DISCOVERY OF TRACKWAYS OF HOPPING DINOSAURS IN THE LITHOGRAPHIC LIMESTONES OF CERIN (UPPER KIMMERIDGIAN, AIN, FRANCE) PALEOECOLOGICAL IMPLICATIONS[*]

by

PAUL BERNIER, GEORGES BARALE, JEAN-PAUL BOURSEAU, ERIC BUFFETAUT, GEORGES DEMATHIEU, CHRISTIAN GAILLARD, JEAN-CLAUDE GALL and SYLVIE WENZ

---

[*] Original citation: Bernier, P., G. Barale, J.-P. Bourseau, E. Buffetaut, G. Demathieu, C. Gaillard, J.-C. Gall, & S. Wenz. 1984. Découverte de pistes de dinosaures sauteurs dans les calcaires lithographiques de Cerin (Kimmeridgian Superieur, Ain, France): implications paleoecologiques. *Geobios, Mémoire speciale* 8:177-185. Translation © Matthew Carrano, University of Chicago, 1996.

INTRODUCTION

The Lithographic Limestone Formation of Cerin, classically attributed to the upper Kimmeridgian, lies in the central part of the Jura chain, in the south of the Ain department (SE France). Exploited in the last century for lithography and construction, it produced a large number of well-preserved fossils (marine and terrestrial vertebrates, invertebrates, plants, etc.) which formed the basis of a number of monographs (cf. P. Bernier *et al.*, 1982, p. 448). Since 1975, the abandoned Cerin quarry has been the object of study, with the intention of reconstructing the paleoecology of this formation. The exploitation of the locality was made bed by bed and at two levels simultaneously (fig. 1):

– in the Lithographic Limestones *sensu stricto* over a surface area of 75 m^2;

– in the basal laminates (bituminous and flint Laminates) over a surface area of 100 m^2. (fig. 1)

The discovery of a locomotion track of a tortoise and of associated sedimentary structures (P. Bernier *et al.*, 1982), showing, for the first time, proof of immersion, permits the proposal of a new paleoenvironmental model. Several seasons of study (principally those in 1981 and 1982) brought to light the footprints of large vertebrates showing a mode of locomotion n unknown prior to the Cenozoic. Recovered in many beds of the two levels under study, they additionally show some features new to the understanding of the environment of the locality.

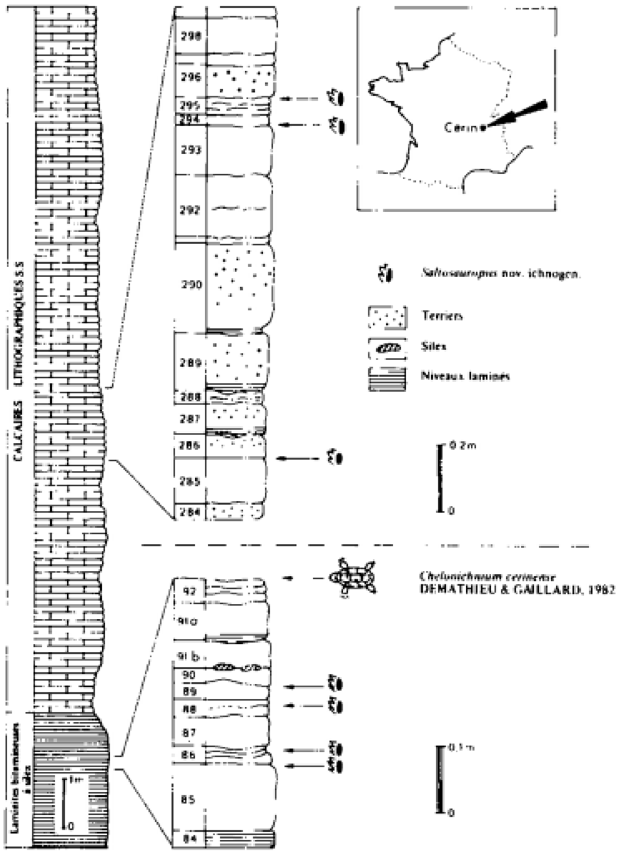


Fig. 1 – Location of the *Saltosauropus*-bearing beds (lithographic limestones of Cerin).

DESCRIPTIVE STUDY OF THE TRACKS (G. DEMATHIEU and C. GAILLARD)

SALTOSAUROPUS nov. ichnogen.

TYPE SPECIES: *Saltosauropus latus*.

ETYMOLOGY:

After the mode of locomotion of the animal which made the track.

DIAGNOSIS:

Tridactyl trackway of a bipedal reptile traveling in bounds. The line joining two feet in phase is slightly less than perpendicular to the direction of movement. The ratio of the length of the jump to the total width of the trackway is greater than 1.

SALTOSAUROPUS LATUS nov. ichnogen.

HOLOTYPE:

Print G2 of trackway A (bed 295 A). Sample deposited in the Collections of the Department of Earth Sciences – Université Claude Bernard, no. 400 002 (fig. 2A). For reasons of illustration quality, it was judged preferable to figure the cast rather than the original piece (pl. 1, fig. 3).

HYPODIGM:

The group of prints from beds 295 A, 285 as well as trackways A of bed 89 and A, B, C, D and E of bed 85. One part of the prints is conserved either in the form of original pieces or in the form of casts.

ETYMOLOGY:

After the great space existing between the prints of two feet in phase.

TYPE LOCALITY:

Town of Cerin-Marchamp (Ain). Site of paleoecological study – old Cerin quarry. Locality no. 5 090 01 23 01. Belley 1/25.000, no. 5/6, IGN XXXII-31, X = 850.200 km, Y = 91.600 km.

TYPE LEVEL:

Lithographic Limestones *sensu stricto*, bed no. 295 A, upper Kimmeridgian (fig. 1).

DIAGNOSIS:

Digits II and III large, joined at their bases, III slightly larger than II, IV slender, not always printed and separated from the other two. Axis of foot turned towards the interior of the trackway making an angle of 10–60° with this axis. Length of foot less than the width. Proximal edge of digits nearly rectilinear. Ratio of the stride to the interior width of the path is between 1 and 2.

DESCRIPTION:

The trackways are in fact completely new to vertebrate paleoichnology (fig. 3 and 4). Two prints in the same phase of locomotion are at a distance of 5 to 9 times the average width of the autopodium (tabl. 4) and two pairs in phase (stride) from 4 to 18 times the average width of the autopodia. The feet are bent which adds to the uniqueness of the tracks and complicates their interpretation.

The prints introduce the two following aspects of the trackways: the tracks, shorter than wide, appear more often than the ends of two digits (short type – fig. 2B), or else longer with the digital parts more developed in length (long type – fig. 2A). All are consistent with a distinct roll giving the form of the axis, with presumed digit III, an angle directed towards the interior of the trackway that varies from 30° to 80°. Digits II and III make deeper depressions than IV. The distance from the tips of digits II-III is a stable character and similar among the prints made by the short type or the long type (tabl. 1). The claws are massive and long enough for the second and third digits, more slender and shorter for the fourth. The pads are not clearly visible on the prints of the long type. For some of these latter, the prints of the digits are sometimes abnormally long. The depressions are not always very deep. They generally do not exceed 4 cm, that is a little for the autopodia of the narrow surface: 125 cm^2 for the long type, 40 cm^2 for the short type.

Regarding the statistical study completed on the prints (Demathieu, 1970), in particular the length of the toes, only the preserved tracks of the long type were considered. For only 3 characters (width of print, distance of the ends of digits II-III, and obliquity) a second statistic was established, bringing the totality of measures made on the prints clearer than those made on the long or short type (tabl. 1, 2, 3). The variabilities on the order of 10-15% can be considered normal for the prints of animals of different sizes. The obliquity (inclination

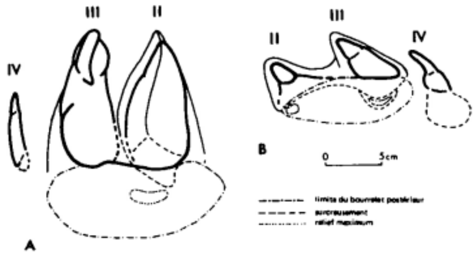


Fig. 2 – A – Long print type from a left pes (holotype – AG2-295 A).
B – Short print type from a right pes (YD4-295 A).

TRACKWAYS	PEDES	AUTOPODIA						
		II (mm)	III (mm)	IV (mm)	Length (mm)	Width (mm)	Obliquity (degrees)	d (II-III) (mm)
Bed 295 A	D 1							66
	D 2							67
	G 2	115	115	65	115	160	80	
	D 3	155	165		165	180	65	65
B	D 3	130	150		150	170	50	56
	G 3	100	125	95	130	170	60	60
T	D 1					190		
	G 1					180		
	D 2					210		
	G 2					210		
Y’	G 1				60	180	30	65
Bed 285 X	A 12	35	55	40	60	170	50	63
A	A 6	45	55		70	210	55	60
	AG 3	60	67	65	87	150	65	58
B	B 10	108	125		130	135	50	67
	B 11					180	60	64
	B 13	97	103	96	115	145	48	62
C	C 9	123	135		139	151	55	59
	C 12					230	30	
	C 10	115	120	90	130	170	45	70
E	BD 1	47	51	53	65	150	50	56
	DG 1	126	147	119	170	180	68	70
Bed 89	AD 1					170		
Bed 85	AG 1					150		65
	AG 2					130		70
	BD 1					155		60
	BG 1					160		
	BD 2					170		
	BD 3					160		
	BD 4					150		
	CD 5					100		65
	DD 2					145		55
	ED 1					95		55
	ED 2					110		65

Table 1: *Saltosauropus latus*
Numerical data.

CHARACTERS	NUMBER	MEAN (mm or °)	STANDARD DEVIATION (mm or °)	VARIABILITY (%)	CONFIDENCE INTERVAL FOR THE MEAN AT 5% THRESHOLD (mm or °)		CRAMER TEST		
							ASYMMETRY	VARIABLE TEST	PROBABILITY OF EXCEEDING THE VARIABLE (%)
Ungual II	9	119 mm	17.60 mm	15	105 mm	133 mm	0.915	1.28	20
Ungual III	9	132 mm	19.42 mm	15	116 mm	147 mm	0.361	0.50	62
Ungual IV	5	93 mm	19.24 mm	21	69 mm	117 mm	-0.255	0.32	75
Length L	9	138 mm	19.83 mm	14	122 mm	154 mm	0.540	0.75	45
Width l	9	162 mm	15.74 mm	10	150 mm	175 mm	0.607	0.85	40
Width (t)	32	163 mm	30.27 mm	19	152 mm	174 mm	-0.168	0.41	68
d (II, III)	8	64 mm	5.20 mm	8	59 mm	68 mm	-0.248	0.33	74
d (II, III) (t)	22	62 mm	4.61 mm	7	60 mm	65 mm	-0.161	0.33	74
Obliquity q	9	58*	11, 41*	20	49*	67*	0.874	1.22	22
Obliquity q (t)	15	54*	13, 19*	24	47*	62*	0.274	0.47	64

Table 2: *Saltosauropus latus*
Statistical parameters of certain measured characters.

CHARACTERS	NUMBER	MEAN	STANDARD	VARIABILITY		CORRELATIONS

		(mm or °)	DEVIATION (mm or °)	(%)	CONFIDENCE INTERVAL FOR THE MEAN AT 5% THRESHOLD (mm or °)		COEFFICIENT	COEFF. THEORETICAL MINIMUM
III/II	9	1.111	0.077	7	1.05	1.18	0.901	0.666
III/II (t)	13	1.153	0.144	13	1.16	1.25	0.980	0.553
L/I	9	0.852	0.091	11	0.78	0.93	0.669	0.666
I/d (II, III)	8	2.569	0.317	12	2.30	2.84	0.143	0.707
I/d (II, III) (t)	21	2.473	0.481	19	2.25	2.70	0.091	0.433
L/III	9	1.052	0.055	5	1.00	1.10	0.927	0.666
L/II	9	1.169	1.108	9	1.08	1.26	0.788	0.666
I/III	9	1.247	0.145	12	1.13	1.36	0.630	0.666
I/II	9	1.382	0.166	12	1.25	1.51	0.592	0.666

Table 3: *Saltosauropus latus*

Statistical parameters of ratios of certain measured characters and correlations.

BED	TRACKWAY	STRIDE	TRACKWAY WIDTH (mm)	PES WIDTH (mm)
295	A	1685	1095	163
295	B	–	875	163
295	T	2015	1004	198
295	Y	2415	1020	180
89	A	1915	740	170
85	A	1390	805	140
85	B	1347	788	159
85	C	893	625	100
85	D	715	–	145
85	E	590	580	103

A: Mean of measured parameters on each trackway.

CHARACTERS	OBSERVED COEFFICIENT	MINIMUM SIGNIFICANT VALUE OF THE COEFFICIENT
Stride/trackway width	0.796	0.707
Stride/pes width	0.851	0.666
Trackway width/pes width	0.806	0.666

B: Mean correlation of ratios of certain measured characters of the trackways.

Table 4: *Saltosauropus latus*

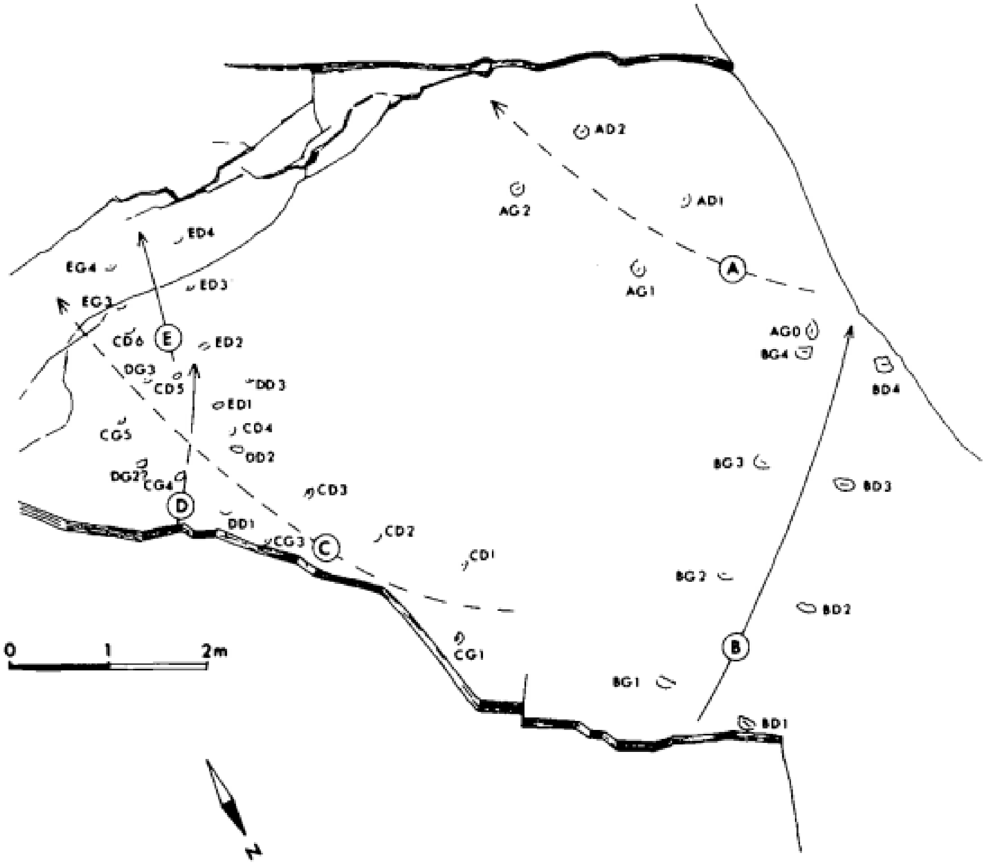


Fig. 3 – Distribution of *Saltosauropus latus* on the upper surface of bed 85. Note the presence of 5 trackways of which 2 (A and B) are probably those of adults and 3 (C, D, and E) are of young animals. Also note that there are very clearly 2 trackway directions, each involving 1 adult and 1 or 2 juveniles moving in the same direction. It could very well be 2 passages of an adult animal accompanied by its young (A + C, B + D, E).

of the axis of III relative to the axis of the roll) is strong: 24% for the global sample, revealing an irregularity in the position of the foot independent of the length of the stride (= length of jump) and the width of the autopodia. The most stable character is the distance of the ends of II-III since this variability is on the order of 7% for the total sample, which permits thinking that the autopodium is placed first on the ends of the toes. The study of ratios shows a drop in the variability in general and particularly in that concerning the basic sample (8 or 9 individuals). The correlations are good for the ratios of measures of length and length/width. All those which use only the width are bad. They show that a functional relationship between the width and the other characters did not exist. The trackways offer variable measures which correspond to differences in size of their makers (tabl. 4) as they show correlations between the stride and the width of the foot (coeff. 0.89) on the one hand and, on the other hand, the interior width of the trackway and the width of the foot (coeff. 0.81).

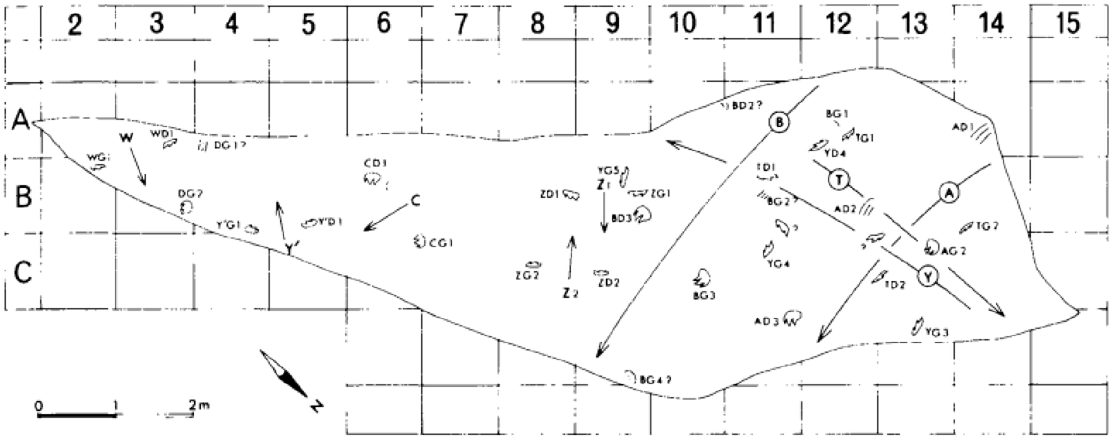


Fig. 4 – Arrangement of *Saltosauropus latus* on the upper surface of bed 295 A.

INTERPRETIVE STUDY OF THE TRACKS

1) MODE OF LOCOMOTION: One can dismiss the hypothesis of a quadrupedal animal easily enough. In effect, that it used an alternate step or a walk, the existence of a single type of print in the trackway suggests homopody. But one does not think that, in the Upper Jurassic, there was a quadrupedal homopodous animal of such a large size and capable of leaving such tracks. Furthermore, products of such an animal, these tracks suppose a particularly surpising movement for a quadruped. The particular case of a quadruped moving alternate feet placing the feet in the prints of the hands could be equally dismissed because there has never been observed the least superposition of prints for this same trackway. In fact, all the observations developed above demonstrate the evidence that these tracks were made by a bipedal animal moving in successive bounds on a soil wet enough to have a certain plasticity. The possibility of traveling in shallow water seems unlikely. Diverse criteria from sedimentological to paleoichnological show elsewhere that immersion, recently proved (Bernier et al., 1982) is a frequent phenomenon in such an environment. The roll which characterizes the rear of the prints can be interpreted as the result of compression attesting to the mechanical reaction of the sediment to the pressure supplied by the autopodium at the moment the animal gathers speed. The support of the foot is made preferentially on digits II and III as attested to by their more deeply marked prints. The abnormal elongation of these shows slippage of the autopodium on slippery soil.

2) COMPARISON WITH OTHER TRACKS: To our knowledge, the discovery of the track of a large bipedal reptile from the Mesozoic has not been described.

Footprint ARSB 95 from the Botucatu Formation, State of San Paolo, Brazil (Upper Triassic or Lower Jurassic) described by G. Leonardi and L. C. Godoy (1980) shows resemblances with *S. latus*: tridactyly, short and thick toes, the line of two in-phase feet perpendicular to the direction of movement, slightly bent feet, small divergence of the digits. But the differences are very significant: the stride is 12 cm, the interior of the path is larger with an area of 2.5 cm, the stride/width ratio of the path is 4.8, and furthermore the hands are sometimes present in front of the feet.

These distinctive characters exclude all identity between the two tracks.

The footprint *Sauropus baratii* Hitchcock, 1837 clearly shows the foot “joints” but shows tracks of resting and not jumping. Finally, *Sarmientichnus* *scaglieri* Casamiquela, 1964 is an elongate track rather similar to the short type of *Saltosauropus latus*. But the large print axis here is parallel to that of the trackway while it is perpendicular for *Saltosauropus latus*.

3) ATTEMPT AT PALEONTOLOGICAL INTERPRETATION: Among known Upper Jurassic vertebrates, amphibians and mammals were too small to have produced such tracks. A large reptile seems the only reasonable hypothesis. Crocodilians can be dismissed because we do not know of any large forms able to move by bounds. On the other hand, this mode of locomotion can be envisioned in bipedal dinosaurs. These latter are found in two different groups: ornithopods (Ornithischia) and theropods (Saurischia). Ornithopods which attained the size of the maker of *Saltosauropus latus* were robust animals, without doubt partly quadrupedal, which one hardly imagines moving in bounds. Moreover, their generally flat phalangeal unguals resembled hooves, which hardly evoke the claws indicated in the Cerin prints. In constrast, the strictly bipedal theropods possessed feet armed with claws. In this group, bounding locomotion could be considered for coelurosaurs, particularly the slender forms that could have been more agile than the more massive carnosaurs. However, the large size of the Cerin animal leaves some doubt, and it is difficult to choose between a large coelurosaur and a gracile carnosaur. The relative weakness of the print of the fourth digit is surprising in a theropod, but it could be due to the bent position of the foot. This would not allow this digit to press down as much as the others. However so, the mode of locomotion indicated by *Saltosauropus latus* is unknown among dinosaurs, although reconstructions of leaping theropods were proposed in the last century. It is certain that, by their occurrence and abundance, the tracks discovered at Cerin constitute the first proof that leaping locomotion was normal in certain dinosaurs.

Inspired by the skeletal proportions of modern bipedal leaping animals such as kangaroos and jerboas (Vialleton, 1924), the dimensions of the dinosaur maker of *Saltosauropus latus* can be estimated according to the lengths of the digits observed on the most marked prints (tabl. 1): the length of the foot could be estimated at 0.50–0.60 m and that of the hind limb at 1.50–1.80 m; the trunk could be on the order of 0.8 to 1.3 m and the total length from 3 to 4.5 m.

However, the highly spread feet (0.70 to 1.40 m) and bent feet clearly differentiate the locomotion of this animal from that of extant jumping vertebrates, as it was bounding with feet together and parallel to the trackway axis. This posture, if our interpretation is correct, seems at least strange and less effective. It is true that the bounds are never very long. They are near the length estimated for the hind limb (around 2 meters); this does not seem to be a remarkable performance. According to the laws of dynamics (P. Appel and S. Dautheville, 1934), the probable speed of the hopping dinosaur at the moment of the bound can be estimated at 16–19 km/h, and the height of the bound (elevation of the barycenter) at 0.30–0.60 m.

PALEOECOLOGICAL IMPLICATIONS

Saltosauropus latus, by its rather high frequency in the formation and abundance in certain beds, proves that the corresponding animal was common in the Cerin paleoenvironment. This track demonstrates the existence of an animal substantially larger than can be predicted only from examination of skeletons known from the locality. These large reptiles imply unsuspected links in the food web. It is thus very reasonable to suppose that the land that they populated was very extensive in order to produce the necessary biomass for their subsistence.

The sedimentological and paleoecological observations accumulated over several years thus allow us to define some characters of the Cerin ecosystem. Enclosed in a vast island complex of coral origin and built of sandy material, the Cerin mudflat was protected from the high sea. Often covered by a thin stretch of water, it was subjected to repeated submersions of short duration. A vegetation with a xerophytic tendency dominated by Bennettitales (G. Barale, 1981) flourished on the neighboring land, which was constantly emerged, and so the substrate enclosed a phreatic sheet of quiet water (P. Bernier, 1983).

Although tied to dry land, large reptiles occasionally ventured onto the exposed muddy expanses. It is possible that they searched for their prey in the remaining pools where they found marine animals trapped in large numbers (crustaceans, fish). The parallel nature of certain juvenile and adult trackways suggests movement of animals in groups.

CONCLUSION

The discovery at Cerin of tridactyl prints of a new type organized in trackways show an unknown mode of locomotion, that by successive bounds. Analysis of the prints suggests that their maker was a dinosaur (theropod?). This reptile is the largest animal known at present from Cerin. Its size and occurrence in the locality imply vast emerging lands nearby.

REFERENCES

APPEL P. & DAUTHEVILLE (1934) – Précis de Mécanique rationelle. *Gauthier-Villars edit.*, Paris, 650 p., 235 fig.

BARALE G. (1981) – La paléoflore jurassique du Jura français: étude systématique; aspects stratigraphiques et paléoécologiques. *Doc. Lab. Géol. Fac. Sci. Lyon*, no. 81, p. 1–336, pl. 1–66 (thesis, Sci. Univ. Lyon, no. 7806, 1978).

BERNIER P (1983) – Les formations carbonatées du Kimméridgien et du Portlandien du Jura méridional. Stratigraphie, micropaléontologie, sédimentologie. *Thèse Sci. Univ. Lyon*. 960 p. dactyl., 220 fig., 35 pl.

CASAMIQUELA R.M. (1964) – Estudios ichnologicos: problemas y metodos de la ichnologia con aplicacion al estudio de pisadas mesozoicas Reptilia, Mammalia de la Patagonia. Buenos Aires, 229 p.

DEMATHIEU G. (1970) – Les empreintes de pas de vertébrés du Trias de la bordure Nord-Est du Massif Central. *Cahiers de Paléontologie*, Paris, 211 p., 76 fig., 83 tabl., 8 pl.

GRAY J. (1968) – Animal Locomotion. *Weidenfeld & Nicolson edit.*, London, 479 p., 251 fig., 8 pl.

HILDEBRAND M. (1974) – Analysis of Vertebrate Structure. *John Wiley & Sons edit.*, New York, 710 p., 364 fig.

HITCHCOCK E. (1837) – Fossil footsteps in sandstones and graywacke. *Amer. Journ. Sci.*, New Haven, vol. XXXII, p. 174–176.

LEONARDI G. & GODOY L.C. (1980) – Novas pistas de tetrapodes da formaçao Botucatu do Estado de São Paulo. *Ann. XXXI Congres. Brasil. Geol.*, Balneario de Camboriu, Santa Catarina, vol. 5, p. 3080–3089, 6 fig.

VIALLETON L. (1924) – Membres et ceintures de vertébrés tétrapodes. Critique morphologique du transformisme. *Doin edit.*, Paris, 710 p., 270 fig.

PLATE 1

Fig. 1 – Cast of a right pes print – long type – bed 295 A – BD3 – x 0.2.

Fig. 2 – Cast of the corresponding left pes print – BG3 – x 0.2.
Note, in both cases, the importance of the rear relief.

Fig. 3 – Cast of the holotype – left pes print of long type – bed 295 A – AG2 – x 0.3.

Fig. 4 – Cast of a right pes print showing a more important sliding (long type without rear relief). Bed 295 A – AD2 – x 0.2.

Fig. 5 – Cast of the successive right pes pring – AD3 – x 0.2.

Fig. 6 – Cast of a right pes print – short type – bed 295 A – YD4 – x 0.3.

Fig. 7 – Cast of a right pes print – short type – beds 295 A – TD1 – x 0.2.

Fig. 8 – Surface of bed 285 showing three pairs of prints of a jumping dinosaur, from the bottom to the top of the photo.

Fig. 9. – Surface of bed 85 showing four pairs of prints from bottom to top, and two pairs of another individual moving from right to left (see fig. 3).

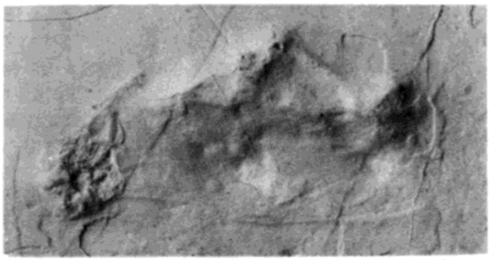

1


2


3

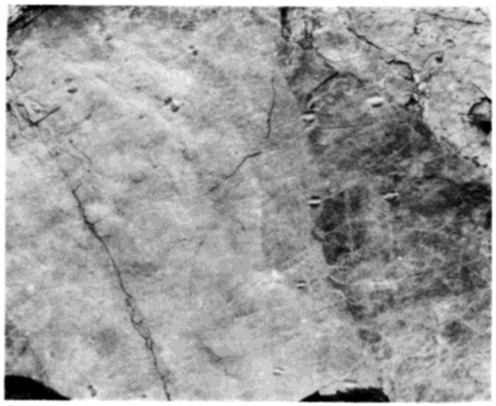

4


5


6


7


8


9