



## Cricket oviposition trace fossils in palaeosols and their stratigraphic significance: The South American Palaeosol Ichnofossil Ages (SAPIAs)



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### ABSTRACT

The first insect trace fossil in palaeosols attributed to the oviposition of crickets is represented by openings composed of two to four, but usually three, perforations with a tripartite pattern. This pattern is compatible with the cross section of the distal ovipositor of some crickets. The new ichnotaxon *Bellosichnus tripartitus* igen. isp. nov. represents a novel architectural design among insect trace fossils in palaeosols. It may reflect true ovipositions or the behavior of testing soil with the ovipositors performed by crickets. In accordance, this trace fossil would be indicative of the surface soil horizon. *Bellosichnus tripartitus* is abundant in the lower section of the Sarmiento Formation (middle Eocene Casamayoran Age) and it is almost absent before and after this interval in other terrestrial successions of Patagonia. It is a trace fossil with high stratigraphic significance. *Bellosichnus tripartitus* and other insect trace fossils in palaeosols with similar stratigraphic significance comprise several assemblages, which are representative of different ages along the Cenozoic of southern South America. Such assemblages are typical of particular ages that are named herein South American Palaeosol Ichnofossil Ages (SAPIAs). The SAPIAs run in parallel with the South American Land Mammal Ages (SALMAs). The SAPIAs would be useful to make predictions not only on ages, but also on possible mammal faunas and palaeoenvironments in understudied palaeontological localities.

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## 1. Introduction

Trace fossils in palaeosols attributed unequivocally to insects could, until now, be included in four ichnofamilies representing four basic architectural designs (Genise, 2000, 2004, 2016; Buatois et al., 2017). Celliformidae, with 7 ichnogenera mostly attributed to bees, are or include chambers with rounded bottoms and flat tops. Krausichnidae, with 15 ichnogenera attributed to ants and termites, include systems of chambers connected by burrows. Pallichnidae, with 3 ichnogenera attributed to beetles and wasps are cylindrical, spherical or ellipsoidal chambers with thin fluidized linings. Coprinisphaeridae, with 8 ichnogenera attributed to beetles, cicadas, and moths are spherical, hemispherical or ellipsoidal chambers with thick discrete linings (Genise, 2016). This scenario is disturbed by the new trace fossil presented herein. *Bellosichnus tripartitus* igen. isp. nov. is not only a new ichnotaxon, but also a new architectural design for trace fossils in palaeosols, produced by a previously undocumented trace maker. This

new insect trace fossil is not composed of chambers as those previously described (Genise, 2000, 2004, 2016; Buatois et al., 2017). Instead it consists of a triple perforation reflecting the penetration of an ovipositor. This new insect architectural design, which can be named “tripartite perforations”, neither strictly represents nesting activities (Calichnia), nor a pupation (Pupichnia) or feeding chamber as in other insect trace fossils. *Bellosichnus tripartitus* is a new kind of insect trace fossil in palaeosols with a novel architectural design, function and trace maker.

Moreover, *B. tripartitus* is significant as a stratigraphic marker. The ichnospecies is almost restricted to a bounded interval of the lower section of the Sarmiento Formation of Patagonia corresponding to the Casamayoran South American Land Mammal Age. The same is also true for other insect trace fossils in Cenozoic palaeosols that comprise assemblages along the Palaeocene – Miocene of southern South America, whose recurrence has been tested along 25 years of research. This frame of assemblages, which will be proposed herein, runs in parallel with that of the South American Land Mammal Ages (SALMAs).

The objectives of this contribution are: 1) to describe and interpret a new insect trace fossil in palaeosols representing a completely new type of architectural design, trace maker, and function; and 2) to analyze and

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highlight the stratigraphic significance of this, and other associated trace fossils, which comprise successive assemblages along the Palaeocene – Miocene of southern South America.

## 2. Geologic and ichnologic setting

### 2.1. Stratigraphy and sedimentology

*Bellosichnus tripartitus* was collected for the first time in 2003 (by ESB) in the lower part of the Sarmiento Formation at Gran Barranca (Chubut Province, Argentina). Subsequent findings were always restricted to the same stratigraphic interval with two exceptions detailed below. The four localities where *B. tripartitus* occurs are Gran Barranca (45°42'56"S, 68°43'17"W), the "Railway Cut" west of Gran Barranca (45°46'6.1"S, 68°49'48"W), Sierra Talquino-Guadal del Diablo (44°49'32"S, 69°1'17"W) including five outcrops: Abra Pepe, Hoyada Ritter, La Bajada, Hoyada Jara and Hoyada Nueva, and Cañadón Vaca (45°12'56"S, 68°3'15"W), in the Chubut Province, Argentina (Fig. 1).

The Sarmiento Formation is a continental pyroclastic succession of middle Eocene–Early Miocene age, extensively distributed in central and northern Patagonia. It bears fossil vertebrate assemblages constituting the standards for several South America Land Mammal Ages or SALMAs (Madden et al., 2010), along with diverse palaeosol trace fossils (Bellosi et al., 2010; Sánchez et al., 2010; Genise, 2016). Internal litho- and biostratigraphy and geochronology of the Sarmiento Formation have been defined with high precision in the type locality, Gran Barranca (Bellosi, 2010a; Ré et al., 2010; Dunn et al., 2013).

The lower part of the Sarmiento Formation comprises the Cañadón Vaca and the Gran Barranca members, both preserving fossils attributed to the middle Eocene Casamayoran SALMA (Cifelli, 1985; Bellosi and Krause, 2014). The Cañadón Vaca Member was dated in 43.00 Ma (Dunn et al., 2015) and includes fossil mammals of the *Vacan* subage (Cifelli, 1985). Stratigraphic relationships suggest an age of 45–42 Ma (Bellosi and Krause, 2014; Krause et al., 2016). The Gran Barranca Member is well constrained at 42.11–38.16 Ma (Dunn et al., 2013) and bears fossil mammals of the Barrancan subage. *Bellosichnus tripartitus* was recovered from two sites. The first site is the "Railway Cut", where this trace fossil occurs in a channel fill modified by pedogenesis 15 m above the marker Bed Y (Fig. 2A). The second site is at the Gran Barranca locality in the marker bed # 9506 or Bed Y (Bellosi, 2010a; Ré et al., 2010), an ash-fall palaeosol with abundant fossil vertebrates (Fig. 2B) dated at 39.86 Ma (Dunn et al., 2013). At Cañadón Vaca (Fig. 1), *B.*

*tripartitus* was recognized in a tuffaceous palaeosol (Andisol) with granular structure from the lower section of the Gran Barranca Member (Fig. 2C).

One of the most complete and thickest outcrops of the Sarmiento Formation is exposed at Sierra Talquino – Guadal del Diablo (Fig. 2D). This succession (187 m) includes pyroclastic mudstones, bentonites, intraformational conglomerates, and numerous andic and non-calcareous palaeosols with diverse trace fossil assemblages (Genise et al., 2015). Kramarz et al. (2015) divided it into three biostratigraphic intervals according to fossil mammals: Casamayoran, Mustersan, and Deseadan beds and an intermediate non-fossiliferous section (Fig. 2D). Almost all specimens of *B. tripartitus* were collected in the lower section corresponding to the Casamayoran SALMA. A single specimen was collected from a Mustersan bed, and another one was found in the uppermost part of the underlying Koluel-Kaiké Formation, which correlates to the Cañadón Vaca Member of the Sarmiento Formation (Bellosi and Krause, 2014; Krause et al., 2016).

Landscapes during the Casamayoran time consisted of rolling plains that frequently received fine volcanic ash falls, small ponds, and ephemeral rivers that reworked pyroclastic sediments (Andreis, 1977; Bellosi, 2010b). Most of the sediments were transformed into andic palaeosols with a diverse degree of development (Bellosi and González, 2010). Most beds bearing *B. tripartitus* correspond to the surface or A horizon of non-calcic, andic Entisols, udic and mollic Andisols and andic Alfisols (Bellosi and González, 2010; Bellosi and Krause, 2014). Several macroscopic and micromorphological pedofeatures observed in the same bed where *B. tripartitus* occurs confirmed that it was produced in a soil: root traces, ped structure, nodules, clay cutans and other insect traces. Palaeosol properties and fossil mammals, reptiles and snails suggest a seasonal, sub-humid to slightly semiarid, warm-temperate climate (Bellosi and González, 2010; Bellosi and Krause, 2014). According to phytolith analyses, Casamayoran landscapes supported open vegetation dominated by palms and grasses, such as palm-grooves, grasslands (Zucol et al., 2010) and dry sclerophyllous forests (Dunn et al., 2015).

### 3. Ichnotaxonomy

*Bellosichnus* Genise and Sánchez, ichnogen. n.

**Diagnosis:** Openings in palaeosols composed of three, or less commonly two or four, relatively short perforations. The perforations are close to each other and when they are three the matrix between them

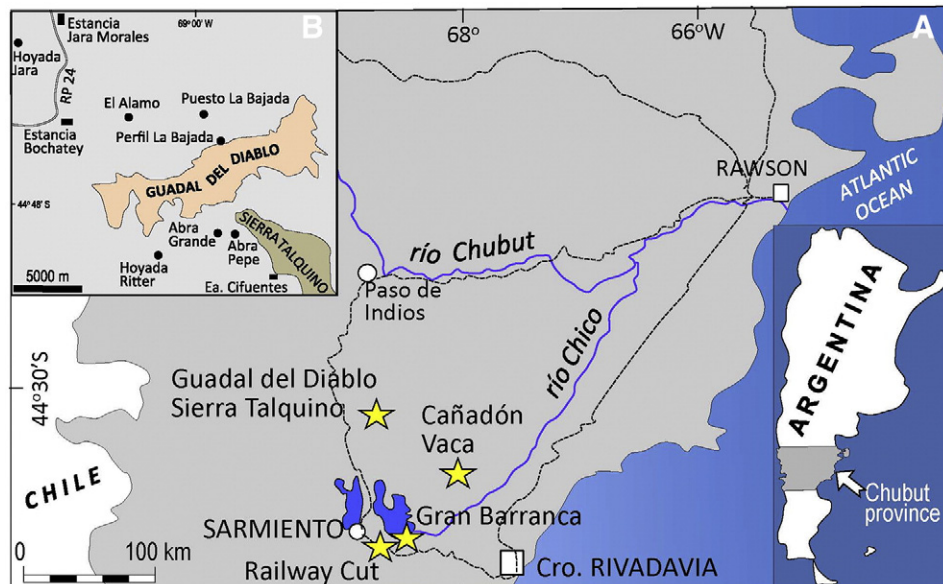
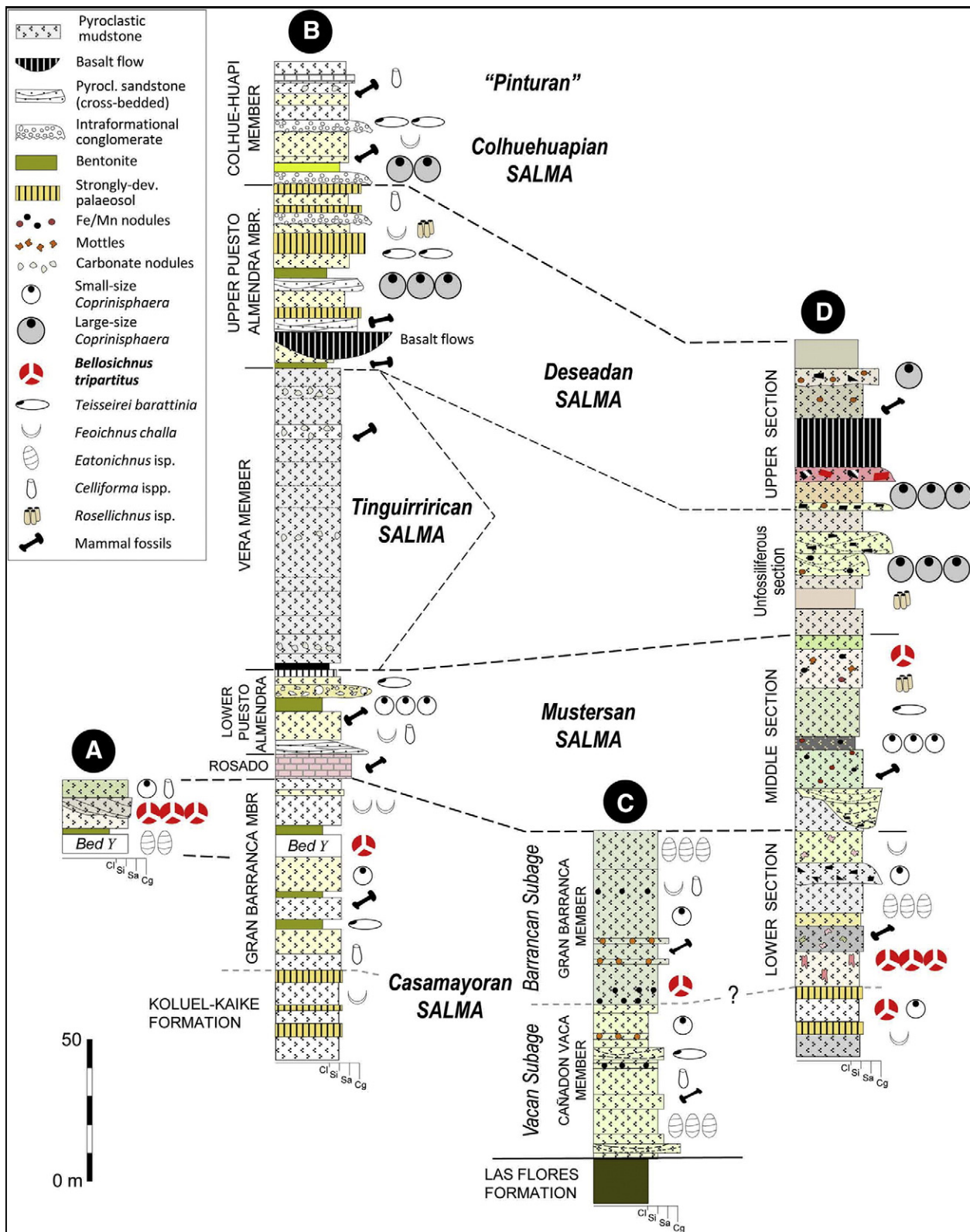


Fig. 1. (A) Studied localities with *B. tripartitus* in the Chubut Province (southern Argentina). (B) Detailed map of the Sierra Talquino-Guadal del Diablo area.



**Fig. 2.** Sedimentary logs from selected localities (see Fig. 1). Distribution of palaeosol trace fossils in members and sections. (A) "Railway Cut". (B) Gran Barranca. (C) Cañadón Vaca. (D) Sierra Talquino-Guadal del Diablo. Relative abundance is represented by repetition of symbols of trace fossils for each member or section.

usually displays a "Y" in plane view. They define a cylinder, constant in diameter, which in some cases may be removed from the matrix as a single structure. In lateral view, the perforations are mostly straight and vertical or straight and inclined, or curved with a distal sub-

horizontal part. In cross section, individual perforations are mostly sub-triangular and elliptical, but also bracket-like, ovoid to round. Perforations may be twisted and cross sections may show different shapes along the trace.



**Comments:** The morphology of this ichnogenus is unique among trace fossils in palaeosols and is not comparable to other known trace fossils. It cannot be included in any defined ichnofamily.

**Etymology:** Dedicated to its discoverer, our colleague and friend, Eduardo S. Bellosi.

*Bellosichnus tripartitus* Genise and Sánchez, ichnosp. n.

**Diagnosis:** Only known ichnospecies, same as for the ichnogenus.

**Etymology:** After the three-folded pattern of its structure.

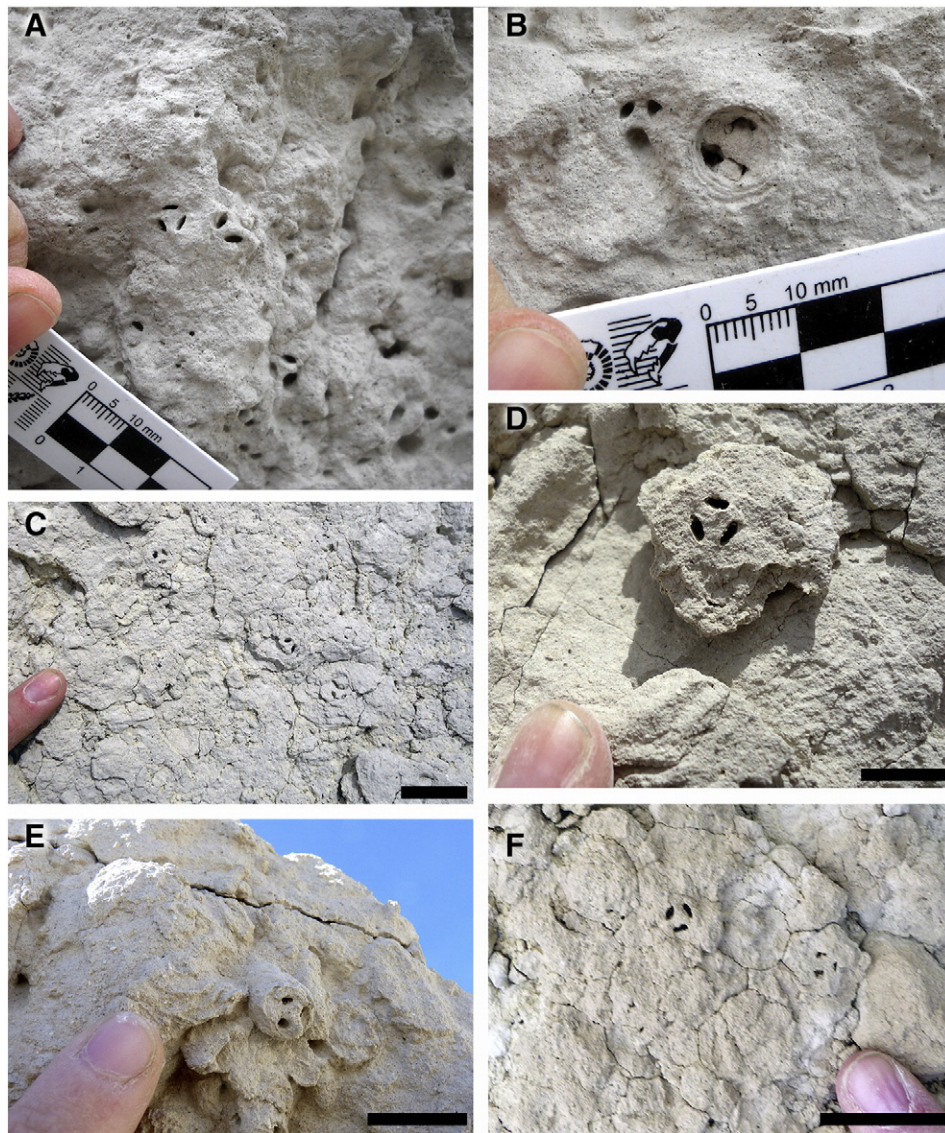
**Holotype:** One specimen sectioned in two pieces (MPEF-IC 4165a, b) from the lower section of the Sarmiento Formation, Hoyada Ritter, Sierra Talquino (Chubut Province, Argentina) (Fig. 3D). It is deposited in the ichnological collection of the Museo Paleontológico Egidio Feruglio (Trelew, Chubut, Argentina).

**Paratypes:** Two specimens from the lower section of the Sarmiento Formation at Sierra Talquino (Chubut Province, Argentina) deposited in the Museo Paleontológico Egidio Feruglio: one specimen sectioned longitudinally from Abra Pepe (MPEF-IC 4115), and a very small specimen from La Bajada (MPEF-IC 4195). One specimen preserved as a tube, which is the first specimen collected, from the Gran Barranca Member of the Sarmiento Formation at Gran Barranca (MACN-Icn

2036) deposited in the ichnological collection of the Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina).

**Examined material:** 130 specimens from the Sarmiento Formation at Sierra Talquino (Chubut Province, Argentina): 31 from Abra Pepe (MPEF-IC 4100–4114, 4116–4131); 37 from Hoyada Ritter (MPEF-IC 4132–4164, 4166, 4167, 4174, 4175); 43 from La Bajada (MPEF-IC 4176–4194, 4196–4219); 15 from Hoyada Jara (MPEF-IC 4220–4234); 4 from Hoyada Nueva (MPEF-IC 4235–4238). 12 specimens from other localities of the Sarmiento Formation in the Chubut Province (Argentina): 3 from Cañadón Vaca (MPEF-IC 4249–4231); 7 from “Railway Cut” (MPEF-IC 4242–4248), and 1 from Gran Barranca (MACN-Icn 2460). 6 specimens from the Kolhue-Kaike Formation at Sierra Talquino (Chubut province, Argentina) (MPEF-IC 4168–4173). All of them deposited in the Museo Paleontológico Egidio Feruglio, with the exception of one (MACN-Icn 2037) that is deposited in the Museo Argentino de Ciencias Naturales.

**Description.** Measurable specimens range in length from 1–2 mm to 37.2 mm ( $n = 67$ ). The more complete ones are more than 10 mm long ( $n = 57$ ). Diameters taken from the outer limit of one perforation to the outer limit of the opposite one range from 2.2 mm to 12.7 mm ( $n =$



**Fig. 3.** *Bellosichnus tripartitus* in situ. (A) Several close specimens at “Railway Cut” occurring along with isolated pits. (B) Two close specimens at “Railway Cut”, one of them (at right) showing a blurred pattern and concentric external rinds. (C) High density of specimens at Hoyada Ritter in Sierra Talquino. Scale: 20 mm. (D) The holotype (MPEF-IC 4165) from Hoyada Ritter at Sierra Talquino. Scale: 10 mm. (E) An inclined specimen, showing a thick wall, exposed in a vertical section at Hoyada Ritter in Sierra Talquino. Scale: 20 mm. (F) Specimens from Site 2 of La Bajada at Sierra Talquino. Scale: 20 mm.



145). In most specimens, the cylinder defined by the perforations is not delimited by an observable discrete wall (Fig. 4A–D). Some specimens are encircled by a wall, 0.4–1.8 mm thick ( $n = 20$ ), composed of more

consolidated soil material. Some of the specimens which show a wall can be detached easily from the matrix as tubular structures (Fig. 3E). The wall may be composed of concentric, incomplete rings (Figs. 3B,



**Fig. 4.** Different morphologies of *B. tripartitus*. (A)–(E) Cross sections. (A) Type 1 (MPEF-IC 4193). (B) Type 2 (MPEF-IC 4149). (C) Type 3 (MPEF-IC 4119). (D) Type 4 (MPEF-IC 4107). (E) Type 5 (MPEF-IC 4182). (F) A specimen at the bottom of a shallow depression (MPEF-IC 4216). (G) Two cross sections of the same specimen (MPEF-IC 4143) showing the twist, at left top and at right bottom. (H) and (I) Specimens with two perforations (MPEF-IC 4176 and 4224, respectively). (J) The specimen with four perforations (MPEF-IC 4207). (K) Longitudinal section showing a common cavity where the perforations open (MPEF-IC 4115). (L) The same specimen showing the opening of two perforations, whereas the third one is exposed along its axis. (M) Small specimen (MPEF-IC 4231) cross-cutting a larger one (MPEF-IC 4230). (N) A specimen (MPEF-IC 4168) cross-cutting a specimen of *Feoichnus challa*. Scales: 5 mm.

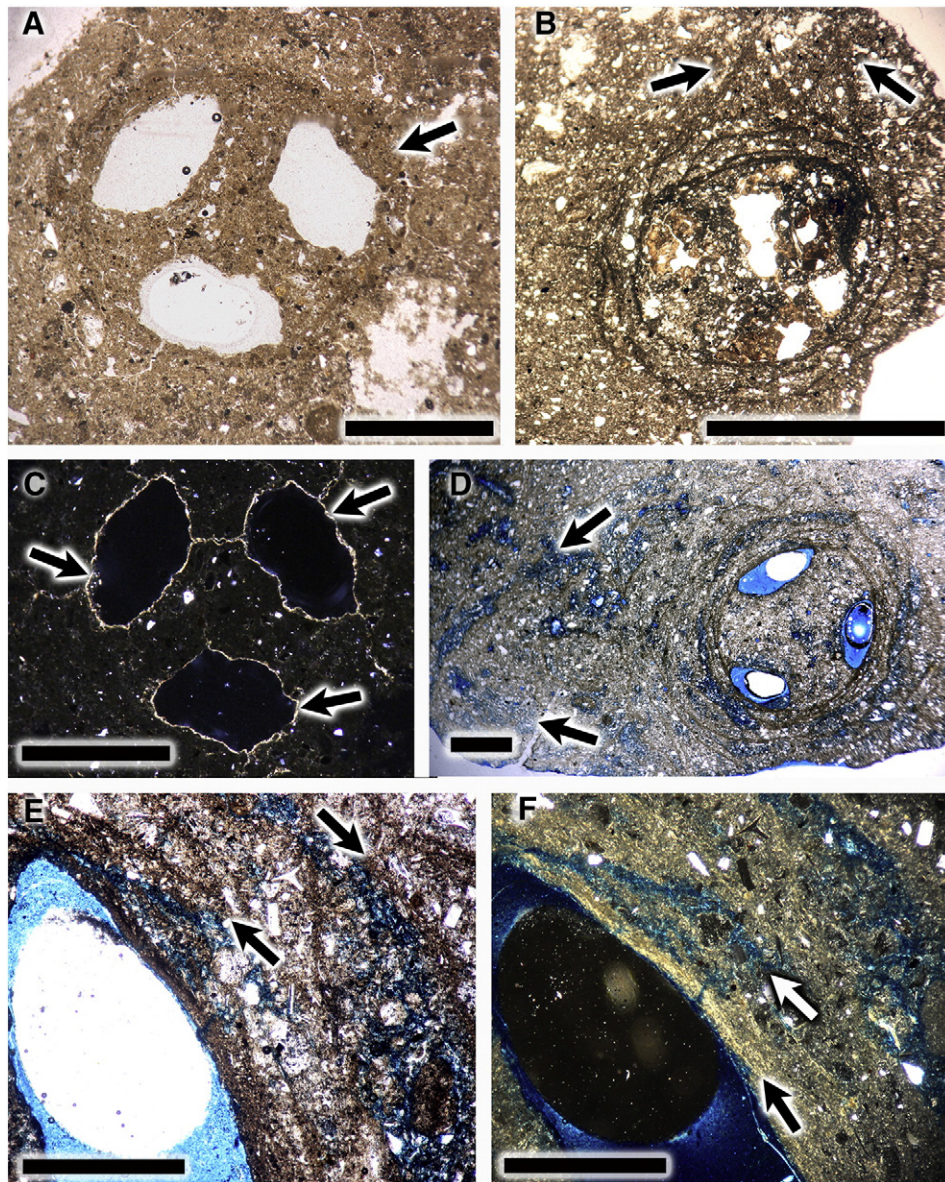


4E, 5). Thin sections show different micromorphologies that explain these different types of preservation. One of the thin sections shows that the soil material among the perforations composing the “Y” shows no micromorphological differences with the soil matrix, except for a circular, stained area including the three perforations, which is slightly darker than the palaeosol (Fig. 5A). Another type of micromorphology shows that the “Y” and the palaeosol matrix are separated by a dark line with Fe–Mn oxides (Fig. 5B, D). Outside this first dark line, there are 3–6 other concentric lines, which are discontinuous in parts or show an irregular pattern (Fig. 5B, D). The lines are 60–80  $\mu\text{m}$  wide, showing a closer grain packing and oriented clay particles (Fig. 5D–F). Besides these concentric lines there are 1–3 lines that extend beyond them defining a somewhat sub-triangular “tail” (Fig. 5B, D). Texture

and mineralogy of the “Y” are similar to the palaeosol, but the former shows smaller pores (Fig. 5D).

Most specimens are straight and vertical ( $n = 50$ ), whereas a few are straight and inclined  $45^\circ$  ( $n = 7$ ) (Fig. 4K). A few specimens, which are curved, show a sub-horizontal deeper part ( $n = 6$ ) (Fig. 3E). In two specimens, the perforations are located in a shallow depression, 10.9–25.0 mm in diameter and 6.7–8.7 mm deep (Fig. 4F). In a few other specimens there are remains of a depression.

Individual perforations are mostly sub-triangular and elliptical, but also ovoid, bracket-like and rounded in cross section (Fig. 4A–E). Thin sections show that the perforations are usually coated by clay cutans (Fig. 5C) or in some cases partly filled with illuviated clay (Fig. 5B). The morphology of the cross sections of the whole structure is defined



**Fig. 5.** Micromorphology of *B. tripartitus*. (A) The central “Y” shows no differences with the matrix, except for a circular area with oxides that is slightly darker than the palaeosol (arrow) (plane-polarized light). Scale: 3 mm. (B) The central part of this specimen, mostly filled with passive filling and illuvial clay, is surrounded by dark lines with oxides, which extend forming a sub-triangular “tail” (arrows) on top (plane-polarized light). Scale: 7 mm. (C) The same specimen in (A) observed under cross-polarized light. Note the clay cutans coating the inner surface of perforations (arrows). Scale: 3 mm. (D) Another specimen showing concentric lines with oxides, a well-defined central “Y” and a sub-triangular “tail” of close packed grains extending to the left (note the blue spaces forming a <) (arrows) (plane-polarized light). Scale: 3 mm. (E) Close up of the dark lines observed under plane polarized light (arrows). Scale: 1 mm. (F) The same close up under cross-polarized light. Note the oriented clay particles (black arrow) and closer grain packing in the lines (white arrow). Scale: 1 mm.

by the shapes and sizes of cross sections of individual perforations. In all cases the symmetry is bilateral because one of the perforations shows a different outline from the other two. Among the 170 observed cross sections, 163 show three perforations, 6 show two perforations, and 1 is composed of four perforations. Specimens showing three perforations can be roughly grouped into five types according to their cross sections, but intermediate shapes are also common (Fig. 4). The aim of defining types is to provide typical examples and to organize the description, rather than to propose a sharply defined classification. The diameter of the different types is mostly similar. The types are ordered towards increasingly smaller cross sections of perforations and a wider central “Y”.

Type 1 ( $n = 56$ ) is probably the most representative and regular in shape: two perforations show sub-triangular cross sections, whereas the third is more elliptical and in many cases ( $n = 30$ ) slightly smaller. The short axes are 1.5 mm on average, whereas the long axes are 2.8 mm on average for the two sub-triangular perforations and 2.6 mm for the more elliptical one (Fig. 4A). Type 2 ( $n = 18$ ) shows two sub-triangular to elliptical perforations, whereas the third is stouter and more rounded. The long axes are 2.9 mm on average and the short axes 1.5 mm for the two sub-triangular perforations, whereas for the third, the long axis is 2.7 mm on average and the short axis is 2 mm (Fig. 4B). Type 3 ( $n = 21$ ) shows two thin and tapered elliptical outlines, whereas the third is less tapered and more rounded. Short axes are 1.2 mm on average, whereas the long axes are 2.4 mm on average. In nine specimens the more rounded perforation is also slightly thinner (Fig. 4C). Type 4 ( $n = 3$ ) shows thin and bracket-like cross sections. The short axes are 0.9 mm on average, whereas the long axes of two of them are 2.6 mm on average and the third one is 2.2 mm (Fig. 4D). Type 5 ( $n = 30$ ) shows smaller and more elliptical to rounded cross sections. Short axes are 1 mm on average, whereas long axes of two of them are 2.2 mm on average and the third 1.9 mm (Fig. 4E).

In 44 specimens contained in slabs of matrix it was possible to examine two exposed cross sections and to recognize changes along the longitudinal axis. In 31 cases, involving different types, the cross section remains the same. The longest specimen examined, 21.3 mm long, shows a type 1 cross section and the perforations rotate with depth about 90°. The twist was also observed in other specimens (Fig. 4G). In one specimen, the cross section changes from type 1 to type 2 (16 mm long), in three specimens from type 1 to type 3 (6–11.4 mm long), in two specimens from type 1 to type 5 (8.7–17.8 mm long), in three specimens from type 3 to type 5 (7–10.5 mm long), and in one specimen from type 4 to type 5 (10.5 mm long).

Three specimens show only two perforations and different cross sections. One specimen shows a kidney-shaped single large perforation, as if the two larger perforations of type 3 were fused and the third remained the same (Fig. 4H). The second specimen shows a cross section composed of two large, opposed, plane-convex perforations (Fig. 4I). The third specimen looks like a type 1 cross section in which both perforations are connected by a shallow depression and the third smaller perforation is missing. One specimen shows a cross section with four perforations, delimiting a central “X” instead of a “Y”. Two perforations show elliptical, somewhat curved and tapering cross sections, 3.2 mm long and 1.6 mm wide, whereas the other two are more rounded and 1.9 mm in diameter (Fig. 4J).

Four specimens were sectioned longitudinally to observe the outline of the individual perforations. In two of them the perforations converge in a common rounded, but mostly unshaped cavity (Fig. 4K, L), whereas in other two the perforations end independently.

At two outcrops in Sierra Talquino-Guadal del Diablo, Hoyada Ritter and La Bajada Site 2, the density of *B. tripartitus* in the bedding plane was the highest (Fig. 3C, F). In three squares of 50 × 50 cm, at Hoyada Ritter, densities were 12, 22 and 27 specimens respectively (Fig. 3C). At the “Railway Cut”, a similar high density (28 specimens in 0.25 m<sup>2</sup>) was recorded (Fig. 3A). Some specimens cross-cut each other (Fig. 4M) or other traces (Fig. 4N). Typical densities from the other localities are around 4–5 specimens in 0.25 m<sup>2</sup>.

## 4. Discussion

### 4.1. Interpretation and trace maker of *Bellosichnus tripartitus*

*Bellosichnus tripartitus* is a trace fossil occurring in palaeosols that shows a morphology that cannot be grouped with the other recognizable insect traces in the four described ichnofamilies: Celliformidae, Krausichnidae, Pallichnidae and Coprinisphaeridae (Genise, 2004). It does not represent pupation, feeding or breeding behaviors. The first question to address, therefore, is what type of behavior it represents. The typical tripartite structure is not a burrow with internal constructed partitions because thin sections show that in most cases such partitions are remains of undisturbed soil instead of constructed free-standing walls. The uniform and recurrent shape indicates that the three perforations are not produced independently, but simultaneously and by a single organism. Such simultaneous production of a tripartite morphology is not compatible with an excavated structure (e.g., simultaneous or successive excavation of the three perforations). The more suitable explanation is then that *B. tripartitus* represents penetration in soil surface. The opening is made with a body part capable of leaving the diversity of morphologies recorded, including the typical tripartite one. Its morphology is compatible with punctures in soils made by birds by pecking, looking for prey, in which case the punctures are mostly single or paired (i.e. Genise et al., 2009) or by insects laying eggs with their ovipositors. *Bellosichnus tripartitus* is discarded as a trace produced by bird pecking because of its three-folded structure and it will thus be analyzed as a trace related to soil oviposition by insects.

Different orders of insects have representatives with ovipositors or comparable structures to lay eggs in soils (e.g. Snodgrass, 1933; Scudder, 1961; Emeljanov, 2014). To start with the most improbable trace makers of *B. tripartitus*, many robber flies (Diptera, Asilidae) have spine-bearing structures at the tip of the abdomen to push aside the soil for inserting the abdomen and laying eggs (Oldroyd, 1964; Chapman, 1982). Such behavior would not result in a tripartite structure. Mayflies (Ephemeroptera) have three terminal cerci and some species are burrowers. However, known burrows of mayflies have no indication of a tripartite structure, their cerci are too weak to be used as tools, and mayflies burrow in the bottom or bank substrates of their aquatic environment (e.g. Keltner and McCafferty, 1986; Rasmussen, 1988; Uchman et al., 2017). The ovipositor of Mecoptera (scorpion and hanging flies) is a three-folded tubular structure composed of two gonapophyses and the tergite X (e.g. Cooper, 1974). However, they deposit eggs in preexisting cavities or around rhizoids of moss in soils (Byers and Thornhill, 1983) and the ovipositor is likely not capable of penetrating soils. Some dragonflies (Odonata) lay their eggs in water-logged soils and their larvae live in burrows. However, their ovipositor is very short, weak and shows no three-folded structure (e.g. Matushkina and Klass, 2011). Some stick insects (Phasmatodea) present primary or secondary ovipositors to deposit eggs in soils, but have no compatible structures to produce a three-folded trace and representatives are from Asia and Oceania (e.g. Bradler et al., 2014). Some beetles (Coleoptera) possess extended ovipositors and some beetles lay eggs in soils (e.g. Brust et al., 2012). Tanner (1927) reviewed and illustrated the female genitalia of representatives of 66 families of Coleoptera. Extended ovipositors, mostly of species that lay eggs in plants, are largely membranous and in no case show a three- or six-folded sclerotized, elongate structures capable of leaving a tripartite trace of oviposition.

The Orthoptera (Caelifera and Ensifera) have the greatest potential to be the trace makers: they show ovipositors composed of six well-sclerotized valvae interlocked in different ways, and in some groups they are long and well-adapted to penetrate the soil (e.g. Cappe de Baillon, 1920, 1922; Snodgrass, 1933; Chopard, 1938; Naskrecki, 2001). The Caelifera (short-horned grasshoppers and locusts) are typical representatives of soil-ovipositing orthopterans. Former entomologists made detailed observations on morphology, physiology, behavior and the particular mechanism of oviposition in Caelifera (e.g.



Snodgrass, 1935 and references therein; Rose et al., 2000). Their ovipositors are composed of three pairs of rather short and curved valvae, which work as a digging and egg-laying tool. When laying eggs, the abdomen of locusts extends several times its usual length inside a hole that is made in the soil by the opening and closing of the valvae. The release of eggs is accompanied by a foam secretion that, after hardening, contains the eggs and forms the egg pod (Snodgrass, 1935; Rose et al., 2000) (Fig. 6A–D). The typical oviposition trace of a locust looks like a short vertical or inclined burrow ending in an ovoid enlargement where the egg pod is located (Fig. 6C–D). Such a behavior and resulting trace is not compatible with *B. tripartitus*.

The Ensifera include, among others, the tettigonioids such as the katydids and long-horned grasshoppers (Tettigoniidae) (Fig. 6E) and the true crickets (Gryllidae) (Fig. 6F–G). Both groups have representatives with long ovipositors capable of penetrating the soil. In contrast, Gryllotalpidae, the common mole crickets inhabiting soils, have no external ovipositor (Naskrecki, 2001). In most Tettigoniidae, the ovipositor is long and sword-like, its cross section is elongated dorso-ventrally (Naskrecki, 2001). Detailed illustrations of ovipositors of more than 20 species of Tettigoniidae, Gryllacrididae, and Raphidophoridae by

Cappe de Baillon (1920) show cross sections of the six valvae and the different ways in which they are interlocked. Considering that the penetration of valvae in the soil is interpreted to be responsible for the shape of *B. tripartitus*, cross sections and arrangement of valvae should match those of the new trace fossil. None of these is compatible with *B. tripartitus*. In turn, in most crickets the ovipositor is needle-like and its cross section along most of its diameter is rounded (Naskrecki, 2001), which is more compatible with *B. tripartitus*. Detailed illustrations of ovipositors of species of 13 genera of Grylloidea show that cross sections are rounded, but the shape and how the valvae are interlocked may change along the same ovipositor (Cappe de Baillon, 1922). In Ensifera, typically dorsal and ventral valvae of the same side are interlocked by a ridge-groove mechanism that allows free back and forth movement (Snodgrass, 1933).

Cappe de Baillon (1922) called attention to some species of crickets in which this interlocking is missing at the tip of the ovipositor and the two ventral valvae are coupled between them by the same ridge-groove mechanism instead. Cross sections from the base to the tip of the ovipositor of *Acheta domestica* (Cappe de Baillon, 1922, Figs. 26 to 33) show that, in contrast to the rest of the ovipositor, where valvae of the



**Fig. 6.** Extant Orthoptera and ovipositors. (A) and (B) *Tropidacris collaris* (Acrididae, Caelifera) showing the short ovipositor (arrow). (C) and (D) Egg pods of *T. collaris* showing the typical drop shape and eggs. (E) A katydid (Tettigoniidae, Ensifera) showing the long sword-like ovipositor (arrow). (F) and (G) Field cricket (Grylloidea, Ensifera) showing the long needle-like ovipositor (arrow).



same side are coupled (Fig. 7A), at the tip, ventral valves are interlocked between them, whereas the dorsal valves are free (Fig. 7B). The same is true for the tip of the ovipositor of *Gryllomorpha uclensis* (Fig. 7C), *Eugrylloides panteli* (Fig. 7D), and *Arachnocephalus vestitus* (= *yersini*) (Fig. 7E). Cappe de Baillon (1922) also recorded this interlocking mechanism in ventral valves of *Nemobius*, *Trigonidium* and *Paranemobius*, and in other species of *Gryllomorpha* and *Eugrylloides*.

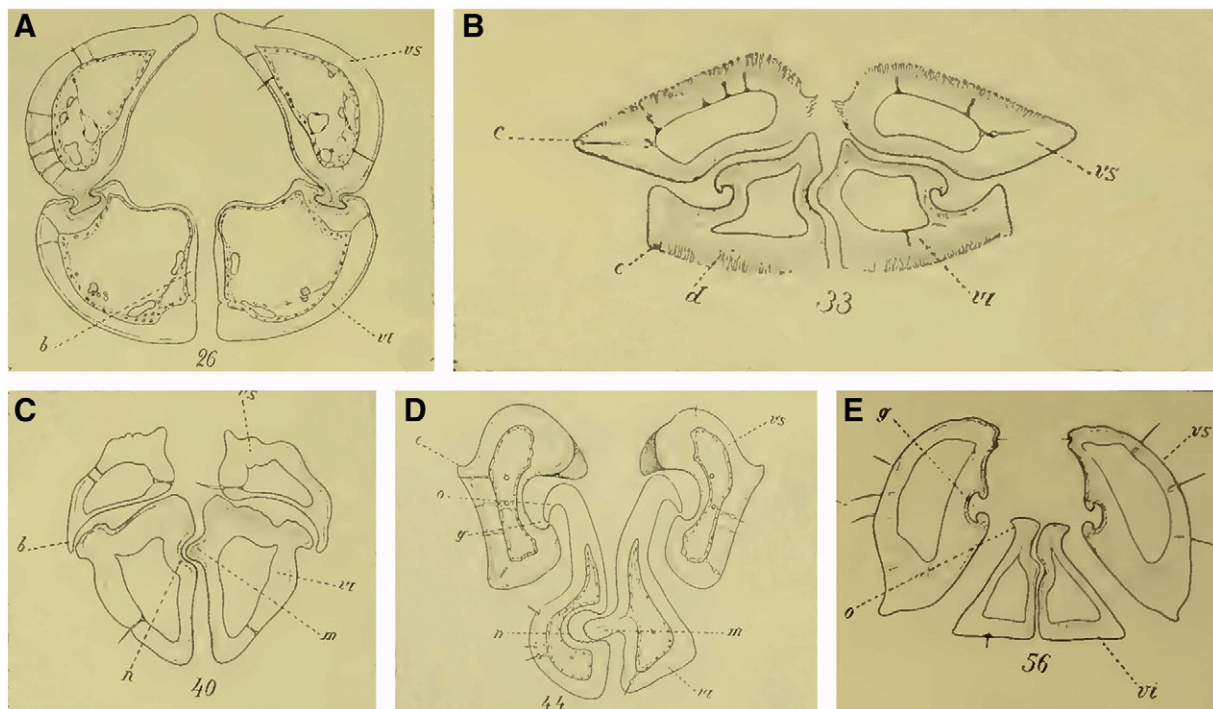
In accordance with these data, it seems more likely that *B. tripartitus* is the trace left by the distal part of the ovipositor of some species of crickets. If so, it had to be a large species considering the maximum diameter recorded of 12.7 mm and that only the distal end of the ovipositor would have been involved. Other possibilities would be a group of crickets with a different mechanism of locking for valves, or one in which the locking of ventral ones would involve the complete ovipositor. The different types of cross sections found (Fig. 4) show that, in most cases, *B. tripartitus* represents the penetration of two individual dorsal valves together with a single penetration of the fused ventral ones. In accordance, the central “Y” is considered as inverted and the figures are oriented following this interpretation. The changes from type 1 to type 5 along the long axis show that with increasing depths the sections of valves decrease distally (Fig. 4A–E). Some specimens demonstrate also that some rotation was involved in penetration (Fig. 4G). Specimens showing two punctures suggest other potential types of valves interlocking. In one case, the two dorsal valves appear to be locked as well (Fig. 4H). The other specimen would be expectable for a typical Ensifera ovipositor with the interlocking of dorsal and ventral valves from the same side (Fig. 4I). The specimen showing four punctures indicates that the ovipositor was composed of four valves, as expected in crickets, in this case each free from the others. The elliptical punctures are similar to the larger ones of type 3 morphology. The rounded ones are as if the third puncture of type 3 would have unfolded in two. It may represent some malfunction of the locking mechanism. These specimens reinforce the assumption of the bilateral symmetry of the producing apparatus and the cricket hypothesis.

The different macro- and micromorphologies found in typical *B. tripartitus* can be interpreted under the light of cricket behavior. Is *B.*

*tripartitus* representing true ovipositions of crickets or only penetrations of the ovipositor in the soil? Most specimens showing three perforations and possessing no external concentric rings or dark lines in thin sections may represent the usual behavior of a cricket thrusting its ovipositor into the soil as a test, without laying any eggs (e.g. Stringer, 2001). This behavior may also be an explanation for the central “Y” not being erased by the passing egg and for the thin sections which show that it is composed of undisturbed soil. The dark-stained circular area surrounding the perforations may represent some small discharge of liquid organic secretion for penetrating the soil as in true ovipositions (Bérengruier, 1907), which later favoured oxidation and slight cementation (Fig. 5A). This cementation, consolidating the soil, resulted in the preservation of a cylindrical 3D structure (Fig. 3E). A single penetration of the ovipositor would result in a clear three-folded puncture with no, or only slight, modification of the soil.

Diameters of *B. tripartitus* range from 2.2 mm to 12.7 mm, indicating that the penetration of the soil was produced by individuals of a wide range of sizes. It may be that fertile females of one species showed a great range of sizes, or that more than one species was involved. However, a more likely possibility is that the small *B. tripartitus* represents the penetration of soil by different larval instars of the same species of cricket, in such case, involving no laying of eggs. The species *Deinacrida rugosa* (Gryllacridoidea) has nine larval instars; the valves are well developed by the 7th instar, when the ovipositor is 6–7 mm long. During instars 8th and 9th the ovipositor grows up to 22 mm long and up to 28 mm long in the adult (Ramsay, 1965).

The other type of micromorphology shows concentric packed lines with oxides around the perimeter (Fig. 5B, D–F), compatible with the concentric rings present around some specimens (Figs. 3B, 4E), which may be the result of true oviposition. Soil packing combined with discharges of liquid organic matter, resulting in lines of oxides in thin sections, resembles the multilayered lining of *Teisseirei barattinia* and pupation chambers of sphinx moths (Genise et al., 2013). In the case of crickets, the liquid organic matter would be the secretions discharged by cricket ovipositors to penetrate the soil while laying eggs (Bérengruier, 1907; Cappe de Baillon, 1922; Snodgrass, 1933). Cappe



**Fig. 7.** Original illustrations of sections of cricket ovipositors by Cappe de Baillon (1922). (A) *Acheta domestica*, proximal section (figure 26). (B) *Acheta domestica*, distal section (figure 33). (C) *Gryllomorpha uclensis*, distal section (figure 40). (D) *Eugrylloides panteli*, distal section (figure 44). (E) *Arachnocephalus vestitus*, distal section (figure 56). Note that in B, C, D and E the dorsal valves are unlocked each other, whereas the ventral are locked producing potentially an inverted Y-shape space among them.

de Baillon (1922) described that in *Nemobius* the ovipositor is beaten against the soil accompanied by a quick movement of the valvae; such behavior is repeated several times while deepening the hole. The egg is immersed in an abundant liquid secretion when passing through the ovipositor. In many cases the secretion overflows and is poured in the soil, which becomes moistened (also observed by Bérenguier, 1907). Once the egg is laid, the ovipositor is withdrawn from the soil with the same movements. Snodgrass (1933) described that *Gryllus assimilis* cleans the soil with the ovipositor, which is then buried to its full length by the movements of the two valvae at each side that glide rapidly back and forth. Then the egg passes along the ovipositor and is extruded into the bottom of the excavation. After oviposition, *Gryllus assimilis*, repeatedly thrusts the ovipositor down at successive shorter depths to pack the soil above the egg. Apart from the secretions released in oviposition, crickets prefer soils already soft and wet to lay eggs (Chopard, 1938).

If this micromorphology of *B. tripartitus* represents true ovipositions: where was the egg? There are two possibilities: the egg is originally located below the trace or on top. The repeated movements during the withdrawal of the ovipositor, combined with a moistened substrate may be responsible for the repeated packing of sediment as evinced by concentric lines, and also for the presence of the sub-triangular area encircled by darker lines if some lateral movements are involved. In moistened substrate, the valvae would have left their trace during their withdrawal from the soil and not during their penetration as in the specimens representing the more simple morphology. Accordingly, the egg would have been laid below the trace. Even when a cavity was found at the bottom of the trace in two specimens, their different sizes and irregular shapes, as well as their absence in all other specimens, suggest that this structure is not an egg chamber or even part of the trace. The other possibility is that this micromorphology reflects the difficult penetration of the ovipositor into a drier soil, instead of its withdrawal, and the egg was laid on top of the trace, possibly in a depression as shown in Fig. 4F. In this case *B. tripartitus* would represent “the trace of the tool”: the cricket made a tripartite hole with the ovipositor and then laid the egg more shallowly in it, leaving at the bottom the traces of the valvae. In contrast, the hole over the egg would have been filled with a plug of structureless soil material.

Despite the location of the egg, the interpretation of *B. tripartitus* as oviposition of crickets, which are usually made from the soil surface, suggests that this trace fossil would be an indicator of the surface horizon of a palaeosol, as *Teisseirei barattinia* (Genise et al., 2013). Its occurrence with traces that are expected to be deeper in soils, such as *Coprinisphaera*, *Eatonichnus* or *Feoichnus*, would indicate that soils were cumule showing a continuous growth of the upper horizons. During this process pedo- and bioturbation could probably destroy many specimens, whereas others were finely preserved.

#### 4.2. Ichnostratigraphic significance of *Bellosichnus tripartitus* and associated trace fossils. The South American Palaeosol Ichnofossil Ages

Ichnological studies on the middle Eocene–early Miocene Sarmiento Formation of Patagonia, particularly at the locality of Gran Barranca, conducted over the course of 25 years have shown that the diversity of trace fossil assemblages changes along the sequences (Bellosi et al., 2010), together with changes in density, size and diversity of *Coprinisphaera* (Sánchez et al., 2010). In some cases, these are major changes involving the alternation of two different ichnofacies: the *Coprinisphaera* and the *Celliforma* Ichnofacies. In other cases, changes involve replacement of assemblages within the *Coprinisphaera* Ichnofacies (Genise et al., 2015). The new research in extended outcrops of the Sarmiento Formation at Sierra Talquino–Guadal del Diablo, confirmed that *B. tripartitus* occurs almost exclusively in the lower section of the Sarmiento Formation, corresponding to the Casamayoran South American Land Mammal Age (SALMA). *Bellosichnus tripartitus* is then a trace fossil with a high stratigraphic significance. Probably the crickets that

produced it became extinct or disappeared from the region. This result combined with changes of ichnoassemblages along the sequences observed at Sierra Talquino–Guadal del Diablo, showed that it is possible to propose a framework on the evolution of ichnoassemblages belonging to the *Coprinisphaera* Ichnofacies along the middle Cenozoic of Patagonia (Genise et al., 2015).

This evolution of ichnoassemblages of the *Coprinisphaera* ichnofacies occurred in similar environments. All the Patagonian units bearing palaeosols from the middle Eocene to the middle Miocene constitute a uniform pyroclastic succession with minor stratigraphic discontinuities (Bellosi, 2010a; Bellosi et al., 2014) (Fig. 8). These units originated in the same fluvio-aeolian depositional setting and show similar tuffaceous facies (Bellosi, 2010b). All of them include similar andic, well-drained and very weakly to moderately developed palaeosols (Bellosi and González, 2010; Bellosi et al., 2014). Preservation of surface horizons is common and not exclusive of palaeosols bearing *B. tripartitus* (Bellosi and González, 2010). The palaeoclimate inferred from these palaeosols do not vary significantly along this interval (Bellosi and González, 2010). In such stratigraphically complete and environmentally stable context, involving neither great depositional changes nor stratigraphic gaps, the SALMAs have been the most useful tool to estimate ages until recent years when radiometric ages have been more frequently utilized. In this scenario, the changes of ichnological assemblages have a similar stratigraphic value to SALMAs (Ré et al., 2010; Dunn et al., 2013). These ichnoassemblages can be used as age indicators along the Cenozoic

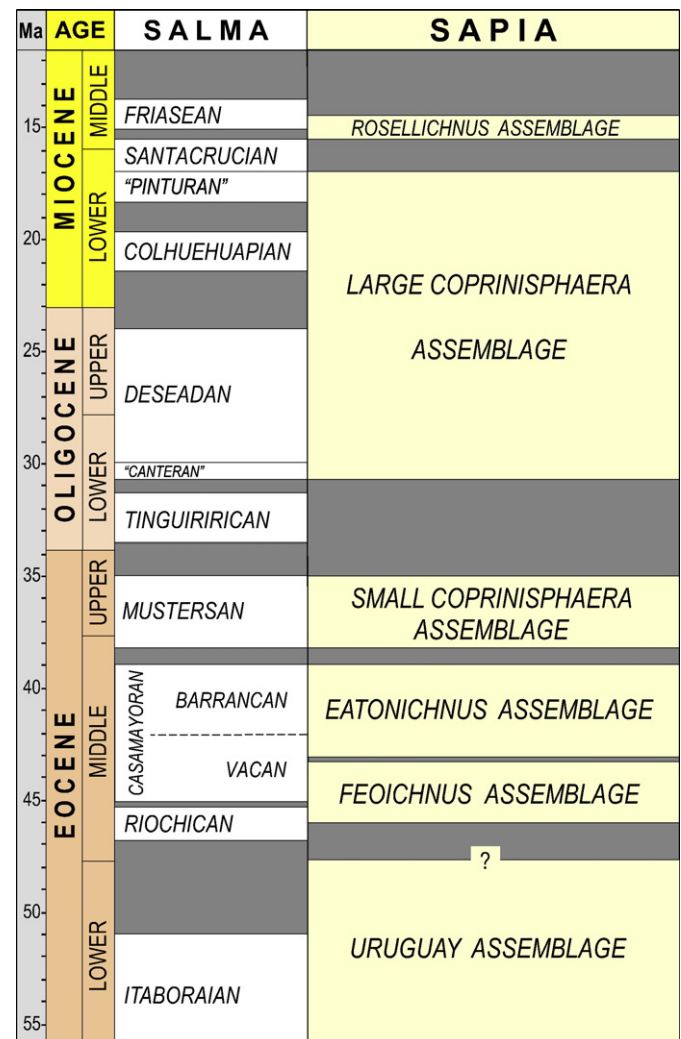


Fig. 8. Stratigraphy of the South American Palaeosol Ichnofossil Ages (SAPIAs), and its correspondence with the South American Land Mammal Ages (SALMAs).



under the new name of South American Palaeosol Ichnofossil Ages (SAPIAs) in parallel to the well-known SALMAs. The SAPIAs reflect temporal variations in these uniform pyroclastic sequences, which in most cases are not revealed by other observable parameters, with the exception of mammal faunas; therefore, they are particularly useful in localities where no mammal remains are present. The SAPIAs would be useful to make predictions not only on ages, but also on possible mammal faunas in understudied palaeontological localities. This frame can be also extended to extra-Patagonian formations, such as the early Eocene Asencio Formation of Uruguay (Bellosi et al., 2016; Genise, 2016) (Fig. 8). The stratigraphic value of the SAPIAs would join other previous examples of trace fossils and ichnoassemblages with restricted bio- and chronostratigraphic distribution: *Cruziana* and *Rusophycus* ichnospecies, Arthropycid stratigraphy, and the Jurassic-Cretaceous tetrapod footprints (Buatois and Mángano, 2011).

South American Cenozoic palaeosols, particularly those extending from the early Eocene to the middle Miocene, contain the most diverse assemblages of insect trace fossils worldwide, most of them representing the *Coprinisphaera* Ichnofacies (Genise et al., 2000; Genise, 2016). This interval comprises about 40 m.y., but *B. tripartitus* is restricted to only 5 m.y. during the middle Eocene. Other insect trace fossils also show their own acme zones. Of additional importance is that different assemblages, in which trace fossils belonging to the *Coprinisphaera* Ichnofacies are included, are exclusive of successive intervals along the Cenozoic of South America.

The oldest and most diverse assemblage is represented in the early Eocene Asencio Formation of Uruguay by ichnospecies of *Uruguay*, *Palmiraichnus*, *Corimbatichnus*, *Elipsoideichnus*, *Krausichnus*, *Monesichnus*, *Rebuffoichnus*, *Teisseirei*, *Cellicalichnus*, and *Coprinisphaera* as dominant trace fossils (Genise, 2016; Bellosi et al., 2016). Despite this diversity, *B. tripartitus* is absent. The next assemblage occurs in the upper part of the middle Eocene Koluel-Kaike Formation from Patagonia and it is dominated by *Feoichnus challa* Krause et al., occurring with a few small-sized *Coprinisphaera*, *Taenidium barretti* (Bradshaw) and *Skolithos* isp. (Krause et al., 2007, 2008; Bellosi et al., 2010). A single specimen of *B. tripartitus* occurred within this assemblage at Sierra Talquino (Figs. 1 and 2).

More diverse assemblages of the *Coprinisphaera* ichnofacies are represented in the Middle Eocene–early Miocene Sarmiento Formation (Bellosi et al., 2010; Sánchez et al., 2010). *Bellosichnus tripartitus* is almost restricted to its middle Eocene lower section (Cañadón Vaca and Gran Barranca Members and equivalents), where it occurs along with *Eatonichnus* isp., *Feoichnus challa*, few *Coprinisphaera* of small size, and *Taenidium barretti*. *Eatonichnus* isp., in the same outcrops, is also limited to this part of the section (Krause et al., 2015). *Chubutolithes gaimanensis* Bown and Rattcliffe, which occurs in other localities of the Sarmiento Formation in Chubut Province (Krause and Genise, 2004), is also limited to the middle Eocene lower section. The middle–upper Eocene section (Lower Puesto Almendra Member and equivalents), where a single specimen of *B. tripartitus* was found, shows an assemblage characterized by a high density (40–100 specimens/m<sup>2</sup>) of small sized *Coprinisphaera* (21–60 mm, mean equatorial diameter: 34.5 mm): *C. murguiai* (Roselli), *C. lazai* (Sánchez et al.), *C. kheprii* Laza, *C. tonnii* Laza and *C. kraglievichi* (Roselli), associated with *Feoichnus challa*, *Teisseirei barattinia* Roselli, and a few *Celliforma rosellii* Genise and Bown. A single specimen of *Rosellichnus patagonicus* Genise and Bown was also collected (Bellosi et al., 2010; Sánchez et al., 2010).

Younger deposits of the Sarmiento Formation, bearing the same type of palaeosols (Andisols) with preserved surface horizons, show no specimens of *B. tripartitus*. The assemblages occurring along the Oligocene–lower Miocene interval are characterized by the appearance of *Coprinisphaera* of large size (60.5–78.5 mm), disappearance of the smallest specimens (21–27 mm), shift in the mode to larger size classes (mean equatorial diameter: 49 mm), decrease of density (7 specimens/m<sup>2</sup>), and a minor decrease of ichnodiversity (Sánchez et al., 2010). They are recorded in the upper part (Oligocene–lower Miocene) of the

Sarmiento Formation (Upper Puesto Almendra, Collhue–Huapi members and equivalents) and in the early Miocene Pinturas Formation (Bellosi et al., 2010; Sánchez et al., 2010; Bedatou et al., 2015).

The next assemblage corresponding to the lower–middle Miocene Santa Cruz Formation is probably a case of the *Celliforma* ichnofacies, showing moderate to low diversity and abundance, and bearing mostly *Celliforma* and *Fictovichnus* (Genise and Bown, 1994; Krapovickas, 2012; Zapata et al., 2016). During the middle Miocene, the last diverse Patagonian assemblage corresponding to the *Coprinisphaera* ichnofacies was recorded from the tuffaceous La Pava Formation in Chubut Province (Bellosi et al., 2014; Cantil et al., 2015; Sarzetti et al., 2015). This assemblage is dominated by *Rosellichnus patagonicus*, *Coprinisphaera tonnii*, *Coprinisphaera akatanka*, and *C. murguiai* (Bellosi et al., 2014; Cantil et al., 2015; Sarzetti et al., 2015).

The recognizable assemblages–SAPIAs named after the dominant trace fossil, their ages and their relationships with SALMAs are (Fig. 8):

1. *Uruguay* assemblage–SAPIA: dominated by *Uruguay* ispp, *Monesichnus ameghinoidi*, small-sized *Coprinisphaera*, *Teisseirei barattinia*, *Palmiraichnus castellanosi* and *Rebuffoichnus casamiquelai*. It may correspond with a pre Riochican SALMA probably involving the Itaboraia (about 56–51 Ma).
2. *Feoichnus* assemblage–SAPIA: dominated by *Feoichnus challa*, few to absent small-sized *Coprinisphaera*, *B. tripartitus*, *Taenidium* isp., *Skolithos* isp. It corresponds with a pre–Casamayoran SALMA, probably including the Riochican SALMA.
3. *Eatonichnus* assemblage–SAPIA: dominated by *Eatonichnus* isp., *B. tripartitus*, *Feoichnus challa*, *Chubutolithes gaimanensis*, *Taenidium* isp.. A few small-sized *Coprinisphaera* may be also present. It corresponds with the Casamayoran SALMA (45–38 Ma).
4. Small-sized *Coprinisphaera* assemblage–SAPIA: dominated by *C. murguiai*, *C. lazai*, *C. kheprii*, *C. tonnii* and *C. kraglievichi* of small sizes in high numbers, associated with *Feoichnus challa*, *Teisseirei barattinia*, and very few *Celliforma rosellii*. A single specimen of *Rosellichnus patagonicus* and another of *B. tripartitus* have been collected until now, respectively. It corresponds with the Mustersan SALMA (38.2–35 Ma). In the following interval (late Eocene–early Oligocene) palaeosol trace fossils are very scarce, with only few *Coprinisphaera* and it is represented in the Vera Member of the Sarmiento Formation that corresponds to the Tinguirirican SALMA.
5. Large-sized *Coprinisphaera* assemblage–SAPIA: appearance of *Coprinisphaera* of large size and disappearance of the smallest specimens. The ichnodiversity of the other trace fossils is slightly lesser than the small-sized *Coprinisphaera* SAPIA, and *B. tripartitus* is absent. This assemblage corresponds to the Deseadan SALMA (29–24 Ma). This ichnodiversity remains with minor changes and some loss of ichnodiversity during the Collhuehupian SALMA (21–20 Ma) and the Pinturan SALMA (19–18 Ma).
6. *Rosellichnus* assemblage–SAPIA: dominated by *Rosellichnus patagonicus*, *Coprinisphaera tonnii*, *C. akatanka*, and *C. murguiai*. This assemblage probably corresponds to a pre- or early Friesean SALMA.

The middle Miocene Cerro Azul Formation from La Pampa (Argentina), corresponding to the Huayqueriense SALMA, bears an association compatible with the *Celliforma* Ichnofacies (Cardonatto et al., 2016). Younger, Pliocene–Pleistocene palaeosols successions bearing insect trace fossils representative of the *Coprinisphaera* ichnofacies from South America, such as those occurring in several localities of Argentina and Ecuador (e.g. Genise et al., 2000; Cantil et al., 2013; Sánchez et al., 2013), currently have too low or null ichnodiversity to comprise assemblages that can be included in this framework.

## 5. Conclusions

*Bellosichnus tripartitus* is a new insect trace fossil from palaeosols that shows a morphology distinct from previously described continental

trace fossils. It represents a new architectural design that can be traced back up to the middle Eocene. Its morphology is composed of two to four, but usually three, perforations displaying a tripartite pattern, compatible with the distal part of the ovipositor of some crickets. It is the first insect trace fossil in palaeosols attributed to the oviposition of crickets. *Bellosichnus tripartitus* may reflect true ovipositions or just the behavior of crickets of testing soil with the ovipositors. Accordingly, *B. tripartitus* may be indicating the surface soil horizon.

*Bellosichnus tripartitus* is abundant in, and mostly restricted to, the lower section of the Sarmiento Formation (middle Eocene). It is also completely absent before and after this interval resulting in a trace fossil with potentially high chronostratigraphic significance. *Bellosichnus tripartitus* and other insect trace fossils in palaeosols with similar stratigraphic significance comprise assemblages, which are representative of different ages along the Cenozoic of Southern South America. Such assemblages are named herein as South American Palaeosol Ichnofossil Ages (SAPIAs), which run in parallel with the South American Land Mammal Ages (SALMAs).

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