An assemblage of large-sized insect traces in paleosols from the middle miocene of northern Patagonia related to the climatic optimum

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ABSTRACT

A new assemblage of large insect trace fossils is recognized in paleosols of the middle Miocene pyroclastic deposits from extra-Andean north Patagonia. This assemblage includes *Racemusichnus jacobacciensis* igen. isp. nov., the largest trace fossil in paleosols attributed to solitary insects. *R. jacobacciensis* is represented by clusters of two to seven thickly walled cylinders horizontally orientated in the paleosol. The cluster arrangement, its orientation, the large size and wall of the cylinders suggest a dung beetle, probably a representative of the Geotrupidae as the possible trace maker. The new ichnoassemblage, also comprising large-sized specimens of *Coprinisphaera ispp.*, *Teisseirei barattinia* and *Feoichnus challa*, belongs to the *Rosellichnus* assemblage-SAPIA of the *Coprinisphaera* Ichnofacies. Mollic paleosols along with the trace fossils, mammal remains and previous data for this unit suggest an open grassy habitat compatible with high productive grass savannas, under a temperate-warm and seasonal subhumid climate. This assemblage of large-sized trace fossils is attributed to highly productive ecosystems related to the rise of temperature occurred during the Middle Miocene Climatic Optimum.

1. Introduction

Insect trace fossils in paleosols in combination with pedogenic features is one of the most powerful tools that has been used in the last years to disentangle ecological and climatic conditions of terrestrial paleoecosystems (Genise et al., 2000; Sánchez et al., 2010; Bellosi et al., 2016; Genise, 2016; Sarzetti et al., 2017; Cantil et al., 2020). South American ichnology of paleosols has a long history and tradition arising in the first half of the last century (Sauer, 1955; Frenguelli, 1938, 1939; Roselli, 1939) and it has been contributing a lot since then to interpret paleoenvironments from different areas of the region (Verde et al., 2007; Genise and Farina, 2011; Cantil et al., 2013; Sánchez et al., 2013; Catena et al., 2016; Genise et al., 2016; do Nascimento et al., 2019). Particularly, Patagonia has been one of the most studied areas, which has been favored by extensive outcrops with paleosols spanning from the Jurassic to the Miocene (Bedatou et al., 2008; Genise et al., 2008, 2017, 2020; Bellosi et al., 2010; Genise, 2016). In this context, recent ichnological research on the middle Miocene La Pava Formation of northern, extra-Andean Patagonia (Nullo, 1978) has resulted in significant information on the evolution of necrophagous habitats in dung beetles

(Cantil et al., 2020), the appearance and evolution of Diphaglossinae bees producing curved cells (Sarzetti et al., 2014, 2017) and paleoenvironmental reconstructions (Cantil et al., 2015, 2020; Sarzetti et al., 2017; Sánchez et al., 2018). This research on new localities of the La Pava Formation in the Rio Negro province of Patagonia, in combination with previous information for this unit allows us to present herein the ichnology of paleosols formed during the Middle Miocene Climatic Optimum. The only antecedent of paleosol trace fossils related to Cenozoic climatic events is the dwarfism of specimens recorded in the Paleocene-Eocene Thermal Maximum of North America (Smith et al., 2009).

The objectives of this contribution are: (1) to describe a new insect trace fossil and ichnoassemblage in paleosols from the middle Miocene of Patagonia, (2) to analyze the possible affinities of the new trace fossil with dung beetles (Geotrupidae), (3) to assess the sedimentary facies and paleosols of the La Pava Formation in order to infer the ancient landscape and soil-forming factors in combination with the ichnological data; (4) to integrate the new trace fossil association to the *Rosellichnus* assemblage-SAPIA of the *Coprinisphaera* Ichnofacies, in order to refine the palaeoenvironmental inferences from the La Pava Formation, and

(5) to analyze the possibilities that the large-sized trace fossils of this new assemblage may be linked the Middle Miocene Climatic Optimum.

2. Materials and methods

The trace fossils described herein were collected at five localities near Ingeniero Jacobacci, Río Negro province (Argentina) (Fig. 1), where the La Pava Formation crops out, during two field trips carried out in October 2017 and March 2018. From a total of 180 specimens collected, 27 come from Estancia Huanuluan Norte (EHN) (41°19′27.6″ S, 69°51′27.7″ W), 51 from Estancia Huanuluan - Cantera Nueva Inferior (EHCNI) (41°23′01′ S, 69°55′20.31″ W), 48 from Estancia Huanuluan - Cantera Nueva (EHCN) (41°23′30″ S, 69°56′33.2″ W)(Fig. 2A), 26 from Cantera Billy (CB) (41°23′03′ S, 69°48′59.7″ W), and 27 from Naríz Krause (NK) (41°21′22.07″ S, 69°46′08.15″ W) (Fig. 1). Specimens collected were deposited in the Museo de Ciencias Naturales, Antropológico e Histórico "Jorge H. Gerhold" (MJHG-NCP), Río Negro province, Argentina. Previously, they were prepared and studied in detail in the laboratory at the División Icnología of the Museo Argentino de Ciencias Naturales, Buenos Aires province (Argentina). Each specimen was photographed, labelled, examined, measured and identified to ichnospecies level when it was possible. Most of them were also sectioned to study and measure internal structures. Seven specimens, four isolated cells (MJHG-NCP 168, 170, 171, 172) and three clusters attributed to *Racemusichnus jacobacciensis* igen. isp. nov. (MJHG-NCP 178, 179, 189), were utilized to obtain CT images using a Philips Brilliance 64 CT scanner (images taken each 0.08 mm). CT images were obtained before preparation to ensure that all internal characters were present without any modification.

The acronyms of collections that house the specimens studied are: MJHG, Museo de Ciencias Naturales, Antropológico e Histórico "Jorge H. Gerhold", Ingeniero Jacobacci, Río Negro province, Argentina; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires province, Argentina.

3. Geological setting

The studied insect trace fossil assemblage was recovered from the La Pava Formation. This unit, along with the Collón Curá Formation, constitutes the infill of several Miocene intermontane basins in the North Patagonia broken foreland (Bilmes et al., 2013). In this case we explored the Jacobacci depocenter, SW of the Rio Negro province, Argentina (Fig. 1). The La Pava Formation consists of stacked brownish paleosol profiles developed in pyroclastic sediments (Nullo, 1978). Coira (1979) and González et al. (2000) included diatomite beds in this unit, but they correspond to the Collón Curá Formation. Thickness shows significant variations, in average 12 m (Agua de la Pava, Carri-laufquen lake), but it exceeds 100 m at EHCN (Fig. 2A), where trace fossils are more abundant.

The La Pava Formation lies unconformably upon several units. At Ea. Huanuluan it covers the Paleocene-Eocene Huitrera Formation, but in others sectors it overlays different basalt flows, such as the early Miocene (20 Ma) Cerro Petiso Formation and the early-middle Miocene Quiñelaf Formation (Asiain et al., 2017) or post-plateau basalts (Kay et al., 2007). North of Ingeniero Jacobacci, and probably related to the last unit, it is exposed the late Oligocene-early Miocene Basalto Carri Laufquen, a sequence of tuffs, tuffaceous sandstones and conglomerates followed by basalt flows. The La Pava Formation is covered in transition by the Collón Curá Formation, a fluvio-deltaic, lacustrine and eolian succession of fine whitish tuffs and diatomites, which bears fossil plants and abundant fossil vertebrates (Bellosi et al., 2014; Bucher et al., 2019b). Mammal remains from this unit and from the La Pava Formation were assigned to the middle Miocene Friasian/Colloncuran SALMA (Kramarz et al., 2018).

The precise age of the La Pava Formation in Ingeniero Jacobacci is unknown. The La Pava Formation was considered late early-early middle Miocene because of its transitional contact below with the Collón Curá Formation in several localities. The Collón Curá Formation possesses numerous isotopic dates mostly in the range 16.1–13.3 Ma (Flynn and Swisher 1995; Bilmes et al., 2013; Dunn et al., 2015). The first
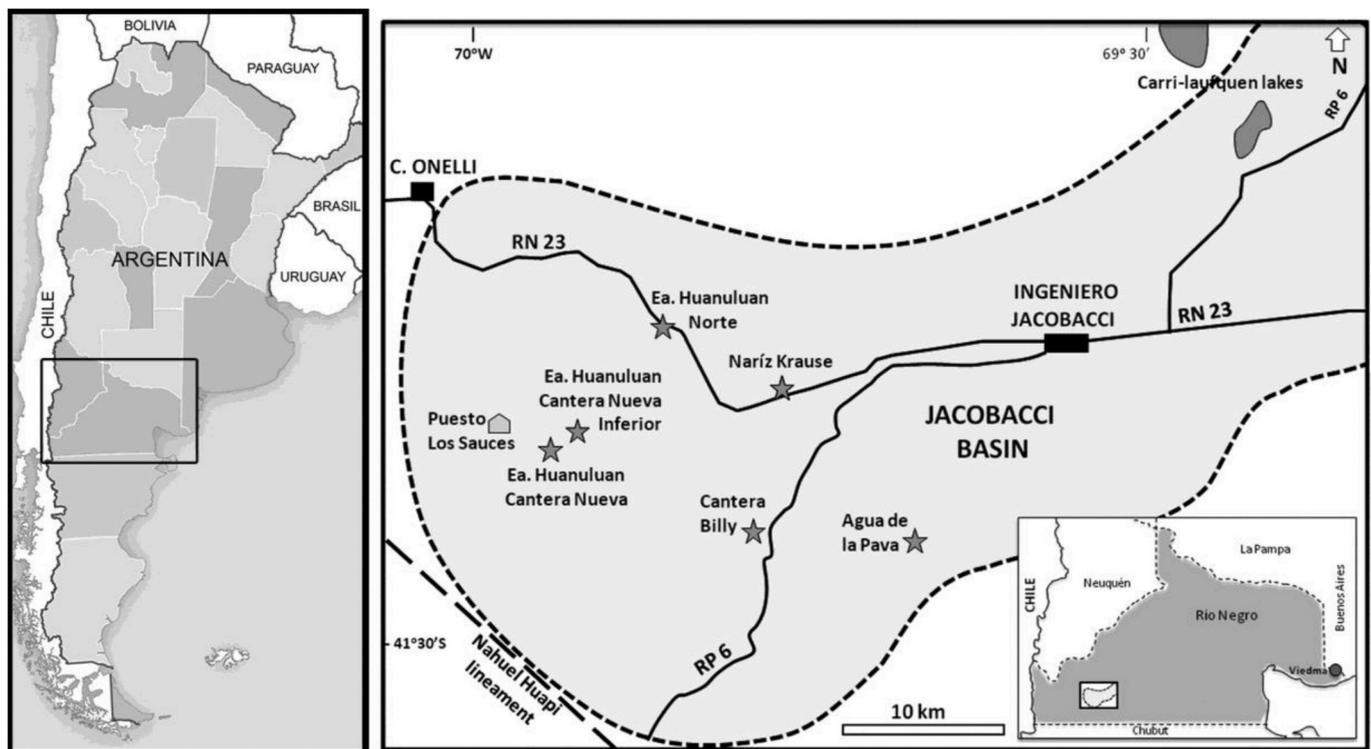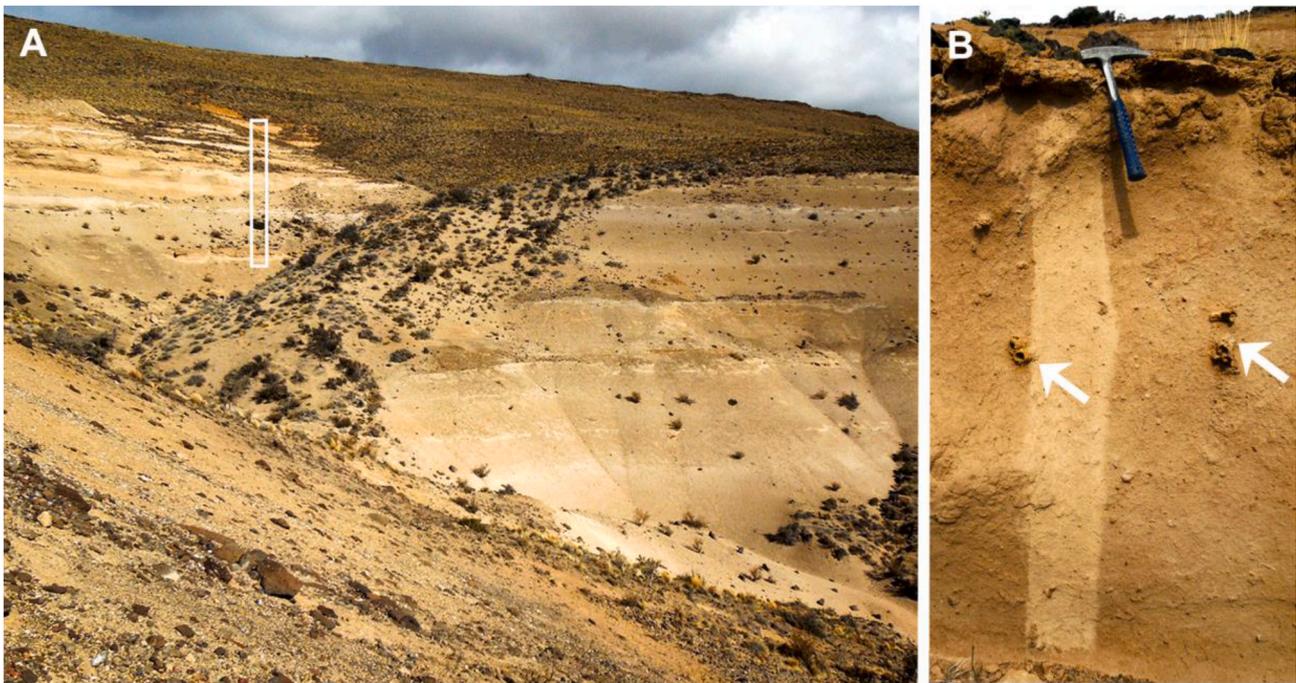

Fig. 1. The Miocene Jacobacci basin in the Rio Negro province, northwestern Patagonia (Argentina). The studied localities of the middle Miocene La Pava Formation are indicated with stars.

Fig. 2. A) Outcrops of the La Pava Formation (middle and upper sections) at Estancia Huanuluan - Cantera Nueva (EHCN). The white box shows the stratigraphic interval with paleosols bearing *Racemusichnus jacobacciensis* igen. isp. nov. B) Three specimens of *Racemusichnus jacobacciensis* igen. isp. nov. preserved *in situ* in a paleosol located in the lower part of the interval marked (white box).

isotopic dates of the La Pava Formation in Paso del Sapo basin indicate an age of ~15.0–14.6 Ma (Bucher et al., 2019a), but a recent radiometric date from Piedra del Águila basin (D'Elia et al., 2020) show an older age (18.85 Ma). Thus, the La Pava Formation would be older than the Santa Cruz and Pinturas Formations (Perkins et al., 2012) and correlated to the Colhue-Huapi Member of the Sarmiento Formation (Re et al., 2010), which is incongruent with paleontological data. Considering radiometric dates and the presence of Friasian/Colloncuran mammals at Ingeniero Jacobacci, we assumed an early middle Miocene age for the La Pava Formation.

3.1. Lithofacies and sedimentation

To characterize the sedimentary facies of the La Pava Formation, the more complete profile (100 m) from EHCN was selected (Figs. 1 and 2A). Considering the high number of paleosols (n = 53), a remarkable proportion of the original sedimentary properties were modified by soil-forming processes (Fig. 3). Three main facies were differentiated: pyroclastics mudstones, very fine tuffs and conglomerates. The first two comprise 80% of the deposits and almost always show pedogenic features. Pyroclastic material is largely (>70%) constituted by glass shards, along with quartz and plagioclase. Beds show tabular morphology. They extend laterally over hundred meters, sometimes parallel to underlying topography (i.e. mantle bedding). These facies are also dominant in other studied localities. At EHCN, articulated fossil mammals were recovered from two massive pyroclastic mudstones (Kramarz et al., 2018).

Subordinate facies include two types of conglomerates with tuffaceous matrix, generally not modified by pedogenesis (Fig. 3). The first one is a fine, massive or horizontally-bedded, matrix-supported conglomerate, showing a flat and sharp lower contact. Clasts are intraformational, moderately-to well-sorted, and are 2 cm in mean diameter. They are concentrated in the upper 20 m of the unit, but at Agua de la Pava this facies occurs in the lowermost part. The second type is more common in the lower and middle sections, and consists of lenticular, 1–1.7 m thick bodies of coarser, matrix-supported conglomerates, with

erosive and irregular lower contacts. They fine upward and show cross or horizontal bedding. Clasts are 4–20 cm in diameter, intraformational or derived from basalt rocks. Some bodies change laterally to clast-supported conglomerates exhibiting larger (up to 80 cm) and imbricated clasts. A thick conglomerate, in the middle part of the EHCN section, also preserves fossil mammals (Kramarz et al., 2018).

The high frequency of paleosols and homogeneity of the fine pyroclastic deposits indicate that prevalent sedimentation was discontinuous and subaerial. This pattern is congruent with the dominant massive pyroclastic mudstones and very fine tuffs showing mantle bedding, interpreted as distal, volcanic ash fallout deposits on extensive, flat or undulating, vegetated land surfaces, similar to loessic plains (Bellosi, 2010). Despite the absence of diagnostic sedimentary structures (Fig. 3), it is probable that a minor part of the pyroclastic mudstones corresponds to overbank deposits on floodplains. Sediment accumulation was frequently interrupted, allowing modification by soil-forming processes. The scarce proportion of overthickened paleosol horizons (i.e. cumulative paleosols) suggests that sedimentation rate was very low or null, and exceeded by pedogenesis. Intraformational, matrix-supported conglomerates of the upper section probably originated as debris or hyper-concentrated flows (Smith, 1986). Coarser and erosive conglomerates accumulated in fluvial channels, which were less frequent during the late depositional stage. Because conglomerates are generally not pedogenically modified, they must have been quickly covered by finer deposits (pyroclastic mudstones), indicating that eolian deposition was very recurrent. The general sedimentary scenario is envisaged as a fluvial system located in a perivolcanic setting, with gravelly rivers and extended plains that received abundant eolian tephric sediments and overbank materials near watercourses. The studied sections probably correspond to central parts of the Jacobacci basin (Fig. 1). In the nearby Comallo area (basin?), 30 km to the NW, Rabassa (1978) identified an exhumed La Pava paleorelief, with a fluvial network partially controlled by faults and deep incised valleys.
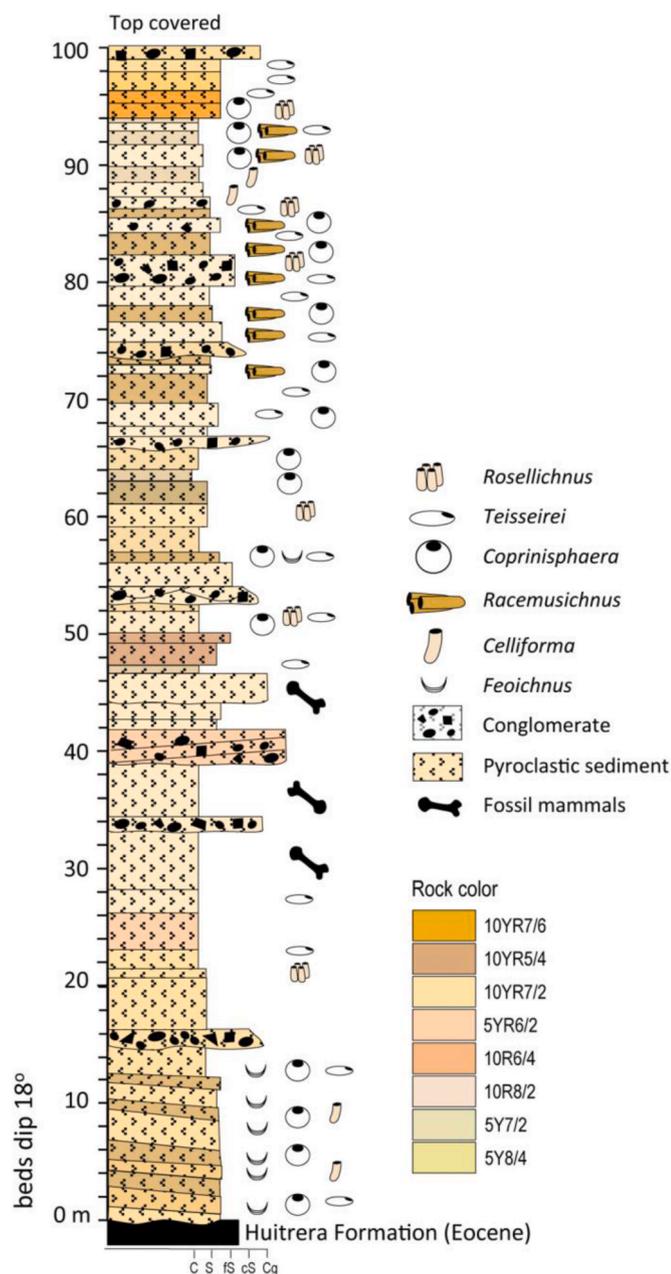
Fig. 3. Sedimentary section of the La Pava Formation at Cantera Nueva, Estancia Huanuluan (EHCN), showing stratigraphic distribution of paleosol trace fossils. Granulometric scale: C = clay, S = silt, fS = fine sand, cS = coarse sand, Cg = conglomerate.

3.2. Paleosols and environment

Fifty-three successive profiles of six types of paleosols were logged in the 100 m thick section at EHCN (Figs. 2A and 3), and defined according to lithology, horizonation, structure, color, trace fossils and micromorphology. Parent material in all cases is mostly composed of vitric ash, and free carbonate is not present. Burial alteration was considered when recognizing and interpreting some pedofeatures. A combination of near-surface processes altered paleosols, including partial depletion of organic matter and burial gleization (Retallack, 2001). Compaction and reddening (dehydration of ferric hydroxides) had slight effect. The degree of development of paleosols varies from very weak to strong and was used to define the pedotypes. Paleosols showing weaker development are common in the lower section (between 15 and 50 m) and near

the top (between 80 and 90 m) (Fig. 3). They are greyish orange pink or pale yellowish brown, exhibit A-C (pedotype 1) or A-AC (pedotype 2) profiles, and formed in conglomerates and pyroclastic mudstones preserving original bedding. Rhizoliths vary from scarce to abundant, but insect trace fossils are rare (*Coprinisphaera, Rosellichnus*) or absent (see Systematic Ichnology). Some examples of the pedotype 2 show slickensides. Micromophology is characterized by a very scarce illuviation and asepic microfabrics. A slightly more-developed variety presents iron nodules and wavy Fe–Si rich crusts. These pedotypes are comparable to andic Entisols.

The second group comprises weakly to moderately developed paleosols (pedotype 3), mostly located in the middle section (between 25 and 80 m), with profiles exhibiting A-Bg-C horizons (Fig. 3). They formed in massive pyroclastic mudstones and are moderate orange pink to moderate yellowish brown in color. Clayey rhizoliths are very common in A and B horizons. Surface horizons also present thick platy peds, crumb structure and slickensides; while subsurface horizons show mottles, well-developed Fe–Mn nodules, and wavy Fe–Si rich crusts. In thin sections, high porosity, scarce illuviation and mosepic and skelsepic microfabrics is observed. The insect trace fossils are diverse, but not abundant. *Rosellichnus* and *Teisseirei* are the more recurrent in A horizons, while *Coprinisphaera* and *Racemusichnus* occur at higher depths. Paleosols of the pedotype 3 are classified as udic Andisols. A particular aquic variety, observed at NK locality, only preserves abundant *Loloichnus*.

Moderately developed paleosols (pedoype 4) occur in low proportion. The complete profile displays A-Bw-BC/C horizons, formed in pyroclastic mudstones. Surface horizons are darker (moderate yellowish brown) and show platy and granular peds, and fine clayey rhizoliths. Subsurface horizons are pale reddish brown, more rooted and show columnar and granular/crumb structure. Granular/crumb peds result from intense rooting by herbaceous plants and earthworm burrowing, which produce mollic characteristics (Retallack, 2001). In thin-sections, moderate illuviation, high porosity, and mosepic or bimasepic microfabrics are recognized. Among the abundant invertebrate trace fossils, *Feoichnus, Coprinisphaera, Teisseirei* and *Rosellichnus* are the most common. The pedotype 4 is compared to mollic Andisols.

Strongly to moderately-developed paleosols (pedotypes 5 and 6) appear near the base and near the top of the EHCN section (between 4–10 m and 90–100 m) (Fig. 3). They formed in pyroclastic mudstones and exhibit A-Bt-C (pedotype 5) or A-Bt1-Bt2-C (pedotype 6) profiles, brown colours are similar to pedotype 4, with darker values upwards. Surface horizons show platy and granular/crumb structure, cracks and trace fossils of roots and insects (*Teisseirei, Coprinisphaera*). Subsurface horizons present crumb peds inside larger blocky peds. They are subdivided according to the rhizolith density and the size of blocky structure. Insect trace fossil are numerous (*Celliforma, Coprinisphaera, Racemusichnus, Fictovichnus*). At EHN, Bt horizons exhibit diffuse boxwork ichnofabric (Bedatou et al., 2009) and galleries of small vertebrates. Under microscope, subsurface horizons show high porosity, very evident argillans, blocky peds, and bimasepic microfabric. Pedotypes 5 and 6 are compared to andic-udic Mollisols.

In general, described soil features and pedotypes record similar soil-forming processes, but differ in their intensity or the time they operated. Main horizonation processes included bioturbation inferred from granular/crumb structure, diffuse boxwork ichnofabric, and abundant rhizoliths and invertebrate trace fossils. Lessivage is recognized by well-developed clay cutans and the b-fabric in subsurface horizons (Bt) (Buol et al., 2011). Decalcification produced removal of carbonates. Andisolization is reflected in high secondary porosity (Buol et al., 2011). Subordinate processes were melanization of surface horizons with organic matter, and hydromorphism deducted from drab-haloed root traces and mottles.

At a geological scale, some of the "active" factors controlling soil-forming processes remained nearly constant during La Pava time. For instance, stratigraphic distribution of facies and bed configuration along

with unchanging lithology (vitric tuffs) indicate relatively uniform topographic setting, geomorphological processes, and parent material, respectively. Iron (ferric) nodules, subsurface clay enrichment and traces of insects attest to well-drained soil profiles. Climate and resulting biota can be assessed by several preserved pedofeatures. Silicified ferruginous crusts in some Andisols result from silica releasing during weathering of volcanic ash in dry soils (Chadwick et al., 1987; Buol et al., 2011), a process enhanced by earthworm activity (Cantil et al., 2020). Lack of carbonates and the presence of clay skins, ferruginous nodules and high biomass (at least below-ground) inferred by abundant trace fossils and the diffuse boxwork ichnofabric, suggest temperate-warm, seasonal subhumid conditions. This climate is similar to that of the unit in northwestern Chubut province (Bellosi et al., 2014; Bucher et al., 2019b; Cantil et al., 2020) and southern Neuquén province (D'Elia et al., 2020). The assemblage of insect trace fossils corresponds to the *Coprinisphaera* Ichnofacies, ascribed to open plant communities dominated by grasses (Genise et al., 2000; Genise, 2016). This is validated by the mollic Andisols and Mollisols and by the abundant grass phytoliths recovered from paleosol and *Coprinisphaera* samples from Paso del Sapo basin (Cantil et al., 2020). Altogether, these data suggest a plant community comparable to grass savannas. The time of development ("passive factor") is linked to landscape stability and successional colonization, in turn manifested in the degree of development of paleosols (Retallack, 2001). In the inferred La Pava paleo-landscape, with extensive sheets of tephric loess, environment stability was mainly governed by frequency and intensity of ash fallouts (Bellosi, 2010; Bellosi and Krause, 2014). Thus, weaker developed paleosols that record early successional communities under frequent and intense ash fallouts lack or include very scarce insect trace fossils; while stronger developed paleosols, which register stable landscapes and intermediate to late-successional communities, bear a high number of insect trace fossils.

4. Systematic ichnology

Ichnofamily Coprinisphaeridae Genise, 2004
Ichnogenus *Racemusichnus* Sánchez, Genise and Bellosi igen. nov. urn:lsid:zoobank.org:act:6176BD43-EF18-4D9F-9175-56349A1217CB
Type ichnospecies. *Racemusichnus jacobacciensis* isp. nov., only known ichnospecies.

Diagnosis. Horizontal cluster of 2–7 slightly curved or sinuous cylinders, each one showing a circular aperture at one extreme (proximal) and a rounded and blind end at the opposite extreme (rear), a discrete thick wall with a rough internal surface, and a circular outline in cross-section. The internal cavity mostly contains a passive filling or it is empty. In clusters with more regular shape, cylinders may be aligned and/or interspersed with their apertures on the same vertical plane and sharing part of its walls, or they may be opened at different planes in the more irregular clusters.

Remarks. *Racemusichnus* is included in the ichnofamily Coprinisphaeridae because the chambers that composed the cluster are surrounded by a discrete thick wall, which can be easily detached from the matrix (Fig. 2B). There are no other Coprinisphaeridae similar to *Racemusichnus*. *Quirogaichnus* is the only ichnogenus of the ichnofamily that is composed of several chambers, but the latter are small loose spheroids clustered in an excavated chamber. The remaining ichnogenera never show clusters. Outside Coprinisphaeridae, the presence of clusters is very common in Celliformidae. There are three ichnogenus showing clusters: *Uruguay*, *Rosellichnus* and *Corimbatichnus*, but all of them are composed of small cells with different arrangement, preserving spiral closures and discrete walls in the two former, or devoid of discrete walls and opened to a convex surface in the later. All of those characters are absent in *Racemusichnus*. Finally, another ichnogenus comparable with the new one is *Loloichnus* that is described as mainly straight to gently curved, vertical to oblique, thickly lined burrow of constant diameter and with blunt ends. In both ichnogenera, the burrows/

cylinders show a circular to sub-circular cross section and a relatively thick wall. The burrows of *Loloichnus* differ from the cylinders of the new *R. jacobacciensis* in its orientation in the paleosol (i.e. major axes vertical/oblique versus horizontal), absence of clustering (i.e. burrows do not share the wall, sometimes are only in contact), bioglyphs on its inner surfaces (*R. jacobacciensis* cylinders lack bioglyphs), and its blunt extremes, whereas in *Racemusichnus* the rear is blind and rounded.

Occurrence. All the specimens collected (n = 11, MJHG-NCP 177–179, 189, 216–222), came from the middle Miocene La Pava Formation at Estancia Huanuluan-Cantera Nueva, Ingeniero Jacobacci (Río Negro province, Argentina), and are housed in the Museo de Ciencias Naturales, Antropológico e Histórico "Jorge H. Gerhold", Ingeniero Jacobacci (Río Negro province, Argentina).

Etymology. *Racemus*, derived from the Latin, and meaning a crowded set of things arranged with some cluster resemblance (the new ichnospecies looks like a bunch of bananas); and *Ikhnos*, derived from the Greek, meaning trace.

Racemusichnus jacobacciensis Sánchez, Genise and Bellosi isp. nov. urn:lsid:zoobank.org:act:80A100BB-1C46-474C-8729-38709F2AF32F.
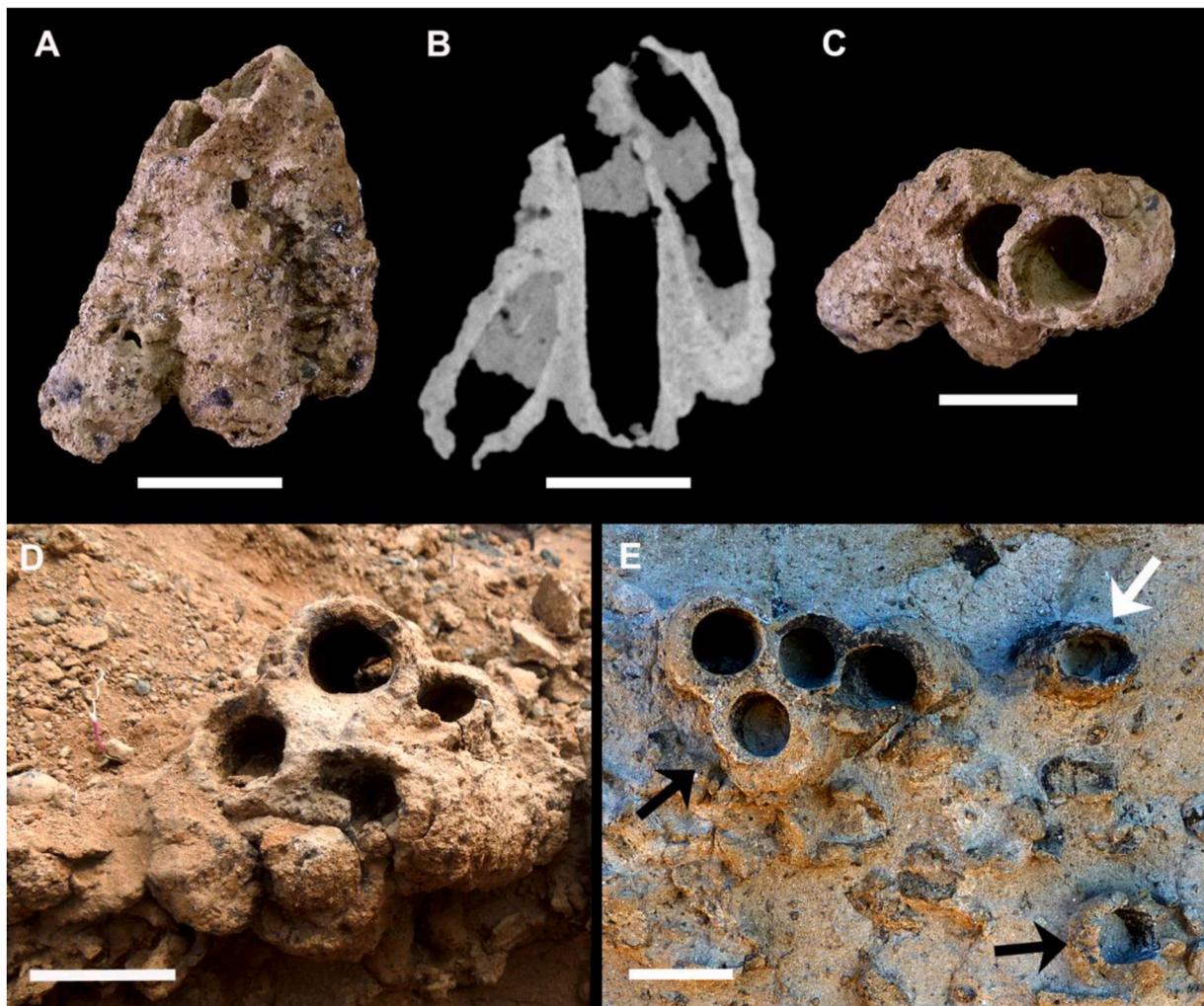
Holotype. MJHG-NCP 189 a-c, a cluster composed of three cylinders, came from the middle Miocene La Pava Formation at Estancia Huanuluan-Cantera Nueva, Ingeniero Jacobacci (Río Negro province, Argentina).

Paratype. MJHG-NCP 178 a-f, a cluster composed of six cylinders, came from the middle Miocene La Pava Formation at Estancia Huanuluan-Cantera Nueva, Ingeniero Jacobacci (Río Negro province, Argentina).

Etymology. After Ingeniero Jacobacci (Río Negro province), the city near the localites where all specimens were collected.

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

Description. Considering the arrangement of the cylinders in the cluster, the more common regular ones show the apertures opened more or less in the same vertical plane, and up to 3 cylinders aligned in a row (Fig. 4C, E). In some clusters the aperture of one cylinder can be blocked by other cylinder. In the irregular cases, the cylinders are horizontal displaced, showing its apertures in different vertical planes. The measurements of the specimens described below are displayed in Table 1. The holotype (MJHG-NCP 189) is composed of three complete, aligned curved cylinders parallel to each other, with different long axis inclination relative to the horizontal plane (Fig. 4A–C). The cylinder 189a shows no aperture because its proximal extreme is blocked by the middle cylinder (189 b). The latter shows the aperture partially blocked by 189c, which shows its aperture totally open. The cluster shows specimens of *Lazaichnus fistulosus* Mikuláš and Genise (2003). The paratype (MJHG-NCP 178) is composed of six incomplete, straight cylinders, broken near the rears (Fig. 4D). In five of them (178a-e), the apertures are roughly in the same vertical plane and almost in contact with each other, sharing parts of its walls. In the sixth cylinder (178f), the proximal extreme is located in another vertical plane, between 178b and c, and emerging about the middle length of them. Only two of the six are preserved as almost complete cylinders (178c and e) with an opened aperture. Some cylinders show specimens of *Lazaichnus fistulosus* Mikuláš and Genise (2003). On the external surface of the wall of 178 d there are preserved two attached curved cells, one of them preserved as a wall fragment, and the other as a complete cell, 30 mm long and 13 mm in maximum diameter (MJHG-NCP 240). These cells are comparable with those of the *Rosellichnus patagonicus* Genise and Bown (1996). One of the cells is connected with a horizontal tunnel that intersects 178e, emerging from its rear. Specimen MJHG-NCP 177 is also composed of six cylinders, but only three (177a-c) are relatively complete structures that are slightly curved, roughly parallel to each other, and showing one of its extremes (proximal?) opened almost in the same vertical plane. The cylinder 177d is a small fragment, located between 177a and c, and its long axis is inclined 45° with respect to 177a. Cylinders 177e and f are smaller fragments that are located between 177a and b, and cross-cut each other. In these fragmented cylinders, the

Fig. 4. *Racemusichnus jacobacciensis* igen. isp. nov., new trace fossil from the middle Miocene La Pava Formation at the Rio Negro province, Argentina. (A) Top view of the holotype (MJHG-NCP 189) composed of three complete and curved cylinders aligned in a row. The orientation of the cluster is horizontal in the paleosol; (B) CT image of the holotype (MJHG-NCP 189) showing well defined cylinders; (C) Front view of the holotype (MJHG-NCP 189) showing the proximal extremes of the cylinders, two of them opened and only one showing the complete section; (D) The paratype (MJHG-NCP 178) *in situ* in the paleosol; (E) Section of a paleosol preserving two specimens of *Racemusichnus jacobacciensis* (black arrows), one as a cluster and the other as a single cylinder, and a specimen of *Teisseirei barattinia* (white arrow). Scale bars = 5 cm.

internal surface of the wall is exposed showing very small pits and ir-regularities. In two cases (177b and c), there are also preserved circular to elongated pits, 2–4 mm in diameter and 5–7 mm long, which are assigned to *Tombownichnus pepei* Sánchez and Genise (2009). This identification is tentative because they show no ovoid mound preserved. Specimen MJHG-NCP 179 is composed of 5 cylinders; two of them (179a-b) are aligned, with 179c interspersed between them, all preser-ving the apertures more or less in the same vertical plane and sharing part of its walls. Only one, 179c, is a complete structure preserving the rear. Cylinders 179d and 179e are fragments located between 179a and b. The cylinder 179d is parallel to 179b, and 179e cross-cut 179d almost perpendicularly. The only entire cylinder (179c) preserves a rhizolith (58.4 mm long and 8 mm width) on the external surface of its wall. Specimen MJHG-NCP 220 is composed of three incomplete cylinders (220a-c), two of them are parallel (220a and b) and the remaining (220c), which is preserved as a small longitudinal fragment of the wall, is interspersed and in contact with the other two. The cylinders 220a and 220b are slightly curve. Both show irregular inner surfaces of the wall, and cylindrical borings crossing the whole wall that are compatible with *Tombownichnus plenus* Mikuláš and Genise (2003). Cylinder 220a also preserves circular to elongated pits without ovoid mounds, excavated in the internal surface of the wall that could be tentatively attributed to

Tombownichnus pepei Sánchez and Genise (2009). Specimen MJHG-NCP 221 is composed of three incomplete cylinders (221a-c) that are simi-larly distributed than in the previous case, and one of them (221c) is also preserved as a longitudinal fragment of the wall revealing its internal surface. The cylinders 221a and 221b are slightly curve, and aligned. The internal surfaces of both show a manganese coating and tiny rhi-zoliths. Specimen MJHG-NCP 222 is composed of three incomplete cylinders (222a-c), aligned and parallel, arranged as in the holotype (MJHG-NCP 189). The cylinder 222a is preserved as a small fragment of the wall attached to the cylinder 222b, which is located between the former and 222c. The latter are strongly curved. Specimen MJHG-NCP 223 is composed of 7 incomplete cylinders clustered as follows: 223c, d and f are aligned and parallel arranged, sharing the walls at different points along its long axes; 223e is interspersing 223c and 223d; 223g is located perpendicularly over 223c and f, and crisscrossed by 223e; 223a and 223b are aligned each other, and parallel to 223c-d-f, but with their long axes inclined about 30° with respect to the axes of the former three. The cylinders 223a (curve) and 223b (sinuous) are longitudinal frag-ments revealing the internal surface of the wall. The cylinders 223c (curved), 223d (sinuous) and 223f (straight) are fragments showing no rears preserved. The cylinder 223e is sinuous and without rear, and 223g is a straight fragment preserved as a longitudinal portion of the wall. The

Table 1

Measurements of *Racemusichnus jacobacciensis* igen. isp. nov. specimens. The bold letters in the collection numbers indicate which cylinder is complete in the cluster. All measurements are in mm.

MJHG-NCP	Cylinders of the cluster	Length	Diameter	Aperture	Wall thickness
177	**Aa**	88.7	31.2		7.0
	b	89.6	32.8		6.3
	c	112.0	36.6		8.0
	d	52.0			6.4
	e	35.0			
	f	50.0			
178	a	97.5	33.3		4.2
PARATYPE	b	104.6	32.5		6.5
	c	114.8	30.5	18.9	6.7
	d	86.1	32.5		6.0
	e	112.1	31.2	21.0	5.8
	f	39.0	24.2		3.9
179	a	96.4	33.2		4.9
	b	89.2	26.6		4.4
	c	91.0	33.5		4.3
	d	65.0	20.3		5.6
	e	40.0	23.5		5.6
189	**a**	129.0	37.3		
HOLOTYPE	**b**	112.0	35.4	23.4	5.2
	c	113.6	37.4	22.9	7.2
220	a	107.0	34.2		5.9
	b	98.0	30.0		4.0
	c				
221	a	71.5	30.0		5.8
	b	78.0	30.1		5.1
	c	69.0			5.4
222	a	59.6			5.6
	b	109.0	31.1		7.8
	c	100.0	33.6		6.8
223	**a**	98.0	31.7		7.1
	b	109.0	29.0		6.3
	c	71.0	31.0		4.6
	d	91.5	34.1		7.2
	e	93.1	38.3		8.5
	f	69,1	31.8		7.1
	g	95.5			7.4
224	a	79.1	32.2		7.5
	b	82.0	36.0		8.9
	c	83.6			6.5
225	**a**	97.7	36.0		6.9
	b	87.0	28.9		6.0
	c	60.0	27.8		6.7

internal surfaces of all the cylinders are partially covered by manganese and tiny rhizoliths. The specimen MJHG-NCP 224 is composed of three fragmentary cylinders: 224a is preserved as a longitudinal fragment of the wall located parallel to 224b, which is a long fragment crisscrossed by 224c that is preserved as a longitudinal and curved fragment of the wall. A specimen of *Tombownichnus plenus* Mikuláš and Genise (2003) is boring the wall of the cylinders 224a and 224b. The specimen MJHG-NCP 225 is composed of three cylinders, one preserved as a long fragment (225a), and the other two as a longitudinal fragments of the wall (225b y c). The two former are aligned and parallel arranged each other, whereas 225c shows its long axis slightly inclined (10° approximately) related to the long axes of the other two. The cylinder 225a is crisscrossed by 225c near its rear. The cylinder 225a is straight, whereas 225b and 225c are curve. The former preserves a rounded hole (14 mm in diameter) excavated in its wall 20 mm from an extreme, which also crosses the wall of 225b. The whole cluster shows specimens of *Lazaichnus fistulosus* Mikuláš and Genise (2003).

Ichnogenus *Coprinisphaera* Sauer, 1955

Coprinisphaera murguiai (Roselli, 1939).

Diagnosis. Spherical to sub-spherical chambers with a discrete wall, that shows at one pole a medium-sized hole (about ¼ of its diameter). There are no remains of a secondary chamber or additional structures (modified from Genise, 2016).

Occurrence. All specimens collected came from the La Pava Formation: five specimens from EHCNI (MJHG-NCP 103, 104, 147–149); six specimens from EHN (MJHG-NCP 65, 66, 70–73); nine specimens from EHCN (MJHG-NCP 151, 152, 154, 156, 157, 160, 214–216); ten specimens from CB (MJHG-NCP 86–88, 92, 95, 96, 98–101); and five specimens from NK (MJHG-NCP 90–93, 95).

Description. Specimens are 24.5–75.4 mm in equatorial diameter (mean: 51.1 mm, n = 35), 25.6–67.1 mm high (mean: 48.8 mm, n = 35), the wall is 2.9–17.8 mm thick (mean: 11.2 mm, n = 26), and the medium-sized diagnostic hole is 6.5–17.8 mm in diameter (mean: 12.4 mm, n = 34) (Fig. 5A). Seven specimens (MJHG-NCP 66, 70, 72, 73, 103, 151, and 216) preserve small irregular tunnels excavated in the wall and infillings that are attributable to *Lazaichnus fistulosus* Mikuláš and Genise (2003). Four specimens (MJHG-NCP 101,152, 160, 196) show *Tombownichnus plenus* Mikuláš and Genise (2003), 4–7 mm in diameter, excavated in the wall. The mean size of *Coprinisphaera murguiai* measured by locality is: EHN: 47.4 mm in equatorial diameter and 44 mm high (n = 6); EHCNI: 51.5 mm in equatorial diameter and 49.7 mm high (n = 5); EHCN: 59.2 mm in equatorial diameter and 55.5 mm high (n = 9); CB: 45.8 mm in equatorial diameter and 43.3 mm high (n = 10); NK: 51.2 mm in equatorial diameter and 52.5 mm high (n = 5). *C. murguiai* shows the largest specimens (n = 6) of all recorded ichnospecies and all of them come from EHCN (ED: 60.0–75.4 mm) (Fig. 5A).

Coprinisphaera lazai Sánchez et al., 2013.

Diagnosis. Spherical to sub-spherical chambers with a discrete wall, that shows at one of its poles, a hemispherical, small chamber whose concavity is opened to the exterior. This secondary chamber occupies all the wall thickness and shows a narrow passage in the center that connects it to the main chamber (modified from Genise, 2016).

Occurrence. All specimens collected came from the La Pava Formation: one specimen from EHN (MJHG-NCP 74); one specimen from EHCN (MJHG-NCP 155); one specimen from CB (MJHG-94); and one specimen from NK (MJHG-NCP 195).

Description. Specimens are 28.6–68.1 mm in equatorial diameter (mean: 46.6 mm, n = 4), 27–68.8 mm high (mean: 44.4 mm, n = 4), and the wall is 4–15.4 mm thick (mean: 9.7, n = 2) (Fig. 5B). The hemispherical secondary chamber is 7.7–12.9 mm in diameter (mean: 10.1, n = 4), and the narrow passage between chambers is 2.5–6.4 mm wide (mean: 4.3 mm, n = 4). Comparing the size of the four specimens of *Coprinisphaera lazai*, each one belonging to different localities the specimen from EHCN (MJHG-NCP 155) is the largest in equatorial diameter and height, which are 68.1 mm and 68.8 mm, respectively.

Coprinisphaera tonnii Laza, 2006.

Diagnosis. Pear-shaped and thick walled *Coprinisphaera* internally composed of a main chamber and a secondary, smaller one, located in the upper protuberance. Both chambers are not separated externally by a deep neck or constriction but internally are clearly apart and may be connected by a small passage (taken from Cantil et al., 2013).

Occurrence. All specimens collected came from the La Pava Formation: one specimen from EHN (MJHG-NCP 67), and another from EHCNI (MJHG-NCP 146).

Description. Specimens are 40–43.9 mm in equatorial diameter (mean: 41.9 mm, n = 2), 43.8–48.8 mm high (mean: 46.3 mm, n = 2), and the wall is 10.3–10.7 mm thick (mean: 10.5 mm, n = 2). The secondary chamber is 6.6–6.8 mm in diameter (mean: 6.7 mm, n = 2) (Fig. 5C). One specimen (MJHG-NCP 146) shows a small passage connecting both chambers that is 7.7 mm wide. The remaining specimen (MJHG-67) preserves *Lazaichnus fistulosus* Mikuláš and Genise (2003).

Coprinisphaera akatanka Cantil et al., 2013.

Diagnosis. Bi-spherical and thin-walled *Coprinisphaera*. They consist of a main, larger chamber and a secondary, smaller one, externally separated by a deep neck or constriction. Internally, both chambers may be connected by a rounded and open passage (Cantil et al., 2013).

Occurrence. One specimen collected that came from the transition La Pava-Collón Curá Formations at EHN (MJHG-NCP 69).

Description. The specimen is 28.5 mm in equatorial diameter and
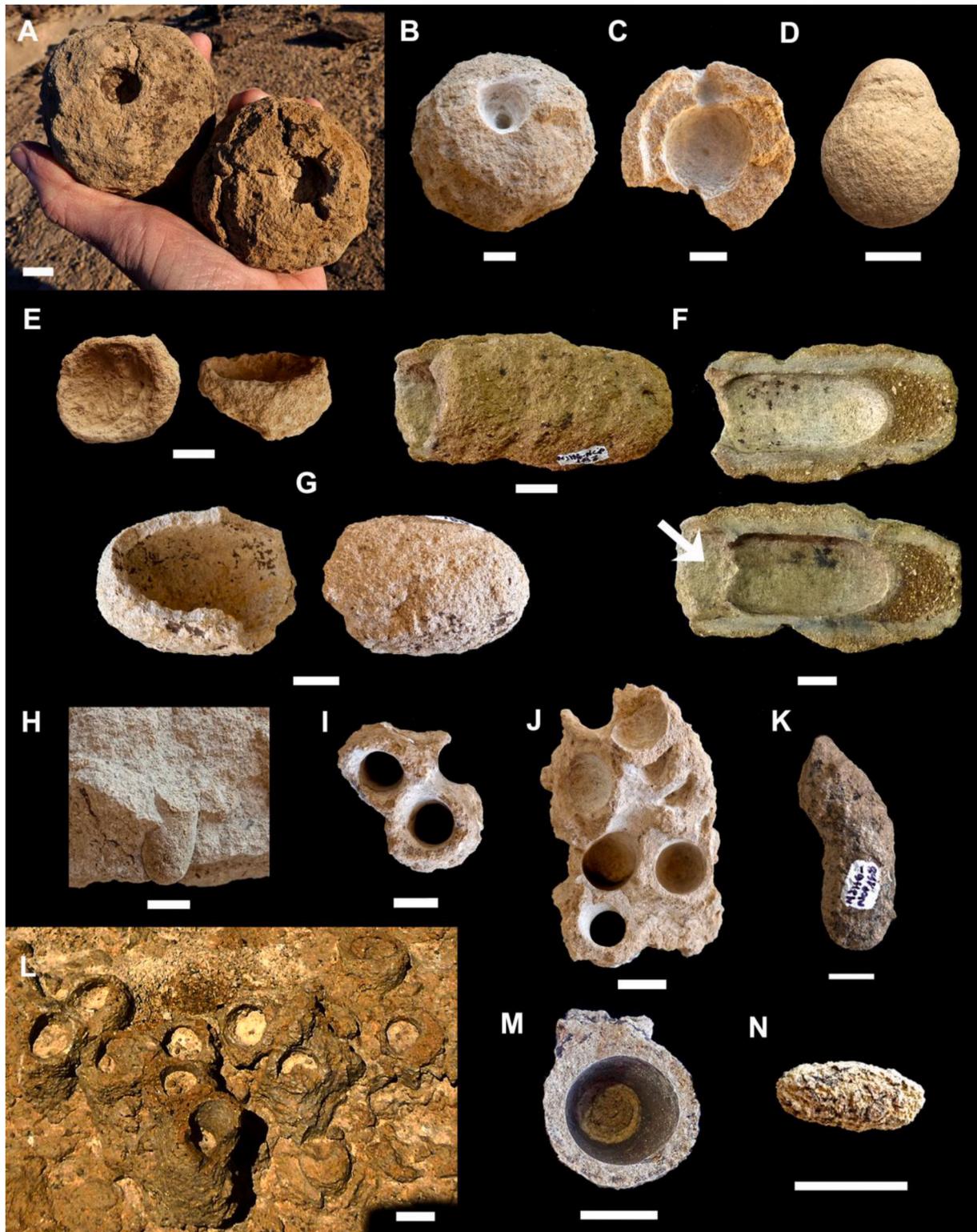
Fig. 5. Other insect traces from the middle Miocene La Pava Formation at the Rio Negro province, Argentina. (A) Two large specimens of *Coprinisphaera murguiai* photographed in the field; (B) *Coprinisphaera lazai* (MJHG-NCP 94); (C) *Coprinisphaera tonnii* (MJHG-NCP 69); (D) *Coprinisphaera akatanka* (MJHG-NCP 67); (E) A specimen of *Feoichnus challa* (MJHG-NCP 115) showing the upper concave surface (left) and the lateral aspect (right); (F) A specimen of *Teisseirei barattinia* (MJHG-NCP 183) showing the external aspect (left) and the longitudinal section (right) displaying the main chamber, antechamber (white arrow), the wall and the rear composed of a double layer separated by a porous zone; (G) A specimen of *Rebuffoichnus casamiquelai* (MJHG-NCP 159) showing a thin, smooth and well defined wall (left), and the external surface (right); (H) Side view of a *Celliforma rosellii* (MJHG-NCP 60) preserved as a cast in the paleosol; (I) *Rosellichnus patagonicus* (MJHG-NCP 164) composed of a row of two almost complete cells in contact with a fragment of a third one; (J) Top view of *Rosellichnus patagonicus* (MJHG-NCP 175) showing superimposed rows of cells; (K) External aspect of an isolated cell (MJHG-NCP 168) of *Rosellichnus patagonicus* showing the curved neck; (L) Top view of *Rosellichnus patagonicus in situ*; (M) Cross section of other isolated cell (MJHG-NCP 166) showing the spiral cap; (N) A specimen of *Fictovichnus gobiensis* (MJHG-NCP 77). Scale bars = 1 cm.

26.8 mm high, with a wall 3.3 mm thick (Fig. 5D). The secondary chamber is 17.8 mm in equatorial diameter and 10.8 mm high, with a wall 5.3 mm thick. Both chambers are connected by a passage 6.4 mm wide. This single specimen was only found in the level that records the transition between La Pava and Collón Curá Formations at EHN in the Río Negro province. In contrast, *C. akatanka* was frequently recorded in localities of the La Pava Formation from the Chubut province (Cantil et al., 2020).

Coprinisphaera ispp.

Occurrence. All the specimens collected came from the La Pava Formation: one specimen from EHN (MJHG-NCP 68); one specimen from EHCN (MJHG-NCP 153); eight specimens from CB (MJHG-NCP 84, 85, 89–91, 93, 97, 102); and one specimen from NK (MJHG-NCP 202).

Description. Specimens grouped in this section are fragmentary showing no diagnostic characters, which are 40.6–70.9 mm in equatorial diameter (mean: 49.3 mm, n = 11), 38.8–48.6 mm high (mean: 43.4 mm, n = 4), whereas the wall is 7.3–16 mm thick (mean: 10.1 mm, n = 10). Three specimens (MJHG-NCP 99, 102, 153) show other traces excavated in the wall, as small burrows and holes, attributable to *Lazaichnus fistulosus* Mikuláš and Genise (2003) and *Tombownichnus plenus* Mikuláš and Genise (2003), respectively. The mean size of *Coprinisphaera* ispp. measured by locality is: EHN: 48.5 mm in equatorial diameter and 38.8 mm high (n = 1); CB: 47.8 mm in equatorial diameter (n = 8) and 44.9 mm high (n = 4); EHCN: 70.9 mm in equatorial diameter (n = 1); NK: 40.6 mm in equatorial diameter (n = 1).

Ichnogenus *Feoichnus* Krause et al., 2008

Feoichnus challa Krause et al., 2008.

Diagnosis. Usually hemispherical, upwardly concave, pan or dish-shaped structures, more rarely conical, and lacking any active filling. Internal surface is lined, smooth and regular, or in some cases with a surface texture constituted by irregular ridges with a knobbly appearance. External surface is rough and irregular, without ornamentation. Some specimens may show a succession of several lined layers at the base or laterally. A common feature is the presence laterally of a small, sub-vertical to sub-horizontal groove, which in some cases shows a smooth surface with longitudinal striations or arise from a hole in the wall (Krause et al., 2008).

Occurrence. All specimens collected came from the La Pava Formation: thirty eight specimens from EHCNI (MJHG-NCP 105–124; 128–145) and four specimens from NK (MJHG-NCP 201; 203–205).

Description. Specimens are 12.5–37.3 mm in external diameter (mean: 27.9 mm, n = 42), 7.3–44.1 mm high (mean: 23.9 mm, n = 42), the lateral wall is 1.9–10 mm thick (mean: 4.7 mm, n = 42), the depth is 2.2–24.1 mm (mean: 11.8 mm, n = 41), and the base is 6.8–19.6 mm thick (mean: 12.2 mm, n = 16) (Fig. 5E). The specimens are conical (n = 22) or more pan-shaped (n = 20). Eleven specimens (MJHG-NCP 108, 110, 111, 114, 119, 123, 133, 136, 141, 143, and 144) show a sub-vertical to sub-horizontal groove excavated on the external surface of the wall. Some specimens show an irregular texture in the concave surface but no clear ridges with a knobby appearance as can be observed in specimens of other localities. Six specimens (MJHG-NCP 107, 109, 111, 115, 121, and 134) preserve *Lazaichnus fistulosus* Mikuláš and Genise (2003). Considering the external diameter, the specimens of *Feoichnus challa* coming from EHCNI show a size ranging from 12.5 mm to 37.3 mm (mean: 27.9 mm, n = 38). In the case of NK, the size of the few specimens collected range from 21.2 mm to 31.3 mm (mean: 27.7 mm, n = 4).

Ichnogenus *Teisseirei* Roselli, 1939

Teisseirei barattinia Roselli, 1939.

Diagnosis. Elongated, sub-cylindrical, horizontal to sub-horizontal structures, depressed all along its length, with an elliptical cross-section and a multilayered wall. A circular aperture located at one end, may be preceded by a rounded, non-depressed antechamber, separated from the main chamber by a constriction. The opposite end is rounded and blind. The internal surface of the chamber may bear densely packed, short, sub-rectangular to sub-triangular pits, covering the entire surface (taken from Genise et al., 2013).

Occurrence. All specimens collected came from the La Pava Formation: two specimens from EHN (MJHG-NCP 75, 76); eighteen specimens from EHCN (MJHG-NCP 158, 161–163, 180–188, 217–219, 227, 228); one specimen from CB (MJHG-NCP 80); and three specimens from NK (MJHG-NCP 197–199).

Description. Specimens are preserved as empty or filled chambers, 47.2–100 mm long (mean: 70.9 mm, n = 17), 25.7–62.4 mm wide (mean: 40.6 mm, n = 24), and 23–53.7 mm high (mean: 35.2 mm, n = 19). Specimens show a distinct wall that is 5.5–13.7 mm thick (mean: 9.2 mm, n = 24) (Fig. 5F). The antechamber is 7.5–23.7 mm long (mean: 15.1 mm, n = 15), 15.2–31.5 mm wide (mean: 21.9, n = 14), 13.1–21.5 mm high (mean: 18.4 mm, n = 12), and the constriction between chamber and antechamber is 12.1–23.2 mm in diameter (mean: 16.8 mm, n = 14). Eight specimens (MJHG-NCP 161, 181, 182, 184, 187, 217, 218, 228) show the wall of the rear end composed of a double layer separated by a more porous zone (Fig. 5F). This is a new character not described before for this ichnospecies. Six specimens (MJHG-NCP 75, 182, 186, 187, 217, 228) show small holes, 2.4–9 mm in diameter, perforating the wall, which are attributable to *Tombownichnus plenus* Mikuláš and Genise (2003). Six specimens (MJHG-NCP 80, 163, 180, 184, 187, and 188) show *Lazaichnus fistulosus* Mikuláš and Genise (2003). One specimen (MJHG-NCP 198) preserves two small, close and elongated chambers, 5 mm long, excavated on the internal surface of the wall that could be compatible with *Tombownichnus pepei* Sánchez and Genise (2009). The size of *Teisseirei barattinia* measured by locality is: EHN: 52.7 mm long (n = 1) and 33.5–44.0 mm wide (mean: 38.8 mm, n = 2), EHCN: 50.8–100 mm long (mean: 74.8 mm, n = 14), 29.1–62.4 mm wide (mean: 41.9 mm, n = 18) and 23–53.7 mm high (mean: 36 mm, n = 17), CB: 47.2 mm long and 25.7 mm wide (n = 1), and NK: 57.5 mm long (n = 1), 31.2–46.9 mm wide (mean: 38.7 mm, n = 3) and 26.5–29.4 mm high (mean: 28.0 mm, n = 2).

Ichnogenus *Rebuffoichnus* Roselli, 1987

Rebuffoichnus casamiquelai Roselli, 1987.

Diagnosis. Sub-cylindrical to oblate, horizontal to sub-horizontal structures whose exterior aspect of the wall is rough or lumpy, whereas the interior is smooth or shows a faint surface morphology. The ellipsoidal internal chamber has circular cross section and shows no antechamber. The wall may be perforated by a rounded medium size hole either terminal or medial (modified from Genise, 2016).

Occurrence. The specimen collected (MJHG-NCP 159) came from the La Pava Formation at EHCN.

Description. The specimen is preserved as a fragment, 38.1 mm long and 28.6 mm in diameter, with a thin, smooth and well defined wall, 3.2 mm thick. There are no remains of fillings (Fig. 5G).

Ichnofamily Celliformidae Genise, 2000

Ichnogenus *Celliforma* Brown, 1934 *Celliforma rosellii* Genise and Bown, 1994.

Diagnosis. Cylindrical to barrel shaped chambers preserved as empty spaces in the rock matrix or as their internal molds. They show a rounded bottom and a flat top, which may be slightly depressed and with a surrounding rim (modified from Genise, 2016).

Occurrence. Two specimens came from the La Pava Formation at CB (MJHG-NCP 82) and NK (MJHG-NCP 200); five specimens came from the transition La Pava-Collón Curá Formations at EHN (MJHG-NCP 60–64).

Description. The specimens are preserved as empty flask-like structures or as a cast with their long axes vertically oriented in the rock matrix (Fig. 5H). They are incomplete, 11.1–17.6 mm long (mean: 14.2 mm, n = 6), whereas the most complete one (MJHG-NCP 64) is 27.1 mm long. Maximum diameters range from 8.5 mm to 12.7 mm (mean: 10.3 mm, n = 7). Specimens collected in EHN (in Collón Curá deposits) show a lining of dark material, probably manganese oxide, which covers partial or completely the internal surface of the chamber. There are no remains of a discrete wall surrounding the cells.

Ichnogenus *Rosellichnus* Genise and Bown, 1996.

Rosellichnus patagonicus Genise and Bown, 1996

Diagnosis. Cluster of vertical and parallel cells with discrete linings and smooth inner surfaces, which are arranged in one or two rows. Cell bottoms are rounded, whereas the tops may be flat or exhibit curved necks. The cells are mostly open and the upper part of the cluster is flat (modified from Sarzetti et al., 2017).

Occurrence. All collected specimens came from the La Pava Formation: seven clusters (MJHG-NCP 150, 164, 174, 175, 209–211) and 12 isolated cells (MJGH-NCP 165–168, 170–173, 207, 208, 212, 213) from EHCN; three isolated cells from EHCNI (MJHG-NCP 125–127) and one from CB (MJHG-NCP 78).

Description. Clusters are composed of two to five vertical and parallel cells arranged in one to two rows. When two rows are present cells of one row accommodate between two consecutive cells of the other row, resembling a comb-like arrangement (Fig. 5I and J). Cells are open, no spiral cup is preserved, and some cells show remains of the curved neck. From the seven collected specimens, only one is composed of two attached cells preserving the base of the curved neck (MJHG-NCP 211). The cluster MJHG-NCP 209 is composed of three almost complete cells, arranged in a triangle (one of them preserving the base of the curved neck), and MJHG-NCP 150 and 164 are composed of two almost complete and attached cells in contact with a longitudinal fragment of a third cell (Fig. 5I). The cluster MJHG-NCP 210 is composed of a row of three almost complete cells, one of them preserving the base of the curved neck, and a fourth cell of other row in contact with two of the former. The remaining two clusters (MJHG-NCP 174 and 175) are composed of five cells, both showing undefined rows (Fig. 5J). These specimens preserved attached cells at different levels. Some cells show parts of the curved necks and in both specimens some bottoms of other fragmented cells are located on these necks. These cases are probably reflecting cross-cutting relationships of independent clusters constructed at different times (Fig. 5L). The cells of the clusters are 21.1–46 mm long (mean: 32.4 mm, n = 14), 10–18.4 mm in maximum diameter (mean: 14.2 mm, n = 18), and the wall is 2.3–4.1 mm thick (mean: 3.1, n = 24). Isolated cells (n = 16) show the same morphology of those in the clusters, and are recovered from the same paleosol as more complete cells preserving well-defined curved necks (Fig. 5K). Most specimens are open, but five of them preserve the spiral cap (MJHG-NCP 166–168, 171, 207) (Fig. 5M), character that is reported here for the first time (Sarzetti et al., 2017). These cells are 16.1–47.6 mm long (mean: 33.1 mm, n = 14), 13.7–16.3 mm in maximum diameter (mean: 15 mm, n = 14), and the wall is 1.9–3.7 mm thick (mean: 2.6 mm, n = 15).

Ichnofamily Pallichnidae Genise, 2004.

Ichnogenus *Fictovichnus* Johnston et al., 1996. *Fictovichnus gobiensis* Johnston et al., 1996.

Diagnosis. Ellipsoid to ovoid chambers, horizontal to sub-horizontally oriented, showing rounded extremes and smooth surface in casts detached from matrix. There is no flat surface near one extreme (modified from Genise, 2016).

Occurrence. The specimen collected (MJHG-NCP 77) came from the La Pava Formation at CB.

Description. The specimen is preserved as an ellipsoidal internal cast, 13 mm long and 5.8 mm in maximum diameter (Fig. 5N). The outer cast preserved in the rock matrix was not collected but recorded by photographs.

Ichnofamily indet. *Loloichnus baqueroensis* Bedatou et al., 2008.

Diagnosis. Mainly straight to gently curved, vertical to oblique, thickly lined burrows of constant diameter. They are mostly passively-filled and sub-circular in cross section, upward Y-branching and pelletal fillings may be present. Inner surface of lining showing transversal, parallel, and adjacent elongated grooves, which are semicircular in cross section. The burrow filling, when detached from the lining may show a knobby surface texture. Burrow endings are blunt and chambers are absent (Bedatou et al., 2008).

Occurrence. All specimens came from the La Pava Formation at NK: twenty specimens distributed as follow: MJHG-NCP 229–235 individual specimens, MJHG-NCP 236 and 237: two samples with three specimens each one, MJHG-NCP 238: a sample with two specimens, and MJHG-NCP 239: a sample with five specimens.

Description. Specimens are vertical to oblique burrows, empty or passively-filled, with a discrete wall. These traces are preserved in dense patches in the paleosol where individual burrows show different orientations. In some cases, its walls are in contact each other and samples were collected as groups of burrows. They are 25.5–98 mm long (mean: 67.2 mm, n = 19), 26–33.4 mm wide (mean: 30.6 mm, n = 16), and the wall is 4.9–10.1 mm thick (mean: 6.8 mm, n = 20).

5. Discussion

5.1. Interpretation of <u>Racemusichnus jacobacciensis</u> and the analysis of its possible trace makers

The cluster arrangement, its orientation (sub-horizontal to horizontal), the large size and the well defined wall of its cylinders give to this trace a distinctive combination of characters that enables the creation of a new ichnogenus. Only a few specimens were found in the paleosol preserved as individual cylinders, so we infer that these specimens could represent a first step of the cluster construction.

Each cylinder as well as clusters of the new trace fossil resembles nesting structures constructed by some coprophagous dung beetles among Scarabaeidae (Scarabaeinae) and Geotrupidae (Taurocerastinae and Geotrupinae) (Halffter and Edmonds, 1982) (Fig. 6). These dung beetles construct nests that are mainly composed of excavated burrows in the soil below dung pads, in some cases forming galleries. Some burrows are built to house brood masses, which according to the definition by Halffter and Edmonds (1982), are a quantity of provision (dung or carrion), receiving an egg, which has been packed into the blind end of a tunnel or tunnel branch, or into an enlargement of a tunnel. The shape is determined by the original cavity. It can be cylindrical (i.e., sausage shaped) to oval or spheroid. The chamber housing the egg can be located in different positions inside the provision. The cylindrical brood masses resemble *R. jacobacciensis*.

Among the Scarabaeidae, species of Onthophagini and Onitini, and some of Oniticellini, Dichotomiini, Ateuchini, and Phanaeini (Scarabaeinae) are typical producers of cylindrical brood masses. Some examples are species of *Digitonthophagus, Onthophagus, Bubas*, *Onitis*, *Chironitis, Euoniticellus, Dichotomius, Canthidium, Ateuchus, Gromphas,* and *Oruscatus,* among others (Fabre, 1897; Halffter and Edmonds, 1982; Cabrera Walsh and Gandolfo, 1996; González-Vainer and Morelli, 1999; Salerno and Zunino, 2002; Sánchez and Genise, 2008; Genise, 2016; and pers. obs. by MVS). These species show differences mostly related to the number, morphology and distribution of the brood masses in the nests and number and position of the egg inside the brood masses. Most of them are coprophagous, but a few are necrophagous (*Canthidium* sp.) or use debris of ants as provision (*Ateuchus* sp.). The analysis of these differences allows us to refine the possible affinities of *R. jacobacciensis*. *Digitonthophagus gazella* (F.) constructs simple (one brood mass per nest) or compound (more than one brood mass per nest) nests. The former is represented by an elongated brood mass at the bottom of the main shaft. The compound nests show short brood masses arranged in a line along a shaft, vertical or with some inclination, or elongated brood masses in a row and in lateral contact each other (Sánchez et al., 2012)(Fig. 6A). In both types of nests, brood masses show a thin lining of soil material. Other species of *Onthophagus* construct similar nests to *Digitonthophagus*. In *Onthophagus taurus* (Schreber) the brood masses are constructed as successive elongated structures inside a tunnel and separated each other by a plug of soil (Halffter and Edmonds, 1982; Genise, 2016). Neither the orientation of Onthophagini brood masses nor their lining resembles *R. jacobacciensis*. Some species of *Bubas* and *Chironitis* make compound nests composed of cylindrical brood masses branching from a common vertical tunnel (Fabre, 1897; Halffter and Edmonds, 1982; Genise, 2016). Occasionally, in *Chironitis* only a single mass occurs in the lower
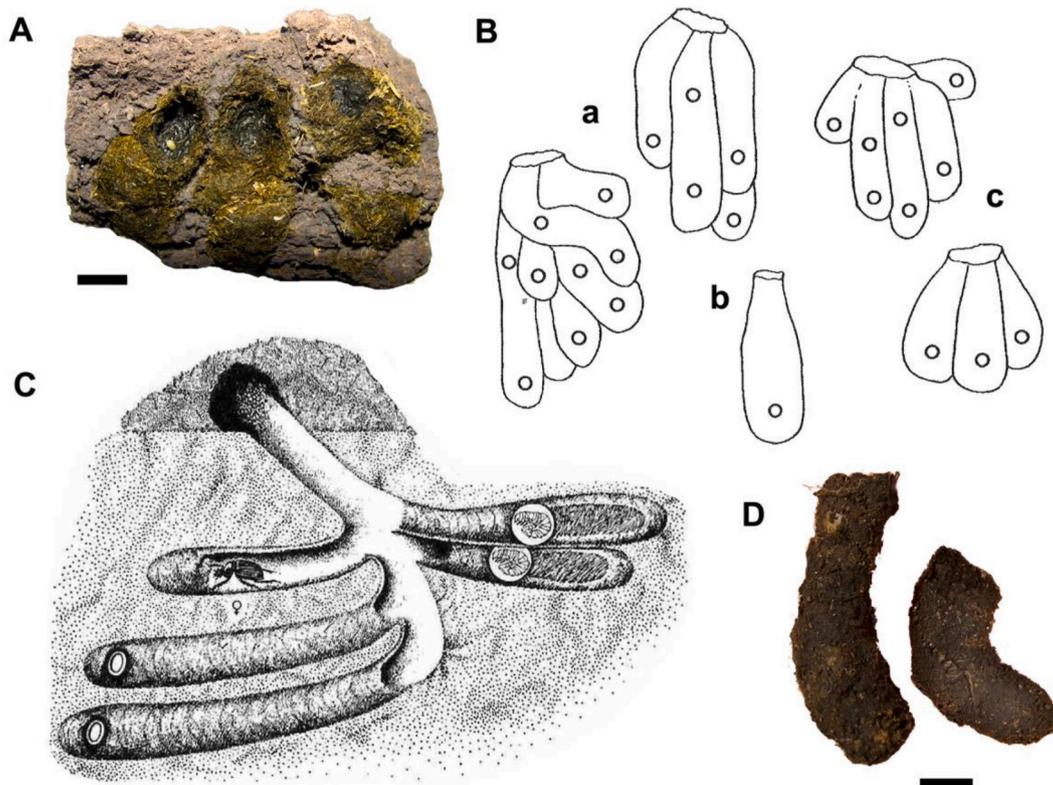
Fig. 6. Some analyzed nests of Scarabaeidae and Geotrupidae dung beetles. A) A compound nest of *Digitonthophagus gazella* (F.) from Formosa province (Argentina) showing elongated brood masses arranged in a row and in lateral contact each other (scale bar = 1 cm); B) Different types of nests of *Onitis alexis* Klug showing cylindrical brood masses: a-compound type (racemose and parallel), b-simple type, c-compound type (racemose and parallel) obtained in laboratory conditions (taken from Salerno and Zunino, 2002); C) Compound and racemose nest of *Geotrupes cavicollis* Bates showing elongated brood masses radiating horizontally from the main straight shaft (taken from Halffter et al., 1985); D) The resulted J-shaped brood masses of *Frickius variolosus* Germain from Chubut province (Argentina)(scale bar = 1 cm).

end of the burrow (Halffter and Edmonds, 1982). These groups of brood masses are always vertical and not comparable with *R. jacobacciensis*. *Dichotomius semiaeneus* (Germar), *Oruscatus davus* (Erichson) and *Gromphas lacordairei* Brullé construct simple nests showing cylindrical brood masses (Cabrera Walsh and Gandolfo, 1996; Sánchez and Genise, 2008). In contrast to *R. jacobacciensis*, all those brood masses are vertical. *Onitis alexis* Klug produces simple or compound nests of cylindrical brood masses according to the type of soil, and also in the number and orientation of the cylinders of the compound nests (Fig. 6B). The latter consists of 7 ± 3 closely pressed brood masses (Fig. 6Ba). In laboratory conditions, *O. alexis* revealed two compound nest architectures: a branched or racemose type showing brood masses radiating sub-horizontally from the main shaft, and the parallel type showing vertical brood masses parallel to each other (Fig. 6Bc). In clay soils, this species builds simple nests of a single tunnel where an elongated brood mass is formed in its bottom (Salerno and Zunino, 2002) (Fig. 6Bb). *Racemusichnus jacobacciensis* resembles the clusters of sub-horizontal, thick-walled cylinders of the compound racemose nests of *Onitis*. However, Onitini are typical European dung beetles, and the most related American group are the Eurysternini (Philips et al., 2004; Ocampo and Hawks, 2006), which show a complex nesting behaviour and very different nests (compound nest of brood balls) not comparable to *R. jacobacciensis* cluster. The Scarabaeidae, then, are not the best candidates as producers of *R. jacobacciensis*.

Some species of Geotrupidae also construct cylindrical brood masses in their nests. Taurocerastinae and Geotrupinae are coprophagous, showing nests that may be composed of a single mass at the main tunnel bottom or having several masses, straight or curved, radiating from the main tunnel. *Geotrupes cavicollis* Bates constructs compound and racemose nests of elongated brood masses radiating horizontally from the

main straight shaft (Halffter and Edmonds, 1982; Halffter et al., 1985) (Fig. 6C). It is remarkable that during the construction, the female begins each brood mass by placing dung on the internal surface of the excavation making a wall, and afterwards on the bottom of the branch (Fig. 6C). The final nest can show up to five brood masses that are separated by a few centimetres and, in other cases, the masses are practically in contact and parallel (Fig. 6C). The nests of *Geotrupes hornii* Blanchard, *G. stercorarius* (L.), *Trypocopris vernalis* (L.), *G. mutator* Marsham, *G. spiniger* Marsham, *Typhoeus typhoeus* (L.) and *Mycotrupes gaigei* Olison and Hubbell, are also compound and racemose as those of *G. cavicollis* (Halffter et al., 1985). The nests of *Geotrupes cavicollis* share some features with *R. jacobacciensis*. Even though they are not described as a cluster, the cylindrical brood masses emerging from the main tunnel are horizontal and closely constructed. Also, this is a large species distributed in America.

Among Taurocerastinae, *Frickius variolosus* Germain constructs simple nests where a single vertical burrow housed at the bottom a brood mass that is provisioned by layers of dung arranged in menisci (Fig. 6D). The resulted brood mass is J-shaped (Sánchez et al., 2012; Genise, 2016) (Fig. 6D). *Frickius variolosus* was already interpreted as a modern analog of *Scaphichnium hamatum* Bown and Kraus from the Cenozoic of USA (Sánchez et al., 2012). *Taurocerastes patagonicus* (Philippi) is an endemic species of Patagonia (Chile and Argentina) showing medium to large-sized specimens, but little is known about its nesting behaviour. Howden and Peck (1987) described the nest as an unbranched and irregular burrow, inclined about 70°, 10–35 cm long, ending in a provision of dung 5–7 cm long and 2–3 cm in diameter. This is a large species adapted to the Patagonian steppe (Howden and Peck, 1987) similar to the grassy habitats postulated for the La Pava Formation (Cantil et al., 2020; Sarzetti et al., 2017; Sánchez et al., 2018) and

congruent with the paleo-Mollisols recognized in Ingeniero Jacobacci basin. Paleopedological analysis show that *R. jacobacciensis* is more common in strongly developed paleosols that record late-successional communities in stable paleolandscapes. The size, possible cylindrical brood masses, and ecological preferences of *Tauroceras patagonicus*, as well as the horizontal and cylindrical walled-brood masses of *Geotrupes* spp., suggest that some Geotrupidae could be the possible trace maker of *Racemusichnus jacobacciensis*.

5.2. *Rosellichnus* assemblage-SAPIA in La Pava Formation. Chronological and palaeoenvironmental significance

The South American Palaeosol Ichnofossil Ages (SAPIAs) is a novel concept based on the stratigraphic significance of insect trace fossil assemblages in palaeosols included in the *Coprinisphaera* Ichnofacies (Genise et al., 2017). The SAPIAs comprise several assemblages of traces that are representative of different ages along the Cenozoic of southern South America, and run in parallel with the South American Land Mammal Ages (SALMAs). Among those, the youngest one belongs to the *Rosellichnus* assemblage-SAPIA, which was recorded from the La Pava Formation in the Chubut province. This assemblage is dominated by *Rosellichnus patagonicus, Coprinisphaera tonnii, C. akatanka, C. murguiai*, and is related to the Friasian/Colloncuran SALMA (Genise et al., 2017).

The new findings in the La Pava Formation of the Río Negro province reported herein allow an update the *Rosellichnus* assemblage-SAPIA. The richest localities, Estancia Huanuluan Cantera Nueva and Cantera Nueva Inferior, preserved a great diversity of ichnospecies and most of them could be collected in large numbers. The ichnospecies recorded there were the classical components of the *Rosellichnus* assemblage-SAPIA, mentioned above, but also *Coprinisphaera lazai, Feoichnus challa, Teisseirei barattinia, Fictovichnus gobiensis, Rebuffoichnus casamiquelai*, and the new ichnospecies *Racemusichnus jacobacciensis*. Considering the entire pool of traces recorded, including the new ones and their interpretations (Genise, 2016), they attest for the presence in soils of Diphaglossinae bees (*Rosellichnus*), necrophagous and coprophagous dung beetles (*Coprinisphaera* and *Racemusichnus*); chafers or weevils (*Fictovichnus* and *Rebuffoichnus*); sphinx moths (*Teisseirei*), and cicadas (*Feoichnus*) (Genise et al., 2002, 2013; Sánchez et al., 2010; Genise, 2016; Sarzetti et al., 2017; Cantil et al., 2020). *Tombownichnus plenus* and *Lazaichnus fistulosus* also record the presence of such kleptoparasites and detritivores as Aphodinae beetles and earthworms (Sánchez and Genise, 2009).

The Friasian/Colloncuran SALMA, mostly recorded in the Chilean and Argentine Patagonia, include marsupials (insectivores/omnivores to carnivores) and several types of placental mammals including caviomorph rodents, xenarthrans, astrapotheres, litopterns and notoungulates (Vucetich, 1977; Bondesio et al., 1980; Marshall, 1990; Scillato-Yané and Carlini, 1998; González-Ruiz et al., 2011; Bostelmann et al., 2012; Vera et al., 2019). Pascual and Ortíz J. (1990) considered that this assemblage records a turnover of mammal faunas, with the extinction and reduction in abundance of several taxa. New findings recently reported from the La Pava Formation at Ingeniero Jacobacci by Kramarz et al. (2018) include *Proeutatus, Prozaedyus*, Glyptodontidae (Cingulata), *Palaeothentes* (Paucituberculata), *Astrapotherium*? (Astrapotheria), and two species of *Toxodontidae* (Notoungulata). These authors observed that the toxodontids are comparable to those of the Colloncuran fauna indicating that its advent in Norpatagonia precedes the deposition of the Collón Curá Formation involving also the La Pava Formation. Mammal trophic types were dominated by grazers, which increased notoriously in relation to the preceding fauna (Ortíz J. and Cladera, 2006). Therefore, some of the medium to large toxodontids and astrapotheres would be the dung providers for the construction of the large *Coprinisphaera* and *Racemusichnus*.

The La Pava andic paleosols formed in landscapes that supported protracted and disturbing ash falls. However, alternate lapses of stability, highly fertile soils and suitable environmental conditions enabled,

with recovery time, the development of a highly productive and stable ecosystem recognized by the assemblage of diverse insect trace fossils and the mammal fauna. Considering that the *Rosellichnus* assemblage corresponds to the *Coprinisphaera* Ichnofacies and the previous (Sarzetti et al., 2017; Cantil et al., 2020) and current paleoenvironmental inferences for the La Pava Formation, it could be surmised that the above mentioned diversity of invertebrates would have been cohabiting with medium to large mammals in an open grassy habitat compatible with grass savannas, under a temperate-warm and seasonal subhumid climate (Kramarz et al., 2018; Sánchez et al., 2018; Bellosi et al., in press). Paleopedological analysis show that *R. jacobacciensis* is more frequent in strongly developed paleosols that record late-successional communities.

5.3. The large size of the trace fossils and the Middle Miocene Climatic Optimum

Racemusichnus jacobacciensis is the largest trace fossil in paleosols that can be attributed to solitary insects from all taxa included in Coprinisphaeridae, Celliformidae and Pallichnidae. It is remarkable that along with this large-sized new trace fossil from Estancia Huanuluan Cantera Nueva (EHCN), other specimens from *Coprinisphaera ispp.*, *Teisseirei barattinia*, and *Feoichnus challa* from this locality and Cantera Nueva Inferior (EHCNI) show large sizes too. Previous data on the La Pava Formation from the Chubut province show a similar scenario, in which the locality called Cerrito Terciario records the presence of large-sized *Coprinisphaera* (Cantil et al., 2020). The most complete study about the *Coprinisphaera* sizes reported until now was carried out for the middle Eocene – lower Miocene Sarmiento Formation at Gran Barranca, Chubut province (Sánchez et al., 2010). In that analysis, involving 1196 specimens of the ichnospecies *C. murguiai, C. kheprii, C. tonnii, C. kraglievichi* and *C. lazai*, equatorial diameters range from 21 mm to 66.4 mm. The specimens were grouped in five size classes, which were: (I) 21.0–27.3 mm, (II) 27.4–35.6 mm, (III) 35.7–46.4 mm, (IV) 46.5–60.4 mm, and (V) 60.5–78.6 mm. The last size class representing 2.56% of the total sample appeared in the early late Oligocene and along with other shifts in the size classes was related to the appearance of large mammals capable of producing large dung pads (Sánchez et al., 2010). In the lower Miocene Pinturas Formation, Santa Cruz province, the equatorial diameter of 202 specimens of *Coprinisphaera* including *C. murguiai, C. kephrii* and *C. kraglievichi* ranged from 29.4 to 69.3 mm (Cantil pers. comm.). Specimens from the size class V represent 5% of the sample. *Coprinisphaera murguiai, C. lazai, C. tonnii* and *C. akatanka* were recorded from the La Pava Formation in the Chubut province (Cantil et al., 2020). The obtained measures of equatorial diameter by locality were for Paso del Sapo, 22.3–53.4 mm (n = 176), for El Petiso 35.8–46.5 mm (n = 10), and for Cerrito Terciario 22–83.3 (n = 88) (Cantil et al., 2020). The last locality was the only one showing specimens larger than 60.5 mm (size class V), which represent 3.65% of the sample from all localities and 9% of Cerrito Terciario. The 53 specimens of *Coprinisphaera* described herein range from 24.5 to 75.4 mm and those larger than 60.5 mm (size class V) compose the 13.2% of the total sample and all of them came from EHCNI and EHCN. These data show that the range of sizes in *Coprinisphaera* remains similar along these formations, whereas the size of specimens shows a shift towards the largest class size (V). This class represents 2.56% of the total sample in the Sarmiento Formation, 5% in the Pinturas Formation, 3.65% in the La Pava Formation of the Chubut province, and 13.2% in La Pava Formation of the Rio Negro province. The largest class is represented only in Cerrito Terciario from the La Pava Formation in the Chubut province and in EHCN from the La Pava Formation in the Rio Negro province. Krause et al. (2008) reported that the equatorial diameter of 204 specimens of *Feoichnus challa* coming from the lower middle Eocene to the lower middle Miocene of Patagonia (Koluel-Kaike, Sarmiento and Pinturas Formations) ranged from 5 mm to 40 mm. These authors suggested that the range of size would correspond to different developmental stages of a single producer, or to individuals of the same stage but with differences in food availability. In

this case, the minimum value of the range is shifted from 5 mm in older formations to 12.5 mm in La Pava Formation at EHCNI, where most of the specimens were collected and to 21.2 mm at NK, where only four specimens were collected. These results show that the range is shifted to larger specimens in EHCNI as in *Coprinisphaera*. Specimens of *Teisseirei barattinia* reported from the middle Eocene – lower Miocene Sarmiento Formation at the Chubut province were 27–90 mm long (n = 80), 12.4–49 mm wide (n = 136) and 8.0–30.0 mm high (n = 102), with an exceptional large specimen showing 115 mm long and 70 mm wide (Genise et al., 2013). The range found in the La Pava Formation at Ingeniero Jacobacci is shifted to larger specimens, being the minimum values of length 47.2 mm, wide 25.7 mm and high 23 mm. Considering only the specimens from EHCN the shift is even more evident because the minimum values are 50.8 mm, 29.1 mm and 23 mm respectively.

This is the first reported case of a whole trace fossil assemblage from a paleosol showing large-sized traces, indicating that a common paleoenvironmental factor affected the size of insects that produced these traces. Body size in insects has been related to several interplaying factors, among which the temperature, either directly or indirectly, has been one of the most documented ones. Insects depend on environmental temperature to regulate their physiological functions, which make them extremely vulnerable to this factor (González-Tokman et al., 2020). Recently, global warming has triggered a lot of new field and laboratory research on the different responses of insects including changes in body size (e.g. Sheridan and Bickford, 2011; Wu et al., 2019). It has been demonstrated that the increase of metabolic rates at higher temperatures in insects result in smaller body sizes allows them to decrease their metabolic rates to resist heating (Sheridan and Bickford, 2011; González-Tokman et al., 2020). The renowned Bergmann's rule predicts that body size of many animals, originally endotherms, varied with latitude and altitude, resulting in larger bodies at higher latitudes and altitudes (i.e. Bergmann's clines). Many latitudinal and altitudinal clines recorded in the field and also laboratory experiments, also in insects, have supported this rule since its proposal (Bergmann, 1847; Atkinson, 1994; Craig Stillwell and Fox, 2009; Meiri, 2011).

However, other evidence contradicts this rule, particularly in ectothermic organisms and when other interplaying factors are considered, such as phylogenetic inertia, growth rates, food availability, seasonality, precipitation, and atmospheric hyperoxia, among others (Kaiser et al., 2007; Chown and Gaston, 2010; Meiri, 2011; Beerli et al., 2019). Some of these cases showing opposite clines to those predicted by the original Bergmann's rule are known as the converse Bergmann's rule (Chown and Gaston, 2010; Beerli et al., 2019). Probably as old as the Bergmann's rule is the observation of field naturalists that tropical insects are larger than those of temperate zones (Beerli et al., 2019). These authors studying the variation of body size in sphingid moths, incidentally the producers of *Teisseirei* (Genise et al., 2013), found that body sizes were only weakly related to latitude or climatic factors and they were more likely related to food availability in tropics and also to phylogeny. According to Vermeij (2016) large size in animals is an ecological condition for defence and feeding regulated by abundance of food resource and recycling; involving not only selection of large size, but also enough oxygen, food and environmental stability. Other classical example of body sizes independent from Bergmann's rule and climate is the gigantism of some insects during the Paleozoic, which has been related to atmospheric hyperoxia and hyperbaria or as a response to predation by vertebrates (Chown and Gaston, 2010). Coleoptera of different taxa from North America show that larger-bodied species follow the Bergmann's rule, whereas smaller species follow the converse Bergmann's rule (Tseng and Soleimani Pari, 2019).

The ichnofossil record has already provided an example of body size changes related to a paleoclimatic event. During the Paleocene-Eocene Thermal Maximum (PETM) in the Bighorn Basin of Wyoming, USA, insect trace fossils in paleosols show a reduction in size of 30–46% (Smith et al., 2009). Along with the rise of temperature, the PETM involved a decrease of about 40% of the mean annual precipitation as attested by paleoflora and paleosols and an increase of atmospheric CO_2 (Wing et al., 2005; Kraus and Riggins, 2007; Smith et al., 2009; Kraus et al., 2013). Authors related the dwarfism to several possible causes and the interplay among them, such as the replacement of fauna better adapted to warmer and drier conditions, phyletic decrease of body size, impacts on growth rates and the nutritional value of their food sources (Smith et al., 2009). The case of the La Pava Formation would be the second case of change in body size reflected by trace fossils in paleosols linked to a paleoclimatic event. Pyroclastic sediments of the La Pava Formation were deposited during the Middle Miocene Climatic Optimum (Westerhold et al., 2020). In contrast to the record of the PETM, under dry climate, resulting in the decrease of size in trace fossils (Smith et al., 2009), the result of the change for the MMCO is an increase in size.

How a climatic optimum can produce an ichnoassemblage composed of large-sized insect traces is difficult to ascertain because of the interplay of different possible causes and the restriction of data when analyzing a paleoecosystem with no chances of conducting experiments as in extant ones. The data show that in most cases and in comparison with older formations the size ranges of the trace fossils were shifted to large size classes, involving the lack of record of the younger small-sized producers, whereas in *Coprinisphaera* the size range remained similar and there was an increase in number of specimens of the largest size class. Since the large size of traces is recorded in particular localities, it is assumed that such increase is not a direct result of higher temperatures, which would have produced a similar increase in all of them, but to an indirect effect. The large size in specimens of *Coprinisphaera* has been traditionally linked to the large size of herbivores producing large dung pads (Sánchez et al., 2010, 2013; Cantil et al., 2020), whereas the range of size in *Feoichnus challa* to the size of the producers or food availability (Krause et al., 2008). From all factors mentioned as possible causes of body size increase in ectothermic organisms, temperature increase, phylogenetic inertia, growth rates, seasonality, precipitation and hyperoxia would have affected similarly all localities. The different body sizes recorded in studied localities indicates that no matter the factor it acted unevenly and accordingly indirectly on them. In contrast, food availability would be the factor that could show variability among localities. Accordingly, the simplest explanation for this assemblage of large trace fossils may be the increase of availability in particular localities produced by the MMCO, resulting in larger insects and traces.

6. Conclusions

1. The new insect trace fossil *Racemusichnus jacobacciensis* igen. isp. nov. is a cluster of two to seven thickly walled cylinders horizontally orientated in the paleosol that is only recorded for the middle Miocene La Pava Formation at the Río Negro province.

2. The cluster arrangement, its orientation (sub-horizontal to horizontal), the large size and the well defined wall of the cylinders that conform *Racemusichnus jacobacciensis* igen. isp. nov. suggest a Geotrupidae dung beetle as the possible trace maker.

3. Facies and paleosol analysis allow inferring a fluvial depositional system located in a perivolcanic area and dominated by frequent ash falls. Quiescence lapses favored formation of soils, which vary from andic Entisols and near-mollic Andisols to udic Mollisols according to the time of landscape stability.

4. The new assemblage of trace fossils presented herein can be included in the *Rosellichnus* assemblage-SAPIA of the *Coprinisphaera* Ichnofacies, which along with the mollic paleosols and mammals recorded and previous data for this Formation suggest an open grassy habitat compatible with grass savannas, under a temperate-warm and seasonal subhumid climate.

5. *Racemusichnus jacobacciensis* is the largest trace fossil in paleosols attributed to solitary insects and occurs in the La Pava Formation of the Rio Negro province with several ichnospecies of *Coprinisphaera*, *Teisseirei barattinia* and *Feoichnus challa* that compared with older formations show shifts in their ranges towards larger specimens. The

increase of size for this assemblage is attributed the increase of productivity in particular localities produced by the MMCO, resulting in larger insects and traces.

Author contribution

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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