A REVISION OF THE TRIASSIC AND JURASSIC TETRAPOD FOOTPRINTS OF ARGENTINA AND A NEW APPROACH ON THE AGE AND MEANING OF THE BOTUCATU FORMATION FOOTPRINTS (BRAZIL)

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RESUMO UMA REVISÃO DAS PEGADAS TRIÁSSICAS E JURÁSSICAS DE TETRÁPODES DA ARGENTINA E UMA NOVA ABORDAGEM SOBRE A IDADE E O SIGNIFICADO DAS PEGADAS DA FORMAÇÃO BOTUCATU (BRASIL). São expostos os resultados de uma expedição pela Argentina, durante a qual foi examinado o material icnológico argentino referente aos tetrápodes, dos Carbonífero ao Pleistoceno. São descritas, classificadas, ilustradas e revisadas, aqui, de maneira preliminar, apenas as icnofaunas argentinas de idade triássica e jurássica. Tais dados são comparados com as icnofaunas de tetrápodes da Formação Botucatu, no Estado de São Paulo. Esta icnofauna é de difícil classificação, posto que se trata de uma associação completamente nova. Deve ser mencionado que o material não é, em geral, de boa qualidade. As associações triássicas da Argentina, representadas pelas localidades de Lás Higueras, Campo de Ischigualasto, Quebrada Los Rastros, Rio Los Tarros-Sur Pagancillo e Los Mencuos, são caracterizadas pela presença, em quantidades variáveis, de terápsides e poucos arcosaurios, entre os quais predominam os tecodontes quadrúpedes. Os mamíferos são raros. Pelo contrário, no associamento jurássico de Laguna Manantiales, há uma predominância de mamíferos, acompanhada de quatro formas dinossaurianas, e ausência de terápsides e tecodontes quadrúpedes. A Formação Botucatu, nos arredores de Araquara, possui um icnofauna na qual predominam os mamíferos primitivos, acompanhados de poucos dinossauroideos bipèdes e poucos terápsides atribuídos tentativamente a Tritylodontoidea. A comparação detalhada entre a estrutura das diversas associações permite atribuir a Formação Botucatu, pelos menos no Estado de São Paulo, ao Jurássico Inferior ou Médio.

Palavras-chaves: Pegadas de tetrápodes, Jurássico, Triássico, Formação Botucatu, Argentina, Brasil.

ABSTRACT A description and a revision of the Triassic (Lás Higueras Ischigualasto, Quebrada Los Rastros, Rio Los Tarros-Sur Pagancillo and Los Mencuos) and Jurassic (Estância Laguna Manantiales) tetrapod ichnofaunas of Argentina and of the Botucatu Formation at Araquara (São Paulo, Brazil) are given. The structures of these ichno-associations are compared. The Triassic Argentinean ichnofaunas present therapsids and archosaurs, specially quadrupedal thecodonts. Mammals are very rare. In the Jurassic (Oxfordian) ichnofauna of Estância Laguna Manantiales, mammals, accompanied by four dinosaurian forms, predominate. There are not obviously either therapsids nor quadrupedal thecodonts. The Botucatu Formation, whose age was up to now uncertain and is herein discussed, presents at Araquara a rich ichnofauna. This includes many mammals, a few bipedal dinosaurs and some theromorphoid footprints, tentatively attributed to Tritylodontoidea. The Botucatu Formation, at least in the outcrops of the State of São Paulo and particularly in the Araquara area, might be put into a period of time between the Rhaetian and Middle Jurassic, with a greater probability for Lower Jurassic or the lowest section of the Middle Jurassic.

Keywords: Tetrapod footprints, Jurassic, Triassic, Botucatu Formation, Argentina, Brasil.

ARGENTINEAN ICHNOFAUNAS Introduction As part of a program of summary and revision of all Latin American localities of fossil tetrapod footprints, one of the authors (G.L) travelled extensively throughout Argentina during late 1981.

Outcrops in several provinces were visited and nearly all ichnological material pertaining to tetrapods (Permian to Holocene) in the field and in scientific institutions throughout the country was analyzed (Fig. 1).

The following report presents the results of the expedition for Triassic and Jurassic ichnofaunas.

Los Mencuos (Province of Rio Negro) One of authors (G.L.) was able to visit the quarries, specially those of the flagstones for sidewalks for around the city of Los Mencuos, in the Patagonian "meseta" about 500 km west of Viedma. Some quarries, collectively referred to as "La Cantera Nueva" (The New Quarry) (Pl. IV.A), almost always contain coarse, pinkish-yellow tuffaceous material of an unnamed formation attributed to the Upper Triassic (Norian-Lower Rhaetian). Only one set of unclassifiable theromorph footprints was found.

About 2 km further north, in the Tschelig Ranch, the small quarries collectively referred to as "Cantera Tschelig" or "La Vieja" of the same formation and scattered over a broad area.

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Plate I — Archosaurian footprints from Argentina.

Plate II - Therapsid tracks from Triassic of Argentina.

Plate II - Prancha TI - Pistas de terápsides do Triássico da Argentina.
Plate III - Miscellaneous footprints from Argentina.


were visited. Here, however, the rocks are finer grained and
gray color (gray-green closer to the upper surface of the layers). While the material of "La Nueva" Quarry seems alluvial, that of "Cantera Tschergi" seem to represent deposits laid down in small lakes or lagoons on a fluvial floodplain. Footprints in the latter are abundant and usually of good to excellent quality. The following examples were found:

A. A trackway of *Gallegosichnus garridoi* Casamiquela 1964
and five trackways of cf- *Gallegosichnus garridoi* (PL VIII).

B. Three trackways of a probably new theromorphoid form, that will be illustrated when the slab MACN 18198 of the Argentinean Museum is described (PL III.A; VLB).

C. Three trackways, one of which was *in situ* with more than 20 footprints, of the form illustrated but not named in Casamiquela (1964). These trackways were made by a small quadrupedal animal, and present the following characteristics: stride is about 28 cm; oblique pace is about 16 cm; trackway width is 16 cm-18 cm; pace angulation is about 125°. The footprints are small round or elliptical and in sets, each presenting an axis forming an angle with the midline of 21° to 33°. Neither Casamiquela nor the authors could observe morphological details; hence it is impossible to determine the direction of the gait, or whether there is an overstep, and to distinguish hands and feet. From the dimensions and general pattern, these trackways can be defined as theromorphid or mammaloid.

D. Two examples of a small mammaloid trackway with a lateral marginal overlap, reminiscent of forms from Botucatu Formation, in the State of São Paulo, Brazil (PL VLB).

E. At least ten other unclassifiable theromorphid trackways. It was not possible to collect this material which consists of about 24 trackways. These finds were registered at the Paleontology Department of the Argentinean Museum of Buenos Aires.

The ichnofauna of Los Menucos listed above confirms the diagnosis of Casamiquela (1964, 1975a): it is a local, endemic almost exclusively therapsidian ichnofauna containing at least eight or ten forms, all of which are small- to medium-sized. The presence of primitive mammals cannot be excluded. The commonest form is *Gallegosichnus garridoi*. The abundance of specimens and the possibility of discovering additional forms bespeak the importance of doing systematic and statistical studies at the site.

The Museum of Ingeniero Jacobacci (Province of Río Negro). The museum of Natural Science, Archeology, Ethnology and History, was organized by R.M.Casamiquela, and besides some small slabs of little importance with dinosaur and early mammal footprints from the Estância Laguna Manantiales (Province of Santa Cruz), presents five excellent slabs from Los Menucos, but collected by Casamiquela from the sidewalks of the city of San Carlos de Bariloche, in the low Andes, around 200 km west of Los Menucos. The unpublished material includes:

A. A slab* about 45 cm x 36 cm with a *Gallegosichnus garridoi* trackway with three hand-foot sets; one set of another individual of the same species; a set of an individual of larger dimensions, maybe of the same species imprinted when the mud was still soft (PL VII.A).

B. A slab of 30 cm X 50cm with an excellent trackway consisting of two sets of footprints of *Gallegosichnus garridoi* (PL VIII.C).

C. A trackway of *Rogerothrichnus aguilerae* Casamiquela 1964 with five sets which the hands and feet are in anteroposterior contact but not in overlap as in the holotype (see below). Also in this case, the smaller autopodium is found behind the larger autopodium; it seems that the larger is the foot, and this oversteps the hand. The dragmarks, probably left by the foot, consist in this case, of four or five parallel lines formed by the dragging of five nails, or better, of five small hoofs (Pis. III.B and VII.A-B).

D. A trackway of five sets, without morphological details, of the group described above in item C) of the previous section.

Miguel Lillo Fundation (San Miguel de Tucumán) This institution, situated in the city of San Miguel de Tucumán, Northwest Argentina, has one of the two largest ichnological collections in that country. The following tetrapod ichnosaurs are found in the collection:

A. Late Triassic ichnofauna of the headwaters of the Río Los Turros-Sur Paganico, La Rioja. It includes 15 small, reddish slabs numbered LPV (Laboratory of Vertebrate Paleontology) from LPV 3452, (Pis. I.H-I.K-M, O and Q-S), with complete or incomplete, almost exclusively chirottheroid footprints. Some of them, as a second, less probable hypothesis, could belong to small Prosauropoda. LPV 3441 (complete foot; Pis. I.R and V.F), 3448 (complete foot; Pis. I.Q and V.D) and 3452 (complete set; Pis. I.O and V.E) are exceptionally well preserved. Three of the four indeterminate footprints (LPV 3439, 3445 and 3447) seem to belong to quadrupedal forms, LPV 3445 is a short lacertoid footprint PL I.H-I).

B. Ichnofauna of the Estância Laguna Manantiales (Province of Santa Cruz) which includes:

1. 19 slabs of gray-green tuff with trackways of, almost always excellent quality, *Ameghinichnus patagonicus* Casamiquela 1964 sometimes accompanied by trails of coleopters. LPV 2743 shows a set of hands and feet that present crescents of tuffaceous sand pushed back by the feet of the animal as it climbed a dune as also observed in the eolian Botucatu Sandstones in the State of São Paulo, Brazil. In general, the sediments of Laguna Manantiales seem to have been wet and plastic when the footprints were made.

2. Three quadrupedal trails of *Delatorrichnus goyenechei* Casamiquela 1964 (PL I.D).

3. Four footprints of three different individuals of *Wildeichnus navesi* Casamiquela 1964. The material comes from the Chon Aike Formation, radiometrically dated at 160 Ma. Late Jurassic according to Uren (1981) (Pis. I.B-C and V.G).

C. Ichnofauna of Las Higuera (Province of Mendonza). The material consists of nine small slabs of fine sandstones to micaceous siltstone of a brown to a deep red color, coming from the Higuere Formation correlatable with the Los Rastros Formation of Middle-Late Triassic age (museum numbers between LPV 2730 to 2741 and 3520) (PL II).

Almost all of them present isolated footprints of the theromorphid type in sets or very short trackways. Particularly noteworthy are:

1. The set of hands and feet (LPV 2738), very much like *Dicyonodontus Liliestern 1944 attributed to cynodonts*.

2. LPV 3520 bears four footprints (a total of five) accompanied by the characteristic sand-crescent of the dune environment.

3. LPV 2730, a left footprint close to *Dicyonodontus* (Pis. II.B and VI.D). Very clearly preserved in this footprints are the impressions of the dermal plates, which are oval and bigger in the central part of the plant, round and smaller, ten in all, around the lateral margin. This arrangement corresponds to what is observed on the autopodia of some modern reptiles. The presence of dermal plates on a footprint, of a type generally attributed to cynodonts or bauriamorphs, contrasts with a footprint covered by hairs and/or bristles published by Ellemberger (1976), also attributed tentatively to cynodonts.

4. LPV 2741 is a theromorphid footprint with fingers having relatively long nails (PL II.F).

5. LPV 2735 (Pis. IE and IV.E), a slab much larger than the others, presents an incomplete hand-foot set of an
Plate IV — Footprints from Argentina.

Archosaurian. The hand has four fingers; the foot appears to be tetradactyl, but the slab is incomplete exactly at the point where a fifth finger in abduction may have existed, so that doubts still remain as to its classification. It could be of prosauropod or chirotherian origin. In either case, the

therapsid-archosaurian association is interesting. Same outcrop gave the Chirotherium hiquerense Rusconi 1952 (= Ch. bartill Kaup 1835) (PI. I.U).

D: Trackways of Rigalites of the "Quebrada Los Rastros" (Province of San Juan; Los Rastros Formation) (PI. III.G). In the gallery of the museum of the Lillo Fundation, a short trackway of the Rigalites Heune 1931 b is on display which shows a hand-foot set and the sucessive foot.

Argentinean Museum of Natural Science (Buenos Aires) The collection consists of the following items: A. Ichnofauna of the Estancia Laguna Manantiales. Nine

Plate VII — Tetrapod trackways from Argentina. A-B: Trackways of Rogerbaletichuns aguilerai. Note the scratches left by the feet dragging across the ground, which seem to be constant characteristic of this form. Unlike in the holotype, the feet overlap the hands; Los Menucos - Tschering Quarry. C: Holotype of Palacioschnus zettii. D: A mammaloid trackway, form illustrated but not named in Casamiquela (1964); Los Menucos - Tschering Quarry. E: Slab with several theromorphoid footprints; Rio Los Tarros. A-B-C: Museo de La Plata. E: Fundación Miguel Lillo. A-B: MLP 60-XI-31-5. C: MLP 60-XI-31-6. E: LPV 2740. Graphic scale in centimetres

slabs with trackways of Ameghinichnus patagonicus numbered MACN (Museo Argentino de Ciencias Naturales) 18616 a 18623, and the slab MACN 18528 with a hand and foot set of a quadrupedal trackway of Delatorrichnus goyenechei. The foot is particularly well preserved: on the fourth toe are four pads, and a claw and a large distal pad are evident on the third toe (Pis. I, F, III.C and IV.C).
Plate VIII - Trackways of Gallegosichnus garridoi from Los Menucos, Argentina.

A: Holotype. B: Slab with trackways of three individuals. C: Two fine hand-foot sets. D: Trackway of Gallegosichnus type. Observe the overstep and the dimension of the hands in relation of the feet. E: Three trackways which show the variability of the position of the hands in relation to the feet.


B. A slab of the Tscherig Quarry of Los Menucos, with a trackway (cast) of three incomplete sets not very well preserved (MACN 18198). It seems to be a different form from the others published in Casamiquela (1964, 1975a) and it is relatively common in Los Menucos. The general pattern is typically theromorphoid, perhaps a long-legged and running cynodont. Morphological details are not clear (Pis. III.A and VLB).

La Plata Museum The famous La Plata Museum has the largest ichnological collection in Argentina and in Latin America as well, collected almost entirely by Dr. R. M. Casamiquela in th 60's and early 70's.

A complete list of the material, which contains around 140 slabs with trackways or isolated footprints, will be given elsewhere. The most interesting pieces are commented here:

1. Shimmelia chirotheroides: both the holotype and the paratype are of poor quality and not well preserved, but they are without a doubt, chirotherian. Probably the genus should be maintained since the footprints present distinct characteristics, some of which are: the hand is in a backwards and medial position in relation to the foot; the hand is very large; the third toe is squeezed between the second and the fourth toes and is impressed only in correspondence of the ungual phalange. In relation to the description of Casamiquela (1964), the authors should add that the claws are very visible; and that the fifth toe does not seem to be falciform (Pis. I.P.T and V.H).

2. Calibarichnus ayestarani: the hand-foot set is very fine. The plates II.C and VI.F show in detail the ungal pads of the sole and palm.

3. Rogerbaletichnus aquilerai (R. aquilerani in errore): to the description in Casamiquela (1964) the authors should add that

Plate IX - Dinosauroid tracks in sidewalks of Araraquara.

A: Mammaloid or dinosauroid tracks showing biped "ricochet" gait. B-F: Dinosauroid tracks from sidewalks. Graphic scale in centimetres

Branca IX - Pegadas dinossauro)dês nas calçadas de Araraquara. A: Pista mamíferoide ou dinossauroide mostrando um andar do tipo "ricochete". B-F: Pegadas dinossauroides provenientes de calçadas. Escala gráfica em centimetros
the toes are almost always very visible in the form of small subpolygonal hoofs and the fifth finger has the form of a sharp falciform nail. The constancy of these characteristic, and of the dragging walk, was mentioned above (Pis. III.A and VII.A-B).

4. Palaciosichnus zettii: it does not seem that the very particular form illustrated in Casamiquela (1964) must be maintained for the toes. Probably, ignoring the cavities that depend on erosion, it is a very common trackway that looks like Dicynodontipus (Pis. II.G and VII.C).

5. Gallegosichnus garrido: the very good preservation of the morphological details can be seen in plates 11 and VII1. The plate VIII. E shows a large, previously unfigured slab, with three trackways of good quality (without matriculation number). The variability of the position of the hand in relation to the foot should be noted.

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B. Ichnofauna of the Estância Laguna Manatiales. This comprises the richest part of the collection, with about 100 pieces. The collection consists of the following items:

1. Sarmientichnus scagliai: this has an extremely interesting bipedal gait, usually monodactyl, but sometimes presenting two or three toes. This phenomenon of variability of dactyly is characteristic also of a small dinosaur from Botucatu Formation in the State of São Paulo, Brazil. The two formations are probably both Jurassic, and it is possible that the two trackmakers may have originated from the same group. The authors need to note that the Sarmientichnus feet constantly raised three sprinklings of wet sand: two laterally and a smaller one in the middle (PL V.A-B).

2. Wildeichnus navesi: this small dinosaurian trackway possibly should be subdivided into more than one ichnospecies because of the different relative length of the toes, among
other details (Pis. I.A.G.N. and IV.D).

3. Delatorrichus goiyenechii: the hand is frequently bidactyl but sometimes, as in the holotype itself, a third toe is clearly visible. Some digital pads are also observed here, particularly on the fourth, but sometimes also on the third finger (PL IV. D).

4. Ameghinichnus patagonicus: the number and beauty of specimens are very impressive. Besides the commonest form, skillfully described and interpreted in Casamiquela (1964, 1975b), the authors should note some different forms; including a gigantic form (for examples: MLP - Museo de La Plata - 60-X-31-13; PL. III.E); and some trackways in which the footprints, from the abducted position of the first and fifth toes, are a little reminiscent of some crocodilian footprints (manus).

C. The collection also includes a series of large plaster cast of some hand-foot sets of Rigalites ischigualastianus Huene 1931 b that were probably made from moulds prepared with wet newspaper by Huene at Campo de Ischigualasto (Huene 1931b) (PL III.G).

D. Slabs with footprints from Germany in the collection include some beautiful slabs with Chiotherium footprints and two large slabs with Ichnotrithix Pohlig 1885 footprints. This material was probably obtained through exchange.

BOTUCATU FORMATION ICHNOFAUNA (BRAZIL)

Introduction The Botucatu Formation has a very extensive outcrop in South America, on both sides of Paraná Basin. From north to south, on its eastern side it crosses the Brazilian states of Minas Gerais, São Paulo to Rio Grande do Sul, extending also into Uruguay; on its western side, the Brazilian states of Goiás and Mato Grosso do Sul, extending southward into Paraguay and Northern Argentina. The calculated extent of this formation, according to Sanford & Lange (1960), is about 1.300.000 km². Yet, despite this enormous outcrop, its date is not known with any precision. The reason for this is the environment: it represents a hot, dry continental interior, where conditions were never less than semi-arid and widely those of a desert. In these sediments body fossils of animals and plants do not occur, nor pollens. All that can be said with certainty (on their date), is that about 120-140 Ma ago, volcanic activity produced the flood basalts over almost the whole area (Cordani & Vandoros 1967). Whether there was a time interlude between the deposition of the sediments and the volcanic episode is uncertain. It's possible that the sediments inter finger with the basalts in places, but this has not yet been conclusively demonstrated.

Vertebrate footprints and invertebrate trails in the Botucatu Sandstone were first observed in 1913 by Brazilian mining engineer Joviano Pacheco, but were only much later reported in print by German vertebrate palaeontologist Friedrich von Huene (Huene 1933a). They were noticed in the flagstones of a pavement in the town of São Carlos, about 40 km southeast of Araraquara (Fig. 1). So far as the authors can determine, the flagstones came from the Santa Agueda quarry in Ouro district, a quarry presently inactive, near Araraquara.

One of the authors (G.L.) found the Ouro quarries initially in 1976. At that time four or five quarries were still being actively worked, the stone being used for making sidewalks and facing buildings; but a decline in demand has brought the progressive closure of most of these quarries and at present only the largest, São Bento, remains open. An account of the sedimentology, paleo-environment and palaeoecology of this quarry was published in Leonardi (1980).

Between 1976 and the present, natural exposures, quarries and town pavements throughout the eastern outcrop of the Botucatu Formation, from Rio Grande do Sul to Minas Gerais, were explored by one of the authors (G.L.), special attention being paid to those in the three northern states. The recovery of fossils was starting. Vertebrate footprints were found in four Brazilian states - from Sacramento (Minas Gerais); Araraquara, Brodôsqui, Rifaina, Analândia and Botucatu (São Paulo); Jacarezinho (Paraná); Santa Cruz do Sul and Tramandai (Rio Grande do Sul) - a belt 2.500 km long (Leonardi 1977, 1980, 1981 Leonardi & Godoi 1980, Leonardi & Sarjeant 1986).

The Ichnofauna of Araraquara The vertebrate tracks from the Ouro quarries and in the sidewalks of Araraquara are almost always of poor quality, the footprints being simply a rounded or elliptical cavity furnishing no morphological details. Characteristically this cavity is accompanied by a crescent sandstone ridge, always in the direction of the
forest dip, representing the sand displaced by the foot of the animal during its progression across the slopes of the dune. The parameters of such tracks frequently enable them to be classified, despite their quality, provided that a good specimen of the same type has been also found.

Firm identification and descriptions depend necessarily on the better specimens and it is on basis of these that the comments below are made. The fauna seems to be completely endemic and, therefore, quite new to science. This factor causes problems in the classification and interpretation of the footprints, but adds greatly to their interest. As noted earlier, this was a very arid environment, like a desert or semi-desert highland.

The Araraquara ichnofauna (tetrapsods) comprises three principal groups:

A. Dinosaur trackways (Pis. IX and X). These are always bipedal, with an elevated pace angulation (up to 180°) and the foot is always tridactyl. This group includes two or three forms of relatively large dinosaurs, having a stride of up to 2 m; some medium-sized animals with a stride of 1m-1.5m; and some smaller types. These are without doubt the footprints of agile, highly mobile reptiles, including the largest animals of this desert environment. Some had thin, clawed toes and were apparently carnivorous dinosaurs (Theropoda). The larger types are found. Since the age of the Botucatu Formation is almost certainly Jurassic (see below), these footprints present a difficult problem. They had been Permian or Triassic, they might easily have been accounted for as the footprints of theophis footprint Laoporus. However, their late date makes such an interpretation difficult. The opinion of the authors is that they are footprints of a late-surviving group of mammal-like reptiles, the Tritylodontoloidea (Fourie 1962, 1968, Ginsburg 1961,1962).

B. Theromorphid trackways (PL XI). These are quadrupedal tracks, with a medium pace angulation. The footprints are of elliptical outline, the largest axis transverse to the mid-line. The claws are partially or completely separated from the palm or the sole pad and are sometimes modified into hooves. The stride is between 15 cm and 50 cm. Eight to ten different types are found. Since the age of the Botucatu Formation is almost certainly Jurassic (see above), these footprints present a difficult problem. They had been Permian or Triassic, they might easily have been accounted for as the footprints of therapsids and no thecodonts. Four forms of dinosaurs, three tridactyl, attributable to a thecodont to a mammal; no therapsids; no mammals. It is an ichnofauna that includes a majority of quadrupedal therapsids (64.3% of the individuals); and a minority of bipedal archosaurs. It is an exclusively archosaurian fauna, but with just one lacertoid footprint.

Los Mencos (Norian to Lower Rhaetian). Six forms of therapsids, with 46 individuals all together: Galagosichnus garridoi and cf. G. garridoi (16 individuals; 34.8%); Calibarichnus ayestaranus (1; 2.2%); Palacotichnus zettii (1; 2.2%); Rogerbaleichnus aguleraei (2; 4.4%); (all these taxa were instituted by Casamiquela 1964); Sianiparichnus bonneti Casamiquela 1975a (1; 2.2%); the unnamed form of the MACN 18198 specimen (4; 8.7%); another theromorphid form (11; 24%); one form of quadrupedal thecodont: Shimmelia chirotheroides Casamiquela 1964 (2; 4.4%); two bipedal trackways perhaps attributable to Prosauropoda (2; 4.4%); two mammaloid forms attributable to mammals or to Theriodontia (5; 10.9%); one unclassifiable form with sprawling gait: Ingenierichnus serrai Casamiquela 1964 (1; 2.2%). It is a large ichnofauna of 46 individuals with large predominance of therapsids (36 individuals, 78.3% of the individuals; 6 forms, 54.5% of the forms). Among them, Galagosichnus garridoi and cf. G. garridoi has 16 individuals (34.8%; 44.4% of the therapside). The second place is for mammaloid trackways (5 individuals, 10.9%; 2 forms, 18.2%). The third place is for the archosaurs (4 individuals, 8.6%; 2 forms, 18.2%). It is a therapsid fauna (89.2% of individuals; 72.7% of the forms) with a few archosaurs.

Jurassic Argentinean Ichnofaunas Estancia Laguna Manantiales (Upper Jurassic, Probably Oxfordian). No therapsids and no thecodonts. Four forms of dinosaurs, three of them bipedal: Wildeeschischnus navesi (biped; 21 individuals; 9.9%); Sarmientichnus scagliai (biped; 16; 7.5%); Delatorrichnus goyenechei (quadrupedal; 19; 9%); an unnamed form (biped; 1; 0.5%); one form attributed to early mammals: Ameghinichnus patagonicus (155; 73.1%). It is a large ichnofauna with 212 individuals, with an evident predominance of mammalian individuals (73.1%). However, small dinosaurian individuals are abundant (57; 26.9%). Bipedal dinosaurs are represented by 38 individuals (17.9%). As in the form number, dinosaurs predominate with four forms (80%).

**Comparative Structure of the Argentinean and Brazilian Ichnofaunas**

Triassic Argentinean Ichnofaunas Las Higueras (Middle to Upper Triassic). Three forms with nine individuals attributable to Theriodontia; one individual of Chirotherium huergense; a set of incomplete footprints attributable to prosauropodians or to Chirotherium. It is an ichnofauna with a large predominance of therapsids, as for the number of individuals (81.8%); and a minority of quadrupedal archosaurs. No mammals.

Campo de Ischigualasto (Upper Landianian). Two individuals of Rigaletes ischigualastianus, attributed to quadrupedal thecodonts. It is a totally quadrupedal archosaurian ichnofauna.

Quebrada Los Rastros (Lower Carnian). One individual of Rigaletes ischigualastianus.

Rio Los Tarros - Sur Pungancillo (Upper Triassic). Nine individuals, probably of the same form, attributable to Chirotherium sp.; one small footprint of the dinosauroid group, bipedal, tridactyl, attributable to a therodont to a dinosaurian; no therapsids; no mammals. It is an ichnofauna that includes a majority of quadrapedal therapsids (64.3% of the individuals); and a minority of bipedal archosaurs. It is an exclusively archosaurian fauna, but with just one lacertoid footprint.
Brazilian Ichnofauna (Botucatu Formation) Ara-
raquara (discussed age). For statistical purpose, 100 slabs
(ARG5 to ARG9 149) were chosen; within them one finds:
seven theromorphoid forms, with eight individuals, attributable to Theriodonta (Tritylodontidae)
(7.7% of the individuals); 29.2 of the forms) eight dinosauroid forms (all bipedal) with 29 individuals, attributable to bipedal dinosaurs and/or to bipedal thecodonts, depending on the age of the Botucatu Formation; nine mammaloid forms with 67 individuals. Among these, Brusilichnium elusivum presents 43 individuals (41.3% of the sample; 64.2% of the mammaloids). No quadrupedal thecodonts. It is a large and varied ichnofauna of 104 individuals in which mammaloid individuals predominate (64.4%); dinosauroid (27.9%) and theromorphoid individuals (7.7%) fill respectively the second and the third places. As for the forms numbers (24 forms in all) figures are respectively 37.3%, 33.3% and 29.2%.

COMPARISON AMONG ICHNOFAUNAS
The comparison between the structure of the ichnofauna of the Botucatu Formation, Triassic and Jurassic ichnofaunas of Argentina can supply new data on the age of the Botucatu Formation and its ichnofauna. The five more important among the Triassic Argentinean ichnofaunas present, as for the individual numbers, the following characteristics (Tabs. 1 and 2):
1. Two of them present a large therapsidian majority, but three of them have no therapsids at all (81.8%, 0%, 0%, 0%, 78.3%, Mean (M) = 32%; absolute % (A) = 60.8%).
2. All of them include quadruped thecodonts (13.7%, 100%, 100%, 50%, 0%, 10.9%, M = 22.2%; A = 6.8%).
3. The fauna presents little or no therapsid material at all (4.5%, 0%, 0%, 4.3%, M = 3.2%; A = 4.7%).
4. Generally they do not present mammaloid trackways. This kind of material seem to begin in the very late Triassic terrains (Norian to Rhaetian) (9%, 0%, 0%, 0%, 10.9%, M = 2.2%; A = 6.8%).
5. Quadrupedalism seems to be almost universal as for the individuals (100%, 100%, 100%, 50%, 7.1%, 4.3%, M = 56%; A = 20.9%).
6. The mammaloid/archosaurian ratio (32%/58.4%) 0.55, as for the percentual of individuals.
7. The mammal/archosaurian ratio is almost nil (0.04), as for the percentual of individuals.
8. The therapsidian/archosaurian ratio is (32.2%/58.4%) 0.59, as for the percentual of individuals.

On the contrary, the only Jurassic Argentinean ichnofauna presents the following characteristics:
1. No therapsidians (0%).
2. No thecodonts, and specially no quadrupedal thecodonts (0%).
3. The fauna includes a good deal of bipedal dinosaurs. The dinosauroid material includes 26.9% of the individuals and 80% of the forms; 17.9% of the individuals and 60% of the forms are bipedal.
4. One only mammaloid form (perhaps with three varieties, one of them overwhelming) predominates as for the individuals number (73.1%).
5. Quadrupedalism is rarer than in the Triassic with 82.1% of the individuals and only 40% of the forms, but is always strong.
6. The therapsidian/archosaurian ratio (which is also the mammal/archosaurian ratio) is (73.1%/26.9%) 2.72, as for the percentual of individuals.

The situation as for the Araraquara ichnofauna is as follows:
1. It includes a small number of therapsid individuals, but a large number of forms (7.7% of the individuals and 29.2% of the forms).
2. No quadrupedal thecodonts (0%)
3. It includes a good percentual of dinosauroid trackways as for the individual percentual (27.9%), more or less as at Estância Laguna Manantiales; however the forms percent is lower than of that locality (33.3%).
4. The mammal percentual is high, but not so high as at Estância Laguna Manantiales, as for the individuals (64.4% against 73.1%); it is higher than at Estância Laguna Manantiales as for the forms (37.5% against 20%).
5. 63 trackways and 14 forms are quadrupedal; 41 trackways and ten forms are bipedal. In this ichnofauna, where a number of mammaloid trackways present hopping gait, bipedalism is rather common (39.4% of the individuals and 41.7% of the forms), and quadrupedalism rate is relatively low (60.6% of

### Table 1 - The ichnofaunas of the Triassic and Jurassic of Argentina and the ichnofauna of the Botucatu Formation of Araraquara (Brazil). The table shows the number (N), the percentages (%) of the forms (F) and the individuals (I) of the ichnofaunas and of their groups (systematic and functional groups). Minimum (*). The specimen LPV 2735 (*) of las Higuerae is evaluated here as 0.5 in two squares because of its doubtful classification; it is necessary to remember that it is a quadrupedal archosaurian

<table>
<thead>
<tr>
<th>LOCALITY</th>
<th>LAS HUGERAE</th>
<th>TRIASIC</th>
<th>ARGENTINEAN</th>
<th>NO LOS TAMPAROS</th>
<th>NOorable</th>
<th>ORIO</th>
<th>TOTAL TRIASIC</th>
<th>ARGENTINEAN</th>
<th>BRAZILIAN</th>
</tr>
</thead>
<tbody>
<tr>
<td>THERAPSIDIAN</td>
<td>3</td>
<td>9</td>
<td>90iben</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>6</td>
<td>5</td>
<td>13</td>
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<td></td>
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<td>6</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>DINOSAUROIDS</td>
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<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>6</td>
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<td>11</td>
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<tr>
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<td>1</td>
<td>1</td>
<td>6</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>FORMS INDET</td>
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<td></td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>6</td>
<td>5</td>
<td>11</td>
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<tr>
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<td>1</td>
<td>6</td>
<td>5</td>
<td>11</td>
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<tr>
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<td>1</td>
<td>1</td>
<td>6</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>BIPEDALITY</td>
<td></td>
<td></td>
<td></td>
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<td>1</td>
<td>1</td>
<td>6</td>
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<td>1</td>
<td>6</td>
<td>5</td>
<td>11</td>
</tr>
</tbody>
</table>
Table 2 - The table compares the structures of the ichnological association and their numerical values. The column "TRENDS" shows graphically the behaviour of the data, for example the increase or decrease of the number of forms and individuals from Triassic to Jurassic. The column "AGE" points to the meaning of the data for the dating of the Botucatu Formation

<table>
<thead>
<tr>
<th>GROUPS</th>
<th>TRIASSIC ARGENTINEAN LOCALITIES</th>
<th>JURASSIC BRAZILIAN LOCALITY</th>
<th>JURASSIC ARGENTINEAN LOCALITY</th>
<th>TRENDS</th>
<th>AGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>THERAPSIDANS</td>
<td>32 %</td>
<td>7.7 %</td>
<td>0 %</td>
<td>Tr/J</td>
<td>J</td>
</tr>
<tr>
<td>QUADRUPED THECODONTS</td>
<td>56 %</td>
<td>0 %</td>
<td>0 %</td>
<td>Tr/J</td>
<td>J+J</td>
</tr>
<tr>
<td>DINOSAUROIDS</td>
<td>3.2 %</td>
<td>27.9 %</td>
<td>26.9 %</td>
<td>Tr/J</td>
<td>J+J</td>
</tr>
<tr>
<td>MAMMALOIDS</td>
<td>2.2 %</td>
<td>64.4 %</td>
<td>73.1 %</td>
<td>Tr/J</td>
<td>J+J</td>
</tr>
<tr>
<td>QUADRUPEDAL FORMS</td>
<td>85.7%</td>
<td>58.3%</td>
<td>40%</td>
<td>Tr/J</td>
<td>J+J</td>
</tr>
<tr>
<td>QUADRUPEDAL INDIV</td>
<td>93.9%</td>
<td>60.6%</td>
<td>82.1%</td>
<td>Tr/J</td>
<td>J+J</td>
</tr>
<tr>
<td>BIPEDAL FORMS</td>
<td>9.5%</td>
<td>41.7%</td>
<td>60%</td>
<td>Tr/J</td>
<td>J+J</td>
</tr>
<tr>
<td>BIPEDAL INDIV</td>
<td>4.7%</td>
<td>39.4%</td>
<td>17.9%</td>
<td>Tr/J</td>
<td>J+J</td>
</tr>
<tr>
<td>THERAPSIDANS/ARCHOSAURIANS</td>
<td>0.55</td>
<td>0.28</td>
<td>0</td>
<td>Tr/J</td>
<td>J</td>
</tr>
<tr>
<td>MAMMALOIDS/ARCHOSAURIANS</td>
<td>0.04</td>
<td>2.31</td>
<td>2.72</td>
<td>Tr/J</td>
<td>J+J</td>
</tr>
<tr>
<td>THERAPSIDANS/ARCHOSAURIANS</td>
<td>0.59</td>
<td>2.58</td>
<td>2.72</td>
<td>Tr/J</td>
<td>J+J</td>
</tr>
</tbody>
</table>

the individuals and 58.3% of the forms).

6/8. The therapsid/archosaurian ratio is medium (0.28); the mammal/archosaurian ratio (231) and the therapsid/archosaurian ratio (2.58) are high.

CONCLUSION ON THE AGE OF THE BOTUCATU FORMATION In spite of the difficulties coming from the very different number of the individuals examined by the authors (from 1 to 212), as well as from the differences of environment and geographic distance, the data allow the authors to point out the following results (Tab. 2): the ichnofauna of the Botucatu Formation, in Araraquara, seems to fit in intermediate position between the Triassic and Jurassic ichnofaunas of Argentina, with a greater Jurassic affinity. The items 1 and 2 of the table 2 show a progressive diminution of therapsids and of quadruped thecodonts from Triassic to Jurassic, passing through the ichnofauna of Araraquara. The items 4, 6 and 7 show a gradual increase of mammaloid forms, both in absolute meaning and in number of archosaurs, with the great increase of mammals, increase also the amount of therapsids, notwithstanding the diminution and later disappearance of therapsids.

The situation is not clear with reference to items 3 and 5. In item 3 the percentage of dinosauroid individuals is slightly higher in Araraquara than in Estância Laguna Manantiales; but referring to forms, the percentage becomes gradually different from Triassic faunas, passing through the fauna of Araraquara, till the Argentinean Jurassic fauna (10% - 33.3% - 80%). In item 5, the bipedaly “is higher in Araraquara than Estância Laguna Manantiales, considering all bipedal trackways, including those that do not represent habitually bipedal animals, but apparently quadruped mammals while resting, or going after hunt, or feeding, that go with a jumping gait when running away, perhaps just to adapt to a dune-desert environment. Also today deserts have many animals of this kind. But if the authors consider only bipedal dinosauroid trackways, the ones that are bipedal sensu stricto the percentages are: Argentinean Triassic 2.3%; Araraquara 29%; Argentinean Jurassic 17.9% with reference to the number of bipedal dinosauroid forms, their percentages increase gradually Argentinean Triassic 10%: Araraquara 33.3%; Argentinean Jurassic 60%. On the other hand, the structure of Araraquara association seems generally nearer to that of Jurassic fauna than to those of Triassic faunas, as could be observed in items from 2 to 7. The only item that seems to indicate more Triassic than Jurassic affinity values is the presence of a comparatively high number of theromorphoid trackways in the Botucatu Formation (7.7%). Facing the clear Jurassic aspect pointed out all the others items (2-7), this fact may be explained, for the moment, in two ways:

1. These trackways must be attributed either to one or the other of the Triassic infraorders of Theriodontia suborder, and particularly, to the Cynodontia is Owen 1860. In this case the Araraquara fauna ought to be dated to the Uppermost Triassic (Rhaetian); a Lowermost Jurassic age might be accepted (Hettangian), if the authors deem likely a hypothetical loitering of a group of cynodonts or other theriodonts, in special, arid highland environment, geographically and ecologically isolated.

2. The trackways could be attributed to a population of medium/large-sized Tritylodontoidea (or Tritylodontidae); some of them with relatively gigantic size of forms, such as for example Tritylodontoidea maximus Fourie 1962, of the Cave Sandstone, Uppermost Triassic of South Africa. In this case the Araraquara fauna could be dated back to Early or Middle Jurassic, since this group, at least in Europe, got till the Bajocian at the very least.

In conclusion, the Botucatu Formation, at least in outcrops of State of São Paulo and particularly in the Araraquara area might be put into a period of time between the Rhaetian and Middle Jurassic, with greater probability for the Lower Jurassic or the Lowermost section of Middle Jurassic.
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REFERENCES


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