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Lavinipes Cheminii Ichnogen., Ichnosp. nov., A Possible Sauropodomorph Track from the Lower Jurassic of the Italian Alps

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A new ichnotaxon is described from the Lower Jurassic (Upper Hettangian—Lower Sinemurian) carbonate tidal flats on the central-eastern Italian Alps. The narrow-gauge trackway is that of a large quadrupedal dinosaur. The pes is functionally tetradactyl with three rounded antero—medially directed digits, and the manus is pentadactyl. This quadrupedal form is close to *Otozoum* and *Pseudotetrasauropus jaquesi* both traditionally related to sauropodomorph trackmakers. The similarity with *Otozoum* is so marked that *Lavinipes* and *Otozoum* could be cogeneric. But the overall evidence today is that the *Otozoum* trackmaker was generally bipedal, whereas the trackmaker of *L. cheminii* is fully quadrupedal. The manual prints of *L. cheminii* show five short clawless digits and are different from the tetradactyl slender toed manual prints of *Otozoum.* The possible sauropodomorph affinity of the *L. cheminii* trackmaker is here discussed with an attempt to a revision of the Late Triassic—Jurassic tracks which have been traditionally related to sauropod and prosauropod.

Keywords Dinosaur footprints, ornithischian tracks, sauropod tracks, *Otozoum,* Lower Jurassic, Italian Alps

INTRODUCTION

The Lower Jurassic dinosaur tracksite at the Lavini di Marco is one of the richest in Europe (Fig. 1). Three dinosaur tracks were discovered for the first time in 1989 by Luciano Chemini. Many other footprints and tracks have been found by systematic field explorations of the site carried out since 1991 (Leonardi and Mietto, 2000). The footprints and tracks testify the presence of theropods, sauropods, and small-sized primitive ornithischians. Large quadrupedal tracks have been attributed to *Parabrontopodus*-like ichnogenus (Leonardi and Mietto, 2000) and assigned to primitive sauropods. Other bipedal or facultative bipedal tracks were attributed by the same authors to "iguanodontid-like" trackmakers; "however, we cannot ignore, another hypothesis: that the trackmaker could be a sauropod" (Leonardi and Mietto, 2000). A sauropod affinity for these tracks was also suggested by Lockley and Meyer (1999), who did not create any new ichnotaxon because of the poor preservation of the tracks.

Some well-preserved trackways that show quadrupedal locomotion have been recognized only recently and allow the erection of the new ichnotaxon that is described in this paper.

GEOLOGICAL SETTING

The trampled sediments have been ascribed to the middle part (peritidal unit) of the Lower Member of the Calcari Grigi formation late Hettangian—early Sinemurian in age. The tracks (Fig. 2) are slightly impressed on the top of a sedimentary layer consisting of alternating stromatolitic laminae and light gray peloidal mudstones, dark gray bioclastic wackestones, and reddish mudstones (Avanzini et al., 1997). A continuous layer of dark-gray wackestone, about 10 mm thick, containing *Thaumatoporella parvovesciculifera*, is intercalated within the inter-supratidal stromatolitic bindstones. This continuous layer, probably a storm layer, grades into hazel-colored mudstone spotted by iron oxides and then capped by a fine grained breccia or by a laminated mudstone-wackestone with evidences of pedogenetic rubefaction. This rubefacted horizon is characterized by iron-rich glaebules, clotted micrite, and cir-

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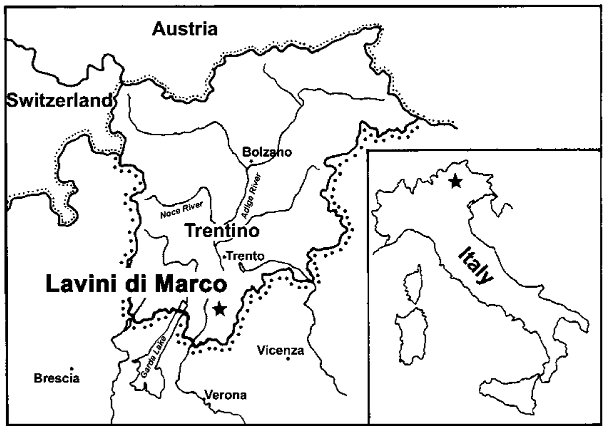

FIG. 1. Sketch map showing the location of the Lavini di Marco ichnosite where *Lavinipes cheminii* igen., isp. nov. were recognized.

cum-granular cracking, all features indicative of supratidal conditions. SEM observations and EDAX analyses reveal that the red, pedogenetic horizons consist of a mixture of dolomite, limestone, clay, and iron oxides (Avanzini et al., 1997).

The trampling of dinosaurs is responsible for the deformation of the substrate as indicated by the convolution of the mud associated with some prints and by the embedded angular red clasts derived by breakage of already lithified sediments. This deformation caused the opening of irregular and/or sheet-like voids between the arched laminae, which were subsequently filled by dolomite.

Stable isotopic data are mostly consistent with a diagenetic environment dominated by marine water, which is particularly marked in the dolomitized stromatolites. The environment of deposition of this layer could have been a coastline or a transitional belt, subjected to strong marine influence and semi-arid climate.

In the Lavini di Marco Jurassic tidal flat, the footprint preservation results generally from a combination of sediment textures and diagenesis (Avanzini et al., 1997). Dinoturbation might have promoted dolomitization, and dolomite precipitation may have contributed to the fossilization of the tracks. It is also possible that immediate cementation occurred via precipitation of NaCl after evaporation of saline waters.

SYSTEMATIC ICHNOLOGY

The terms concerning vertebrate palaeoichnology mainly follow Leonardi (1987) (Fig. 3). To avoid repetition in the systematics the authors and years of publication of the ichnotaxa will only be listed at the first mention.

Lavinipes ichnogen. nov.

Etymology: From Lavini di Marco, the locality in which the tracks have been discovered.

Type horizon and locality: As for the type ichnospecies.

Diagnosis: Narrow trackway of a quadrupedal animal with footprint length of about 43 cm and with no space between

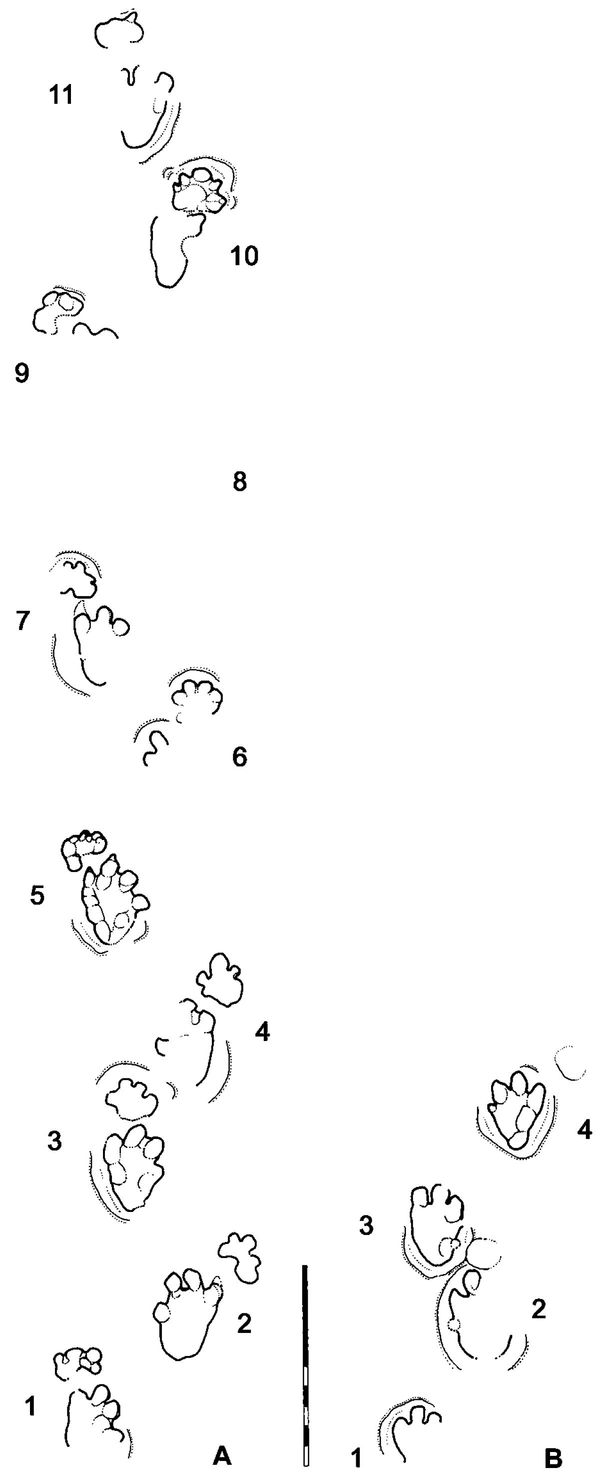

FIG. 2. Line drawing of *Lavinipes cheminii* igen., isp. nov. trackways. **(A)** The best-preserved trackway ROLM 577. **(B)** The poorly preserved ROLM 192, without manual prints. Scale bar: 1m.

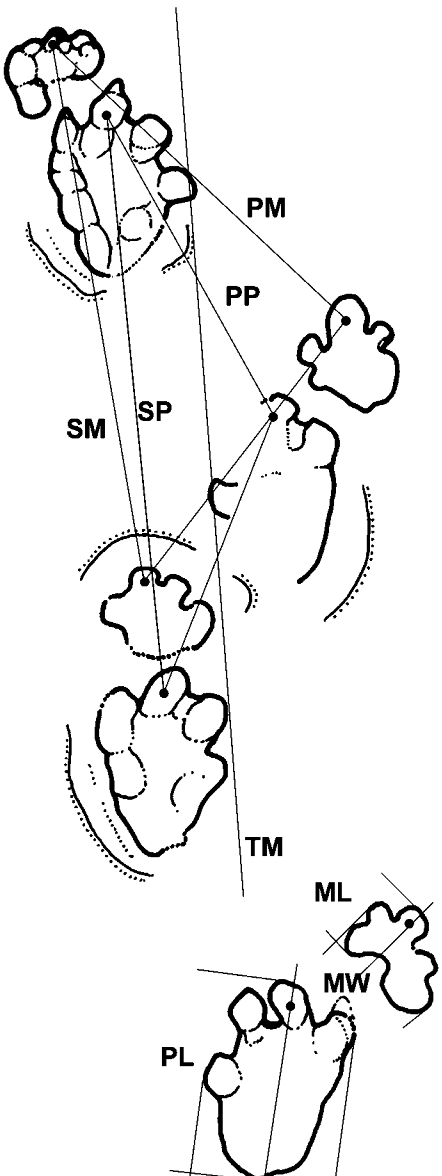

FIG. 3. Line drawing of the segment of the *Lavinipes cheminii* igen., isp. nov. trackway ROLM 577 chosen as holotype with indication of the most relevant parameters measured. PP, pes pace length; PM, manus pace length; SP, stride pes; SM, stride manus; TM, trackway midline; ML, manus length; MW, manus width; PL, pace length; PW, pace width.

trackway midline and inside margin of pes tracks. Pes axis longer than wide with long axis parallel to the midline or slightly rotated inwards (up to –12°). Pes tetradactyl with three short anteriorly directed digits and a small digit I. Digit impressions with inward rotation. Manus tracks pentadactyl or semicircular (pronounced heteropody—manus/pes ratio 0.44) and placed externally to the hind foot (Fig. 2).

Remarks: The new ichnogenus is distinguished from Early Jurassic taxon *Otozoum* Hitchcock, 1847 by the different morphology of manual prints that in *Otozoum* are tetradactyl with high divarication between the slender digits (Rainforth pers. comm.) and from *Tetrasauropus* Ellenberger, 1972, by the slender clawless manus and pes prints and narrower trackway. *Lavinipes* is also distinguished from *Parabrontopodus* Lockley et al., 1994a, by the relatively longer digits III (both in the pes and manus), the prevalence of pes digit IV, the inward rotation of the digits and by the inward rotation of the footprints with respect to the midline (in *Parabrontopodus* there is outward rotation of the foot and digits).

The tetradactyl pes of *Lavinipes* seems close to the stegosaur-like trackway reported by Le Leouff et al. (1999), but this latter specimen show more elongated digits without the well-marked pedal digit IV and a tridactyl smaller manual print. The roughly triangular pedal prints of *Lavinipes* and the crescent-shaped manual prints are similar than those of *Deltapodus* Whyte and Romano, 1994; however, the trackway of *Deltapodus* is wide gauge and different than *Lavinipes*.

The position of the manual prints with respect to the trackway seems peculiar in *Lavinipes*. The midlines of the manual prints, are lateral to the midline of the pedal prints and in most cases a major portion of the manual prints are lateral to the lateral margins of the pedal prints in difference to those of *Parabrontopodus*, *Breviparopus* Dutuit and Ouazzou, 1980 and *Brontopodus* Farlow et al., 1989, and more similar than those of *Tetrasauropus* and *Pseudotetrasauropus*.

***Lavinipes cheminii* ichnosp. nov.**

(Figs. 2–8)

Etymology: In memory of Luciano Chemini, the discoverer of the Lavini di Marco ichnosite.

Type horizon and locality: Lower Jurassic (Upper Hettangian—Lower Sinemurian) Calcari Grigi Formation at Lavini di Marco ichnosite, Rovereto (Trento), Italy.

Material: One trackway made up of at least 10 sets (ROLM 577) and another poorly preserved trackway made up of 4 pedal prints (ROLM 192) (Fig. 2).

Holotype: Rubber cast of manus-pes set 5 from the ROLM 577 trackway and fiberglass replica of ROLM577 2–5 manus—pes set.

Paratypes: Rubber cast of ROLM 577/10 manus print, rubber cast of ROLM 192/4 pes print.

Topotype: Trackway ROLM 577 that has been left *in situ*.

Repository of plaster casts: Museo Tridentino di Scienze Naturali—Trento, Italy.

Description—based on holotype: Narrow-gauge trackway of a quadrupedal dinosaur with no space between trackway midline and inside margin of pes tracks. Manus pentadactyl; pes functionally tetradactyl with three rounded anteriorly directed digits (II, III, IV) and a medially directed digits I. Manus laterally directed; pes directed slightly inward with respect to the midline. Manus impressions placed antero-laterally with respect to the pes impressions (Figs. 2, 3, 4). The maximum external width of the trackway is 92 cm. Oblique pace: pes 74 cm, manus 92 cm. Stride: pes 134 cm, manus 135 cm. Pace angulations: pes 128°, manus 95°. The ratio of stride to footprint length is about 3. (Table 1).

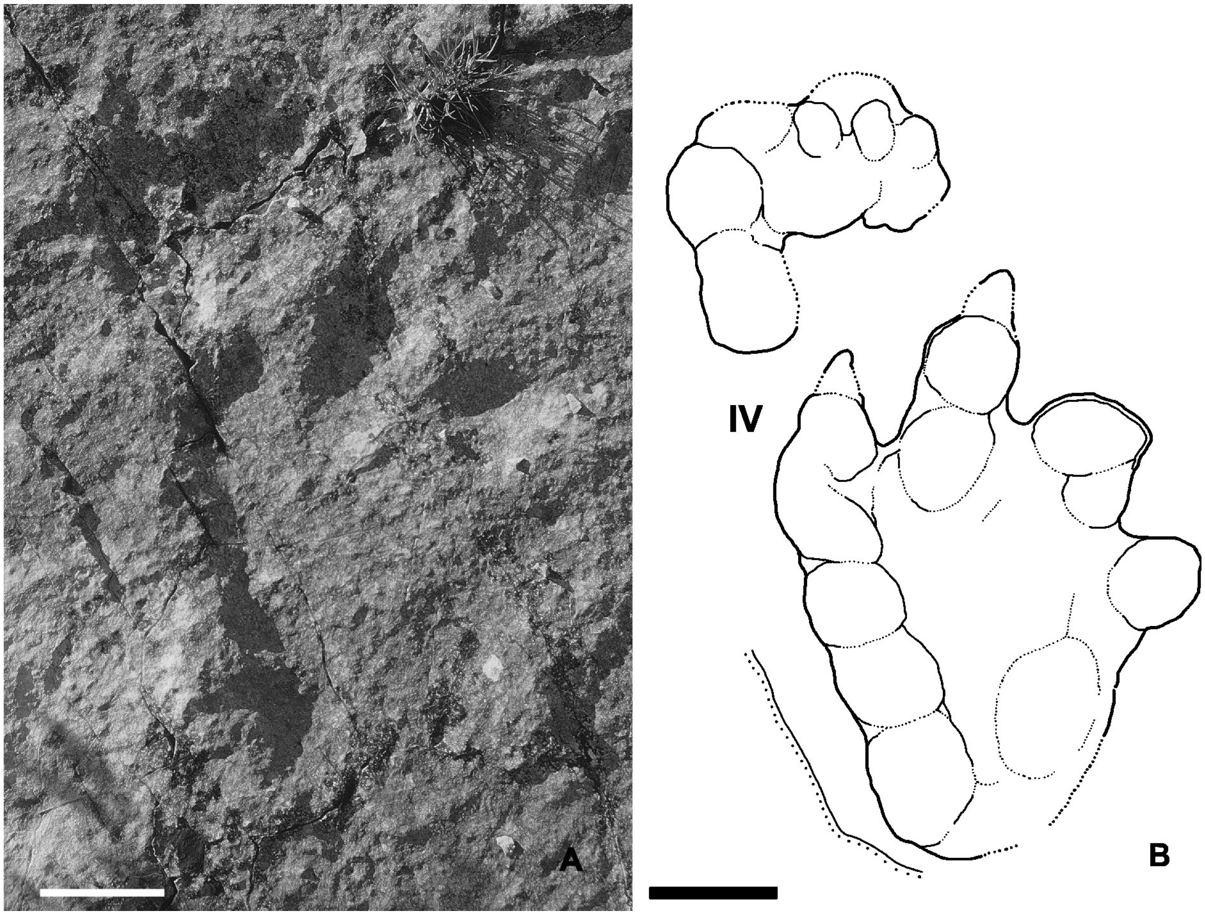

FIG. 4. Holotype of *Lavinipes cheminii* igen. isp. nov. (MTSN ROLM577.5). Lower Jurassic Calcari Grigi Formation, Lavini di Marco tracksite, Italy. Scale bar: 10 cm.

TABLE 1
Data of the trackway ROLM 577. Measurements in cm and in degrees. (M, manus; P, pes; x, average; σ, standard deviation).

	Pace			Stride			Pace angulation			Length			Width			Divarication from midline	
	M	P		M	P		M	P		M	P		M	P		M	P
1–2	102	74	*1–3*	136	131	*1–3*	85°	120°	*1*	15	—	*1*	24	30	*1*	+18°	0°
2–3	98	76	*2–4*	140	135	*2–4*	103°	136°	*2*	20	46	*2*	25	31	*2*	+30°	+2°
3–4	77	78	*3–5*	127	134	*3–5*	94°	129°	*3*	20	44	*3*	25	31	*3*	+5°	–12°
4–5	93	80	*4–6*	137	135	*4–6*	96°	129°	*4*	24	43	*4*	24	30	*4*	+15°	–2°
5–6	92	68	*5–7*	134	126	*5–7*	98°	134°	*5*	18	45	*5*	23	32	*5*	+15°	–5°
6–7	86	67	*6–8*	—	—	*6–8*	—	—	*6*	20	—	*6*	25	—	*6*	—	—
7–8	—	—	*7–9*	135	140	*7–9*	—	—	*7*	18	39	*7*	25	—	*7*	0	–5°
8–9	—	—	*8–10*	—	—	*8–10*	—	—	*8*	—	—	*8*	—	—	*8*	—	—
9–10	98	77	*9–11*	140	137	*9–11*	98°	123°	*9*	20	—	*9*	26	—	*9*	+40°	—
10–11	87	74							*10*	20	41	*10*	27	—	*10*	+5°	–5°
									11	16	42	*11*	24	—	*11*	—	+5°
x	**92**	**74**		**135**	**134**		**96°**	**128°**		**19**	**43**		**25**	**31**		**+16°**	**–3°**
σ	7	4		4	4		5°	5°		2	3		1	1		12°	4°

Pedal print longer than wide (L = 43, W = 31 cm) (Fig. 5). Digit III is the longest digit and protrudes 5 cm (average) in respect to II and IV. Digits II and IV are subequal in length; digit I is the smaller and appearing as a single pad positioned in the medial part of the footprint. The digits are connected to ample and rounded hypexes. Digit IV continues proximally, as a long depression that characterizes the lateral margin of the whole footprint. The base of digit IV corresponds with the proximal margin of the foot; there are recognizable traces of five phalangeal and/or phalangeo-metatarsal pads. Divarication angles of the pes digits are I–II = 15°, II–III = 14°, III–IV = 25°; total divergence I–IV = 45°. The terminal last phalanx of every digit is rotated inwardly. The claw marks on digits III and IV are short and triangular. No claw prints are preserved on digits I and II (Fig. 6).

Manual prints are small, wider than long (L = 19 cm, W = 25 cm), pentadactyl and mesaxonic, sometimes U-shaped and outwardly rotated, located laterally in respect to the foot and externally in respect to the midline. The axis of the manual print is lined up to the axis of the digit IV of the foot (Figs. 2, 5, and 6). Digits show rounded margins and rather ample hypexes. Digit I print is turned toward the midline, digit III is the longer, rounded and wider, digits II and IV are equal in length and general shape, and digit is V outward turned. The proximal margin of the print is generally concave with an anteriorly directed broad indentation in the middle, but sometimes with trace of an ample and convex heel. No claw marks are preserved (Fig. 7).

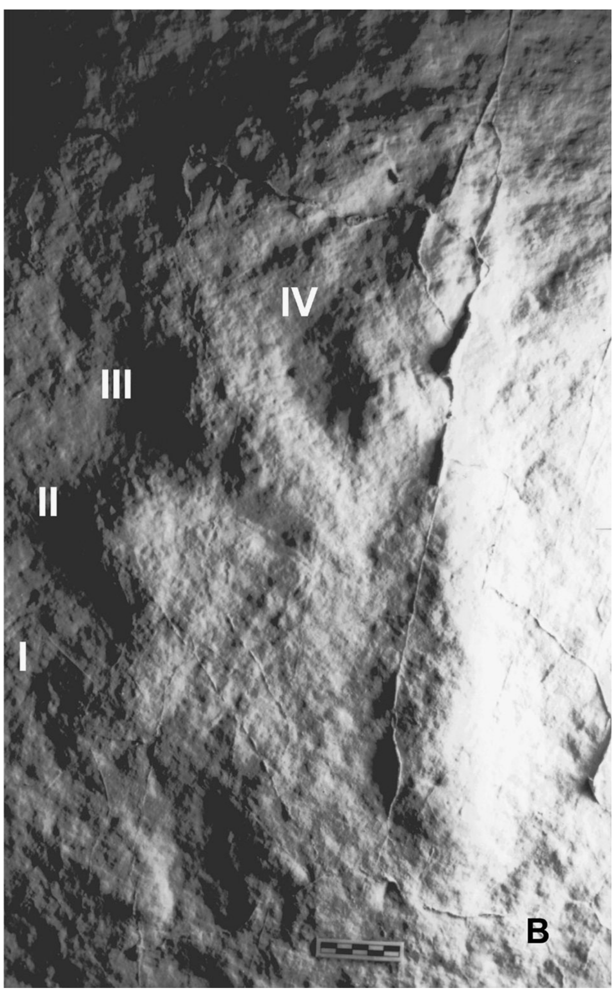

FIG. 5. *Lavinipes cheminii* igen. isp. nov. Plaster cast of manus-pes set ROLM577.5. Light from the right side. Scale bar: 5 cm.

Remarks: The most evident characteristic of the pedal footprints is their elongated shape with a long "heel" produced by the whole of digit IV resting on the ground. This is evident in sets ROLM577/3, ROLM577/5, and ROLM 192/4. Digit IV shows traces of four connective pads and a proximal pad probably corresponding to the phalangeal-metatarsal articulation. Digit III shows traces of two pads while digits I–III are characterized by the impression of a single elongated pad. The claws on digits III and IV, when present, are short and triangular, inward turned, like the digit, toward the midline of the trackway. The manus has a U-shaped morphology and only in some prints five digits are recognizable. Generally only manual digit prints II, III, and IV are well preserved. Digit III is always prominent and protrudes up to 11% with respect to group II–IV. The lateral margin, in correspondence to digit V, is more robust with a broad indentation in the posterior margin (Fig. 8).

DISCUSSION

Lower Jurassic trackways that show clearly evidences of facultative or obligate quadrupedal locomotion are relatively rare. *Lavinipes* differs from *Moyenisauropus* Ellenberger (1974) and from *Anomoepus* Hitchoch, of the Lower Jurassic of Lesotho and of the western U.S., including the form described by Gierlinski (1991), from the upper Hettangian of Poland and named *Moyenisauropus karaszevenkii* Gierlinski, 1991 recently interpreted as a possible basal thyreophoran footprint (Gierlinski, 1999; Gierlinski et al., 2001; Lockley and Meyer, 1999; Le Leuff et al., 1999). Like the above-mentioned forms, *Lavinipes* is digitigrade in the strict sense of the word (i.e., here is never the imprint of a real heel-tarsus/metatarsus), but digits II–IV are much shorter, broad, and hooflike. Moreover the trackmaker of *Lavinipes* was much larger and stouter, with a general different foot and manus structure.

The unnamed track of a purported large quadrupedal thyreophoran dinosaur reported by Le Leuff et al. (1999) from the Hettangian of central France is comparable with *Lavinipes* in having a narrow trackway and a tetradactyl pes (L = 25 to 32 cm). However, the smaller tridactyl manus (L = 16 to 18 cm), the longer and slender distal phalanges of II–IV digits, the isolated distal end of digit I situated slightly posterio-medially to the impression of phalanx I of digit II, the shorter digit IV and the marked inward rotation of the foot (about 20°), are in disagreement with the characters of *Lavinipes*.

The earliest true stegosaurids have a tridactyl pes and have been found in the Bathonian beds of England. Conjectural predictions of stegosaurid footprint characters show a relatively

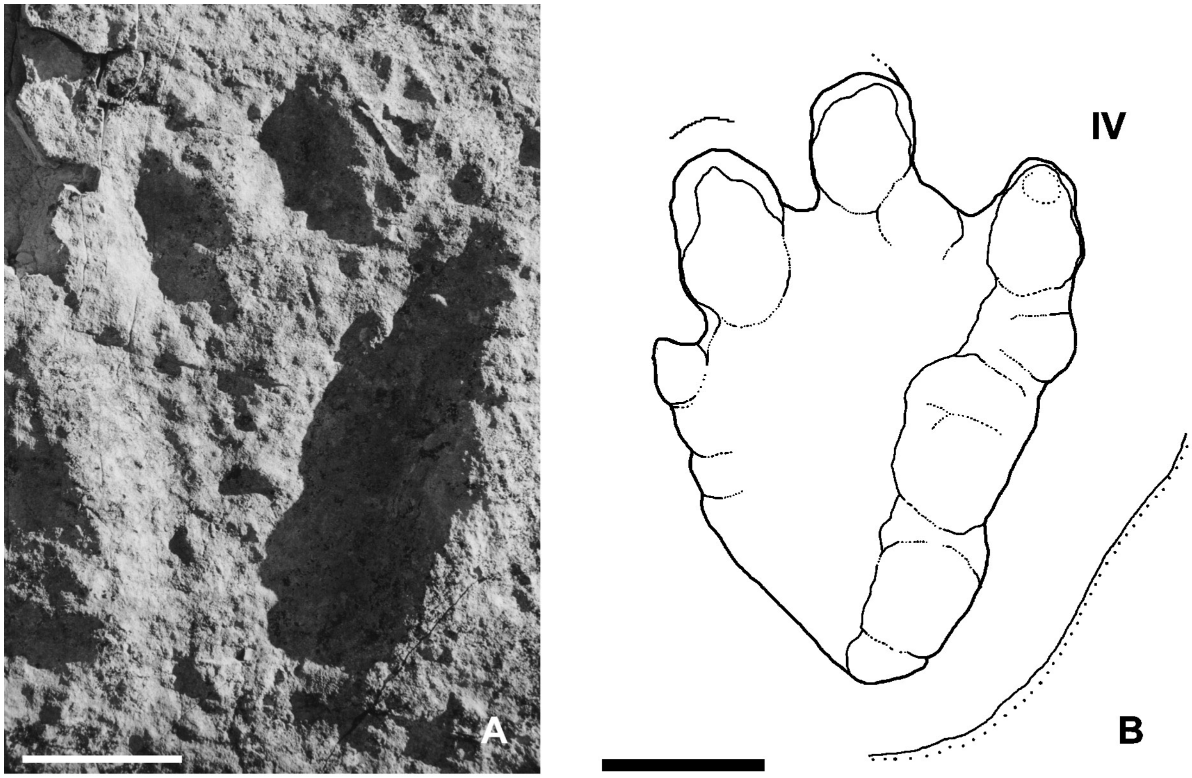

FIG. 6. Paratype of *Lavinipes cheminii* igen. isp. nov. (MTSN ROLM 192.4 pedal print). Scale bar: 10 cm.

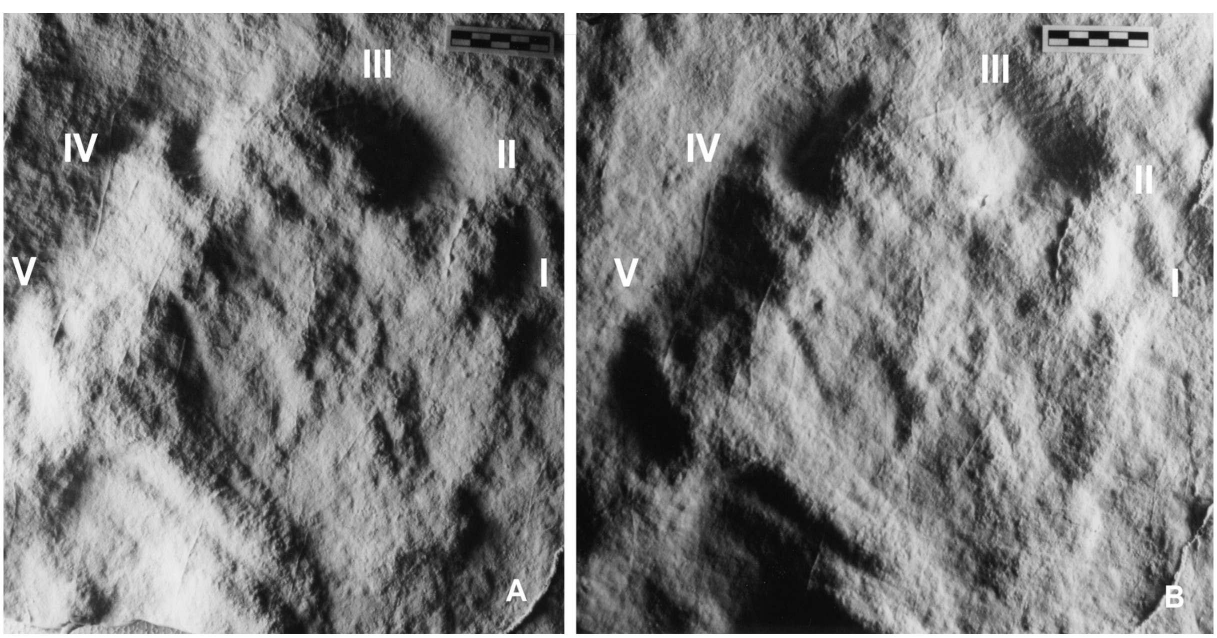

FIG. 7. Plaster cast of *Lavinipes cheminii* igen., isp. nov. manual print ROLM 577.10. **(A)** with the light from the left side. **(B)** with the light from the right side. Scale bar: 5 cm.

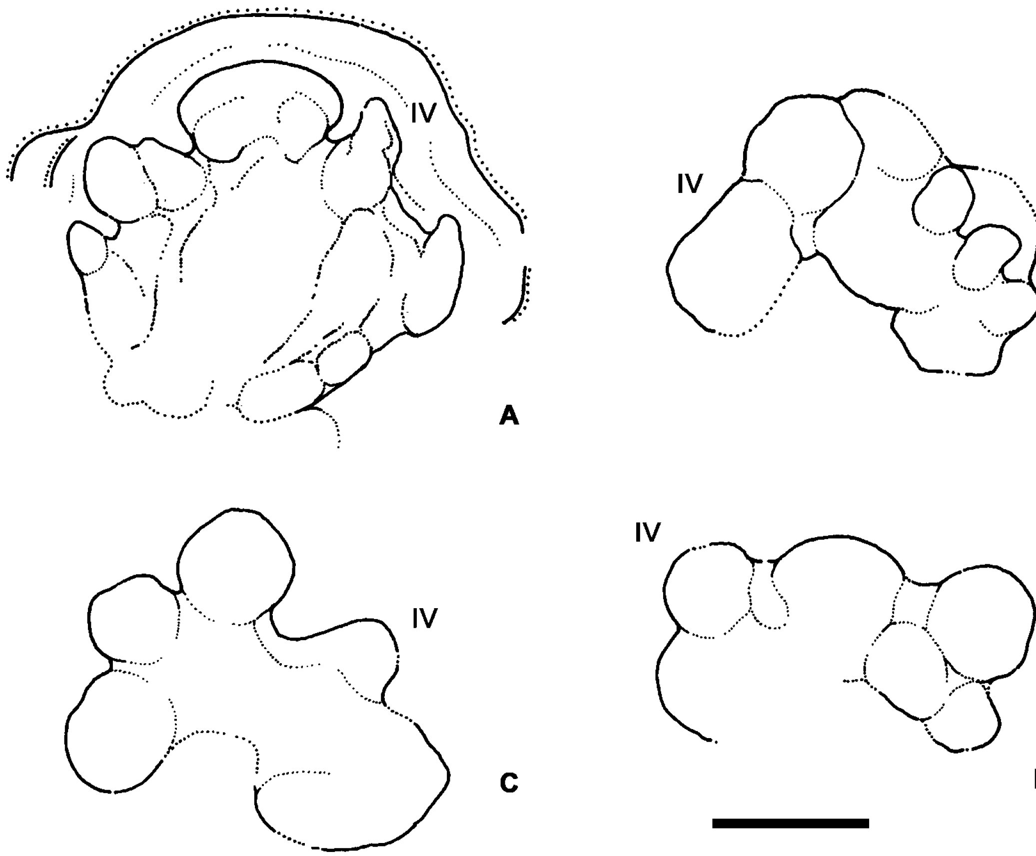

FIG. 8. Line drawing of some *Lavinipes cheminii* igen., isp. nov. manual prints. **(A)** ROLM 577.10, **(B)** ROLM 577.5, **(C)** ROLM 577.1, **(D)** ROLM 577.2. Scale bar: 10 cm.

large tetradactyl manus print and tridactyl mesaxonic pes prints (Thulborn, 1990; Whyte and Romano, 2001). The first formally described stegosaur tracks were reported from the Upper Jurassic (Lockley and Hunt, 1998) and assigned to the ichnogenus *Stegopodus*, but unnamed stegosaurid footprints with tridactyl manus and pes have recently been found by Gierlinsky and others (2001) in the Upper Jurassic of Poland. They are smaller and have more elongated digits than *Lavinipes*. Another possible ichnogenus related to Jurassic basal quadrupedal ornitischia is *Deltapodus brodericki* Whyte and Romano, 1994, a trackway of Aalenian age in England (Lockley and Meyer, 1999; Whyte and Romano, 2001; Romano and Whyte, 2003). In *Deltapodus brodericki* the footprints are roughly triangular, and the manual footprints are crescent-shaped, very close to *Lavinipes*. However, the trackway is wide gauge with pace angulation of about 90°, slight negative (outward) rotation of the pedal print, and wider manual prints.

Sauropodomorph are the only other quadrupedal dinosaurs present in the Upper Hettangian-Upper Sinemurian interval from the U.S., Africa, and Europe (Lockley et al., 1994b). The first study of Upper Triassic track successions, in which abundant sauropodomorph tracks occur, was conducted by Ellenberger (1955, 1970, 1972, 1974) in Southern Africa. Among these tracks, there are two related ichnogenera: *Tetrasauropus* and *Pseudotetrasauropus* (Ellenberger, 1972). *Tetrasauropus* tracks were generally large and produced by quadrupedal animals, whereas *Pseudotetrasauropus* tracks were more variable in size and in most cases were made by bipedal animals. Lockley and Meyer (1999), in their attempt to revise prosauropod track nomenclature, concluded that *Tetrasauropus* represents a quadruped trackmaker with robust, fleshy feet that are not separated into elongate digits, and that *Pseudotetrasauropus* is essentially identical to the bipedal *Otozoum*.

Tetrasauropus unguiferus Ellenberger 1972 show robust feet (L = 44 cm) with a smaller manus (L = 32 cm) situated anterolateral to the pes. The digits on both the manus and pes appear to be curved inward with respect to the trackway midline. The pes is functionally tetradactyl. Digits II, III, and IV are almost equal in size and pronounced with evident scratch marks, digit IV is short and parallel to digit III, digit I is the shortest. There is a functional prevalence of digit IV that is marked along the lateral margin of the footprint. The manus show four digits with robust and arched claws (Fig. 9A).

Lockley et al. (2001) stated that the *Tetrasauropus* trackways are similar to the later sauropod tracks such as *Brontopodus* and related forms (see above). For this reason it was re-

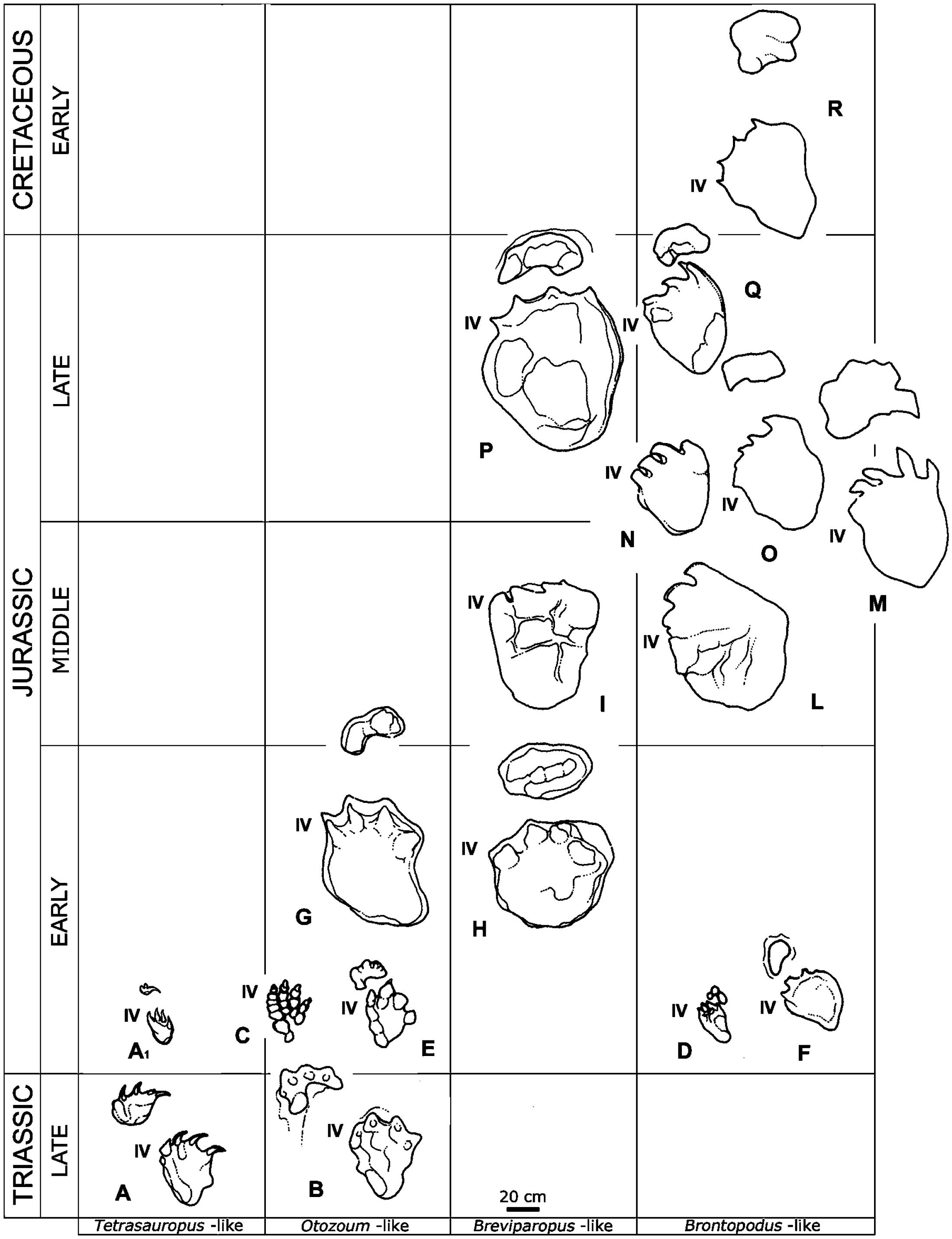

FIG. 9. Differences in sauropodomorph tracks between Late Triassic and Early Cretaceous. On the basis of pedal print morphology the sauropod ichnotaxa are here subdivided into four main groups: *Tetrasauropus*-like, *Otozoum*-like, *Breviparopus*-like and *Brontopodus*-like. **(A)** *Tetrasauropus unguiferus* from the Late Triassic of Southern Africa (after Ellenberger, 1972, mod.); (A1), *Navahopus* from the Early Jurassic of Northern America (after Baird, 1980, mod.). **(B)** *Paratetrasauropus jaquesi* from the Late Triassic of Southern Africa (after Ellenberger, 1972, mod.). **(C)** *Otozoum moodii* CU-MWC 181.11 from the Lower Jurassic of eastern U.S.A. (after Lockley, 1990, mod.). **(E)** *Lavinipes cheminii*. **(D)** *Parabrontopodus* sp. from the Lower Jurassic of Poland (after Gierlinski, 1997, mod.). **(F)** unnamed from the Lavini di Marco (after Leonardi and Mietto, 2000, mod.). **(G)** morphologic group 1 from the Lower Jurassic of Morocco (after Ishigaki, 1988, mod.). **(H)** morphologic group 2 from the Lower Jurassic of Morocco (after Ishigaki, 1988, mod.). **(I)** morphotype A from the Middle Jurassic of Yorkshire (after Romano et al., 1999, mod). **(L)** morphotype B from the Middle Jurassic of Yorkshire (after Romano et al., 1999, mod). **(M)** unnamed from the Middle Jurassic of Portugal (after Santos et al., 1994, mod.). **(N)** unnamed from the Late Jurassic of Spain (after Garcia Ramos et al., 2000). **(O)** unnamed from the late Jurassic of Portugal (after Santos et al., 1994, mod.). **(P)** *Breviparopus thagbaloutensis* from the late Jurassic of Morocco (after Dutuit and Ouazzou, 1980, mod.). **(Q)** *Parabrontopodus mcintoshi* from the Late Jurassic of the U.S.A. (after Lockley et al. 1994, mod.). **(R)** *Brontopodus birdi* from the Early Cretaceous of the U.S.A. (after Farlow et al., 1989, mod.). All the left prints are drawn at the same scale. Scale bar: 20 cm.

cently suggested that the trackmaker of *Tetrasauropus* was not a prosauropod (Ellenberger, 1972; Baird, 1980; Haubold, 1984; Thulborn 1990) but a primitive sauropod (Lockley et al., 2001). However, the inward rotation of the digits, the longer digit III, the functional prevalence of the digit IV is very different from the own characters of the true sauropod tracks. For this, it may be preferred to consider *Tetrasauropus* closer to prosauropods than to sauropods. *Lavinipes* differs from *Tetrasauropus* due to its slender manus and pes without arched claws and the much narrower trackway.

An ichnogenus related to *Tetrasauropus* is *Navahopus* Baird 1980, known from the Lower Jurassic Navajo Sandstone. The pes print is smaller but close to *Tetrasauropus* and shows a recurved manual digit I . The manual digit I suggests that *Navahopus* was made by a prosauropod (Baird, 1980); however, Lockley (Lockley and Hunt, 1995; Lockley and Meyer, 1999) consider *Navahopus* close to the sinapsid trackmaker of *Brasilichnium*. The pedal prints of *Navahopus* are less elongated than those of *Lavinipes*, the pedal unguals are more marked, and the peculiar morphology of the manual prints is different than those of our specimen.

Pseudotetrasauropus Ellenberger 1972 was named for material from the upper Triassic Molteno Formation of Lesotho and include nine different species, namely *P. acutunguis*, *P. augustus*, *P. bipedoida*, *P. curtus*, *P. dulcis*, *P. francisci*, *P. mekalingensis*, *P. elegans*, *P. jaquesi* (Ellenberger et al., 1970; Ellenberger, 1972). Olsen and Galton (1984), in their systematics appendix, consider *Pseudotetrasauropus* as a possible synonym of *Brachychirotherium*, while Lockley and Hunt (1995) and Lockley and Meyer (1999) affirm that some (bipedal) *Pseudotetrasauropus* tracks are particularly interesting because they are close to the Early Jurassic track *Otozoum*. Rainforth (2000, 2001, 2002) contests this attribution and observes that *Pseudotetrasauropus* shows only four phalanges in digit IV, thus distinguishing it from *Otozoum* (five phalanges in digit IV) and suggests a crocodilomorph or rauisuchian trackmaker for this ichnogenera. This observation seems to be inconsistent, as the *Pseudotetrasauropus* tracks are often poorly preserved, and it is preferred to consider Lockley and Hunt's (1995) observations valid while awaiting further investigations. The ichnogenus *Pseudotetrasauropus* includes bipedal (*acutiunguis*, *augustus*, *bipedoida*, *dulcis*, *francisci*, *mekalingensis*) and quadrupedal (*elegans*, *jaquesi*) forms that show generally rounded digit termination (Ellenberger, 1972; Lockley and Hunt, 1995; Hunt et al., 1993; Lockley and Meyer, 1999). Among the quadruped forms, *Pseudotetrasauropus jaquesi* seems close to *Lavinipes cheminii* (indeed, Ellenberger, 1972, considers *P. jaquesi* a functional quadruped expression of *P. augustus* and admits that this latter is similar to *Otozoum*) (Fig. 9B). The pes of *P. jaquesi* is tetradactyl, more long than wide (L = 48.5, W = 37.0 cm), with a pronounced third digit. The digits are short, slightly inward rotated and marked only by the distal phalanx. There is a functional prevalence of digit IV that is marked by a depression along the lateral margin of the footprint. The manus is pentadactyl with regularly spaced digits and digits I–IV particularly evident (L = 45, W = 37 cm). Also in the manus digit III is the most developed. The trackway is relatively narrow gauged. The similarity with *L. cheminii* is in the general shape of the foot, which has a well-marked heel print, and in the functional prevalence of digit IV. Digit I in *P. jaquesi* is slightly more forward than *L. cheminii*. The manus of *P. jaquesi* is similar but bigger in proportion to the pes than it is in *L. cheminii* (manus/pes ratio = 0.90 in *P. jaquesi* and 0.44 in *L. cheminii*) and it is relatively wider and more arched.

Otozoum is one of the classic Lower Jurassic Connecticut Valley ichnogenus first described by Edward Hitchoch between 1836 and 1865 (Hitchoch, 1836, 1845, 1847, 1856, 1858, 1865; Lull, 1904, 1915, 1953). *Otozoum* is a large pentadactyl but functionally tetradactyl footprint, made by a digitigrad facultative biped dinosaur. Digit III is the longest, digits II and IV are subparallel, subequal in length and only a little shorter than digit III (Fig. 9C). The pes is rotated slightly outward from the trackway midline (Rainforth, 2000). There were reports of a small four-toed manus in association with *Otozoum* footprints of the specimen (A.C. 5/14) (Lull, 1904, 1953), but it was never convincingly demonstrated that the footprints were part of a regular sequence made by an animal progressing quadrupedally. Rainforth (2000, 2002, pers comm.) stated that the animal was evidently bipedal but stooped down, and both the manus print preserved on the A.C. 5/14 (Lull, 1904, 1953) slab are tetradactyl. There are many similarities with *L. cheminii*. The general dimensions and morphology of the tetradactyl pes are comparable, even if in *Otozoum* the digits are always evident and not included in the tissue of the pes. Also characteristic is the presence of well-marked pads on the lateral margin of the pes prints in both *L. cheminii* and *Otozoum*. But the overall evidence today is even stronger that the *Otozoum* trackmaker was generally bipedal except when it stooped down (Lockley and Hunt, 1995; Rainforth, 2000, 2002), whereas the trackway of *L. cheminii* is fully quadrupedal. The manual prints of *L. cheminii* are stout and pentadacty, different to those reported for *Otozoum*. The comparison with *Otozoum* seems possible but not completely convincing.

In *Parabrontopodus* sp. reported by Gierlinski (1997) from the Polish Hettangian, the manual prints are semicircular, broader than long, significantly smaller than the pes and situated antero-laterally to the pes (Fig. 9D). In the manual prints a wide and rounded digit III is recognizable. On the medial side traces of digit II can be seen, while on the lateral margin an elongated track can be related to digit II and IV prints. The manual print compares well with our sample and, together with *P. jaquesi*, is the most similar among the late Triassic and early Jurassic sauropodomorph manual prints. However, in this *Parabrontopodus* sp. specimen, the pes has four anteriorly directed pointed digits similar to other sauropod-like tracks at Lavini di Marco (Leonardi and Mietto, 2000) but different to the digit morphology of *L. cheminii*.

The unnamed sauropod tracks reported by Leonardi and Mietto (2000) at Lavini di Marco are narrow gauge and resemble the ichnogenus *Parabrontopodus* of the Upper Jurassic of USA

(Fig. 9F). The diagnostic features suggested by Leonardi and Mietto (2000) are: quadrupedality with marked heteropody, characteristic shape of the manual (crescent-like) and pedal prints, strong positive (outwards) divarication, short pointed digits on the hind feet and, when present, also in the fore feet, with hypexes open, blunt and rounded; relatively high pace angulation (about 120°). The pes differs from that of *L. cheminii* due to the consistent outward rotation, the absence of traces of digit III and for the traces of sharp forward pointing claws. The manus impressions are different from *L. cheminii*, always deformed by the pes with a very narrow U-shape either without traces of digits or with narrow digits pointing forward.

Large unnamed footprints attributed to sauropods and separated into two morphological groups are known from the Lower Jurassic (Pliensbachian) of Morocco (Ishigaki, 1988). The first group has pedal prints with four large digit impressions, a very long heel mark, and manual prints that show no digit impressions (Fig. 9G). The trackway is wide gauge with a shape that is rather different from those that are usually seen in well-preserved sauropod hind foot tracks, in which claw marks are laterally directed and digit I usually leaves the largest most clearly visible impressions (Farlow, 1992). Given the differences in hind foot track shapes between known sauropod trace fossils it has been speculated that the tracks were not made by true sauropods, but rather by specialized descendants of melanosaurids or blikanasaurids (Farlow, 1992). Farlow (1992) affirmed that it is intriguing to note that the hind foot of this group is superficially similar to that of *Otozoum*. The general outline of this morph is relatively close to morph described herein. However, the much larger size of the tracks and the decidedly wider trackway make this comparison unlikely. The second Moroccan group has rounded manual prints within digit impressions (Fig. 9H). The pes tracks are very short with clawless digital impressions. The trackway is narrow gauge and has features similar to those of typical narrow gauge sauropod ichnites. Notwithstanding the fact that the narrow gauge trackway is similar to ours, the morphology and the size of the manus and pes are different.

Several other sauropod print morphotypes are reported from the Jurassic and from the Cretaceous; they are briefly described and compared to *Lavinipes*.

Two different sauropod print morphotypes were reported from the lower Middle Jurassic of Yorkshire (England) by Romano et al. (1999). The ichnospecies A shows a pes that is oval in outline with a straight inner antero-lateral margin and three (but possibly five) curved digit prints (Fig. 9I). These ichnospecies bear a very strong similarity to the pes print of *Brontopodus birdi*, particularly in their shape, digit impressions, and size (Romano et al., 1999) and therefore is quite different from *L. cheminii*. Ichnospecies B shows a pes with a bell-shaped outline, a broadly rounded heel, nearly straight anterior margin, and three distinct lateral digit prints (I–III) (Fig. 9L). The manus print (not in the trackway) is broadly semicircular in outline with one or two deep, narrow indentations on the convex anterior margin, and up to two broader indentations along the posterior margin. The pes print of ichnospecies B shows differences from *Brontopodus*-like footprints with a more symmetrical shape. Romano et al. (1999) suggest a comparison with *Breviparopus taghbalutensis* Dutuit and Ouazzou 1980, but the pes digits are larger and more strongly indented than those from Morocco. The manus also is quite different. Comparison with *L. cheminii* does not suggest any similarity.

Well-preserved but unnamed sauropod footprints are reported from the Middle Jurassic and Upper Jurassic of Portugal (Lockley et al., 1993; Santos et al., 1994; Meyer et al., 1994; Lockley et al., 1994c). The Fatima (Pedreira do Galinha) trackways are wide gauge, with large elongated pes prints with outward-directed digits and are therefore similar to *Brontopodus* (Fig. 9M) (Santos et al., 1994). However, the tracks are distinctive in having a very large manus tracks (1:2) with a well-developed impression of digit I relative to all other known sauropod trackways. Both manus and pes are different to *L. cheminii*. The sauropod tracks preserved at Lagosteiros Bay, near Cabo Espichel, show an elongated pes with five outward claws in the frontal part (Fig. 9O) (Lockley et al., 1994c). The manus is small and arched without digit prints. The tracks are *Brontopodus*-like and different from *L. cheminii*.

Breviparopus thagbaloutensis Dutuit and Ouazzou, 1980 (Upper Jurassic of Morocco) has typically sauropod pes with claw marks directed slightly inward or outward, as in *Brontopodus* (Fig. 9P). The manus prints of *Breviparopus* are quite similar to *Parabrontopodus*, more wide than long, crescent shaped, without digit prints (Ishigaki, 1989), and are quite different to *L. cheminii*.

Also the pes of *Parabrontopodus mcintoshi* Lockley et al. 1994a of the Upper Jurassic of the western U.S. is different from *L. cheminii* (Fig. 9Q). The manus is also quite different, more wide than long, semicircular and decidedly smaller than the pedal print, and without clear digital prints (Lockley et al., 1994a).

The classic Early Cretaceous pes tracks of *Brontopodus birdi* Farlow et al., 1989 shows footprints that are more long than broad, with large, laterally directed claw marks at digits I–III, a small claw at digit IV, and a small callosity or pad mark at digit V (Fig. 9R). The pes tracks appear different in their shape to *L. cheminii*. Well-preserved manus tracks in the *Brontopodus* type specimen are U-shaped. Slight indentations in the medial and lateral sides of the manus tracks suggests that digits I and V of the forefoot were separated by soft tissues from digits II–IV, which were themselves bound together by soft tissues to form a crescent shaped anterior portion of the manual print. There are no indications of either a large digit I claw or cushioning pad of connective tissue behind the bones of the manus (Farlow, 1992; Farlow et al., 1989). The manus is therefore much more symmetrical and placed inside the trackway than those of *L. cheminii* are. The trackway is broad, with manual and pedal prints well away from the trackway midline different from the narrow trackways of *L. cheminii*.

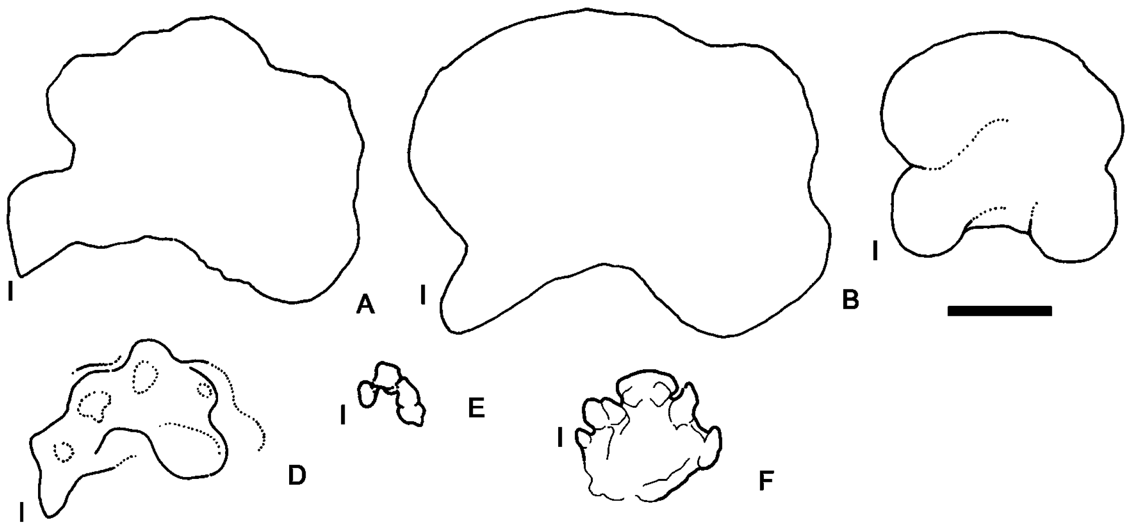

FIG. 10. Manual prints of sauropods. **(A)** unnamed from the Middle Jurassic of Portugal (after Santos et al., 1994, redrawn). **(B)** unnamed from the Middle Jurassic of Portugal (after Santos et al., 1994, redrawn). **(C)** *Brontopodus birdi*, Albian, Texas (after Farlow et al., 1989, redrawn). **(D)** *Pseudotetrasauropus jaquesi*, Late Triassic, Southern Africa (after Ellenberger, 1972, redrawn). **(E)** *Parabrontopodus* sp. (after Gierlinski, 1997, redrawn). **(F)** *Lavinipes cheminii*. Scale bar: 20 cm.

On the basis of pedal print morphology the examined sauropod ichnotaxa seem to be subdivided into four main groups (Fig. 9). One group is characterized by elongated and pentadactyl pedal prints with four inward arched and clawed digits, a well-developed digit IV along the lateral margin of the foot, and a very short digit I in medial margin (i.e., *Tetrasauropus*). A second group is characterized by pedal prints that are elongated with four inward digit marks, a well-developed mark of digit IV along the lateral margin of the footprint, and a digit I print in the middle, medial margin (i.e., *Otozoum*). A third group is characterized by a wide pedal print with anteriorly (or slightly outwardly) directed claw or digit marks, (i.e., *Breviparopus*). A fourth group is characterized by pedal prints that are longer than broad, with large, outwardly directed claw marks at digits I–III, a small claw at digit IV, and small callosity or pad mark at digit V (i.e., *Brontopodus*).

The manual morphology seems less defined (Fig. 10). Only the more derived sauropod ichnotaxa (the *Brontopodus*-like group) have been recently subdivided into three groups distinguished by the configuration of digit I (Dalla Vecchia, 1999; Dalla Vecchia et al., 2000). One group is characterized by manual prints with a well-developed impression of the digit I claw (i.e., cf. *Brontopodus* from the middle Jurassic of Portugal) (Fig. 9M; Fig. 10A). A second group is characterized by a manual print with an intermediate development of a digit I print (i.e., cfr. *Brontopodus* from Upper Jurassic of Portugal) (Fig. 9O; Fig. 10B). A third group is characterized by a manual print without a claw mark on digit I and with rounded digital prints I and IV (i.e. *Brontopodus birdi*) (Fig. 9R; Fig. 10C).

L. cheminii would seem to be a synonym of *Pseudotetrasauropus* (cfr. *P. jaquesi*) or *Otozoum*-like track when comparing the pes morphology with known tracks of Jurassic facultative quadrupedal dinosaurs (Fig.11). The manus, however, is more sauropodan (*Brontopodus*-like) in their general shape and, among late Triassic-early Jurassic quadrupedal dinosaurs, results in some way comparable only with *Pseudotetrasauropus* (cfr. *P. jaquesi*). Thus we can affirm that this ichnospecies show a marked affinity to taxa traditionally related to early sauropodomorph.

POSSIBLE TRACKMAKER IDENTIFICATION

In the Late Triassic and Early Jurassic, the Sauropoda must have had a relatively long and almost completely unknown evolutionary history during which they coexisted with large bodied, heavily built sauropodomorphs, like the Melanosauridae and Plateosauridae prosauropods (Coombs, 1975; Galton, 1985; Sereno, 1989; Upchurch, 1995, 1997a, 1998; McIntosh, 1997; Barrett, 1999; Buffetaut et al., 2000; Yadagiri, 2001; Wilson, 2002).

There has been some debate over the gaits of prosauropods. In general the light-bodied thecodontosaurids have been regarded as the most bipedal form, with the large heavily built plateosaurids and melanosaurids considered to be facultative bipeds and obligate quadrupeds, respectively (VanHeerden, 1997). Prosauropods and certain basal archosaurian pedes are similar in general structure and would be expected to leave similar tracks (Thulborn, 1990). Thus, true prosauropod trackways could only be recognised for certain when these animals walked quadrupedly, leaving the characteristic manus prints that are functionally tetradactyl with digits III and IV of similar length and a first digit with a large claw lifted away from the substrate (Thulborn, 1990). The prosauropod manus, with its unusual structure, has played an important role in studies of the

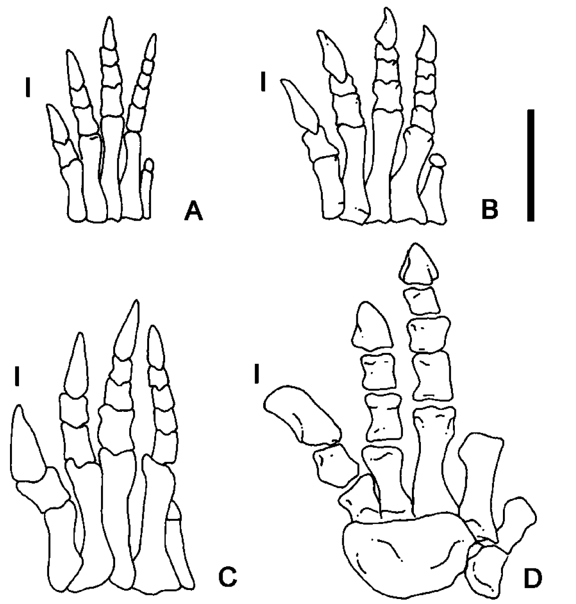

FIG. 11. Foot skeletons of various prosauropod dinosaurs. **(A)** *Massospondylus*. **(B)** *Yunannosaurus*. **(C)** *Lufengosaurus* and the ancestral sauropod *Vulcanodon*. **(D)** (redrawn after Raath, 1972; Cooper, 1984; Galton, 1990; Thulborn, 1990). Scale bar: 10 cm.

palaeoecology of this group, and Cooper (1981), on the basis of the manus structure, suggested that not all the heavily built prosauropods are quadruped (Upchurch, 1997b). For example the manus of medium sized *Massospondylus* i.e., was unsuitable for bearing any weight during quadrupedal locomotion (a similar conclusion was proposed for *Plateosaurus*) (Upchurch, 1997b; VanHeerden, 1997).

Several quadrupedal ichnogenera have been attributed to Prosauropoda (i.e., *Tetrasauropus*, *Navahopus*, and *Pseudotetrasauropous*) but the bipedal *Otozoum* are the only tracks convincingly attributed to this ichnotaxon (Baird, 1954, 1957; Thulborn 1990; Farlow, 1992; Lockley and Hunt, 1995; Lockley and Meyer, 1999; Rainforth, 2000, 2002; in press), although Gierlinski (1995) contest this attribution and consider *Otozoum* related to Thyreophoran.

A structure of the pes similar to that of the heavily built prosauropods is recognizable also in the earliest sauropod hind feet. In prosauropods such as *Lufengosaurus* and *Massospondylus* the ungual of digit I is only about 10% longer than the ungual of the second digit (Wilson and Sereno, 1998), and the digit IV is well developed (Fig. 12). In sauropods, in contrast, the ungual of pedal digit I is 25% longer than the ungual of the second digit, sauropod therefore exhibits a strong decreasing gradient in ungual size from digit I to digit IV (Wilson and Sereno, 1998).

In prosauropods the unguals of pedal digits II–IV are moderately flattened with subequal height and depth proximally (Galton, 1971; Cooper, 1981; Galton, 1990). In sauropods, in contrast, these unguals more closely resemble that of pedal digit I, are transversely compressed, and are always claw-shaped, with a depth that is significantly greater than width throughout their length (Dodson, 1990a, 1990b; McIntosh et al., 1992; Sereno, 1999). The first ungual in the basal sauropods *Vulcanodon karibaensis* Raath, 1972 (Lower Jurassic of Southern Africa) and *Kotasaurus yamanpalliensis* Yadagiri, 1988 (Lower Jurassic or Cretaceous of India) is flattened and sickle-shaped (Raath, 1972; Cooper, 1984; Wilson and Sereno, 1998; Yadagiri, 2001), more similar to those of prosauropods than those of sauropods. In *Antenonitrus ingenipes* Yates and Kitching, 2003 also, the first metatarsal is shorter than metatarsal II–IV with an elliptical section greater than any other metatarsal (Yates and Kitching, 2003). On the basis of the morphology of the pes of *Vulcanodon*, Farlow (1992) affirmed that in a conjectural footprint one would expect digit I to leave the stoutest but not the longest mark. In *Vulcanodon* and *Antenonitrus*, digit III is relatively much longer than the others, and the unusually broad proportions of the unguals in pedal digits II and III appear to be unique among sauropodomorphs (Wilson and Sereno, 1998; Yates and Kitching, 2003). The penultimate phalanges of digits II and III are considerably longer in comparison to their respective metatarsals than in later sauropods and resemble those in prosauropods (Cooper, 1984). In prosauropods the pedal unguals of digits II and III have a distinctly flattened plantar surface, similar to those of *Vulcanodon*. In eusauropods, in contrast, the pedal unguals of digits II and III resemble the sickle-shaped ungual of pedal digit I. In the earliest known sauropod *Antenonitrus*, therefore, the metatarsal V is reduced, suggesting that it bore little if any weight (Yates and Kitching, 2003) and so the pes could be functionally tetradactyl. In prosauropods the ungual of pedal digit IV is only slightly shorter than that of pedal digits II and III. In eusauropod, in contrast, the unguals of pedal digit IV is rudimentary or absent.

In prosauropods the manual digits were not specialized for weight support. Thus unguals are present on digits II and III, which are successively longer than digit I. Digits IV and V retain at least a pair of vestigial phalanxes. In the habitual quadruped basal sauropod *Antenonitrus* the manus retained a strongly twisted and mobile pollex that maintained the grasp-

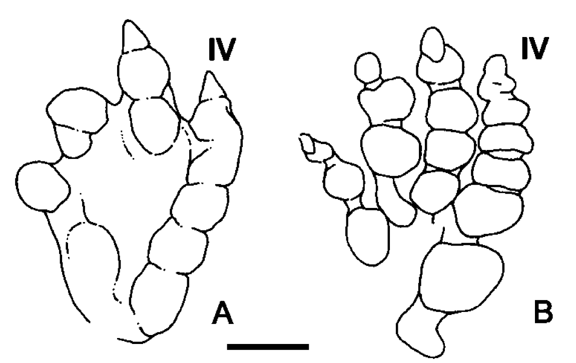

FIG. 12. Comparison between *Lavinipes cheminii* pedal print ROLM 577.5 **(A)** and *Otozoum* CU-MWC 181.11. **(B)** footprint (redrawn after Lockley, 1990). Scale bar: 10 cm.

ing ability seen in prosauropods (Yates and Kitching, 2003). No manual phalanxes were recovered with known skeletal material of more derived *Vulcanodon*. The modification noted in the manus of all sauropods, therefore, may characterize *Vulcanodon*, which was clearly an obligatory quadruped. In eusauropod, manual digits II and III are shortened so that all but the first are subequal in length. Eusauropods are thus characterized by the loss of unguals in digits II and III and the additional loss of at least one nonterminal phalanx in digit III. The shortening of middle digits of the manus and loss of their respective unguals reduces the disparity in the length of digits II–IV and appears to be an adaptation for weight support (Wilson and Sereno, 1998). It has recently become evident that the manual morphology of sauropods has taxonomic importance (Upchurch, 1994; Wilson and Carrano, 1999; Dalla Vecchia et al., 2000). Less-derived sauropods, such as diplodocidomorphs and *Camarasaurus*, had a well-developed claw on manual digit I and phalanges on the digits, whereas *Brachiosaurus* had a small claw on digit I and less-developed phalanges. Titanosaurids had neither claws nor phalanges. This could correspond to the subdivision of the sauropod ichnotaxa into three groups distinguished by the configuration of manual digit I illustrated above (Fig. 9).

The *Lavinipes* footprint is characterized by the marks left by a wide and flattened digit I located on the middle medial margin of the footprint. This position does not correspond with the position of digit I in derived sauropods. A better comparison is provided by the position of ungual I of several heavily built prosauropods such as *Lufengosaurus* or *Yunnannosaurus* and with the flattened ungual I of *Vulcanodon* (Fig. 12). The longer digit III and the general morphology of *L. cheminii* could be well superimposed on the skeletal structure of heavily built prosauropods or basal sauropods (as *Vulcanodon* and *Antenonitrus*) than more derived sauropods. The lack of digit V in of *L. cheminii* is coherent with the osteology for both prosauropods and basal eusauropoda (cfr. *Antenonitrus*). The blunt and triangular claws of *L. cheminii* seem more similar to those of *Vulcanodon* and basal eusauropoda than those of prosauropoda.

The pentadactyl manual prints, without a well-developed print of ungual I, digits II and III short without their respective unguals, digit II and IV of the same length, resemble instead those of relatively evolved sauropods like eusauropoda. For this reason it is possible that a primitive sauropod closed to basal eusauropoda but relatively derived from an ichnological point of view, could be considered the maker of *Lavinipes cheminii* tracks.

CONCLUSION

The most evident characteristic of the pedal footprints of *Lavinipes cheminii* is their elongated shape with a longer digit III and a marked impression of the digit IV. The pendadactyl manual prints have a U-shaped morphology with apparently clawless digits. This habitual quadrupedal form is very close to *Otozoum* and *Pseudotetrasauropus jaquesi*, both traditionally related to sauropodomorph trackmakers.

The similarity with *Otozoum* is so marked that *Lavinipes* and *Otozoum* could be cogeneric. But the overall evidence today is that the *Otozoum* trackmaker was generally bipedal, whereas the trackway of *L. cheminii* is quadrupedal and the manual prints of *L. cheminii* are stout and pentadactyl, different from the tetradactyl slender-toed manual prints of *Otozoum*.

If compared with the Jurassic sauropodomorph ichnotaxa, *Lavinipes cheminii* reveals both primitive and derived characteristics. This ichnotaxa could be classified as a sauropod on the basis of the pentadactyl U-shaped manual prints, and the quadrupedal narrow-gauged trackway. However, certain characteristics, such as the elongated tetradactyl *Otozoum*-like pes, indicate a prosauropod condition. For this reason the *Lavinipes cheminii* trackmaker is here considered to be one of the earliest sauropods related in some way to the basal eusauropoda.

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REFERENCES

Avanzini, M., Frisia, S., Keppens, E., and Van den Driessche, K. 1997. A dinosaur tracksite in an Early Jurassic Tidal Flat in Northen Italy: Palaeoenvironmental reconstruction from Sedimentology and Geochemistry. *Palaios*, 12:538–551.

Baird, D. 1980. A prosauropod dinosaur trackway from the Navajo Sandstone (Lower Jurassic) of Arizona. *In* Jacobs, L. L. (ed.), Aspects of Vertebrate History, Essays in honour of Harris Colbert. Museum of Northern Arizona Press: 219–230.

Baird, D. 1954. Chirotherium lulli, a pseudosuchian reptile from New Jersey. *Bulletin of the Harvard College Museum of Comparative Zoology, Harvard University*, 111:163–192.

Baird, D. 1957. Triassic reptile footprint faunules from Milford, New Jersey. *Bulletin of the Harvard College Museum of Comparative Zoology, Harvard University*, 117:449–520.

Barrett, P. M. 1999. A sauropod dinosaur from the Lower Lufeng Formation (Lower Jurassic) of Yunnan Province People's Republic of China. *Journal of Vertebrate Paleontology*, 19:785–787.

Buffetaut, E., Suteethorn, V., Cuny, G., Tong, H., Le Loeuff, J., Khansubha, S., and Jogautchariyakul, S. 2000. The earliest known sauropod dinosaur. *Nature*, 407:72–74.

Coombs, J. R. W. P. 1975. Sauropods habits and habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 17:1–33.

Cooper, M. R. 1981. The prosauropod dinosaur *Massospondylus carinatus* Owen from Zimbabwe: its biology, mode of life and phylogenetic significance. *Occasional Papers of the National Museums of Rhodesia, Series B,* 6:689–840.

Cooper, M. R. 1984. A reassessment of *Vulcanodon karibaensis* Raath (Dinosauria: Saurischia) and the origin of the sauropoda. *Palaeontologia Africana*, 25:203–231.

Dalla Vecchia, F. M. 1999. A sauropod footprint in a limestone block from the Lower Cretaceous of Northeastern Italy. *Ichnos*, 6:269–275.

Dalla Vecchia, F. M., Tarlao, A., Tunis, G., and Venturini, A. 2000. New dinosaur track sites in the Albian (Early Cretaceous) of the Istrian peninsula (Croatia). Part I—Stratigraphy and sedimentology. Part II—Paleontology. *Memorie di Scienze Geologiche*, 52:193–292.

Dodson, P. 1990a. Sauropodomorpha. *In* Weishampel, D. B., Dodson, P., and Osmolska, H. (eds.), The Dinosauria. University of California Press, Berkeley: 318–319.

Dodson, P. 1990b. Sauropod Paleoecology. *In* Weishampel, D. B., Dodson, P., and Osmolska, H. (eds.), The Dinosauria. University of California Press, Berkeley: 402–407.

Dutuit, J. M. and Ouazzou, A. 1980. Découverte d'une piste de Dinosaure sauropode sur le site d'empreintes de Demnat (Haut Atlas marocain). *Mémoires Societè Géologique France, N.S.*, 139:95–102.

Ellenberger, P. 1955. Note préliminaire sur les pistes et les restes osseux de vertébrés du Basutoland (Afrique du Sud). *Compte rendus hebdomadaires des séances de l'Académie des Sciences, Paris*, 240:889–891.

Ellenberger, P. 1970. Les niveaux paléontologiques de premiere apparition del mammifères primordiaux en Afrique du Sud et leur ichnologie. Etablissement de zones stratigraphiques détaillées dans le Stormberg du Lesotho (Afrique du Sud) (Trias supérieur à Jurassique). Proceedings and Papers II Gondwana Symposium 1970: 343–70.

Ellenberger, P. 1972. Contribution à la classification des Pistes de Vertébrés du Trias: Les types du Stormberg d'Afrique du sud. (I partie). Paleovertebrata, Mémoire extraordinaire, 1972, Montpellier: 117 p.

Ellenberger, P. 1974. Contribution à la classification des Pistes de Vertébrés du Trias: Les types du Stormberg d'Afrique du sud. (II partie). Le Stormberg superieur—I. Le biome de la zone B/1 ou niveau de Moyeni: ses biocénoses. Paleovertebrata, Mémoire extraordinaire, 1974, Montpellier: 147 p.

Ellenberger, F., Ellenberger, P., and Ginsburg, L. 1970. Les Dinosaures du Trias et du Lias en France et en Afrique du Sud, d'après les pistes qu'ils ont laissées. *Bulletin de la Société géologique de France*, 7:XII, 1:151–159.

Farlow, J. O. 1992. Sauropod Tracks and Trackmakers: Integrating the Ichnological and Skeletal Records. *Zubia, Instituto de Estudios Riojanos*, 10:89–138.

Farlow, J. O., Pittman, J. G., and Hawthorne, J. M. 1989. Brontopodus birdi, Lower Cretaceous sauropod footprints from the U.S. Gulf coastal plain. *In* Gillette, D. D. and Lockley, M. G. (eds.), Dinosaur Tracks and Traces. Cambridge University Press, New York: 371–394.

Galton, P. M. 1971. The prosauropod dinosaur *Ammosaurus*, the crocodile *Protosuchus*, and their bearing on the age of the Navajo Sandstone of northeastern Arizona. *Journal of Paleontology*, 45:781–795.

Galton, P. M. 1985. Notes on the Melanosauridae, a family of large prosauropod dinosaurs (Saurischia: Sauropodomorpha). *Geobios*, 18:671–676.

Galton, P. M. 1990. Basal Sauropodomorpha—Prosauropoda. *In* Weishampel, D. B., Dodson, P. E., Osmolska, H. (eds.), The Dinosauria. University of California Press, Berkeley: 321–344.

Garcia-Ramos, J. C., Aramburu, C., Piñuela, L., and Lires, J. 2000. La costa de los dinosaurios: ruta por el Jurasico de Asturias. Gobierno del Principado de Asturias: 1–33.

Gierlinski, G. 1991. New dinosaur ichnotaxa from the Early Jurassic of the Holy Cross Mountains, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 85:137–148.

Gierlinski, G. 1995. Thyreophoran affinity of *Otozoum* tracks. *Przeglad Geologiczny*, 43, 2:123–125.

Gierlinski, G. 1997. Sauropod tracks in the Early Jurassic of Poland. *Acta Palaeontologica Polonica*, 42:533–538.

Gierlinski, G. 1999. Tracks of a large thyreophoran dinosaur from the Early Jurassic of Poland. *Acta Palaeontologica Polonica*, 44:231–234.

Gierlinski, G., Gazdzicka, E., Niedzwiedzki, G., and Pienkowski, G. 2001. New ornithischian dinosaur footprints in the Jurassic of Poland. *Geological Quarterly*, 45:205–210.

Haubold, H. 1984. Saurierfährten. A. Ziemsen Verlag, Wittenberg Lutherstadt. 230 pp.

Hitchcock, E. 1836. Ornithichnology—Description of the footmarks of birds (Ornithichnites) on New Red Sandstone in Massachusetts. *American Journal of Science*, Series 1, 29:307–340.

Hitchcock, E. 1845. An attempt to name, classify and describe the animals that made the fossil footmarks of New England. *Proceedings of the American Association of Geologists and Naturalists*, 6:23–25.

Hitchcock, E. 1847. Description of two new species of fossil footmarks found in Massachusetts and Connecticut, or of the animals that made them. *American Journal of Science, Series 2,* 4:46–57.

Hitchcock, E. 1856. Additional facts respecting the tracks of the *Otozoum moodii* on the Liassic sandstone of the Connecticut Valley. *Proceedings of the American Association for the Advancement of Science*, 9:228.

Hitchcock, E. 1858. Ichnology of New England: A Report on the Sandstone of the Connecticut Valley, especially its fossil footmarks. Natural Sciences of America Reprint, W. White, Boston: 220 pp.

Hitchcock, E. 1865. Supplement to the ichnology of New England. Commonwealth of Massachusetts, Boston: 96 pp.

Hunt, A. P., Lockley, M. G., and Lucas, S. G. 1993. Vertebrate and invertebrate tracks and trackways from Upper Triassic strata of the Tucumcari Basin, east-central New Mexico, USA. *In* Lucas, S. G. and Morales, M. (eds.). The Nonmarine Triassic. *New Mexico Museum of Natural History and Science Bulletin*, 3:199–201.

Ishigaki, S. 1988. Les empreintes de dinosaures du Jurasique inférieur du haut Atlas central marocain. *Notes du service géologique du Maroc*, 44:79–86.

Ishigaki, S. 1989. Footprints of Swimming Sauropods from Morocco. *In* Gillette, D. D. and Lockley, M. G. (eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge: 83–86.

Le Loeuff, J., Lockley, M., Meyer, C., and Petit J. P. 1999. Discovery of a thyreophoran trackway in the Hettangian of central France. *Comptes Rendus de l'Académie des sciences de Paris, Sciences de la terre et des planétes*, 328:215–219.

Leonardi, G. 1987. Glossary and Manual of Tetrapod Paleoichnology, Brazil: Departmento Nacional da Producao Mineral, Brasilia: 117 pp.

Leonardi, G. and Mietto, P. 2000. Dinosauri in Italia, le piste giurassiche dei Lavini di Marco (Trentino) e gli altri resti fossili italiani. Accademia Editoriale, Pisa-Roma.: 495 pp.

Lockley, M. G. 1990. Tracking the rise of dinosaurs in eastern Utah. *Canyon Legacy*, 2:2–8.

Lockley, M. G. and Santos, V. E. 1993. A preliminary report on sauropod trackways from the Avelino site, Sesimbra region, Upper Jurassic, Portugal. *Gaia*, 6:38–42.

Lockley, M. G., Farlow, J. O., and Meyer, C. A. 1994a. Brontopodus and Parabrontopodus ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackway. *Gaia*, 10:135–145.

Lockley, M. G. and Hunt, A. P. 1995. Dinosaur Tracks and other fossil footprints of the western United States. Columbia University Press, New York: 338 pp.

Lockley, M. G. and Meyer, C. A. 1999. Dinosaur Tracks and other fossil footprints of Europe. Columbia University Press, New York: 330 pp.

Lockley, M. G., Meyer, C. A., Hunt, A. P., and Lucas S. G. 1994b. The distribution of sauropod tracks and trackmakers. *Gaia*, 10:1–16.

Lockley, M. G., Meyer, C. A., and Santos, V. F. 1994c. Trackway evidence for a herd of juvenile sauropods from the late Jurassic of Portugal. *Gaia*, 10:27–35.

Lockley, M. G., Wright, J., Hunt, A. P., and Lucas, S. G. 2001. The Late Triassic sauropod track record comes into focus: old legacies and new paradigms. New Mexico Geological Society Guidebook, 52nd Field Conference, Geology of the Llano Estacado: 181–190.

Lull, R. S. 1904. Fossil footprints of the Jura-Trias of North America. *Memoirs of the Boston Society of Natural History*, 5:461–557.

Lull, R. S. 1915. Triassic life of the Connecticut Valley. *Connecticut State Geological and Natural History Survey Bulletin*, 24:1–285.

Lull, R. S.1953. Triassic life of the Connecticut Valley. *Connecticut State Geological and Natural History Survey Bulletin*, 81:1–336.

McIntosh, J. S. 1990. Sauropoda. *In* Weishampel, D. B., Dodson, P., and Osmolska, H. (eds.), The Dinosauria. University of California Press, Berkeley: 345–401.

McIntosh, J. S. 1997. Sauropoda. *In* Currie, P. J. and Padian, K. (eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego: 654–660.

Meyer, C. A., Lockley, M. G., Robinson, J. W., and Santos, V. F. 1994. A comparison of well-preserved sauropod tracks from the late Jurassic of Portugal and the western United States: evidence and implications. *Gaia*, 10:57–64.

Olsen, P. E. and Galton, P. M. 1984. A review of the reptile and amphibian assemblages from the Stormberg of Southern Africa, with special emphasis on the footprints and the age of the Stormberg. *Palaeontologia Africana*, 25:87–110.

Raath, M. A. 1972. Fossil vertebrate Studies in Rhodesia: A new Dinosaur (Reptilia, Saurischia) from near the Trias-Jurassic boundary. *Arnoldia*, 30:1–37.

Rainforth, E. C. 2000. The Early Jurassic ichnogenus *Otozoum*. *Geological Society of America, Abstract with Programs*, 32:67.

Rainforth, E. C. 2001. Late Triassic—Early Jurassic dinosaur ichnofaunas, Eastern North America and Southern Africa. *Journal of Vertebrate Paleontology*, 21:91A.

Rainforth, E. C. 2002. The Pangean ichnite *Otozoum* and *Pseudotetrasauropus*: an example of relationships among and between tetrapod ichnotaxa and skeletal taxa. *Journal of Vertebrate Paleontology*, 22:92A.

Rainforth, E. C. (in press). Revision and re-evaluation of the Early Jurassic dinosaur ichnogenus *Otozoum*. *Paleontology*.

Romano, M. and Whyte, M. A. 2003. Jurassic dinosaur tracks and trackways of the Cleveland Basin Yorkshire: preservation, diversity and distribution. *Proceedings of the Yorkshire Geological Society*, 54:185–215.

Romano, M., Whyte, M. A., and Manning, P. L. 1999. New sauropod dinosaur prints from the Saltwick Formation (Middle Jurassic) of the Cleveland Basin, Yorkshire. *Proceedings of the Yorkshire Geological Society*, 52:361–369.

Santos, V. F., Lockley, M. G., Meyer, C. A., Carvalho, J., Galopin de Carvalho, A. M., and Moratalla, J. J. 1994. A new sauropod tracksite from the Middle Jurassic of Portugal. *Gaia*, 10:5–13.

Sereno, P. C. 1989. Prosauropod monophyly and basal sauropodomorph phylogeny. *Journal of Vertebrate Paleontology*, 9:83A.

Sereno, P. C. 1999. The evolution of dinosaurs. *Science*, 284:2137–2147.

Thulborn, R. A. 1990. Dinosaur Tracks. Chapman and Hall, London: 410 pp.

Upchurch, P. 1994. Manus claw function in sauropod dinosaurs. *Gaia*, 10:161–170.

Upchurch, P. 1995. The evolutionary history of sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London, Series B,* 349:365–390.

Upchurch P. 1997a. A cladistic analysis of sauropod dinosaur phylogeny. *Journal of Vertebrate Paleontology*, 17:82A.

Upchurch, P. 1997b. Prosauropoda. *In* Currie, P. J. and Padian, K. (eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego: 599–605.

Upchurch, P. 1998. The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society*, 124:43–103.

VanHeerden, J. 1997. Prosauropods. *In* Farlow, J. O. and Brett-Surman, M. K. (eds.), The Complete Dinosaur. Indiana University Press, Bloomington and Indianapolis: 242–263.

Whyte, M. A. and Romano, M. 2001. Probable stegosaurian dinosaur tracks from the Saltwick Formation (Middle Jurassic) of Yorkshire, England. *Proceeding of the Geologists' Association*, 112:45–54.

Wilson, J. A. 2002. Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society*, 136:217–276.

Wilson, J. A. and Carrano, M. T. 1999. *Titanosaurs* and the origin of "wide-gauge" trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology*, 25: 252–267.

Wilson, J. A. and Sereno, P. C. 1998. Early evolution and higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology Supplement*, 18:1–68.

Yadagiri, P. 2001. The Osteology of *Kotasaurus yamanpalliensis*, a sauropod dinosaur from the Early Jurassic Kota Formation of India. *Journal of Vertebrate Paleontology*, 21:242–252.

Yates, A. M. and Kitching, J. W. 2003. The earliest known sauropod dinosaur and the first steps toward sauropod locomotion. *Proceedings The Royal Society London*, B: 03PB0009.1–6.