

Small Amphibian and Reptile Footprints from the Permian Carapacha Basin, Argentina

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This paper contains a taxonomic study of the Permian tetrapod ichnofauna from the Carapacha Basin. Tetrapod traces are analyzed in their environmental context and compared with similar faunas from Europe and North America. This ichnofauna is particularly relevant because of the scarcity of Permian tetrapod tracks from South America and also of Permian tetrapod fossils from Argentina. Ephemeral fluvial and shallow lacustrine deposits compose the sedimentary succession of the basin, which is represented by the Carapacha Formation. Most of the tracks have been collected from the upper member of the formation (Urre-Lauquen Member), mainly from freshwater ephemeral lake deposits as well as from playa-lake mudflats. The deposits of this member have been attributed to the early Late Permian on the basis of a *Glossopteris* fossil flora. Ichnotaxonomic designations of tetrapod traces are made on the basis of morphologic features that reflect the anatomy of the producer and special attention has been paid to extramorphologic deformations observed in the track assemblage. A total of four footprint ichnotaxa have been recognized, namely *Batrachichnus salamandroides* (Geinitz, 1861), *Hyloidichnus bifurcatus* Gilmore, 1927, cf. *Amphisauropus* isp. and cf. *Varanopus* isp. These track taxa are associated with two forms of vertebrate swimming traces (*Characichnus* isp. and type A swimming trace) and a possible fish trail. Invertebrate trace fossils include abundant arthropod locomotion traces and *Scoyenia* isp. The ichnofauna is composed of six tetrapod ichnocoenoses that are dominated by tiny amphibian tracks attributed to Temnospondyli (*Batrachichnus* and type A swimming trace) and Seymouriamorpha (*Amphisauropus*), and also contain the footprints of small reptiles, mostly Captorhinomorpha and possibly Pelycosauria (*Hyloidichnus* and *Varanopus*). Even if the ichnofauna of the Carapacha Basin is slightly younger than typical examples from the literature of the Early Permian “red bed ichnofacies” (Hunt et al., 1995b), a comparison is made. However, further detailed case studies are needed to

formally define this “red bed ichnofacies” and its prospective subdivisions.

Keywords Permian, Argentina, Carapacha Basin, lacustrine environment, *Batrachichnus*, *Hyloidichnus*, *Varanopus*, *Amphisauropus*, *Characichnus*, tetrapod swimming traces

INTRODUCTION

Only five occurrences of Late Paleozoic tetrapod footprints from South America are known (cf. Leonardi, 1994). This apparent paucity is surely a reflection of the scarcity of detailed studies. Late Paleozoic tetrapod tracks are highly significant for the understanding of the Carboniferous-Permian tetrapod life of South America as the bone record is almost non-existent, particularly in Argentina (Aramayo, 1993). The oldest Late Paleozoic tracks from South America are purported amphibian footprints from the Carboniferous Chinchas Formation of Northern Chile (Bell and Boyd, 1986). The remaining tracks have been recovered from three Permian basins in Argentina (Eastern Permian, Paganzo, and Carapacha Basins) and from Permian rocks in the Paraná Basin of Brazil. Tetrapod tracks from the Eastern Permian Basin occur in Late Permian eolian dune facies and are dominated by tracks assigned to the ichnogenus *Chelichnus* Jardine, 1850 (Cej and Gargiulo, 1977; Aramayo and Farinati, 1983; Melchor, 1997a, 2001b). The Paganzo Basin has only yielded scarce isolated footprints in eolian sand-sheet facies of the Permian Patquía Formation, which were preliminary compared with the ichnogenes *Dromopus*, and *Gilmoreichnus* by Caselli and Arcucci (1999). However, these tracks are poorly preserved and have not been described in detail. The single record from the Paraná Basin is an isolated swimming trace from the Upper Permian Rio do Rastro Formation (Leonardi, 1987a, 1994). Melchor and Poiré (1992) briefly mentioned the tetrapod footprint assemblage from the Carapacha Basin and Melchor (1997a, 2001b) presented a preliminary report on its composition and

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implications. The senior author discovered this ichnofauna during fieldwork for sedimentological studies on the Carapacha Formation in 1990 and further collection was conducted in successive field trips until 1994. Melchor (1997a) mentioned the existence of a single slab with *Batrachichnus*-like footprints housed in the collection of the Museum of San Rafael (Mendoza Province, Argentina), labeled as coming from Permian rocks of the Sauce Grande Basin (Buenos Aires province). However, the lithology of this slab cannot be found at the referred locality and, contrary to this, the lithology and track morphology are similar to those typical of slabs bearing the vertebrate ichnogenus *Ameghinichnus* Casamiquela, 1964 from the Middle Jurassic of Patagonia.

This paper contains a detailed treatment on the ichnotaxonomy of the vertebrate tracks, an account of the sedimentary facies and paleoenvironmental setting of the footprint-bearing interval, and an analysis of the significance of the Permian tetrapod ichnofauna from the Carapacha Basin. The assemblage is dominated by small isolated footprints and short trackways, mostly assigned to the amphibian ichnogenus *Batrachichnus* Woodworth, 1900; which occurs in shallow lacustrine deposits in association with many invertebrate ichnofossils (essentially arthropod locomotion traces). The invertebrate ichnofossils will be described elsewhere. This ichnofauna is compared with well-known Permian tetrapod ichnofaunas from North America and Europe.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The Carapacha Basin is considered to be a continental half-graben of Permian age located in southern La Pampa province, central Argentina (Melchor, 1995, 1999); between approximately 37° 30'–38° 40' S and 65° 40'–66° 20' W (Fig. 1). The

basin was isolated from the neighboring Late Paleozoic San Rafael and Sauce Grande Basins. The basin filling is about 630 m thick and entirely composed of the Carapacha Formation. The base of the Formation cannot be observed and is covered and intruded by Permian-Triassic volcanic rocks of the Choiyoi Group (Fig. 2). Basement rocks include Upper Cambrian to Lower Devonian metamorphic rocks (Las Piedras Metamorphic Complex), granitoids (Pichi Mahuida Group), and Late Paleozoic

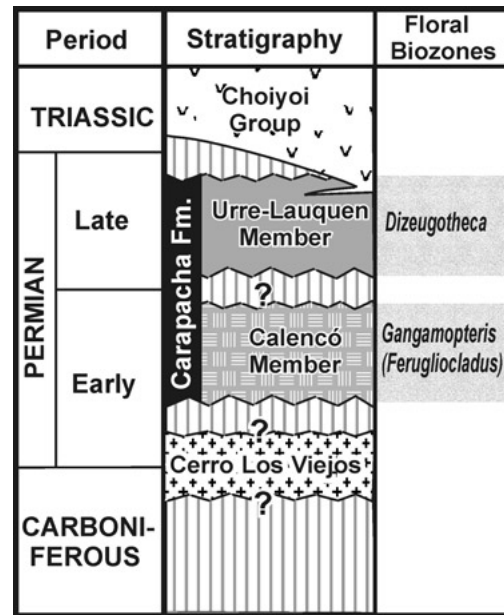


FIG. 2. Stratigraphy and biostratigraphy of the Carapacha Basin and related units. Modified from Melchor (1995).

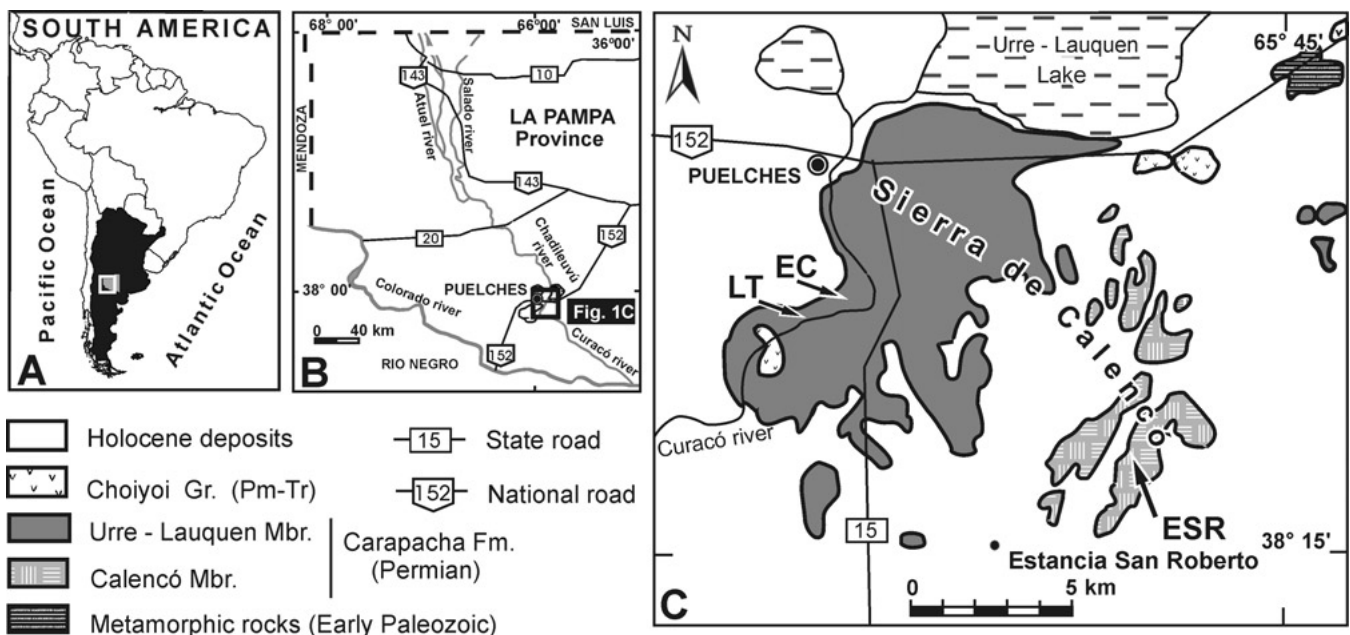


FIG. 1. Location maps. A. Geographical situation of western La Pampa Province in South America. B. Position of the study area. C. Geologic map of the area located south of Puelches town, showing the footprint-bearing localities. ESR: Estancia San Roberto, LT: La Tapera, and EC: El Cañadón.

granite orthogneisses (Cerro de los Viejos Complex) that outcrop in southeastern La Pampa province (Tickyj et al., 1999). Red and gray arkosic or lithic sandstones, mudstones and rare conglomerates compose the Carapacha Formation. It has been divided in two members separated by an unconformity (Fig. 3), the lower Calencó Member and the upper Urre-Lauquen Member (Melchor, 1999). The formation has yielded a typical *Glossopteris* macroflora, which permitted it to be assigned to the Per-

mian (Melchor, 1990; Melchor and Césari, 1991, 1997). More specifically, the taphoflora from the lower member has been dated as late Early Permian and that from the upper member as early Late Permian (Melchor and Césari 1991, 1997). The succession of the basin is dominated by ephemeral fluvial facies with subordinate lacustrine deposits (Fig. 3). The initial filling (Early Permian Calencó Member) is lacustrine and displays an upsection transition from deep to shallow water conditions, associated with poorly developed paleosols, which was replaced by a sandy braided fluvial system (Melchor, 1990, 1995; Melchor and Césari, 1991). During the last stage of sedimentation (Late Permian Urre-Lauquen Member) there was an alternation of ephemeral fluvial deposits dominated by tabular sheetflood sandstones and of shallow lacustrine (freshwater and saline) episodes, including playa-lake facies. Besides leaves and fronds, the formation has yielded plant fructifications (Melchor and Césari, 1997), four gymnosperm wood taxa (Crisafulli et al., 2000), a probable reptile bone (Melchor, 1995), and impressions of freshwater jellyfish (Melchor, 2001a).

The footprint-bearing localities are located south of the town of Puelches (Fig. 1C). The Estancia (farm) San Roberto (ESR) is located 7 km southeast of Puelches town, at the southern end of sierra de Calencó (38° 13' 14" S, 65° 48' 53" W), and two additional localities are near the Curacó river about 5 to 7 km south of Puelches. The later are here named "La Tapera" (LT: 38° 11' 13" S, 65° 55' 31" W) and "El Cañadón" (EC: 38° 11' 06" S, 65° 54' 45" W).

FOOTPRINT-BEARING FACIES AND PALEOENVIRONMENTS

Most of the footprints were recovered from the Urre-Lauquen Member; only one specimen was collected in the Calencó Member (Fig. 3). The tracks were found exclusively in shallow lacustrine deposits where they are commonly preserved in mudstones and siltstones. The footprint-bearing interval from the lower member (Calencó Member) is interpreted as floodplain lakes or ponds, fed by overbank sediments of fluvial origin (Melchor, 1995). Vertebrate traces from the upper member (Urre-Lauquen Member) were mostly recorded from exposed tracts of playa-lake mudflats and of shallow freshwater lakes and ponds. Table 1 contains a brief summary of the sedimentary facies of the Urre-Lauquen Member and its paleoenvironmental interpretation (for detailed descriptions see Melchor, 1995, 1999). Vertebrate traces occur exclusively in the middle part of the Urre Lauquen Member (Figs. 3 and 4). Fig. 4 displays two laterally correlative logs at "La Tapera" and "El Cañadón" localities, the stratigraphic distribution of the facies associations, vertebrate and invertebrate ichnotaxa, and of body fossils.

Sedimentation of the Urre-Lauquen Member of the Carapacha Formation took place under a semi-arid and seasonal climate. At this time interval, the major paleogeographic setting is envisaged as a terminal fan (e.g., Parkash et al., 1983; Kelly and Olsen, 1993), where the deposits of ephemeral channels, proximal and distal sheetfloods composing depositional lobes, fringed by shallow lakes in the distal areas can be recognized (Melchor,

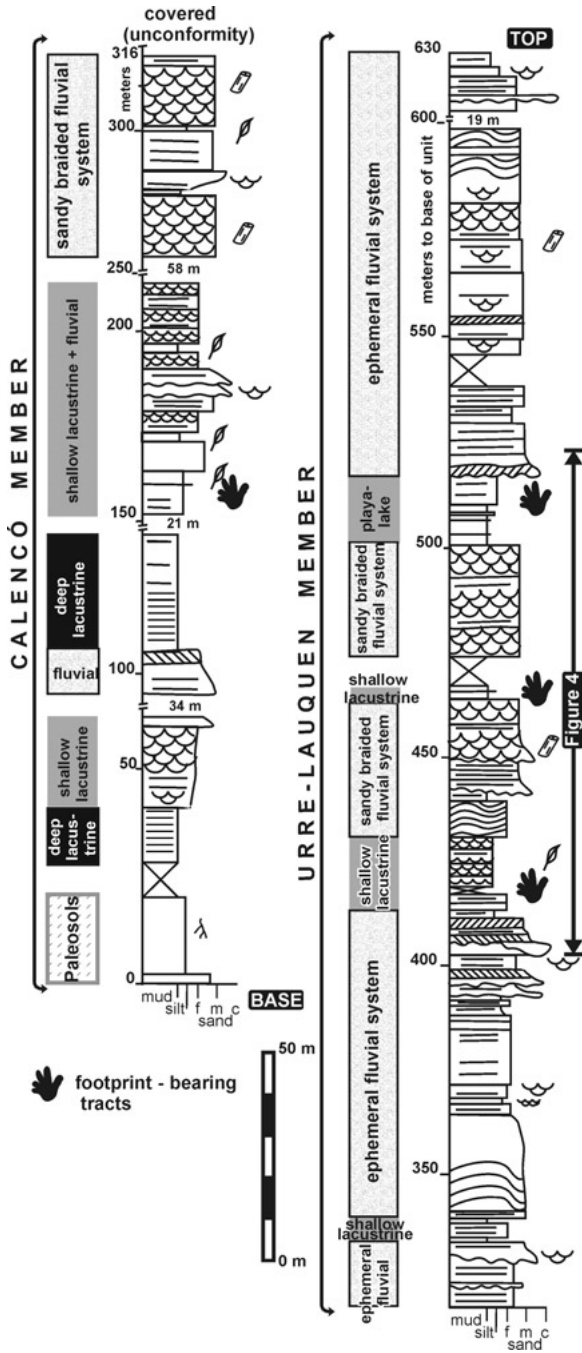


FIG. 3. Schematic stratigraphic column of the Carapacha Basin showing details of both members, position of footprint-bearing tracts and the main environmental setting. Also indicated is the interval represented in detail in Fig. 4. See additional references in Fig. 4. Modified from Melchor (1995, 1999).

TABLE 1

Summary of main facies associations of the Urre-Lauquen Member of the Carapacha Formation (from Melchor, 1995)

Facies associations	Percent thickness	Lithology & sedimentary structure	Fossils & trace fossils	Interpretation
Proximal sandy sheetflood deposits (PS)	45%	Fining-upward 3–6 m thick cycles composed by medium to fine grained sandstones with parallel lamination and parting lineation, massive or rare cross-lamination, rippled top and mud drapes. Tabular beds. Occasional trough cross-bedding. Localized soft sediment folding. Raindrop imprints and mudcracks.	Twig casts. Burrows and arthropod locomotion traces.	Deposits of one or more unconfined currents and occasional reworking by dilute currents. Deformation favored by rapid sedimentation and triggered by seismic shocks.
Distal sheetflood deposits (DS)	14%	Fine-grained sandstone and silstones with trough-cross lamination, climbing ripples, parallel lamination, soft-sediment deformation structures (ball and pillow structure, convolute lamination, load casts). Rare planed-off symmetrical microripples and mudcracks. Common association with subordinate massive or parallel laminated sandstone.	Leaves and twigs. Burrows and arthropod locomotion traces.	Deposition in distal parts of sheetflood lobes.
Wadis (W)	7%	Fining-upward, 2.5–6.5 m thick cycles composed by medium to coarse-grained sandstones with trough cross-bedding bounded by a basal erosive surface, plus finer-grained sandstones with parallel or tabular cross-bedding.	Twig casts.	Ephemeral fluvial channels that feed sheetflood lobes. Concentration of shallow flows and down cutting plus migration of subaqueous dunes.
Sandy braided fluvial deposits (SB)	7%	Red, medium to gravelly sandstones with trough cross-bedding bounded by a basal erosive surface. Common upward transition to massive or parallel-laminated sandstones. Cosets up to 11 m thick. Low variation of paleocurrent indicators. Absence of fine-grained sediments.	Log casts and log permineralizations	Permanent fluvial channels of low sinuosity, transport of sediments as bedload. Large discharge variability.
Playa lake (PL) <i>Lake mudflat</i>	10%	Red, massive or poorly laminated argillite with minor siltstone laminae and thin fine-grained sandstone beds, which display horizontal, undulated or cross-lamination. Gypsum present as thin laminae and small rosettes. Mudcracks, raindrop imprints and tool marks. Common thickening- and coarsening-upward trend.	Leaves. Vertebrate footprints, arthropod locomotion traces, bioturbated horizons.	Dry and partially evaporitic mudflats sourced by distal sheetfloods and associated with saline lakes. Massive stratification due to mudcrack formation and intrastratal evaporite precipitation.
<i>Saline lake</i>		Coarsening- and thickening upward cycles (1–3 m) composed by red laminated mudstone with common convolute lamination, mudcracks and raindrop imprints, gypsum laminae (up to 3 cm thick). Interbedded fine-grained massive or parallel laminated sandstone.	Leaves and twigs, <i>Scoyenia</i> isp.	Deposition in shallow lakes or ponds with mildly saline waters, subject to frequent desiccation and evaporite precipitation at the sediment-water interface.

(Continued on next page)

TABLE 1

Summary of main facies associations of the Urre-Lauquen Member of the Carapacha Formation (from Melchor, 1995)
(Continued)

Facies associations	Percent thickness	Lithology & sedimentary structure	Fossils & trace fossils	Interpretation
Freshwater ephemeral lake (FEL) <i>Drier lakes</i>	16%	Coarsening-upward, 2–6 m thick cycles mostly composed by red argillite with parallel or convolute lamination and interbedded fine-grained sandstones. Mudcracks and water escape structures. Occasional peds, slickensides and septarian nodules.	Leaves, twigs, and rare bones.	Shallow lakes or ponds that received fine grained sediments and were frequently desiccated. Incipient pedogenic modification.
<i>Wetter lakes</i>		Fine-grained sandstones and siltstones with trough cross-lamination, parallel lamination and wavy bedding. Capped by mudstones with common convolute lamination, mudcracks, water escape structures, and microbial wrinkle structures. Mostly organized in fining-upward cycles 2–9 m thick.	Burrows, arthropod locomotion traces, bioturbated texture, diverse invertebrate ichnofossils, vertebrate footprints.	Shallow freshwater, rarely desiccated lakes. Sedimentation above wave base. Long-term lake-level change.

1995). The lacustrine deposits include playa-lake facies (containing mudflat and saline lake deposits) and shallow freshwater facies (Table 1). On the basis of abundant evidence for subaerial exposure, the later deposits can be differentiated between those of drier lakes (frequently desiccated and subject to incipient pedogenesis) and “wetter” lakes (mostly subaqueous). Tetrapod footprints occur in association with diverse invertebrate trace fossils including arthropod locomotion traces (various ichnogenera), *Helminthoidichnites tenius* Fitch, 1850, *Rusophycus stromnessi* (Trewin, 1976), *Scoyenia* isp., *Palaeophycus* isp. and millimeter-thick burrows with probable meniscate structure (Fig. 4). Arthropod locomotion traces appear exclusively in mudflat facies of playa-lakes and in subaqueous parts of freshwater ephemeral lakes (Table 1 and Fig. 4). In addition, a probable fish trail (*Undichna* isp.) has also been identified.

APPROACH

The measurements and terminology used in this paper follow the recommendations of Peabody (1959) and Leonardi (1987b). For the measurements (e.g., footprint size, divergence from midline, and angle between manus—pes), digit III was used as a reference. The ichnotaxonomic attribution of the studied specimens is based on morphologic attributes that reflect the anatomy of the producer (Peabody, 1955). A particular effort has been made to consider any extramorphologic characters (*sensu* Peabody, 1948:296–297) that can result from variations in gait and velocity of the animal and substrate type and consistency (Peabody, 1948, 1955; Haubold et al., 1995; Melchor, 1997b). This is especially the case when the sample size is large enough to show an ample morphologic variation in different substrate and gait conditions. Most tetrapod ichnologists agree that this is the desirable

and “correct” practice, in order to avoid naming extramorphologic variants of tetrapod traces (cf. Haubold, 1996). However, this practice is questionable, especially from the viewpoint of invertebrate ichnology (cf. Bromley, 1997). Some conspicuous extramorphologic tetrapod traces with behavioral connotations, which are recognized on the basis of a large sample size from different stratigraphic intervals and locations, are worth distinguishing and describing in detail. In this case, a judicious use of binomial nomenclature and ichnotaxonomic procedures can be accepted, in order to facilitate the naming and identification of similar traces in other case studies. A good example of the latter practice is the recent erection of the ichnogenus *Characichnos* Whyte and Romano, 2001, for a particular type of tetrapod swimming trace.

Most of the material described in this paper consists of isolated or a pair of footprints, although about 11 trackways have been collected. This scarcity of trackways makes a proper ichnotaxonomic identification difficult for many specimens. The specimens described here are housed at the collection of the Cátedra de Geología Histórica y Regional, Universidad Nacional de La Pampa, Santa Rosa, Argentina (institutional abbreviation GHUNLPam). The specimen number is followed by Roman numerals used to indicate related slabs (usually part and counterpart of the same tracks) and letters to indicate different trackways or isolated tracks in the same slab.

SYSTEMATIC ICHNOLOGY

The described tetrapod traces include distinct footprint ichnotaxa and tetrapod swimming traces. Ichnotaxa are listed in alphabetical order followed by those forms left in open nomenclature.

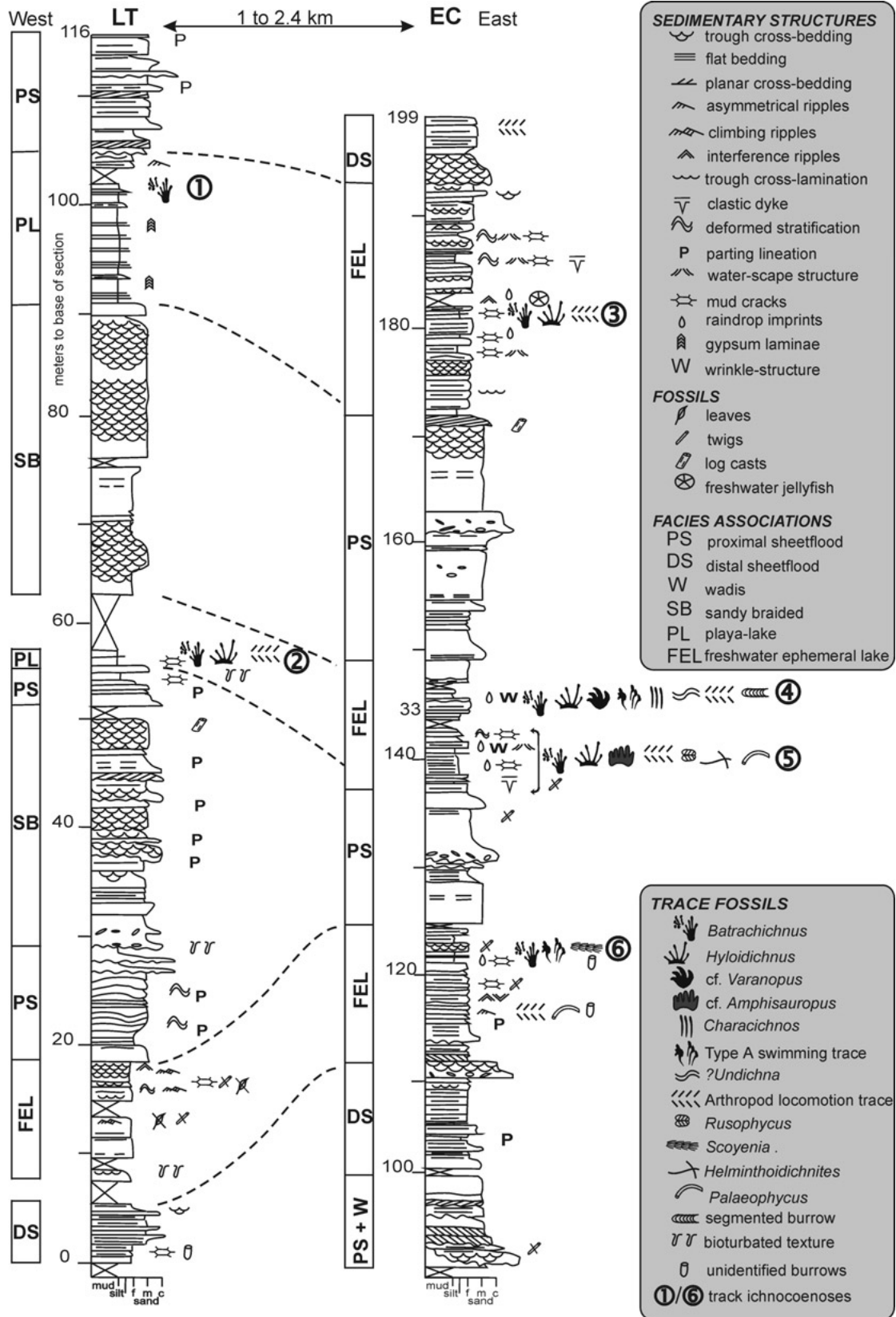


FIG. 4. Laterally correlative sedimentologic sections between La Tapera (LT) and El Cañadón (EC) localities showing the facies associations (see Table 1), vertebrate traces and invertebrate ichnofossils of each ichnocoenoses (1 to 6) of the Urre-Lauquen Member. Dashed lines indicate correlated surfaces. The distance that separates both sections increases upsection because they were measured in adjacent limbs of an anticline. Modified from Melchor (1995).

Tetrapod Footprints

Ichnogenus *Amphisauropus* Haubold, 1970

Type ichnospecies: *Amphisauropus latus* Haubold, 1970.

Diagnosis: Tracks of a quadruped, pace angulation around 90°; impressions plantigrade to semiplantigrade, pentadactyl manus and pes impressions, digit tips rounded, digit IV the longest, manus slightly smaller than pes (from Haubold, 1970:103).

cf. *Amphisauropus* isp.
Figs. 5A, B

1997a *Limnopus* Marsh: Melchor, p. 59.

Referred material: GHUNLPam 3219, 3301-I/II.

Locality: The material was collected from the ESR and EC localities (Fig. 1C).

Description: The specimen 3219 (from EC) contains an incomplete plantigrade footprint showing four straight digits, which is 20.5 mm long and 16.5 wide (minimum value, incomplete footprint). The sole is 10.5 mm long and greater in width than length, sole length is approximately equal to the longest digit (II). Total divarication of digits (I–IV?) is equal to 18°. The specimen 3301-I/II (from ESR) contains two incomplete footprints, including the largest track of the ichnofauna (31 mm long). The best-preserved footprint displays four digits of similar length (probably digits I–IV), which are slightly curved outward and form a small interdigital angle (angle I–III? = 26°). Two digit imprints that are related to the previous footprint represent the remaining partial footprint. In both specimens, it is not possible to determine if the footprints belong to pes or manus.

Discussion: The assignment of these specimens to the ichnogenus *Amphisauropus* is tentative, as the available material is scarce and incomplete. However, they can be easily distinguished from the remaining tracks of the ichnofauna because of larger size, presence of broad soles or palms, and short robust digits with low divarication. These footprints have features that are common to the ichnogenus *Limnopus* Marsh, 1894 (cf. Haubold, 1996), but the lack of trackways or manus-pes sets makes the distinction difficult. However, it is considered that their morphology is closer to *Amphisauropus* because of the compact form, and the relatively wide footprints with short digits of similar length and rounded tips (cf. Baird, 1952; Haubold, 1970, 1973, 1996). Furthermore, the type material of *A. imminutus* Haubold, 1970 displays a relatively small divarication angle in the pes (Haubold, 1970: table 6), which is a feature not seen in the type material of *Limnopus* (Haubold, 1970: table 4). The ichnogenus *Amphisauropus* is commonly recorded in Permian basins of Europe (e.g., Haubold, 1971, 1996; Gand, 1987), although there are rare occurrences reported from Canada (Mossman and Place, 1989) and the USA (Lucas et al., 2001). It is considered as the track of Diadectidae (Haubold, 1970, 1996) or Seymouriamorpha (Haubold and Lucas, 2001b).

Ichnogenus *Batrachichnus* Woodworth, 1900

Type ichnospecies: *Batrachichnus plainvillensis* Woodworth, 1900.

Diagnosis: Small (up to 30 mm in length) quadrupedal trackways with four and five digits on manus and pes, respectively. Narrow trackways, common alternating manus-pes sets, small divergence of manus and pes axes, pace angulation rarely exceeds 90°. Elongated tracks and digit impressions, distal portion of digits rounded. Pes plantigrade, toe IV is the longest, flat and rounded sole with posterior narrowing; manus plantigrade to semiplantigrade, common tail mark (modified after Gilmore, 1927:36; Haubold, 1971:14 and Haubold, 1996:48).

Remarks: Haubold et al. (1995) and Haubold (1996) recently have discussed the taxonomic status of the ichnogenus and its nomenclatural history. They recognized three valid ichnospecies, namely *B. plainvillensis* Woodworth, 1900 (the type ichnospecies), *B. delicatulus* (Lull, 1918), and *B. salamandroides* (Geinitz, 1861). The first ichnospecies is considered by Haubold (1996) as restricted to Carboniferous rocks and in need of revision. The latter two ichnospecies are of Permian age, whereas *B. delicatulus* is commonly used for North American and *B. salamandroides* for European occurrences (Haubold et al., 1995; Haubold, 1996). Haubold et al. (1995) suggested that *B. salamandroides* is the senior synonymous of *B. delicatulus* (Lull, 1918) and *Anthichnium salamandroides* (Geinitz, 1861). The authors accept this equivalence, even if a thorough revision of the ichnogenus is pending. Thus, only the ichnospecies *B. salamandroides* (Geinitz, 1861) is used in this work and no distinction of “provincial ichnotaxa” (i.e., *B. delicatulus* for North America and *B. salamandroides* for Europe) is sustained.

Batrachichnus salamandroides (Geinitz, 1861)

Figs. 6A–J, 7A–F, 8A–E

- 1992 *Anthichnium salamandroides* (Geinitz, 1861): Melchor and Poiré, p. 253, table 2.
- 1992 *Anthichnium* cf. *A. salamandroides* (Geinitz, 1861): Melchor and Poiré, p. 252, table 2.
- 1992 cf. *Batrachichnus* sp.: Melchor and Poiré, p. 252, table 2.
- 1992 ? *Moodieichnus* Sarjeant, 1971: Melchor and Poiré, p. 252, table 2.
- 1992 *Limnopus* cf. *cutlerensis* Baird, 1965: Melchor and Poiré, p. 253, table 2.
- 1997a *Batrachichnus delicatulus* (Lull, 1918): Melchor, p. 59.
- 2001b *Batrachichnus salamandroides* (Geinitz, 1861): Melchor, p. 37, plate 1A, C, D.
- 2001b cf. *Gilmoreichnus* Haubold, 1971: Melchor, p. 37, plate 1F, G.

Diagnosis: Ichnites of very small to small quadrupeds, trackway pattern usually characterized by pace angulation of around 80°–90°, rarely exceeding 100° and 110° for pes and manus, respectively. Pes plantigrade to semiplantigrade, pentadactyl. Pes length less than 20 mm (typically 10 to 15 mm). Digits I to III

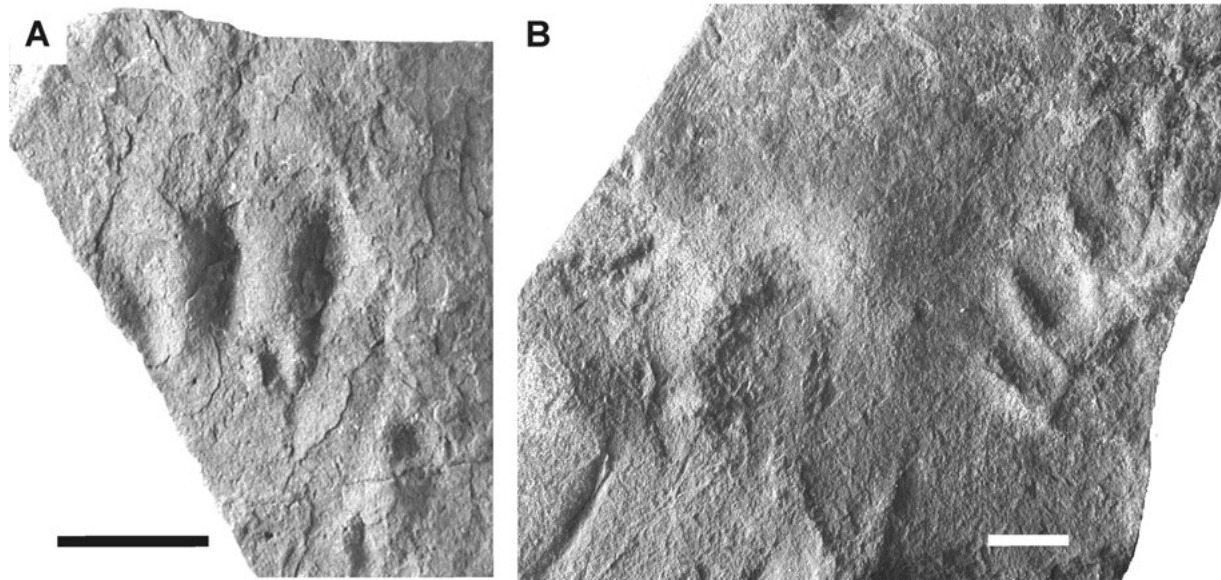


FIG. 5. Footprints compared with *Amphisauropus* Haubold, 1970. **A.** GHUNLPam 3219, concave epirelief. **B.** GHUNLPam 3301-I, convex hyporelief. Scale bar = 1 cm.

closely grouped together with increasing length, IV longest digit and somewhat posterior and lateral. Manus semiplantigrade, tetradactyl, smaller than pes; increasing length of digits from I to III, digit IV diverging outward from the grouping of I–III. Tail-drag may be present (Haubold et al., 1995:143).

Referred material: About 125 footprints on 38 slabs. GHUNLPam 3035, 3050-a/b, 3053, 3054-a/b/c, 3055, 3056-a/b, 3062-a/b, 3063-a/b, 3210, 3211, 3212, 3213, 3214, 3215, 3216-a, 3217-a/b/c, 3218-a/b, 3220-a/b, 3221, 3281, 3282, 3283-b, 3284-b/c, 3286-a/b, 3287, 3288, 3290, 3292-a/b, 3294, 3296-a, 3298, 3299, 12078, 12079, 12081, 12082, 12493-a/b, 12494.

Locality: LT and EC localities near the Curacó river (Fig. 1C).

Description: Measurements on the material attributed to this ichnospecies are shown in Table 2. Except for a few specimens (Figs. 7D, E), all tracks are very shallow (less than 1 mm deep). This ichnospecies includes slender and small quadrupedal trackways with tetradactyl manus and pentadactyl pes, manus-pes sets arranged in an alternating pattern and a pace angulation ranging from 63° to 135° . The pace angulation is larger for the manus (mean = 115°) than for the pes (mean = 71°). Ten short trackways were collected (maximum length = 127 mm), which commonly display a curved tail drag. Manus impressions are more frequent (about 2/3 of the recorded tracks), better preserved and located closer to the midline than the pes impressions (Fig. 6A). Manus and pes are imprinted fairly close to each other although they commonly do not overlap (Figs. 6B, I, J), in some specimens the pes partially oversteps the manus (Figs. 6F, G). Step and stride length are variable and are always smaller for the manus than for the pes. The stride length averages 42.3 mm (manus) and 46.2 mm (pes). The angle between manus and pes of a set is low to moderate and ranges between 0° – 8°

($n = 3$) or between 33° – 35° ($n = 2$). The manus prints average 8.1 mm in length (range 5–12.5 mm) and are slightly longer than wide (mean length / width ratio = 1.1). They are digitigrade to semidigitigrade and commonly display straight and slender digit imprints with rounded and enlarged tips (Figs. 6E, I). The inner digit imprints (I–III) can display two or three pads and occasional pointed tips, although they are rare. In some cases, the imprints of manus digits can join in a common point (Figs. 6E, F), although true palm impressions are rare. The imprint of digit III is the longest and it is followed by those of digits IV, II and I, in decreasing length. Total divarication of manus impressions averages 85° and ranges between 58° and 112° . Relative interdigital angles are variable but in most cases digits I–III are separated from digit IV (Figs. 6E, I, J).

The pes impressions are semidigitigrade (commonly preserved as undertracks) to plantigrade (which correspond to natural molds) and display slender and curved impressions of digits I–IV with rounded tips, whereas the impression of digit V may sometimes be missing (Figs. 6B–E, H). The average length of the pes impressions is 12.9 mm (range = 6.9–23.9 mm) and the tracks are longer than wide (mean length/width ratio = 1.2). In average, pes impressions are about 40% longer than the manual prints. Plantigrade footprints show an oval sole tapered backward, that is up to 7 mm long and 5 mm wide (Figs. 6B–D). The digit length in pes impressions increases progressively from I to IV, the imprint of digit V is the shortest and commonly missing or poorly impressed (Figs. 6C, H). The longer digits (III and IV) can show bifurcated tips (Fig. 6D). Though rare, the imprint of digits I–III can display two or three pads and occasional pointed tips. Total divarication ranges from 62° to 126° (mean = 91°) and seems to be greater for larger forms, although the sample size is small ($n = 7$) and the influence of substrate

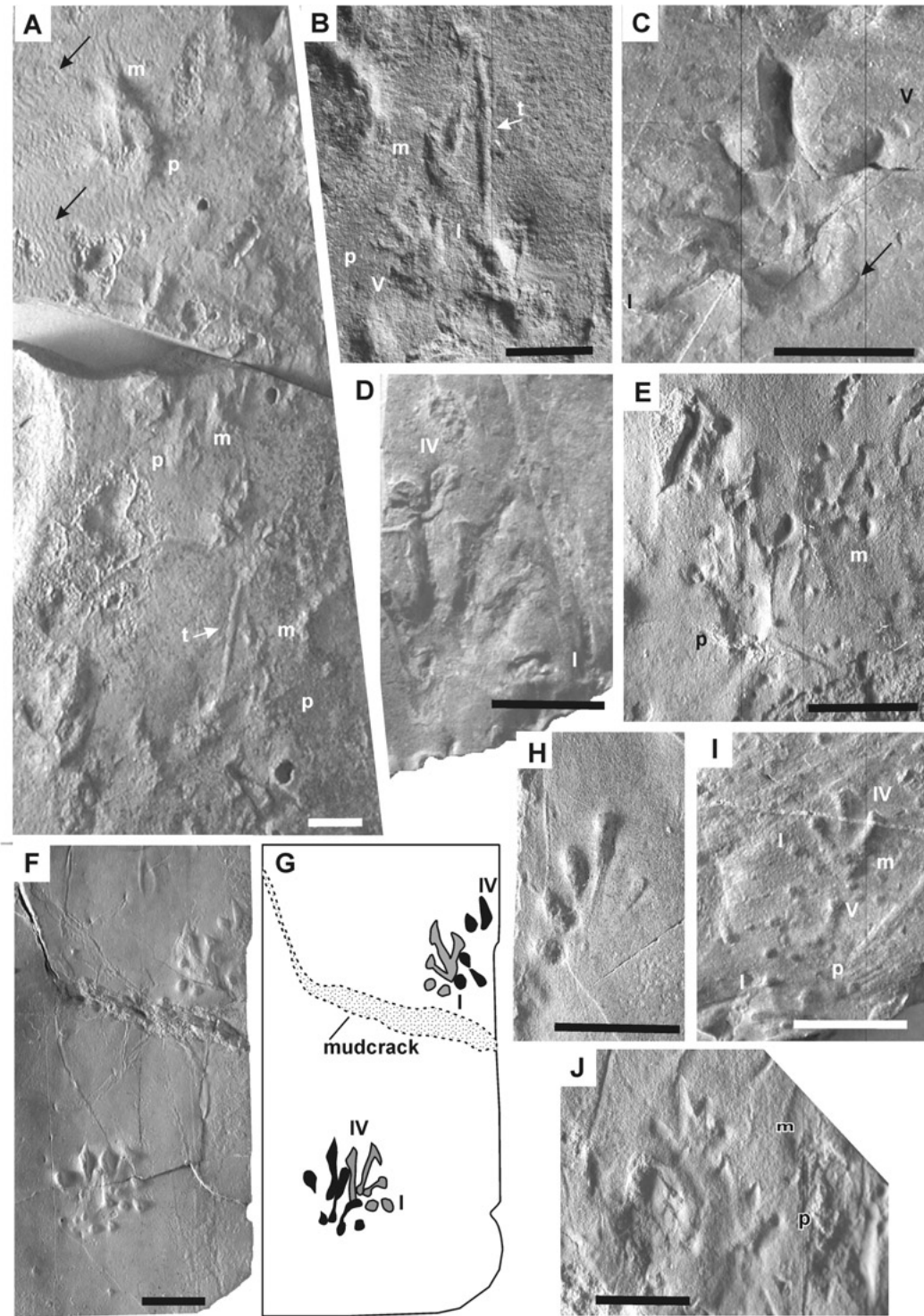


FIG. 6. *Batrachichnus salamandroides* (Geinitz, 1861). **A.** GHUNLPam 3216-I, III, three manus-pes sets and a discontinuous tail mark preserved in convex hyporelief (natural casts). Arrows indicate microbial wrinkle structure. **B.** GHUNLPam 3216-II, left manus-pes set and tail mark preserved as natural molds. This is the counterpart of the first couple of Fig. 6A. **C.** GHUNLPam 3213, isolated right pes impression (natural mold). Note deeply imprinted digits, broad sole and lateral marginal ridge (arrow). **D.** GHUNLPam 3212, isolated left pes impression (natural mold). Note bifurcation on digits imprints III and IV and the elongated rounded sole. **E.** GHUNLPam 3287, unrelated right pes and left manus impressions preserved as concave epirelief (natural molds). **F.** GHUNLPam 3063, two manus-pes sets preserved in convex hyporelief (undertracks). **G.** Interpretative drawing of specimen 3063. The manus are gray and the peses are black. Note marginal overprinting of the manus by the pes. **H.** GHUNLPam 3220-II, isolated right pes impression, convex hyporelief (undertrack). **I.** GHUNLPam 3214, left manus-pes set, convex hyporelief (undertrack). **J.** GHUNLPam 3211, right manus-pes set, concave epirelief (natural mold). Note pointed digit imprints. **m** = manus; **p** = pes; **m1**, **m2**, etc. = consecutive impressions in a trackway; **t** = tail mark; **I** to **V** = digit imprints. Scale bar = 1 cm.

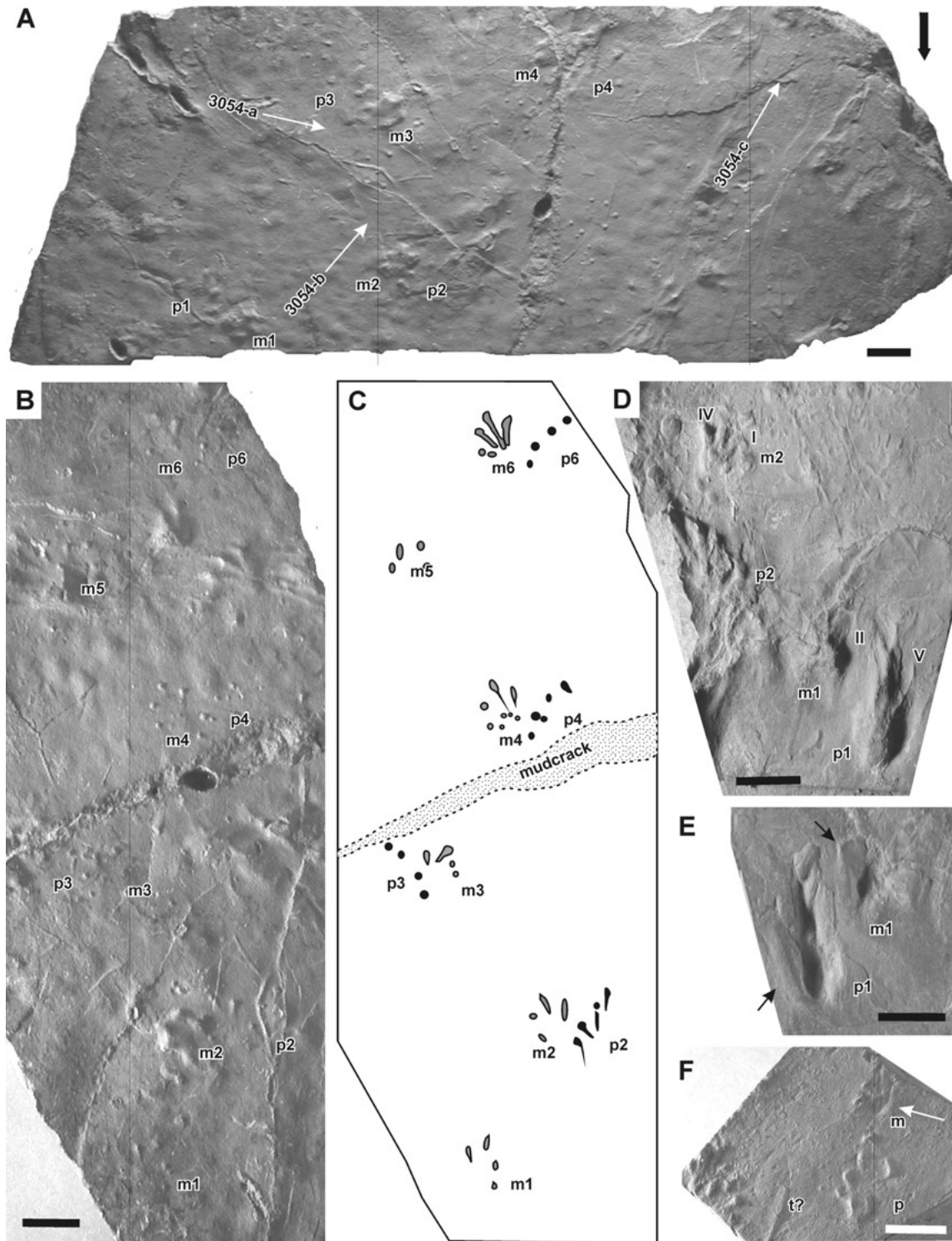


FIG. 7. Extramorphologic variants of *Batrachichnus salamandroides* (Geinitz, 1861). **A.** GHUNLPam 3054, slab with three trackways (3054-a, b, c) showing contrasting preservational modifications, convex hyporeliefs (mostly undertracks). White arrows indicate direction of progression of the trackmaker. Consecutive manus-pes sets (m1-p1, m2-p2, etc.) are labeled only for trackway 3054-b. Black arrow indicates the direction of lighting. **B–C.** Detailed photography and sketch of trackway 3054-a. Manus impressions are colored with gray and pes impressions are black. Note the presence of a mudcrack. **D.** GHUNLPam 3215-I, two manus-pes sets, convex hyporeliefs (natural cast). Note collapse of pes digits in p1 and raindrop imprints in the upper left of the photograph. **E.** GHUNLPam 3215-II, left manus-pes set, concave epireliefs (natural mold), corresponding to m1-p1 set of the counterpart pictured in Fig. 7D. Note marginal ridges of both footprints (arrowed). **F.** GHUNLPam 12081, left manus-pes set (and probable tail mark), pes preserved as convex hyporeliefs and manus as concave hyporeliefs (white arrow). Probable natural casts. Symbols as for Fig. 6. Scale bar = 1 cm.

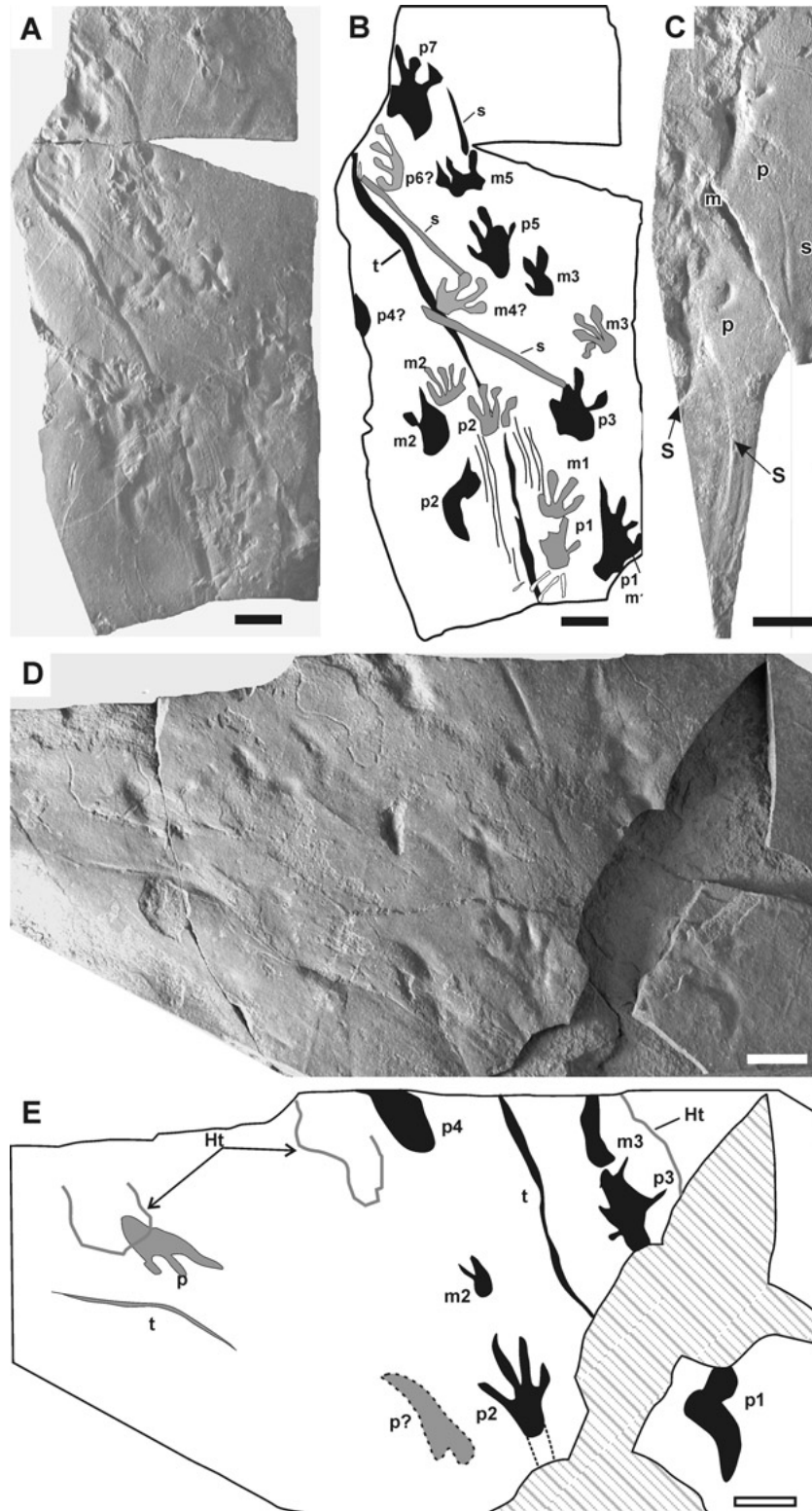


FIG. 8. Extramorphologic variants in *Batrachichnus salamandroides* (Geinitz, 1861). **A–B.** Detailed photography and sketch of slab GHUNLPam 3062. At least two markedly deformed trackways (distinguished by different gray shades in Fig. 8B), and a single partial and unrelated footprint (white). Note fine striations parallel to tail mark in the lower half of the picture. **C.** GHUNLPam 3296, two consecutive right pes impressions, concave epirelief (possible natural mold). Note curved spurs associated with the footprints. **D–E.** GHUNLPam 3218, two partial trackways preserved as concave epirelief (natural molds) and invertebrate trails. The footprints of separate trackways are distinguished by different color. s = spur; Ht = *Helminthoidichnites tenuis* Fitch, 1850. Additional symbols as for Fig. 6. Scale bar = 1 cm.

consistency might be important. Interdigital angles are highly variable, although the angle II–III is commonly the largest. Deeply imprinted footprints (e.g., GHUNLPam 3213, 3215) exhibit an external marginal ridge that bounds the sole (Figs. 6C, 7E).

Discussion: The best-preserved manus and pes footprints are inferred as digitigrade and plantigrade impressions, respectively. The variations observed in the described material are interpreted as essentially related to different substrate consistency and to the preservation as undertracks or transmitted tracks (sensu Heyler and Lessertisseur, 1963: 134). The trackways of slabs GHUNLPam 3054 (Figs. 7A–C) and 12493 are good examples for differences in footprint morphology related to substrate consistency. GHUNLPam 3054 displays three trackways that are interpreted to have been produced under a desiccating substrate (Fig. 7A). Trackway 3054-c, which is inferred to have been produced first, displays blunt footprints with elongated digits and scarce morphologic detail. The second trackway (3054-b) contains semidigitigrade pes impressions and digitigrade manus impressions, even if the digits are not easily distinguished and appear “webbed.” The last trackway (3054-a) is either composed of shallow semidigitigrade impressions or impressions reduced to rounded digit tips (Figs. 7B, C). In this trackway, manus prints are deeper than pes prints and the latter are represented by four dots (tip of digits I–IV, digit V is commonly missing) arranged in an arc with convexity toward the midline. Footprints similar to 3054-c can also be interpreted as undertracks or transmitted tracks.

Pes impressions with broad soles and a marginal ridge may indicate substrates with marked water saturation or under a few millimeters of water, because the soles have probably been enlarged by sliding of the autopodium (Figs. 6C, 7E). Associated manus prints commonly convey little detail and are reduced to “bidactyl” imprints, which probably correspond to digits II and III (Figs. 6B, 8B, 8D). Experimental results with salamanders by Peabody (1959) and Brand (1996) indicate similar results in a subaqueous substrate or in a subaerial substrate with a high water saturation. In the specimen GHUNLPam 3215 the pes impression is relatively deep (1.5–2 mm) and the interdigital angles are markedly reduced (Figs. 7D, E). This is interpreted as an extramorphologic variant produced by collapse of the digits in a pliable substrate. The specimen GHUNLPam 12081 displays a pes preserved as convex hyporelief with a manus preserved as concave hyporelief (Fig. 7F). The inverted relief in the manus print might be interpreted as a result of locomotion in a sticky or adhesive clayey substrate (Brand, 1996).

Other tracks exhibit curved drag marks behind the pes impression (GHUNLPam 3062, 3218, 3296-a; Figs. 8A–D). This is interpreted as the arc described by the limb during progression and suggests sprawling locomotion (Peabody, 1959). Rounded digit tips in amphibian tracks were interpreted by Peabody (1954) as a reflection of the amphibian locomotion, in which the flexible foot is “rolled” forward in the walking movement, and the digit tip is depressed or flexed to facilitate the displacement.

Bifurcated digit tips are confined to longer digits of some footprints (Fig. 6D), as they are the first to touch the ground and the last to leave it (Peabody, 1959). By comparisons with modern salamander trackways, Peabody (1954, 1959) interpreted this feature as reflecting relatively primitive locomotion (cf. Haubold et al., 1995).

B. salamandroides footprints have been attributed to the Temnospondyli, particularly to Eryopoidea (Haubold, 1971, 1996; Haubold et al., 1995; Hunt et al., 1995a). Haubold (1996) suggested that they belong to juvenile Temnospondyli with uniform body proportions and morphology of the autopodium. The value of the gleno-acetabular distance (range = 24–37 mm, mean = 29.6 mm) estimated from the available sample size (n = 6) suggests that the producers were fairly tiny animals. Considering the presence of a tail mark in most trackways and by comparison with the relationships between gleno-acetabular length and stride length versus tail length for salamander consigned by Peabody (1954, 1959), it is estimated that the producers rarely exceeded 70–120 mm in total length.

Ichnogenus *Hyloidichnus* Gilmore, 1927

Type ichnospecies: *Hyloidichnus bifurcatus* Gilmore, 1927.

Diagnosis: Quadrupedal, semidigitigrade. Both manus and pes have five digits. Manus smaller than pes and placed in front of hind foot. Digits terminated either with pellets or having bifurcated ends (Gilmore, 1927:51).

Hyloidichnus bifurcatus Gilmore, 1927

Fig. 9A–E

- 1992 *Hyloidichnus* Gilmore, 1927: Melchor and Poiré, p. 253, Table 2.
 1997a *Hyloidichnus* cf. *H. bifurcatus* Gilmore, 1927: Melchor, p. 59.
 2001b *Hyloidichnus* cf. *H. bifurcatus* Gilmore, 1927: Melchor, p. 37, plate 1B, E.
 2001b cf. *Hyloidichnus* Gilmore, 1927: Melchor, plate 1H.

Diagnosis: Track of a quadruped with a relatively narrow trackway. Pace angulation usually over 100°, higher for the manus than for the pes pattern. Complete tracks are pentadactyl and semiplantigrade with small sole pads. Digit length increase from I–IV with digit V as long as I. Outer digits, particularly V of manus and pes, are often incompletely impressed; digits mainly straight and slender; distal digit tips are sometimes extramorphologically changed to be rounded or bifurcated. Pes length 20 to 50 mm; stride: pes length ratio equal to 4–5:1 (from Haubold et al., 1995: 145).

Referred material: GHUNLPam 3222-a, 3284-a, 3285, 3289, 3293, 3295-a/b, 3296-b. Material probably belonging to this ichnospecies: GHUNLPam 3282, 3297, 3299 and 12077.

Locality: The material was collected from EC and LT localities (Fig. 1C).

Description: Small tracks characterized by pentadactyl pes footprints with slender, long and curved digit imprints

TABLE 3
Measurements on *Hyloidichnus bifurcatus* footprints. See conventions in Table 2.

Specimen # GHUNL	Manus													Pes										
	Pam	Nr.	Digit length					Divarication			Lp	Wp	L/Wp	Digit length					Divarication					
			Lm	Wm	L/Wm	II	III	IV	V	II-V				I-II	II-III	III-IV	I	II	III	IV	V	I-V	I-II	II-III
3222	1											12.6	14.4	0.88	5.1	7.2	10.8	11.6	6.2	84	19	15	33	17
3284-a	1											8.9	9.4	0.95	3.4	4.4	6.8	6.9	3.2	94	60	12	13	16
3293	4											9.2	11.0	0.84	5.9	6.9	7	8.6	2.2	93	33	21	21	26
3295-a	2	7.6	9.8	0.78	5	5.9	6.7	3	93	46	0	60	8.2	13.2	0.62									
3295-b	1	9.6	7.1	1.35	4.9	8.1	7.3	4.2	58	31	0	34												
3296-b	1											7.2	10.8	0.67	5	7.6	13.6	14.5	7	90	49	11	21	23

and narrow crescent-shaped soles. Table 3 summarizes the measurements of the specimens attributed to this ichnotaxa. A single partial trackway was found (GHUNLPam 3293) that contains two manus-pes sets associated with a tail mark, although most impressions are incomplete (Fig. 9A). This partial trackway displays a marked separation between manus and pes (mean = 33.3 mm). The external trackway width is 27.3 mm and the internal trackway width 4.4 mm. Both manus and pes display a concave divarication in relation to the midline, with an angle from 0° to -7° (inward rotation) for the pes. Pace length is 16.8 mm for the pes and 14.3 for the manus. Only two complete manus impressions were found, which appear tetradactyl and digitigrade to semiplantigrade (Figs. 9B, E). They have a symmetrical outline, imprints of digit III and IV are straight, parallel and of the same length. The external digits are of similar length and they are arranged symmetrically. One of the manus impressions is wider than long (7.6 mm long by 9.8 mm wide) and the other displays the opposite relationship (9.6 mm long by 7.1 mm wide). Pes impressions are digitigrade to semiplantigrade, digit length increases progressively from I to IV. If present, the imprint of digit V is about as long as digit I. Digits are slightly curved inward, the tips are oval-shaped and the longer digits seldom display bifurcated ends (GHUNLPam 3285). Mean length of pes impressions is 11.2 mm (range = 7.2–21 mm) and the tracks are wider than long (average length/width ratio = 0.8). The semiplantigrade pes prints show a sharply imprinted sole that is up to 5.8 mm long and 11.2 mm wide, and its crescent shape is a distinctive feature of this ichnotaxa. Total pes divarication ranges from 84° to 94° (n = 4), whereas the angle between digits I–II is commonly the larger and the remaining interdigital angles display a subequal value.

Discussion: The tracks match the description of *Hyloidichnus bifurcatus* by Haubold et al. (1995), who examined the type specimen from the Hermit Shale (Arizona) and additional material from New Mexico. Even if the footprints described in this work are smaller, they exhibit the morphologic features of the type material, after comparison with the photographs published by Haubold et al. (1995: Fig. 8). The ichnogenus *Hyloidichnus* (including original designations and later regroupings) has six named ichnospecies: *H. bifurcatus* Gilmore, 1927; *H.*

withei Gilmore, 1928; *H. arnhardti* Haubold, 1973; *H. tirolensis* Ceoloni et al., 1986; *H. major* (Heyler and Lessertisseur, 1963); and *H. minor* (Heyler and Lessertisseur, 1963). *H. withei* is synonymous with the type ichnospecies (Haubold et al., 1995) and *H. arnhardti* was included within *Batrachichnus salamandroides* (Haubold, 1996). *H. bifurcatus* and *H. major* were considered as significant ichnospecies (Haubold, 2000), although a complete revision of the ichnogenus is pending (Haubold and Lucas, 2001b). *Varanopus microdactylus* (Pabst, 1897) has been considered as belonging to the ichnogenus *Hyloidichnus* by Gand (1987) and Haubold (1996), however, recent re-examination of additional material from the type locality of *Varanopus* (Castle Peak, Texas, USA) indicates that this is a valid ichnogenus and the ichnospecies *V. microdactylus* (Pabst, 1897) is also a distinct morphotype (Haubold and Lucas, 2001a).

The sample size of *Hyloidichnus* footprints analyzed in this study is considerably smaller than those of *Batrachichnus*. However, some significant differences can be used to distinguish both ichnotaxa in the studied ichnofauna. In *Hyloidichnus*, manus impressions are rarer and digit imprints are longer than in *Batrachichnus*; additionally the pes displays a very characteristic sole that is distinguished from the typical oval sole in the plantigrade impressions of *Batrachichnus* (compare Figs. 6D–E with Figs. 9C–D). Further, pes prints of *Hyloidichnus* are wider than long (opposite to *Batrachichnus*). It is not possible to judge if the marked separation between manus and pes as seen in specimen 3293 is representative of the track morphology of *Hyloidichnus* or if it is due to a variation in gait of the producer. *Hyloidichnus* has been attributed to the Diadectidae (Haubold, 1971), Captorhinomorpha (Haubold, 1984; Gand, 1987) or Captorhinomorpha/Pelycosauria (Haubold and Lucas, 2001b).

Ichnogenus *Varanopus* Moodie, 1929

Type ichnospecies: *Varanopus curvidactylus* Moodie, 1929.

Diagnosis: Quadruped, pes pace angulation of 70° to 100°, external trackway width of manus slightly smaller than pes. Footprints commonly arranged in an alternate pattern with pace angulation of 95°; marginal primary crossing possible; average stride: pes length = 4:1. Manus and pes semiplantigrade, the internal portions of the impressions are preferably deeply

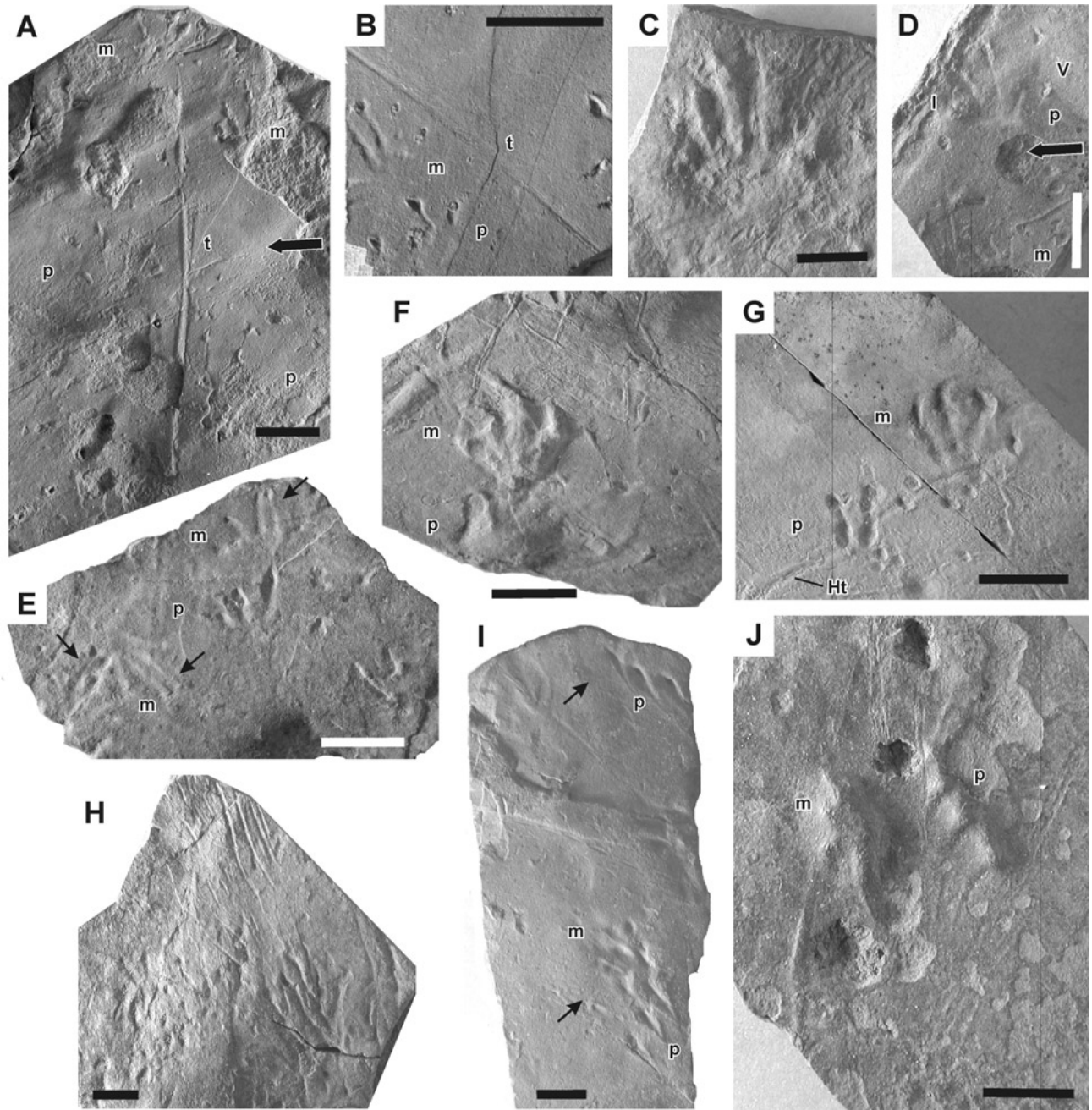


FIG. 9. *Hyloidichnus*, cf. *Varanopus* and swimming traces. **A–E.** *Hyloidichnus bifurcatus* Gilmore, 1927. **A.** GHUNLPam 3293, two manus-pes sets and continuous tail mark, convex hyporelief (natural cast). Large arrow indicates the direction of illumination. **B.** GHUNLPam 3284, manus-pes set and tail mark, concave epirelief (natural molds). **C.** GHUNLPam 3289, single right pes impression, concave epirelief (possible natural mold). **D.** GHUNLPam 3222, pes and partial manus print, concave epirelief (probable undertrack). Large arrow indicates the direction of illumination. **E.** GHUNLPam 3295, one manus-pes set (center top) and about three unrelated partial footprints, concave epirelief (natural molds). Parallelism of digit III–IV is indicated by arrows (compare with Fig. 9B). **F–G.** cf. *Varanopus* isp. **F.** GHUNLPam 3291, left manus-pes set, convex hyporelief (undertrack). **G.** GHUNLPam 3283, manus-pes set, concave epirelief (natural mold) and invertebrate trail. Note large claw marks and marked digital pads. **H–J.** Swimming traces. **H.** GHUNLPam 3300-I, *Characichnos* isp. and obscure digitigrade traces on the left of the photography. **I.** GHUNLPam 3039, type A swimming trace, one complete and one partial right “manus-pes set,” concave epirelief, natural mold. **J.** GHUNLPam 12078, type A swimming trace, one complete “manus-pes set” and associated spurs. s = spur; **Ht** = *Helminthoidichnites tenuis* Fitch, 1850. Additional symbols as for Fig. 6. Scale bar = 1 cm.

impressed, pentadactyl, digit lengths increasing from I to IV, digit V about as long as II, digit tips slightly curved inward, particularly the claws, total divarication of pes (I–V) up to 90°, manus over 100°. Range of footprint length from 20 mm to 30 mm (from Haubold, 1971:30).

cf. *Varanopus* isp.
Figs. 9F, G

Referred material: GHUNLPam 3283-a, 3291.

Locality: EC section (Fig. 1C).

Description: Isolated footprints are distinguished by clear digital pads, moderately curved digits and marked claw marks. Only two incomplete manus-pes sets have been found. Manus impressions are 13.2 and 14 mm long, longer than wide (corresponding widths are 10.6 and 12.5 mm, respectively). They display only four digits, increasing in length from II to IV, whereas digit V is about as long as digit II. All digits show conspicuous triangular claw marks, the largest is 4 mm long by 1.5 mm wide (Fig. 9G). Divarication between digits II–V ranges from 76° to 91°. The pes impression of GHUNLPam 3291 is poorly defined (Fig. 9F). Footprint length is estimated to be about 18 mm and digit length increases from II to IV. The imprint of digit V is considerably shorter than the imprint of digit IV. The angle between manus and pes in this set, using the imprint position of digit IV as a reference, is about 45°.

Discussion: The assignment of this material to the ichnogenus *Varanopus* is not certain because of the small number of specimens available and the poor to moderate preservation. A comparison with the type material of the ichnospecies published by Haubold and Lucas (2001a: Figures 4B and 5), suggests this provisional assignment and also indicates that the closest ichnospecies might be *V. curvidactylus* Moodie, 1929. *Varanopus* has long been envisaged as a poorly defined ichnotaxa (Haubold, 1996), although discovery of additional material from its type locality and formation (Castle Peak, USA and Choza Formation, respectively) revealed that it is a distinct ichnogenus (Haubold and Lucas, 2001a). *Varanopus* tracks have been attributed to indeterminate Cotylosauria (Haubold, 1971) or particularly to the Captorhinomorpha (Haubold, 1984; Gand, 1987; Haubold and Lucas, 2001a).

Tetrapod Swimming Traces

These traces include parallel, elongated furrows or ridges, which commonly appear in groups of three. They can be associated with partial semidigitigrade footprints and a confuse arrangement of imprints. Tracks interpreted as reflecting a swimming behavior are frequently cited in the ichnological literature, although commonly they are not treated in detail. McAllister (1989) revised the existing literature on tetrapod swimming traces. More recent descriptions of this kind of traces include Turek (1989), Smith (1993), Lockley and Hunt (1995:96), Brand (1996), Lockley et al. (1998), McAllister and Kirby (1998), Soler-Gijón and Moratalla (2001),

Whyte and Romano (2001), and Swanson and Carlson (2002). In particular, McAllister (1989) and McAllister and Kirby (1998) revised the criteria employed by previous authors and proposed new features, which might allow identifying subaqueous tetrapod traces. An essential criterion to identify such traces is of buoyancy of the producer, particularly in the form of incomplete and elongated digit imprints or spurs. Other relevant criteria for an aquatic origin of similar traces include (cf. McAllister and Kirby, 1998): preferential impressions of distal digits and the paleoenvironmental context interpreted from sedimentary structures. Diedrich (2000, 2002) even recognized a “scratch mark ichnofacies” represented by reptile swimming traces and tail marks in pond and tidal channel deposits of a Middle Triassic carbonate tidal flat succession from Germany. Some purported brontosaur swimming traces (Bird, 1944) were reinterpreted as undertracks (Lockley and Hunt, 1995:189–191), which highlights the fact that certain undertracks might be confused with swimming traces. The intervals with swimming traces from the Carapacha Formation have been interpreted as shallow freshwater lacustrine deposits that suffered frequent water-level changes (Fig. 4).

Ichnogenus *Characichnos* Whyte and Romano, 2001

Addition to the synonymy list proposed by Whyte and Romano (2001:231).

- 1930 Toe-drag markings: Moodie, p. 557, fig. 11.
- 1963 Traces de nage: Heyler and Lessertisseur, plate XI, figs. 1–2.
- 1980 Griffures et traces de natation: Heyler and Montecat, p. 431–432, plate IV.3–4.
- 1987 Traces de nage: Gand, plate 5E, H, I.
- 1987a Half-swimming footprint: Leonardi, p. 331–333, fig. 1.
- 1994 Half-swimming footprint: Leonardi, p. 46, plate I.7.
- 1998 Reptile subaqueous traces: McAllister and Kirby, p. 45–49, fig. 1.
- 2000 Kratzspuren: Diedrich, figs. 6E, F.
- 2001 Schliefspuren: Diedrich, figs. 3D, 4D.
- 2001 Parallel hypichnial ridges: Schlirf et al., p. 88, fig. 19.
- 2002 Parallel tridactyl traces: Swanson and Carlson, p. 125, fig. 7.
- 2002 Kratzspur: Diedrich, fig. 3B.

Type ichnospecies: *Characichnos tridactylus* Whyte and Romano, 2001.

Diagnosis: Two to four elongate, parallel hypichnial ridges (or epichnial grooves), which may be straight, gently curved or slightly sinuous. The termination of the ridges (or grooves) may be straight or sharply reflexed. Trackway consists of two rows of tracks; the long axes of the tracks are parallel to each other in a straight trackway, and either parallel or oblique to the midline of the trackway (Whyte and Romano, 2001:232).

Discussion: These traces are frequently reported in the literature. Additional recognition in particular case studies will be favored by the formal ichnotaxonomic designation of this

kind of swimming traces. The known stratigraphic range of *Characichnos* is Early Permian-Cretaceous (Whyte and Romano, 2001).

Characichnos isp.
Fig. 9H

Referred material: GHUNLPam 3300 and 3052.

Description: Epichnial traces composed of three to four parallel furrows of uniform width, which display a slightly curved and discontinuous path (Fig. 9H). Individual furrows are up to 1.5 mm wide and the trails are 12–26 mm long and 8–11 mm wide. Some furrows seem to start with digit tip marks and they are associated with incomplete and poorly preserved footprints.

Discussion: Compared with similar traces reported by McAllister (1989), Brand (1996), Whyte and Romano (2001) and Swanson and Carlson (2002), *Characichnos* isp. traces are interpreted as scratches produced by the backward motion of the digits by a partially buoyant tetrapod. Comparison with type A swimming traces suggest that *Characichnos* isp. was produced in slightly deeper water, where only the tips of digits touched the bottom. Even if the described *Characichnos* isp. traces are in the same size range as the other vertebrate tracks of the Carapacha Formation, they cannot be attributed to a distinct group.

Type A swimming trace
Figs. 9I, J

Referred material: GHUNLPam 3039 and 12078. 3300,

Description: This morphotype includes a sharp semidigitigrade pes impression composed of three digit tip imprints related to curved spurs (*sensu* Peabody, 1959:6) and a blunt digitigrade manus impression that can also display an associated single spur parallel to those of the associated footmark (Fig. 9J). The two specimens with these traces are of similar size: about 25–28 mm long by 16–19 mm wide, measured parallel and transversal to the spurs, respectively.

Discussion: The morphology of these traces, especially the presence of curved and elongated spurs, may suggest they were produced by a partially buoyant tetrapod whose digits barely touched the bottom. In this situation, the foot would not encounter much resistance in the substrate and would then continue posteriorly along the arc of the limb (McAllister, 1989). The resemblance in morphology, size, and arrangement of manus and pes between *Batrachichnus salamandroides* and type A swimming traces might suggest a similar producer (compare Figs. 6I–J with Figs. 9I–J). Taking into account the reduced limb length of the producers and the sedimentological evidence, it is inferred that they were probably produced in very shallow water.

DISCUSSION

Extramorphologic Deformations in *Batrachichnus*

The quite large sample size of *Batrachichnus* tracks from the Carapacha tetrapod ichnofauna exhibits an ample morphologic diversity, which is exemplified in Fig. 10. This figure includes footprints that share a similar shape, relative length of digit imprints, total divarication of digit imprints, overall size, and

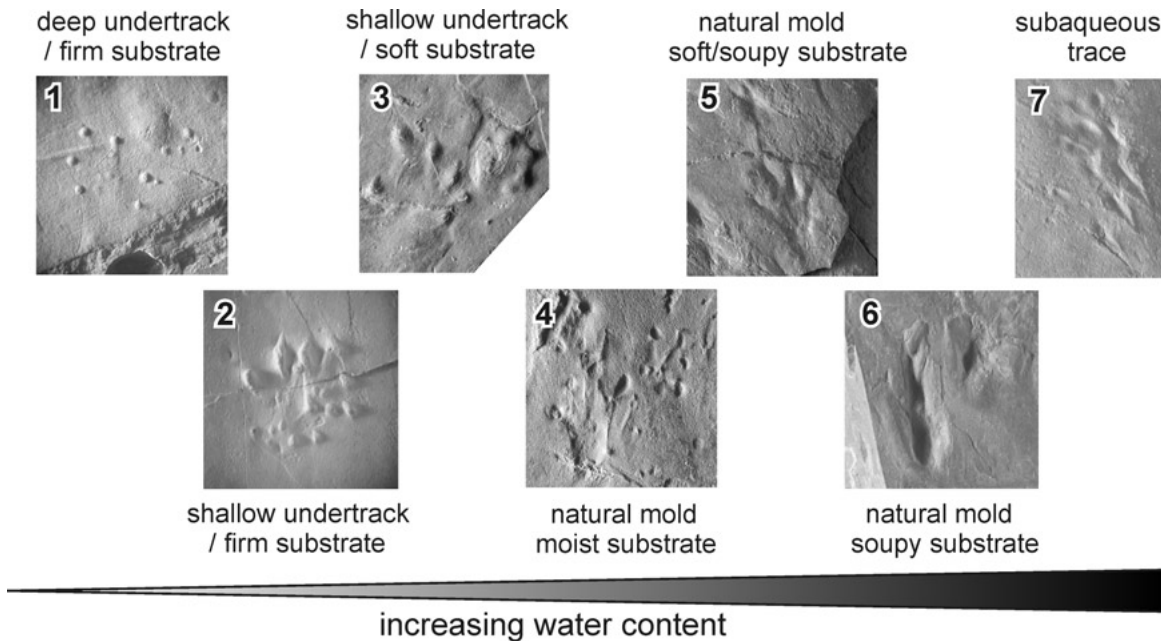


FIG. 10. Influence of substrate consistency on the morphology of *Batrachichnus salamandroides* footprints. 1 = left set, convex hyporelief; 2 = right set, convex hyporelief; 3 = left set, convex hyporelief; 4 = right pes and left manus, concave epirelief; 5 = left set, concave epirelief; 6 = left set, concave epirelief; 7 = right set, concave epirelief. See discussion in the text.

arrangement of manus and pes. Haubold (1996) has pointed out that small footprints (less than 3 cm in size) are particularly prone to suffer extramorphologic deformations. Peabody (1948:296) considered that the main factors that control extramorphologic deformations in footprints are related to substrate type and consistency as well as to gait and variable speed of the producer. Other relevant factors are the inclination of the surface and the effects of diagenesis (Haubold, 1996). In this case, the existence of microbial mats, as suggested by wrinkle structures, might be another important factor. The morphologic variability is interpreted largely as a function of substrate consistency related to water content (Fig. 10, cases 1 to 7). The different distances between manus and pes imply a slightly different speed of the producers. In cases 1, 2 and 4 (Fig. 10) the influence of the substrate consistency is difficult to distinguish from the undertrack fallout phenomenon (*sensu* Goldring and Seilacher, 1971). Case 1 (Fig. 10) illustrates the classical appearance of a manus-pes set represented by rounded tip imprints, which are connected to partial cylindrical digital imprints. The pes impression is recognized by four rounded digit tip imprints (digits I–IV), which forms an arc located behind and external to the midline. Case 2 (Fig. 10) is a more deeply imprinted undertrack, where digit imprints are nearly complete and digit tips appear pointed. The latter feature is interpreted as result of the trace left by the digit during the retraction phase of the movement. Case 3 (Fig. 10) is possibly also an undertrack, but the apparent “web” that displays the manus is indicative of a substrate with soft consistency or can also indicate the presence of a clay drape in the imprinted surface. Case 4 (Fig. 10) portrays one manus and one pes that do not compose a set, but the morphology is representative of this type of preservation. Case 4 is considered to be a true surface track (original mold), which shows plantigrade pes impressions with a shallow sole. Case 5 (Fig. 10) displays surface tracks, including a pes impression with a high divarication angle between digits I–IV and a broad sole, accompanied by a “bidactyl” manus impression. This animal probably walked over thin clay laminae with a high water saturation or which were covered by a few millimeters of water (cf. Brand, 1996). Case 6 (Fig. 10) illustrates deeply imprinted footprints with marginal ridges. The imprint of pes digits form a fairly low divarication angle. By comparison with modern tracks, these features are interpreted to be indicative of a moderately thick clayey substrate with high water saturation. Case 7 (Fig. 10) shows subaqueous traces (type A swimming traces) with very little anatomical information, namely arrangement of digits and general morphology of impressions. This case also implies a different locomotion behavior (swimming against walking or running).

Tetrapod Track Ichnocoenoses

Six ichnocoenoses have been identified in the Urre–Lauquen Member (1–6 in Fig. 4 and Fig. 11) and one from the Calencó Member. The latter has yielded a pair of incomplete footprints recovered from pond deposits in a floodplain setting, which are comparable with *Amphisauropus*. Figure 11 summarizes

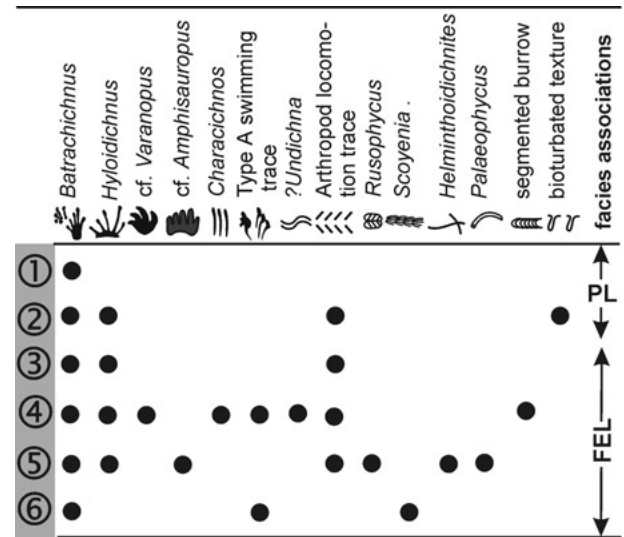


FIG. 11. Summary of trace fossil composition and facies associations for the different ichnocoenoses of the Urre-Lauquen Member of the Carapacha Formation. PL = playa lake, FEL = freshwater ephemeral lake.

the composition and environmental partitioning of the six ichnocoenoses identified in the Urre-Lauquen Member. The lack of large tracks in this association could be a reflection of a sampling bias, because no systematic quarrying has been conducted to date. *Batrachichnus* is present in all ichnocoenoses followed, in order of abundance, by *Hyloidichnus* and arthropod locomotion traces, which are present in four. The relative abundance of the different ichnotaxa is considered as an indication of the participation of different groups in the paleocommunity. Tetrapod traces reveal a paleocommunity dominated by small amphibians (*Batrachichnus* and type A swimming trace assigned to Eryopoidea, and *Amphisauropus* assigned to Seymouriamorpha) and includes small reptiles, mostly Captorhinomorpha (*Hyloidichnus* and *Varanopus*) and possibly Pelycosauria (*Hyloidichnus*). The associated arthropod population was varied, as inferred by the abundance and morphologic diversity of the invertebrate traces. The tetrapod traces were only recovered from mudflats of playa-lakes and from “wet” tracts of freshwater ephemeral lakes (Figs. 4 and 11). The latter yielded most of the tetrapod traces, including ichnocoenoses 4 and 5 that exhibit the greater ichnodiversity (Fig. 4). It is possible that this particular distribution can be related to the apparent preference of the producer of *Batrachichnus* for more aquatic environments, as noted by Hunt et al. (1995b) and Haubold (1996). Comparing the ichnocoenoses developed in roughly correlated intervals of the two sections illustrated in Fig. 4 (for example, ichnocoenosis 2 with ichnocoenoses 4 and 5), it is evident that the vertebrate and invertebrate trace fossil assemblages are most diverse in the deposits of freshwater ephemeral lakes. In ichnocoenosis 6, the coexistence of burrows with scratches that are indicative of desiccated substrates (*Scoyenia* isp.) and of type A swimming traces, seems to be contradictory. However, this can be explained

by a scenario of repeated water–level changes in a shallow lacustrine setting, as inferred from the sedimentological evidence. This implies that the lakes suffered periods of flooding and desiccation and that the same community of organisms produced these traces at different times.

Permian Tetrapod Ichnofacies

The current knowledge of Permian vertebrate ichnofacies is limited. In addition to a revision of the existing literature, more detailed ichnotaxonomical and sedimentological studies on individual cases are needed. Harmut Haubold has led a profound revision of the ichnotaxonomy of Permian tetrapod tracks from Europe and the southwestern USA (e.g., Haubold et al., 1995; Haubold, 1996, 1998, 2000; McKeever and Haubold, 1996; Haubold and Stapf, 1998; Haubold and Lucas, 2001a, 2001b). However, the precise facies assignment and composition of the track ichnoconoses is generally not known and probably is almost impossible to reconstruct without further studies. Such studies are essential to compile a large database and to define distinct ichnofacies (Lockley et al., 1994). The rich ichnofaunas from the Permian sequence of southwest USA (mainly the Robledo Mountains, New Mexico) probably represent a good opportunity to reconstruct the precise environmental setting and composition of different ichnoconoses developed along large environmental gradients (Lucas and Heckert, 1995). Despite this situation, two more or less distinct Permian track assemblages occurring in definite sedimentary facies (prospective ichnofacies) have been distinguished (Haubold, 1996; Hunt and Lucas, 1998; Lucas, 1998). An eolian track assemblage was named the *Laoporus* ichnofacies by Lockley et al. (1994) and *Chelichnus* ichnofacies by McKeever and Haubold (1996). A “red bed ichnofacies,” characterized by the presence of the ichnogenera *Batrachichnus*, *Limnopus*, *Gilmoreichnus* and *Dimetropus* typically occurring in fluvio-lacustrine deposits, was named by Hunt et al. (1995b) and later recognized by Melchor (1997a, 2001b) and Hunt and Lucas (1998). On the basis of their studies in the southwestern USA, Hunt et al. (1995b) proposed a subdivision of this “red bed ichnofacies” into an “*Ichniotherium-Parabaropus* ichnofacies” characterizing inland environments and a “*Dimetropus-Batrachichnus* ichnofacies” for more coastal environments. Hunt et al. (1995b) even proposed a subdivision of the latter “ichnofacies” on the basis of the relative abundance of *Limnopus* and *Batrachichnus*, whereas *Limnopus* is more common in terrestrial deposits and *Batrachichnus* in coastal or partially subaqueous deposits. The tetrapod ichnofauna from the Carapacha Basin includes typical Permian footprint ichnotaxa with cosmopolitan distribution (cf. Haubold, 1996, 2000). It is clearly related to the Permian “red bed ichnofacies,” in particular to the *Batrachichnus*-dominated, “*Dimetropus-Batrachichnus* ichnofacies” of Hunt et al. (1995b). However, this ichnofacies has not been formally defined. All occurrences are of Early Permian (up to Artinskian-Kungurian) age (Haubold, 2000), and especially of late Artinskian age (Haubold and Lucas, 2001b). The upper member of the Carapacha Formation has been dated

as early Late Permian, but a more precise dating is not available. However, Lucas (1998) states that the Early Permian amphibian and reptile groups persisted until Kazanian times. For this reason, it is likely that similar tracks occur in fluvio-lacustrine deposits of Kungurian-Kazanian age.

The composition of the Carapacha ichnofauna is also characterized by the apparent absence of lacertoid tracks of the ichnogenus *Dromopus* Marsh, 1894, which is a common component of Permian ichnofaunas in Europe and in the USA (Haubold et al. 1995; Haubold 1996). Hunt and Santucci (1998) have related the absence of *Dromopus* tracks from the tetrapod ichnofauna of the Hermit Shale (Arizona, USA) to an “inland” variety within the “red bed ichnofacies” because this lacertoid ichnotaxa is common in coastal settings in southwest USA. Consequently, the absence of *Dromopus* in the Carapacha ichnofauna could be related to the inland setting of the basin (cf. Melchor, 1995).

The vertebrate and invertebrate ichnofauna of the Carapacha Basin is comparable in composition, ethology, and sedimentary facies with the archetypical *Scoyenia* ichnofacies of the invertebrate realm (Buatois and Mángano, 1995). However, such an assignment, even if correct, will convey scarce information on the included tetrapod ichnotaxa, and on its precise paleoecological and paleoenvironmental meaning.

CONCLUSIONS

The Carapacha Basin tetrapod ichnofauna reveals the activities of a community of small tetrapods, mainly amphibians (Temnospondyli and Seymouriamorpha) and small reptiles (Captorhinomorpha or Pelycosauria). These animals have inhabited a limited range of shallow lacustrine environments, which were subjected to frequent water–level changes. The moderately abundant material of some footprint types permit the recognition of extramorphologic variants and their grouping within a few ichnotaxa. Footprint taxa were recognized on the basis of morphologic features that reflect the anatomy of the producer. Distinct morphologic variants of tetrapod traces that are recognized from a large sample size and from different stratigraphic intervals and locations should be distinguished as a separate ichnotaxa. This procedure is especially significant when the traces indicate a definite behavior. This is the case with the swimming traces assigned to *Characichnos* Whyte and Romano, 2001, that are discussed in this paper. The identified footprint ichnotaxa include: *Batrachichnus salamandroides* (Geinitz, 1861), *Hylodichnus bifurcatus* Gilmore, 1927, cf. *Amphisauropus* isp. and cf. *Varanopus* isp. These tracks are associated with two forms of swimming traces: *Characichnos* isp. and type A swimming traces (assigned to the producer of *Batrachichnus*).

The Carapacha tetrapod ichnofauna contains Permian ichnotaxa of cosmopolitan distribution and can be compared with the “red bed ichnofacies” of Europe and the USA, particularly with the “*Dimetropus-Batrachichnus* ichnofacies” that occurs in inland settings (Hunt et al., 1995b). However, to formally define one or more ichnofacies for Permian red bed tetrapod

ichnofaunas, more case studies dealing with tetrapod ichnotaxonomy and sedimentary facies are needed.

The presence of *Scoyenia* burrows, tetrapod footprints and desiccated substrates also suggest comparison of invertebrate and vertebrate ichnofossils from the Carapacha Basin with the *Scoyenia* ichnofacies of the invertebrate realm. However, this assignment would be almost meaningless for a vertebrate ichnologist. Researchers with different backgrounds and interests commonly treat invertebrate and vertebrate trace fossils separately. It is considered that the time has come to try and analyze in conjunction the distribution of vertebrate and invertebrate ichnofossils in continental successions with a similar methodology (including ichnotaxonomy). It is hoped that more communication between vertebrate and invertebrate ichnologists and multidisciplinary efforts will improve our understanding of the distribution and significance of continental ichnofossils.

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