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THE REPTILE FOOTPRINTS FROM THE LOWER LIAS OF VEILLON (VENDÉE)

BY

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FOREWORD

In presenting this original work in the *Mémoires* of the Geological Society, we are pleased to thank all those who helped in its realization.

Above all Mr. Gilbert BESSONNAT, to whom we are indebted for the discovery of the footprints of Veillon. Mr. Bessonnat much wished to invite us to study this interesting locality, and we thank him highly.

We contracted a debt of gratitude toward Mrs. Mireille TERS. She brought us her dynamic aid during several visits to Veillon, and we benefited from her perfect knowledge of the Vendée coast.

The students of the geology laboratory of the Catholic Institute of Paris also brought us, on the ground, enthusiastic and effective aid, notably during the five days of active excavation made in March 1966 on the Veillon beach. Among them, Mr. Raymond DESPARMET, very particularly, made all of the visits to Veillon and showed himself a precise collaborator during the excavations, as in the laboratory.

Finally, Mr. P. R. CHAIGNEAU, conservator at the museum of Sables-d'Olonne, was closely interested in our work. He accepted the task of carefully mounting a large slab of footprints in the Sables museum, where they can now be found, particularly well developed.

The plate types were made by Mr. J. LERICHE and we thank him for his work.

The figures of the footprints of various sizes, and still more the trackways, could not be published at the same scale. Note the indicated reduction.

Frontispiece legend

Above: Life picture of the reptiles, pseudosuchians, and dinosaurs in the Veillon estuary during the Lower Liassic. Drawing by Miss D. Humphreys. 1966.
A: Payré Point: discordance of the Hettangian on the mica schists.
B: Veillon Point at low tide. Sandstone slab (no. 5 of the section on p. 8) with numerous reptile footprints.

INTRODUCTION

1. *HISTORY OF THE DISCOVERY AND METHODS OF STUDY*. — The Liassic of the Vendée coast, well exposed on the cliffs south of Sables-d'Olonne, were minutely studied by numerous geologists. We refer to the detailed publications of J. Welsch [1912], P. Butel [1953], G. Mathieu [1948], M. Ters [1961], J. Gabilly [1964], as well as the new edition of the 80,000 scale geological map of Sables-d'Olonne.

Several paleontological beds are found and described in this Liassic. It is curious to note that people have not remarked on, entirely at the base of the sedimentary series, the footprints of reptiles, abundant and sometimes of large size, that we are describing. The fortuitous discovery is due to Mr. Gilbert Bessonnat, chemical engineer. Interested by the nature of the rocks outcropping on the Veillon beach, G. Bessonnat made a detailed section of it and collected by chance, during the summer of 1963, small tracks that intrigued him. When he presented them to us, on the advice of Miss M. Ters, we recognized ten footprints recalling a pes of *Cheirotherium*, as well as two small tridactyl tracks of an entirely different type.

Profiting from the spring tide of 19 March 1965, we made a first visit to Veillon, which permitted localizing the site on the strand (Frontispiece, fig. B) and collected more than a hundred tracks. A second locality, stratigraphically higher by several meters, was discovered there on a limestone slab in the cliff, at the Veillon point [Bessonnat, Lapparent, Montenat and Ters, 1965]. Several visits to the locality were made in April and June; they allowed the collecting of several more new types. In December 1965, some large prints were discovered a little farther north, in the République Cove [Lapparent, Montenat and Desparmet, 1966]. The abundance of tracks following trackways over long distances led us to organize, for the spring tide of March 1966, a very important excavation with the help of students of our laboratory, who were joined by Mrs. Ters and geography students from the Sorbonne. Twenty people in total participated actively in the work.

In the République Cove, a large slab of 20 x 15 m was extracted and revealed an extraordinary richness of trackways of large dinosaurs (text-fig. 14). The locality being submerged with each tide, we only had a limited time to make a description of this slab. All the prints and strides were measured and numbered. Then the slab having been gridded with a 1.30 m mesh, each square, located on the ground by a letter and a figure, was photographed from above at one scale. In certain cases, two photos of the same track, with an overlap of around 50 to 60%, permitted a stereographic view that gave a still more accurate image of the print.

A mold of each trackway was made, either in plaster or Elastomer, a cold-polymerizing synthetic rubber[1]. This last formula presents incomparable advantages for the transport and storage of molds; but its utilization becomes expensive for deep tracks and those of large size. Its use is better for the case of small trackways preserved in fine sediment, without large irregularities.

[1] Rhodorsil Elastomer RTV 105, of which an important sample was graciously offered to us by the Rhône-Poulenc Establishment.

During the same excavation, a 6 m long slab, covered with large counter-impressions, was extracted in several parts and transported to the Sables-d'Olonne museum where it is mounted today. Several other slabs, exceeding a square meter, were extracted and brought to the laboratory. To limit the considerable maximum weight of the slabs, the blank parts were eliminated. For this we used a very convenient rock saw[1].

Finally, we made another visit to the locality in June 1966. Prospectings of other small outcrops of the Lower Liassic near Veillon, at Cayola and the Pissot rock, were made in vain by Mr. Bessonnat and ourselves.

In fact, the clayey-sandy levels bearing footprints are essentially localized in the environs of Veillon. However, near Bourgenay, at the Pissot rock, the detrital facies at the base is somewhat less represented; but it has undergone a secondary silicification, in connection with the mineralized faults that affected the Mesozoic covering.

FIG. 1. — Geological map of the Vendée shoreline.
1: ancient base; 2: Liassic and Jurassic; 3: Cretaceous.

GEOLOGICAL SITUATION OF THE LOCALITY. — The reptile footprint locality that we studied is found between the Veillon point and the République Cove, immediately north of the mouth of the Payré; it is found in the community of Saint-Hilaire-de-Talmont (Vendée), 12 km southeast of Sables-d'Olonne (text-fig. 1).

[1] The apparatus comprises an actuating four-stroke engine, by the intermediary of a 2 m long flexible transmission, a disc of emery powder agglomerated onto a metallic grill. This instrument, easily transportable on the ground, is recommended for the extraction of slabs in place, the same as the ground, whose thickness does not exceed fifteen centimeters.

Here is found the eastern limit of the ancient Vendée massif, essentially formed of Precambrian mica schists, Paleozoic sediments, and Hercynian granites. The Lower Jurassic deposits are transgressive and discordant on the ancient base, in a sometimes spectacular manner, as can be seen in the traditional place of Payré point (Frontispiece fig. A).

The details of the transgression were described by the authors and the oldest level was attributed to the Hettangian. We borrow the detailed section of the Liassic of the Payré estuary from the work of Mrs. Ters (text-fig. 2). The following succession is observed from top to bottom:

FIG. 2. — Stratigraphic diagram of the Lower Liassic of Veillon.
Numbers explained in the text. The fossiliferous levels are indicated by a conventional symbol. Note the discordance of the Lower Liassic on the mica schists and the depression of the pre-Liassic estuary.

13) platy, brown limestone with ripple marks: Cardinies level, with a rich fauna of lamellibranchs, gastropods, brachiopods, and algae indicating the Hettangian [Ters-Fouyé, 1934];
12) crystalline, gray-blue limestone: upper footprint level;
11) nankin yellow limestone;
10) black clay with plant debris;
9) nankin yellow limestone;
8) green clay with plant debris;
7) white limestone with lenses of black clay;
6) green clay;
5) plates of clayey-sandy limestone, gray-green or gray-black, with plant debris, molds of salt crystals, ripple marks, beds of black clay; this level is particularly rich in footprints;
4) green clay, with quartz grains and detrital feldspar;
3) red clay, or quite red and green;
2) white clayey limestone;
1) thick sandstone, with clayey-calcareous cement.

Mrs. Ters was able to show at Veillon the trace of an estuary emerging at this point a the start of the Liassic; the series is thicker, because it is more complete at the base, in the estuarine depression (text-fig. 2).

On both sides of the ancient estuarine depression, only levels *8* to *13* are represented. These must be referred to the Hettangian, although speaking properly, only level *13* has revealed identifiable fossils.

The age of levels *1* to *7* is more disputable. The installation of a sedimentation already quite rich in limestone excludes the Keuper; but it seems prior to the Hettangian. We are rather struck by the resemblance of the facies with those of the classic Rhaetian even in detail, the intercalations of red clay recalling the "Levallois marls" of the Rhaetian of Lorraine. The similarities are also very striking with the Rhaetian of Normandy [Rioult, 1964]. These clayey-sandy beds, which fill the depressions in the pre-Jurassic relief, do nothing but announce the Liassic transgression. This latter is clearly manifest in the marine limestone beds of the upper levels *8* to *13*. But above all,

the paleontological study of the footprints reveals a reptile fauna that has still more affinities with those of the Upper Triassic. Thus we have several arguments converging to distinguish very probably two stages, the Rhaetian and the Hettangian, in the Lower Liassic of the cliffs and beach of Veillon.

It goes without saying that we have used the most current language among French geologists. But it is known that a recent meeting of specialists recommended reattaching the Rhaetian to the Upper Triassic [Pugin, 1964]. In any case, the succession of three distinct terms, Keuper, Rhaetian, and Hettangian, remain well founded.

Thus we think finally, as much for paleontological reasons as due to facies comparisons, that levels *1* to *7* at Veillon, much the richest in reptile footprints, belong to the Rhaetian, defined as being a more recent level than the Keuper, but before the characteristic Liassic.

Practically, the footprints are encountered at all levels of the clayey sandstones outcropping on the strand between the Veillon beach and the République Cove, and the same types of tracks are found in all the beds. The map (text-fig. 3) locates simply the places where the slabs are shown to be particularly rich in tracks.

FIG. 3. — The Veillon coast: main fossiliferous points.
See the explanation of the numbers in the text. The "fish locks" used as benchmarks are figured.

F_1 first locality located in the company of Mr. Bessonnat: slabs with *Grallator* and *Batrachopus*.
F_2 limestone slabs with footprints in the cliff at Veillon point (base of level *12* of the section).
F_3 beds particularly rich in prints, practically on all the layers. Good levels with "mud cracks", ripple marks, molds of salt crystals, and traces of raindrops.
F_4 sandy lignite level, located by Mrs. Ters in April 1965 and covered since.
F_5 slab with counter-impressions, brought to the Sables-d'Olonne Museum.
F_6 République cove locality. Large slab very rich in prints, removed in March 1966. For convenience, in this study we call this surface the "principal slab."
F_7 impressions on the surface of white limestone (level *7* of the section), near the "principal slab."

When the first announcement of the discovery was publicized, in a note presented to the Academy of Sciences on 17 May 1965, we had recognized 200 prints, divided into seven different types. Currently, the material examined shows a thousand prints, belonging to a dozen types at least.

CHAPTER I

DESCRIPTION OF THE FOSSIL TRACES

The footprints recovered at Veillon can be divided into a dozen types that we will now describe.

For convenience, we employ a Linnean binomial nomenclature. But if we give the names of "genera" and "species," it is clearly understood that they are only applied to the prints and do not presuppose the identity of the author of the tracks. Too often, this remains unknown, and we reserve the discussion on the possibilities of attributing them for the following chapter.

The prints are delicate fossils to study, owing to the fact that all kinds of possible causes of mechanical deformations come to be added to the individual variations linked to the author of the tracks. It is therefore convenient to give each "species" a rather wide meaning, which can hold these variations. As a result, we figure as many varieties as possible grouped around the type.

The statistical study furnished good results when the considered sample came from beds of comparable lithological nature and *a fortiori* for populations of a single horizon.

We describe successively:

1) Two forms attributable to quadrupedal pseudosuchian reptiles:
Batrachopus gilberti nov. sp. *Dahutherium* sp.

2) Seven types of tridactyl dinosauroid tracks:
Grallator olonensis nov. sp. *Saltopoides igalensis* nov. gen., nov. sp.
Grallator variabilis nov. sp. *Anatopus palmatus* nov. gen., nov. sp.
Grallator maximus nov. sp. *Talmontopus tersi* nov. gen., nov. sp.
Eubrontes veillonensis nov. sp.

3) Some isolated, unnamed tracks.

I. Quadrupedal footprints

Genus ***Batrachopus*** HITCHCOCK 1845.

The genus *Batrachopus* created by Hitchcock and redescribed by Lull [1953] indicates the tracks of small quadrupeds from the Upper Triassic of Connecticut.

The impression of the manus is small, apparently tetradactyl. The digits are wide and lack claws. The impression of the pes, clearly very large and tetradactyl, shows traces of claws. The order of size decrease of the digits is as follows: III, IV, II, I; the pollex I being particularly reduced.

The difference in appearance and size between the manus and pes recalls that observed in *Cheirotherium*; but these latter are larger and pentadactyl, with a better-developed pollex.

***Batrachopus gilberti* nov. sp.**
Pl. I, fig. 1 to 3 and text-fig. 4.

1. MATERIAL. — We have around 70 manus and pes tracks belonging to this type. Most often they are grouped in pairs (manus and pes of the same side). We particularly note a slab of greenish sandstone with beautiful ripple marks (A XII) bearing a dozen tracks of which 4 pairs alternate, left and right; they could belong to a single trackway, but the stride seems too large.

FIG. 4. — *Batrachopus gilberti* nov. sp.
A: type, x 1. — B: variations (*a*: pair; *b*: different varieties of pes; *c* to *e*: varieties of manus), x 1.

We take for description of the type the right counter-impression of a pair, which corresponds as a result to the impression left by the left manus and pes of the animal. It is preserved in strong relief on a slab of thick, grayish, clayey sandstone. These tracks are besides the first finds made by G. Bessonnat, discoverer of the locality.

2. DESCRIPTION OF THE TYPE. — The manus is small and stocky.

The digits, arranged "in a star shape" are short, with rounded pads, and subequal. Digits II and IV are symmetrically inclined on III following an angle of around 30°. Digit I, smaller, is directed backward and makes an angle of 120° with digit III. Finally, there exists, in a postero-external position, a small trace, less appressed than those of the other four digits, which can only be that of digit V or the trace of the palm. The distal ends of the digits are rounded, lacking claws, and strongly imprinted.

The pes is tetradactyl. The digits are elongate, well separated from one another and slightly inclined. The order of decreasing size, III, IV, II, I, with marked predominance of digit III and accentuated reduction of digit I, is in agreement with the description of the genus. The ends of the digits are rounded, even slightly dilated, without trace of claws. The "heel" is relatively well developed.

The interdigital angles of the pes are as follows: I/II = 30°; II/III = 10°; III/IV = 20°.

DIMENSIONS OF TYPE PAIR. — Total length of pair = 58 mm; distance between the two legs of the pair taken with the heel = 37 mm. — Manus = 21 X 20 mm. — Pes = 38 x 28 mm.

3. OTHER SPECIMENS. — Numerous other specimens complete the description of this type.

None of our tracks, however well preserved, show any clearly individualized phalanges on the manus or pes. The manus track is very polymorphic (text-fig. 4B). Frequently, digit I does not leave a mark; the manus appears tridactyl and the three digits then seem more elongate and not retracted on a rounded pad (Pl. I, fig. 2).

A small counter-impression of the left manus bears under each digit the mark of a small, elongate claw, not projected ahead of the digit, but retracted under it (text-fig. 4Bc). A print of the right manus (text-fig. 4Bd) shows only the impressions of the ends of the digits, as an oval cup with, as in the preceding case, the mark of the claw not extending past the end of the digit. All these variations suggest mobile digits, susceptible to being retracted or slackened following the attitudes of walking.

All the specimens of pedal tracks show the same order of development of the digits. Rather often, a strong claw is marked on digit I; several examples show a well-imprinted claw and sometimes even detached ahead of the other digits (Pl. I, fig. 3 and text-fig. 4Bb).

It happens that the heel of the pes, even as the palm of the manus, is rather unobtrusive. The relative positions of the manus and pes within a single pair are very variable. The manus is in an antero-internal position in the type pair; it can, according to the example, be brought more or less closer to the pes, sometimes to the same height as it.

We have observed three alternating pairs on a ripple-marked slab (A XII). The strides, 177 mm on average, seem too long to be the trackway of a single animal.

SEVERAL DIMENSIONS. — A V pair: manus = 16 x 13 mm; pes = 32 x 31 mm. — A VIII: manus = 22 x 21 mm. — A XII: pes = 33 x 27 mm.
Another pair: manus = 20 x 15 mm; pes = 30 x 24 mm.

4. DISCUSSION. — Concurrently with *Batrachopus*, Lull described two other genera, *Cheirotheroides* and *Comptichnus*, of comparable size and which did not present major differences with *Batrachopus*.

Our small form from Veillon is close to *Batrachopus deweyi* HITCH. from Connecticut. This one differs especially by the shape of the manus, whose digit I is not directed backward as in our species, and by some details in the contour of the pes.

Genus ***Dahutherium*** MONTENAT 1967.

The presence of a second form of quadruped at Veillon, of much greater size than *Batrachopus*, is indicated to us by two isolated tracks. Their interpretation was be facilitated by comparison with other prints that one of us recently recovered in the Triassic of the Daüs plateau near Aubenas (Ardèche)[1]. We will now summarize the characters of this Triassic form, named *Dahutherium*, before examining our specimens from Veillon.

Genus *Dahutherium*: quadrupedal footprint of moderate size; dimensions of the pes: 120 x 80 mm.

The difference in size and form between the manus and pes is very marked. The manus impression is small, probably tetradactyl, although there are often only three visible digits.

The pes is tetradactyl. The order of development of the digits is the same as in *Batrachopus*. The pollex, very reduced, does not leave a discrete trace. The digits are inclined toward the interior, slightly divergent, without differentiated claws.

***Dahutherium* sp.**
Pl. II and text-fig. 5 and 5 *bis*.

The Veillon locality delivered to us two tracks that we can attribute to *Dahutherium*: one counter-impression of the right pes, on a yellowish sandstone; one counter-impression of the manus on a blackish gray sandstone.

— The *pes track* is tetradactyl. Digit III is clearly the longest, with IV, II, I in decreasing order. The digits have a tendency to incline toward the interior. The hallux, very reduced, is lacking a powerful nail. The other digits do not bear traces of a claw. They are elongate and well separated. The heel is moderately developed.

In front of the pes, the trace of a large digit belonging to another type of print comes to mask the eventual location of the manus.

— The *counter-impression of the manus* is tridactyl. The three digits are stocky and have a strong relief. The palm did not leave a trace, no more than the claws (text-fig. 5 *bis*). The lateral digits together make an angle of 90°, the median digit having almost a bisecting position. On this median digit is raised the trace of three short phalanges.

FIG. 5. — *Dahutherium* sp.: Left pes, x 1/2.

FIG. 5 *bis*. — Manus track, x 1.

[1] The description of the Triassic ichnofauna of the Daüs plateau, which includes a dozen different types of tracks, was recently published (Montenat, 1967).

DIMENSIONS. — *Pes*: L = 160 mm; w = 130 mm. — Interdigital angles: I/III = 30°; II/III and IV/III = 20 to 25°.

Manus: 28 x 35 mm.

DISCUSSION. — The manus track is identical in form and size to the specimens of the best prints of *Dahutherium* from Aubenas.

The pes, if it possesses all the principal characters of *Dahutherium*, in particular the size order of the digits and their inclination toward the interior, is larger than the Ardechois type.

We do not specifically name these tracks from Veillon for which more ample materials remain to be found.

II. Tridactyl dinosauroid tracks

Alongside these quadrupedal forms, the essential part of the Veillon ichnofauna is represented by varied tridactyl tracks of dinosauroid type; we will describe them now.

Genus ***Grallator*** HITCHCOCK 1858.

This type of print, frequent in the Triassic of Connecticut, corresponds to bipedal forms, of small and very small size.

The feet are slender; the median digit is long, the phalanges are well marked, with rounded pads and well-marked claws. The trackways show long strides, relative to the dimensions of the foot, and disposed along the same line.

***Grallator olonensis* nov. sp.**
Pl. III, fig. 1, 2 and text-fig. 6.

1. MATERIAL. — We have recovered around 160 impressions and counter-impressions of this species, divided among a dozen slabs and several isolated small slabs, numbered from B I to B XXI, with (*bis*) for the counter-impressions where the hollow print is also possessed.

Nearly all of this material comes from the same bed (locality F 1, text-fig. 3), formed of a fine grayish sandstone, clayey-calcareous, broken into slabs of 1 to 3 cm thickness. Several tracks come from other levels; a small slab (B XI) is made of a very thick, greenish sandstone; four counter-impressions, arranged in a trackway, are preserved on the back of the slab (A XII) bearing the prints of *Batrachopus* (locality F 2).

The type slab (B I) bears 25 impressions on a surface of around a quarter of a meter squared. B I (*bis*) shows a dozen counter-impressions of the same tracks.

2. DESCRIPTION OF THE TYPE (Pl. III, fig. 1 and text-fig. 6A). — These small tridactyl tracks are slender. The very elongate median digit appears supple. It is frequently incurved, with its mobile distal end inclined toward the interior. The lateral digits are reversed on the central axis and withdrawn relative to it. The phalangeal pads are well marked, of elliptical contour, often detached from one another. They number three on the median digit and IV, and two on the internal digit II.

The claws are strong on the three digits, but less pointed than those of other *Grallator*. In particular, that of digit II, the most strongly imprinted, can sometimes simulate a third phalanx. Certain prints are only represented by the distal ends of the three digits, or even only by their claws.

Behind the print of the lateral digits, there is no trace of a heel.

Four impressions that seem to belong to a single trackway, although a little sinuous, are separated by strides of average length 150 to 160 mm for tracks of 43 mm.

The type slab shows equally tracks of the same shape, but smaller and more slender, belonging reasonably to young individuals. Three of these small tracks are ordered

FIG. 6. — *Grallator olonensis* nov. sp.
A: Type, x 1/3. — B: Different examples, x 1.

into a trackway and show a stride of 195 mm for a foot length of 38 mm, that is a ratio of 5/1, testifying to a very elongate stride.

The dimensions of the prints on the type slab vary between 48 x 26 mm and 47 x 29 mm, lowering to 38 x 17 mm for the juvenile tracks. The average dimension is around 44 x 24 mm.

3. OTHER SPECIMENS. — The dimensions are well grouped as the graph shows (text-fig. 8) and separated from those of other *Grallator* from Veillon that we will describe later. Morphologically, these small tracks are equally homogeneous.

Several tracks coming from the same slab show an exceptionally important separation of the lateral digits, which seems to result from the plasticity of the sediment on which the animal walked.

On the reverse of the slab (A XII) with *Batrachopus*, four counter-impressions of our small *Grallator* are arranged in a trackway. The stride is 245 mm for a foot of 44 mm, the ratio being 5.5/1. The foot alternates on a single line; the median digit is found almost on the trackway axis.

4. Discussion. — The slenderness of the foot, the clear predominance of the medial digit, and the considerable elongation of the stride, being able to attain five times the length of the foot, make our small form a typical *Grallator*.

The Connecticut ichnofauna includes several species of *Grallator*, among which the small *Gr. gracilis* has the dimensions of our species. *Gr. tenuis*, of a little greater size, presents equally a supple and incurved median digit. The tracks from Veillon are situated very close to both.

***Grallator variabilis* nov. sp.**

Pl. III, fig. 3; IV to IX; XII, fig. 2; XIII, fig. 1, 2 and text-fig. 7, 9, and 10.

1. MATERIAL. — The tracks that we will describe now form a dense group in which it is difficult to put any order, although we possess an important number of specimens, around one hundred. The statistical study is not sufficient to unravel the problem, in part due to the diversity of provenance of the specimens. The different soils on which these tracks are imprinted are of a varied nature, more of less clayey or sandy, and the shape of the impressions finds itself affected. The counter-impressions in thick sandstone are thickened and often slightly deformed. And then, generally, the variations in size, when they are not important and constant, are not at all significant if one remembers that reptiles have continuous growth during their life.

Faced with this rather heterogeneous collection, we now describe an average type to which are attached a good number of specimens; then we indicate the variations in size and form, which should perhaps constitute species for certain, but insufficiently founded to our senses, at least for the moment.

We take for description of the type a trackway of three feet, observed on the "principal slab" (F 6, text-fig. 3) and of which we have made a mold.

2. DESCRIPTION OF THE TYPE (text-fig. 7). — The shape of this track is that of a typical *Grallator*.

The digits are fine, lacking well-marked phalangeal pads. The median digit is very elongate, the lateral digits tightened against it and slightly inclined. The phalanges number 3 on digits III and IV, and 2 on digit II. There is no heel, but a slight posterior extension to digit IV. The long and sharp claws leave a cuneiform impression.

DIMENSIONS. — Average of the tracks of the type trackway = 123 x 65 mm. — Interdigital angles: II/III = 8°; IV/III = 16°. — Average of the strides = 570 mm, that is a ratio of 4.6/1 with the foot.

The ratio of the stride to the foot corresponds to an elongate stride. The feet are arranged single file, the median digit within the trackway axis, its claw inclined toward the interior (text-fig. 7B).

Fig. 7. — *Grallator variabilis* nov. sp.
A: Type (drawing taken from the "principal slab"), x 1. — B: trackway, "principal slab", x 1/10.

3. OTHER SPECIMENS. — Several other identical tracks were located on the "principal slab." Among the numerous other specimens comparable to the type and collected in various levels, the small differences include the more or less rounded impression of the pads or slight variations in the inclination of the digits. The posterior extension of digit II is perhaps more or less impressed, sometimes absent.

Several strides were measured. One attains 610 mm for a track of 115 mm; ratio 5.3/1. Another is 575 mm with a foot of 138 mm; ratio 4.1/1. Thus the strides are always very long.

SEVERAL MEASUREMENTS:		Interdigital angles	
Slabs		IV/III	II/III
C I	108 x 60 mm	10°	12°
C III.	130 x 75	15°	25°
C $VIII_2$.	141 x 94	17°	22°
C XV_1.	108 x 64	15°	15°
M V.	108 x 63	15°	11°

The counter-impression C XV1 comes from a good level with "mud cracks" at locality F 3 (Pl. VI) of which we figure also two other tracks.

Alongside this first group are placed some tracks morphologically identical to the preceding ones; they accompany them at different levels, but are of a markedly smaller size.

They are found in general less strongly imprinted in their posterior part and do not leave a trace behind digit IV. They are without doubt the tracks left by young individuals, less heavy and therefore sinking less into the sol (Pl. XIII, fig. 2).

DIMENSIONS:		Interdigital angles	
Slabs		IV/III	II/III
C XXVII.	80 x 51 mm	18°	20°
C XXIV.	85 x 48	10°	20°

Several tracks grouped on slab M 1 (coming from locality F 3) are particularly reduced: from 60 x 38 to 67 x 42 mm, but not attaining the breadth of variation of *Grallator olonensis* which differ equally from them by their form (text-fig. 8).

Several other tracks separate themselves more from the type. The essential difference is the fact that the lateral digits are at once more distant from the central axis and more inclined toward it, notably digit IV. The heel is also frequently more marked and rounded. The other characters:

FIG. 8. — Diagram showing the size variations in *Grallator olonensis* (round points) and *Grallator variabilis* (squares).

number of phalanges, pads, development of claws, do not differ from the type. These tracks, which are rare besides, perhaps result simply from a different manner of walking (Pl. XII, fig. 2).

FIG. 9. — *Grallator olonensis* nov. sp.
Different examples showing variations; x 1/2.

Finally, some tail traces, 2 to 3 cm wide, are visible on several slabs, in the middle of a trampling of *Grallator* feet. It is not possible to associate these tail traces with the footprints (Pl. IV, fig. 2). Let us recall that the type trackways of *Grallator variabilis* on the "principal slab" does not show a tail trace.

4. DISCUSSION. — The presence of a *Grallator* of moderate size in the Veillon locality, which we name *Gr. variabilis*, is attested to by a great number of tracks. These reveal a slender animal, with rather thin digits, susceptible as a result to leaving rather variable prints due to the consistency of the soil.

The homology of *Grallator variabilis* in the Connecticut ichnofauna would be *Gr. cuneatus*, of slightly greater size, but which differs above all by the still more forward projected position of the central digit, and by the slightly more divergent lateral digits.

FIG. 10. — *Grallator variabilis* nov. sp.; x 3/4.
Limestone slab; Hettangian; Veillon point.

This is equally with *Grallator variabilis* that we will collect the tracks, impressions and counter-impressions, discovered in the limestone slabs of the cliffs immediately under the nankin limestone. (Pl. IX, fig. 1, 2 and text-fig. 10).

***Grallator maximus* nov. sp.**
Pl. X; XI, fig. 1; XIII, fig. 4 and text-fig. 11 and 14.

1. MATERIAL. — The description of this species rests on several trackways, certain of which contain more than 10 successive feet; they are associated with another type of large track, which we will describe successively, on the "principal slab" found in March 1966.

We have found some tracks at numerous other points in the Veillon locality. The large slab transported to the Sables-d'Olonne museum, and which comes from locality F 5, comprises numerous examples. Several impressions of this type were equally located (F 7) on the surface of a white limestone, at level 7 of the stratigraphic section (see fig. 2).

We take for the type a trackway of a dozen feet from the "principal slab". The mold of a well-preserved right pes will serve as the plastotype.

2. DESCRIPTION OF THE TYPE (Pl. XI, fig. 1 and text-fig. 11 A and B). — This tridactyl track, of large size, is characterized by its relatively straight contour and the weak divergence of the lateral digits. The median digit is clearly carried in front.

FIG. 11. — *Grallator maximus* nov. sp.
A: Trackway, "principal slab", x 1/20. — B: Type, x 1/3. — C: Different examples, x 1/3.

The phalangeal pads, well marked, are three in number on digits III and IV and two on digit II. The proximal phalanx of the medial digit is less imprinted. Besides, the impression of digit ii is wider than that of digit IV. The claws are strong, that of the central digit being particularly long. Those of the lateral digits, shorter, are arranged along the digital axis and are not inclined toward the exterior as in *Grallator variabilis*. In the posterior extension of digit IV there exists a small impression that gives an asymmetrical contour to the rear of the track.

The strides of the trackway are large, 122 cm on average for a foot of 28 cm, that is a ratio of 4.3/1. The feet are arranged single file, the medial digit being very slightly inclined toward the exterior (text-fig. 11 A).

DIMENSIONS OF THE TYPE TRACK: 280 x 165 mm. — Interdigital angles: IV/III = 15°; II/III = 13°.

3. OTHER SPECIMENS. — The measurements of all the prints of *Grallator maximus* observed on the principal slab are reported in the graph (text-fig. 13). We will extract only some values:

Trackways	Six tracks	Five tracks	Eight tracks
Average of foot	23.5 x 15 cm	26.5 x 17.5 cm	27.5 x 18 cm
Average of stride	120 cm	140 cm	171 cm
Ratio	5.1/1	5.2/1	6.2/1

The ratio observed for the trackway with eight tracks corresponds to the proportionally longest stride that we have observed. Generally, this "stride/foot" ratio is around 5. Nevertheless, an exceptionally low value of 3.7 has been registered. All the trackways present the same linear disposition, with a very weak deviation of the median digit toward the exterior. Morphologically, the prints are all very comparable and there is nothing to add to the description of the type.

Several isolated tracks of lesser size, from 16 x 12 cm to 22.5 x 12, discovered at different points in the locality, belong without doubt to young individuals (see Pl. X).

4. DISCUSSION. — Except the size, these tracks do not differ from *Grallator*, of which they possess all the essential characters: preeminence of the median digit, phalangeal impression with rounded pads, tightened lateral digits, slightly inclined, linear trackway with large strides.

The largest species of *Grallator* described up to now, *Gr. formosus* from the Upper Triassic of Connecticut, does not exceed 185 mm in length. Our *Grallator maximus* is thus a little larger still.

By their shape and dimensions, these large tracks also present certain resemblances with *Anchisauripus* from Connecticut. But these latter show the trace of a reverted hallux, which does not exist on our specimens.

These *Grallator* of large size seem to have a vast geographic extension into the Lower Lias. In effect, E. Bölau [1952] figured some comparable tracks from the Rhaetian of Scania, and closer to us, in the Causses region, L. Thaler [1962] made known the locality of St.-Laurent-de-Trèves (Lozère), whose prints are of comparable size and the same form. The trackways also show long strides, as those of which we have just spoken for the Veillon tracks. Certain tracks discovered by P. Ellenberger [1965] in the Hettangian of Sanary (Var) belong equally to this same type.

Genus ***Eubrontes*** HITCHCOCK 1845.

The principal characteristics of this type of large tridactyl tracks, frequent in the Upper Triassic of Connecticut, are as follows: wide print with thick digits, armed with strong

claws, but less pointed than in *Grallator* for example; lateral digits generally less inclined; medial digit less projected forward.

***Eubrontes veillonensis* nov. sp.**
Pl. XXI, fig. 2 to 4; XIII, fig. 3, 4 and text-fig. 12 and 14.

1. MATERIAL. — A group of fifteen trackways that intersect in every direction on the "principal slab" (text-fig. 14). Several other trackways of 3 or 4 strides have been equally observed at different places in the locality. One trackway of 12 feet will serve as the type, and the mold of one of the tracks, deeply sunken, will constitute the plastotype.

2. DESCRIPTION OF THE TYPE (Pl. XI, fig. 2 and text-fig. 12). — This track is first remarkable for its massive aspect. It measures 340 mm long for 280 mm in width. The lateral digits are very slightly inclined toward the median digit and rather removed from it; their impression is wide.

FIG. 12. — *Eubrontes veillonensis* nov. sp.
A: Trackway, "principal slab", x 1/20. — B: Type, x 1/3.

Interdigital angles: III/II = 15°; III/IV = 10°.

The median digit, sunken nearly 4 cm into the sediment, bears the trace of the two last phalanges slightly individualized. It is terminated by a strong and pointed claw, inclined toward the interior of the foot. The median digit is only slightly detached in front relative to the lateral digits. The claw of digit IV is at the level of the middle of the distal phalanx of the central axis.

The internal lateral digit (II) possesses two widely imprinted phalanges. These latter are not well differentiated on digit IV. Both digits are provided with large claws, but less elongate than that of the median digit.

The posterior contour of the print is asymmetrical, longer on the exterior side.

The stride is on average 120 cm for a foot dimension of 34 cm, that is a ratio of 3.5/1. The median digit is slightly oriented toward the exterior, whereas its claw is inclined in contrast toward the trackway axis (text-fig. 12 A). The successive feet are separated a little from the linear arrangement to divide itself into two close parallel lines.

3. OTHER SPECIMENS. — The graph in figure 13 shows the size variations of these prints. The largest that we have observed constitute a trackway of six deeply sunken tracks, having on average 43 x 33 cm (Pl. XI, fig. 4). The stride is short, 113 cm, that is a ratio of only 2.6/1.

FIG. 13. — Diagram showing the size variations in *Eubrontes veillonensis*. Note the difference in the slope of the major axis of each of the two clouds of points.

One can give several other values:

Trackways	Six tracks	Eleven tracks	Five tracks	Three tracks
Average of foot	31.5 cm	33 cm	37 cm	32.5 cm
Average of stride	105 cm	112.5 cm	121.5 cm	163 cm
Ratio	3.3/1	3.4/1	3.2/1	5/1

FIG. 14. — Principal slab. Partial diagram (around 5 x 6 m) showing trackways of *Grallator variabilis*, *Grallator maximus*, *Eubrontes veillonensis*, and *Saltopoides igalensis*.

The exceptionally high ratio observed on the trackway with three tracks was the only such one on our trackways of *Eubrontes*. The majority of values were around 3.5 as on the type trackway.

All the tracks noted are characterized by their wide contour, their thick digits without marked predominance of the median one. The phalanges are sometimes better marked than on the type, but are never separated into pads. One can observe three on the lateral external digit. The central claw is always longer than those of the lateral digits.

4. DISCUSSION. — The assignment of this type of large track to the genus *Eubrontes* seems certain to us. This attribution is reinforced by the characters of the trackway with average strides, on which the right and left pedes are separated a little from the linear arrangement.

The closest American form to ours is *Eubrontes giganteus*, of the same size but with a slightly different contour.

The great number of prints observed on the "principal slab", about thirty trackways, more than 200 footprints, led us to perform a statistical summary. This confirmed the first impression already acquired on the outcrop (text-fig. 13). The dimensions of the tracks are grouped on the graph into two distinct "clouds," corresponding to the two species that we came to describe, *Grallator maximus* and *Eubrontes veillonensis*. The major axis of each of the two clouds has a distinct slope that translates the difference in the length-width ratio of the prints of each of the two groups. The L/w ratio calculated on the types is 1.69 for *Grallator maximus* and 1.21 for *Eubrontes veillonensis*. The first species, *Grallator maximus*, which corresponds to the smallest dimensions, is a relatively slender track with a long median digit; whereas the second form, *Eubrontes veillonensis*, of larger size, is wide with a slightly elongate central digit.

FIG. 15. — *Saltopoides igalensis* nov. sp.
A: Type, x 1/2. — B: Trackway, "principal slab", x 1/20.
C: Another specimen, x 1/2.

The characters of the trackways confirm the distinction between the two genera. In the *Grallator* trackway, the left and right pedes alternate practically on the same line, the stride is long, and the "stride/foot" ratio is generally situated between 1 and 5. In contrast, the foot of *Eubrontes* is separated a little from the trackway axis. The strides are also smaller. Their ratio to the size of the foot is often on the order of 3.4.

Genus ***Saltopoides*** **nov. gen.**

The type of this genus is a trackway from the "principal slab" including six successive feet. The mold of one of them will serve as the plastotype. Several other tracks, impressions and counter-impressions have been found in different beds.

Saltopoides igalensis **nov. sp.**

Pl. XII, fig. 4 and text-fig. 15.

1. DESCRIPTION OF THE TYPE (text-fig. 15 A and B). — The three digits of the track left only the impression of their distal parts, rather wide and bearing claws, with, for the median digit, a very thin trace of the proximal phalanx.

On either side of the very long central axis, the lateral digits are asymmetrically arranged. Digit II is at the same time more slender than the median digit and a little more inclined toward it than digit IV. Behind the track, a small, isolated triangular impression is preserved within the extension of digit IV.

The most original character of the type reside in the shape of the trackway. In effect, the five successive strides, perfectly clear, where left and right pedes alternate clearly, measure from 160 to 176 cm, that is an average of 172 cm. The ratio of the foot to the stride is thus a little more than 11/1! One therefore imagines an animal with slender limbs and very probably jumping.

DIMENSIONS: 155 x 115 mm. — Interdigital angles: IV/III = 19°; II/III = 28°.

2. OTHER SPECIMENS. — Another print from the "principal slab" was able to be brought to the laboratory. It is of the same size and shape as the type, but more completely impressed (Pl. XII, fig. 4).

Digit II shows three phalanges, the first in a very remote position; digit IV has only two. The phalanges of the median digit did not leave distinct traces. The distal end of this latter is inclined toward the interior. The ends of the three digits are deeply sunken with, at the bottom of the depression, the mark of the claw for digits III and IV. That of digit II is well marked in front.

DIMENSIONS: 155 x 120 mm. — Interdigital angle: IV/III = 22°.

3. DISCUSSION. — The asymmetrical disposition of the lateral digits, and above all the trackway characteristics, confer a true originality to this type of print. We cannot compare it currently with any other, and we must create a new genus and species, *Saltopoides igalensis*.

Genus ***Anatopus*** **nov. gen.**

The description of this type of print is based on three isolated tracks, one impression and two counter-impressions, all coming from different levels.

One finely preserved counter-impression will serve as the type.

***Anatopus palmatus* nov. sp.**
Pl. XII, fig. 3 and text-fig. 16.

1. DESCRIPTION OF THE TYPE (Pl. XII, fig. 3 and text-fig. 16 A). — Tridactyl track of a bipedal animal of moderate size. Only the digits are marked, and isolated from one another.

FIG. 16. — *Anatopus palmatus* nov. sp.
A: Type, x 1. — B: Other specimens, x 1.

The median digit, much longer than the other two, is pointed and terminated by a long, fine claw, inclined toward the interior. It seems to bear three phalanges but only the first (proximal) is well individualized. The lateral digits show only a single phalanx. The lateral internal digit (II) is close to the central axis and forms with it an angle of around 30°, whereas the external digit (IV), in contrast, is at the same time more elongate and more inclined (ca. 40°). Its impression is also smaller.

One interesting particularity is the very clear indication of an interdigital membrane. This webbing is well visible between digits II and III and begins on the other side from digit III.

DIMENSIONS: L = 84 mm; w = 96 mm.

2. OTHER SPECIMENS (text-fig. 16 B). — The position of the digits is the same on the other two specimens. One (B 1) shows three pads on the median digit, the distal pad being the most deeply imprinted. The lateral digits are only marked by their distal phalanx, as on the type. The other specimen (B 2) shows only the impression of the ends of the digits, reduced to the claw for the second.

3. DISCUSSION. — Neither of the two latter specimens show any trace of the webbing, but this is sufficiently well indicated on the type in order to retain its existence. Its absence on the two tracks could be due to their particularly digitigrade impression. Besides, the observation of the tracks of recent plantigrades reveals that the imprint of the webbing is very irregularly preserved.

The exceptional elongation of the median digit relative to the lateral digits, represented only by their distal phalanx, the separation of the inclination of these latter, the presence of a web, all these characters constitute a type of original track, of avian form, which cannot yet be referred to any known type. We must therefore employ a new denomination: *Anatopus palmatus* nov. gen., nov. sp.

Genus ***Tamontopus*** **nov. gen.**

A counter-impression on blackish clayey sandstone will serve for the description of this type, of which we possess two other rather mediocre counter-impressions besides.

Talmontopus tersi **nov. sp.**

Pl. XII, fig. 1 and text-fig. 17.

1. DESCRIPTION OF THE TYPE (Pl. XII, fig. 1). — This large tridactyl track is remarkable for the inclination of its lateral digits: III/IV = 30°; II/III = 45°.

The digits are uniformly sharp at the base of their extremity, without differentiated claws. The distal end of the median digit is clearly inclined, probably toward the interior, on which we base our numbering of the other two digits. A fine film of blackish clay, well visible on the sandstone, seems to indicate the presence of a stretched web between the digits.

The heel is important, rounded; a slight constriction individualizes it in the digital region.

The counter-impression has a more distinct relief of the heel and in the proximal parts of the digits.

FIG. 17. — *Talmontopus tersi* nov. sp., x 1/3.

DIMENSIONS: 270 x 230 mm.

The two other specimens do not provide any supplementary information.

2. DISCUSSION. — This type of foot presents clear affinities with the large tridactyl tracks with separate digits and a strong heel that have been attributed to *Iguanodon*.

It is known that these are quite frequent in the Wealden of southern England and also of Hanover. Dollo [1905] described and figured certain of these tracks. None corresponded, according to the authors, to the position of repose: then only the proximal phalanges and the heel were borne, whereas the ends of the digits did not leave a mark. One observes a similar arrangement in our type, where the distal parts of the digits are only very lightly indicated relative to the posterior region, strongly in relief.

Of a much more more modest size than the tracks of *Iguanodon*, our *Talmontopus tersi* is very close to the tracks of the ornithopod from the Hettangian of Sanary (Var) discovered by P. Ellenberger.

III. Unnamed tracks.

We have found still two other types of tracks. They are each represented by only one or two examples and we will limit ourselves to describing them without naming them.

Unnamed track no. 1
Text-fig. 18.

Tridactyl track of small size, remarkable by its stocky aspect. The short and thick digits are armed with claws. The median digit is dominant and the lateral internal digit reduced.

The heel is well developed and shrunken relative to the digital region.

DIMENSIONS: 40 x 29 mm. — Interdigital angles: II/III = 20°; III/IV = 8°.

A second specimen, less strongly imprinted, enters perfectly within the contours of the preceding (dimensions: 37 x 29 mm). It is not impossible that they might be deformed tracks of *Batrachopus*.

Unnamed track no. 2
Pl. XIII, fig. 5.

A tridactyl track of rather small size (97 x 67 mm). The lateral digits are nearly parallel to the median digit and nearly as long as it, notably digit IV. There are three phalanges on digit III, and two on digit II. They are not visible on digit IV.

There are no well-differentiated claws, and the ends of the digits are blunt. The claw is asymmetrical, more supported in its postero-external part.

This track, which does not seem deformed, resembles no other from the Veillon locality.

FIG. 18. — Unnamed track no. 1, x 1.

CHAPTER II

ATTEMPTED INTERPRETATION OF THE TRACKS

1. *TENTATIVE ATTRIBUTION OF THE TRACKS FROM VEILLON*. — After having described the diverse types of footprints encountered at Veillon, we attempt, in light of the paleontological evidence, to evoke their authors. One will see that, often, we will be quickly stopped by the lack of fossils and also by the randomness of the observations resting on the fleeting footprints.

The Triassic of Connecticut in the United States constitutes, from the ichnological point of view, a privileged example. Because of the extraordinary abundance of tracks that are found there; but also by the presence of bony remains, sometimes rather complete, which permit a direct comparison with the tracks. The striking affinities of the Veillon ichnofauna with that of Connecticut lead us to first turn toward this region to attempt to interpret our tracks.

Among others, the bony remains of small, quadrupedal pseudosuchian reptiles with a dorsal cuirasse have been discovered in the Connecticut Valley, of which the best known is *Stegomosuchus*, about fifteen centimeters long. The good state of preservation of the fossil permitted Lull [1953, p. 23] to give a reconstruction of this small quadruped, with an elongate body and rather reduced forelimbs. Some other, less complete remains indicated larger forms, but not exceeding about fifty centimeters.

It is thought that the tracks named *Batrachopus* could have been left by such animals. This opinion, already expressed by Lull [1953], was recently restated by Colbert [1963].

The mobility of the manual digits, sometimes elongate, sometimes retracted in a pad, such that one could induce some observations made on our traces of *Batrachopus*, agrees well with the silhouette of small stegomosuchids. Their reduced forelimbs must have been clearly digitigrades when walking and to support itself more on the ground in other occasions.

Noting the narrow resemblance of the tracks of *Batrachopus* from Connecticut with those from Veillon, one could suppose that we have a very comparable animal. But for the moment, in Europe, no osteological evidence can help us to specify the silhouette.

It should be underlined besides that, up to now, the pseudosuchians were considered to be exclusively Triassic and ended at the Keuper. On the other hand, the comparison with more complete tracks from the Triassic of Aubenas (Ardèche) studied at the same time by one of us (C. M.) allows supposing that the tetradactyl track of *Dahutherium* could equally be attributed to a pseudosuchian.

The tracks named *Grallator* are certainly the most representative of the Veillon fauna, as much by their number as by their variety. These tridactyl tracks, of narrow and elongate contour, with fine digits bearing sharp claws, could be referred to a group of dinosaurian carnivores, of relatively modest size, the coelurosaurians. These small, gracile dinosaurs, clearly bipedal, with very elongate hind limbs, show, in particular, long, fine, and tightened metatarsals, corresponding to a narrow foot such as *Grallator* shows.

In the Triassic, one family of coelurosaurians, the podokesaurids, is particularly flourishing and represented by varied forms. From the Upper Triassic of Scotland comes *Saltopus*, a small podokesaurian, 60 cm long, whose pes, with a very elongate median digit, must have left on the soil a track very comparable to our *Grallator olonensis*. Some other Triassic genera from North America, *Podokesaurus* and *Coelophysis*, of greater size, could have been suitable for the moderate-sized *Grallator*.

The upper Keuper of Thuringia reveals the existence of a heavier coelurosaurian of large size, *Halticosaurus*, but whose pes remains elongate and could correspond by its dimensions to our *Grallator maximus*. Or the Rhaetian of Airel (Manche) has recently shown the bony remains of a coelurosaurian that one of us was able to refer to *Halticosaurus*.

Saltopoides igalensis is probably a predator, judging by its claws. The length of the stride suggests movement in bounds, which confirmes the very digitigrades shape of the trackway prints. The separation of the lateral digits is probably also due to this mode of locomotion. All this suggests a light animal, with slender limbs, perhaps still a coelurosaurian. We remark on this subject because the study of the metapodia of certain small podokesaurians permits supposing an adaptation to jumping [Lapparent and Lavocat, 1955, p. 797].

The tracks of *Eubrontes*, wide, with thick, strongly armed digits, evokes a rather heavy and slightly slender theropod if one considers the strides. It is very probably a carnosaurian theropod of which two families, the teratosaurids and megalosaurids, possess some representatives of large size, but still poorly known, in the Upper Triassic. One could evoke the genus *Gresslyosaurus*, a carnivore whose bones and teeth are noted in different places in the Rhaetian of Europe. We remark here that the footprints reflect well the difference in silhouette between the agile coelurosaurians and the heavier and more massive carnosaurians.

We have already underlined the great resemblances existing between the tracks of *Talmontopus tersi* and those of large ornithopods, such as *Iguanodon*. The lateral digits are inclined, there is no trace of claws, but rather the mark of a large blunt nail; the imprint of the heel is important and individualized relative to the digital region. It seems that there is hardly reason to hesitate to attribute *Talmontopus tersi* to an ornithopod. But it is evidently not a true *Iguanodon* in the Rhaetian.

The ornithopods are only represented in the Triassic by some forms of modest size. Some small tracks of avian form have been reported [F and P. Ellenberger, 1958]. Nevertheless, the the history of the group remains rather obscure until the Upper Jurassic, where the American genus *Camptosaurus* leads to *Iguanodon* in the Lower Cretaceous. The existence of an ornithopod of already large size in the Lower Lias, which is thus revealed to us at Veillon, seems like an important discovery.

Anatopus palmatus represents an especially interesting type of foot. The external elongation of the median digit; the separateness of the small lateral digits, which widens the foot considerably without ceasing to be light; all of this arrangement evokes an animal habituated to movable soils. The presence, highly probable, of an interdigital web confirms this life habit. We would thus be in the presence of an animal living in the swamps, where without doubt it found its nutrition. Its assignment to a precise zoological group is hardly possible at present. Perhaps it is also an ornithopod?

Thus, the footprint locality of Veillon lets us foresee a particularly varied reptile fauna. It includes at least a dozen very distinct forms. For several, it is true, one would wish to know a greater number of examples.

In the current state of our understanding, the confrontation of the Veillon tracks with the acquisitions of the paleontology of the reptiles allows outlining the following relationships:

FOOTPRINTS	FOSSILS KNOWN BY THEIR BONES
— *Batrachopus*	pseudosuchians
— *Dahutherium*	*Idem*
— *Grallator*	coelurosaurian theropod dinosaur
— *Saltopoides*	*Idem* (?)
— *Eubrontes*	carnosaurian theropod
— *Talmontopus*	ornithopod dinosaur
— *Anatopus*	*Idem* (?)

This tentative assignment of the tracks is still, one sees, very approximate. It is that in France, as elsewhere in Europe, the discoveries of terrestrial reptiles in the Triassic and Jurassic are rare and fragmentary. Thus one still has much to discover on the subject of the animals that traversed the beaches of Veillon.

2. *REMARKS ON THE STRATIGRAPHIC SUCCESSION OF THE ICHNOFAUNAS*. — The renewed interest which has benefited ichnology for several years has favored the discovery and description of numerous localities of vertebrate footprints. Now a continuous suite of information is possessed going from the Permian up to the Liassic. We enumerate succinctly these different ichnofaunas, in order to better place the Veillon locality in this context.

PERMIAN. — Let us first say that the Permian ichnofauna is clearly different from those which are encountered successively. The excellent trackways of the Saxonian of Lodève, minutely described by D. Heyler and J. Lessertisseur [1963], reveals an exclusively quadrupedal fauna, with a dominant stegocephaloid: pentadactyl limbs, fore and hind tracks little different, heavy trail before. However, several lighter forms, lacertoids, appear. Very different from those following, this Permian ichnofauna has, in contrast, much greater affinities with those of the Pennsylvanian (upper Carboniferous) of North America [Baird, 1952].

LOWER TRIASSIC. — The forms of the Lower Triassic have not yet been well enough described. The more representative type is *Cheirotherium*, a quadruped with reduced forelimbs, represented by several species in the variegated sandstones and also in the lower Muschelkalk. Several other forms, such as *Chelichnus*, equally quadrupedal, were inherited from the Permian [Haubold, 1965].

MIDDLE TRIASSIC. — The Middle Triassic of the northern and eastern border of the French Massif Central has revealed, these last years, several localities of recently studied prints [Lorenz and Demathieu, 1962; Courel and Demathieu, 1962]. Near Aubenas, another locality shows a series of tracks that are particularly interesting by the association they present.

One remarks there on the persistence of *Cheirotherium* as well as a small lacertoid trace already represented in the Lower Triassic, *Rhynchosauroides*. But above all, there appear several new forms. On one hand, some tridactyl prints attributable to bipedal dinosaurs: some small, close to *Grallator*; others larger, with perhaps a hallux trace preserved. On the other hand, one finds a curious quadrupedal form of large size, almost plantigrade and whose four or five short digits, curved, evoke an "elephant's foot." It is seen further that these tracks can be thought of as a primitive sauropod.

KEUPER. — The ichnofauna of the Upper Triassic of France is little known to us only by the tracks discovered at Anduze (Gard) by P. Ellenberger [1965]. They reveal several tridactyl dinosauroid

forms associated with the same enigmatic quadruped with the "elephant's foot." These latter tracks have recently been attributed to primitive sauropods [P. Ellenberger, 1965; F. Ellenberger and Ginsburg, 1966].

More diversified than the Middle Triassic, these bipedal and quadrupedal dinosaur prints are also of larger size. Neither *Cheirotherium* nor *Rhynchosauroides* is noted.

The recent study of the Triassic prints from the United States, in particular the works of D. Baird [1954, 1957], also bring several supplementary pieces of information on the ichnofaunas of the Upper Triassic. The Upper Triassic formations of Milford (New Jersey) still bear *Cheirotherium* and *Rhynchosauroides*, associated with several theropod prints, notably *Grallator*. In contrast, the localities of the Connecticut Valley, also of Upper Triassic age, whose richness is celebrated, contain neither *Cheirotherium* nor *Rhynchosauroides*, but inversely an association of much richer dinosaurian forms.

It thus seems there are two distinct ichnofaunas in the Upper Triassic of America, the more recent, that of Connecticut, must be rather close to the Rhaetian. The French Triassic localities have not yet been sufficiently inventoried to be able to judge the value of this last subdivision.

RHAETIAN. — The Rhaetian of the Midi of France again delivered only some indications [P. Ellenberger, 1965]. The prints from the Rhaetian of Scania described by E. Bölau [1952] are less varied and include tridactyl forms of large size belonging to *Grallator* and *Eubrontes*.

Some footprints have been found in the Rhaetian sandstones, toward the north of the Sainte-Croix massif in Poland [Samsonowicz, 1929; Karaszewski, 1966]; but we have no precise description.

It is here, at this stratigraphic level, that the rich ichnofauna of Veillon is placed, whose Rhaetian age is highly probable (see p. 9). Two tendencies can be recognized there:

— on one hand, the very marked Triassic affinities. The three most abundant genera represented: *Batrachopus*, *Grallator*, *Eubrontes*, are known equally in Connecticut. One has seen that *Batrachopus* is perhaps attributed to a small pseudosuchian, a group considered until now uniquely Triassic. And to evoke the authors of the tracks named *Grallator* one can easily turn toward the diverse types of coelurosaurians of the Keuper;

— on the other hand, at Veillon there are also forms prefiguring the large dinosaurs of the Upper Jurassic and Cretaceou, notably an ornithopod already attaining a good size.

Thus it seems to be a transitional fauna still connected by numerous links to that of the Upper Triassic, which suits the Rhaetian age of the locality, situated at the boundary between the Triassic and Liassic.

HETTANGIAN. — Following our enumeration, one arrives at the Hettangian localities recently discovered in the environs of Sanary (Var) [P. Ellenberger, 1965] or in the Causses region (Hérault and Lozère) [Thaler, 1962]. One finds there large tridactyl tracks identical to those of Veillon. It is interesting to rediscover at Sanary the tracks of a large ornithopod comparable to our *Tamontopus*. At Saint-Laurent-de-Trèves, near Florac, there exist several tracks of a quadruped with an "elephant's foot." We have not encountered them at Veillon.

Recall, always on the subject of the Hettangian, that bed no. *12* of Veillon showed about twenty tracks of *Grallator variabilis*, identical to those of the lower beds attributed to the Rhaetian.

MIDDLE LIASSIC. — One has still noted the fleeting trackway of a small tridactyl dinosaurian on a

Slab from the Lotharingian of Aveyron, in a zone where high FONDS could emerge temporarily [F. Ellenberger and Fuchs, 1965]. Then, in the higher levels of the Liassic, localities are lacking[1]. The transgression of the Jurassic sea spreads widely at this time and the places likely to preserve tracks for us are much reduced.

It is necessary to await the general regression at the end of the Jurassic to find again the footprints of reptiles. It is also that in the Purbeckian of Dorset, in southern England, good trackways of a large ornithopod have recently been brought to light [Charig and Newman, 1962]. On the coast of Portugal, numerous prints of large theropods have likewise been noted [Lapparent, 1951]. But all these tracks do not show more than affinities with those known to us in the preceding epochs.

It seems that the vertebrate fauna that had blossomed on the vast Triassic continent was perpetuated up to the dawn of Jurassic times. It is only in the middle Liassic that the old European continent was broken up. The continental climates were reduced and differently distributed. This favored among the terrestrial faunas both confrontations and competitions needed to operate an overall renewal (cf. L. Ginsburg [1964]).

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Although still marred by many uncertainties, all these results are interesting. By condition of reason on the sufficiently rich localities, in which the relative frequencies or absences become significant, one can hope to erect a stratigraphic succession of ichnofaunas. Furthermore, the existence of identical forms in well-separated localities allows hope for the possibilities of correlation at a great distance. Also, fossils as particular as reptile footprints could bring a non-negligible contribution to stratigraphic paleontology.

[1] The assignment of good footprints from Demnat in Morocco to the upper Liassic [Lapparent, 1945] is recently discussed: they could be in Cretaceous terrains.

CHAPTER III

ECOLOGICAL EVOCATION

Mrs. M. Ters has shown in her thesis [1961] that the clayey sandstones in slabs at Veillon are localized in a depression that corresponds almost to the current estuary of the Payre River (see fig. 2). It is therefore an old feature of the pre-Jurassic morphology which was found fossilized in this manner, and one thinks that from the Rhaetian a valley, which the current Payre is only a modest survivor, emptied here into the sea. Its estuary must have formed a vast spreading surface where clayey-sandy muds were deposited. One often observed, at the centimeter or millimeter scale, an alternation of more clayey or sandy beds, these latter always being thicker according to the intensity of fluviatile flows.

The counter-impressions of feet in relief are ordinarily formed by a rather thick sandstone, whereas the hollow impressions rest on a fine clayey film. The sequence of the deposits therefore was as follows: arrival of the detrital materials at a time of flooding; then, as the waves diminish, deposition of finer clay particles still in suspension. Following this a period of emersion arises, which sees the passage of animals leaving impressions of their feet on the still-soft soil. This phase of emergence could be sufficiently long so that dessication slits or "mud cracks" were produced. During the following rising, a new delivery of thick materials will come to mold at the same time the footprints and dessication cracks (Pl. VI).

The prints of locality F 5 were impressed on clay that was 1 to 2 cm thick and still very mobile. It resulted in deeply sunken feet, sometimes deformed and often ringed by a pad of mud. Some withdrawal cracks mark the dessication of the clay; then a spread of sand covers the ensemble while molding all the details. This sandy slab with numerous counter-impressions is currently exposed at the Sables-d'Olonne museum. Rather frequently, the filling of sand, under the combined action of its own weight and the humidity it brings, induces deformation in all directions of the subjacent impression. This is located as a result by a slight enlargement (Pl. VII). This remark is to be noted when one wants to evaluate the actual size of the animal. A clayey surface of locality F 3, particularly rich in impressions, is covered by traces of big raindrops that were also molded by the subjacent sandstone (Pl. V, fig. 2).

One notes that the quartz grains of the sediment are remarkable for their very weak degree of wear. All of them are angular, just like the pebbles of conglomeratic lenses dispersed in the series. These materials, pulled out from the nearby crystalline basement, underwent only a very brief transport and were not subsequently covered by the sea. The proximity to the sea was made nevertheless felt by the numerous pseudomorphs of salt crystals which can be found at all levels (Pl. VI). From time to time, the sea comes therefore to erode the flat plains of the estuary. Some recent studies of J Bajard [1966] and R. Mathieu [1966] on the faces of modern sedimentation in Mont-Saint-Michel bay, where one sees ripple marks, "mud cracks," and bird footprints, evokes the manner of the environment that we have tried to reconstruct for Veillon.

Vegetation itself was not absent from this tableau of former times. Carbonized fragments of trunks or floated branches are frequent enough, sometimes with strings of blackish lignitic clay.

It is within this flat landscape, frequently inundated, evoking the estuaries of certain large modern rivers, that the rich reptile fauna evolved, whose footprints revealed their existence to us. The nearly indecipherable trampling that is observed on most of the surfaces leads to the thought that these animals were not only passing to Veillon accidentally, but that they were there amidst their life habitat (frontispiece).

It is curious to note that the carnivores are much more numerous here than the herbivores. This is also the case in most footprint localities. It is possible that the herbivores, ornithopods and sauropods, lived preferably in the wooded marshes where they found nourishment and protection; but these places were less favorable to the preservation of tracks. Whereas theropods, agile runners, preferred vacant spaces and open beaches; it is also there that their tracks had the greatest chance of being preserved.

It could equally be that the small predators of Veillon were nourished especially by mollusks and fishes. A recent observation corroborates our hypothesis. In the Rhaetian of Airel (Manche) are found [Larsonneur and Lapparent, 1966], associated with the bones of the dinosaurian carnivore *Halticosaurus*, coprolites containing scales and small teeth of *Semionotus*, a fish abundantly represented in the same locality. Besides, the long and mobile neck as well as the relatively small teeth equally suggested a piscivorous habit for *Halticosaurus* and other coelurosaurians.

Progressively, the transgression asserts itself and, little by little, the sea invades the valley that opened to Veillon. A this moment, the land could no longer furnish detrital provisions and an essentially calcareous sedimentation is henceforth established. During a time, the advance of the sea is still subject to fluctuations, and on the shores one exposed moment, small dinosaurs left us the trace of their passage: this is the case of the impressions of *Grallator variabilis* spotted on the limestone slab at Veillon point (fig. 1, no. 12). Then, the sea returns further and, without even becoming very deep, spreads itself widely on the old continent of the Vendée. Henceforth, the hordes of terrestrial reptiles were pushed back very far from the former Vendée shores.

In concluding this attempt to reconstruct the past, one cannot but be struck by the resemblances between the Lower Liassic landscapes that we evoked above and the present appearance of the Payré estuary. But on these vast swampy extents, pseudosuchian and dinosaurian reptiles are lacking which, for 180 million years, here traversed these shores on the border of an ancient Atlantic Ocean.

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PLATE I

Batrachopus gilberti nov. sp.

FIG. 1. — Type; x 1.
FIG. 2. — Variety; x 1.
FIG. 3. — Slab with counter-impressions; x 1/2.

PLATE II

Dahutherium sp.

Counter-print of pes; x 1.

PLATE III

Grallator olonensis nov. sp. And *Gr. variabilis* n. sp.

FIG. 1 and 2. — *Grallator olonensis* nov. sp.
1: Type, x 1/3. — 2: other examples from the type; x 1/2.
FIG. 3. — *Grallator variabilis* nov. sp. Another example from the type.

PLATE IV

Grallator variabilis nov. sp.

FIG. 1. — Another example from the type; x 1.

FIG. 2. — Variety; x 1/2. Note the tail trace.

PLATE V

Grallator variabilis nov. sp.

FIG. 1*a* and *b*. — Impression (*a*) and counter-impression (*b*) of the same trace; x 1.

FIG. 2. — Counter-impression from a level with raindrops; x 1/4.

PLATE VI

Grallator variabilis nov. sp.

Note the "mud cracks" and pseudomorphs of salt crystals.

PLATE VII

Grallator variabilis nov. sp. and other traces.
Counter-impressions on thick sandstone; x about 1/3.

PLATE VIII

Grallator and *Batrachopus*; x 1/3.

PLATE IX

Grallator variabilis nov. sp.

FIG. 1. — Counter-impressions on the limestone slab; Hettangian; Veillon point; x about 1/5.

FIG. 2. — Impressions corresponding to the counter-impressions in fig. 1; x 3/4.

PLATE X

Grallator maximus nov. sp.

Example of small dimensions on ripple marks; impression (*a*) and counter-impression (*b*) of the same trace; x 1/2.

PLATE XI

Grallator maximus nov. sp. and *Eubrontes veillonensis* nov. sp.
FIG. 1. — *Grallator maximus* nov. sp. plastotype; x 1/3.
FIG. 2 to 4. — *Eubrontes veillonensis* nov. sp.
2: counter-impression; x 1/3. — 3: plastotype; x 1/3.
4: trackway of *E. veillonensis* of large size; x about 1/30.

PLATE XII

FIG. 1. — *Talmontopus tersi* nov. sp.; x 1/2.
FIG. 2. — *Grallator variabilis* nov. sp. Variety of small size (below); with straight lateral digits (above); x 1/2.
FIG. 3. — *Anatopus palmatus* nov. sp. Type; x 1.
FIG. 4. — *Saltopoides igalensis* nov. sp.; x 1/2.

PLATE XIII

FIG. 1 and 2. — *Grallator variabilis*; x 1/2.
FIG. 3. — Exposure of a trackway of *Eubrontes veillonensis* at low tide.
FIG. 4. — "Principal slab," partial view. Anse de la Republique. Impressions of *Grallator maximus* and *Eubrontes veillonensis*.
FIG. 5. — Unnamed trace no. 2; x 1/2.