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The *Celliforma* ichnofacies in calcareous paleosols: An example from the late Miocene Cerro Azul Formation, La Pampa, Argentina

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ABSTRACT

Invertebrate trace fossils from the late Miocene Cerro Azul Formation (La Pampa, Argentina) are described and compared with known paleosol ichnofacies. The formation is a loess succession punctuated by numerous calcareous paleosols. Trace fossils were recovered from thirteen localities distributed in a wide latitudinal and longitudinal range within La Pampa Province. Paleosols from the northwestern localities display clastic dikes and pedogenic slickensides and are compared with calcic vertisols, which are typical of strongly seasonal and semiarid climate. Paleosols from the remaining localities have a Bt horizon with blocky or prismatic peds and can be compared with mollisols. The depth to the Bk horizon for all paleosols averages 0.54 m, suggesting a mean annual precipitation of 450 mm (± 147 mm), also pointing to semiarid climatic conditions during soil formation. The trace fossil assemblage from the Cerro Azul Formation is of low diversity and abundance and is typified by the presence of the insect trace fossils *Celliforma*, *Rosellichnus*, *Rebuffoichnus*, *Fictovichnus* and *Teisseirei*. The ichnospecies recorded are: *Celliforma germanica*, *Celliforma* cf. *rosellii*, *Celliforma* isp., *Rosellichnus* isp., *Rebuffoichnus casamiquelai*, *Fictovichnus* cf. *sciuttoi*, *Fictovichnus* isp., *Teisseirei barattinia*, *Taenidium barretti*, and cylindrical burrow fills. These trace fossils (along with *Attaichnus kuenzelii*, vertebrate burrows and medium–sized rhizoliths described in previous works) are considered comparable with the *Celliforma* ichnofacies. This ichnofacies is indicative of well-drained calcareous paleosols developed under low vegetation coverage. For the analyzed succession the vegetation was probably dominated by scrubs with minor participation of herbaceous plants. *Coprinisphaera* ispp. (including *Coprinisphaera lazai*, *Coprinisphaera murguiai*, and *Coprinisphaera* isp.) showing a cementation similar to associated late Miocene trace fossils were only recorded, along with *Celliforma* isp., in two localities. This trace fossil assemblage is comparable with the *Coprinisphaera* ichnofacies, suggesting dominance of herbaceous communities and wetter climate than those of the *Celliforma* ichnofacies. Some specimens of uncemented *Coprinisphaera* ispp. were produced during post-Miocene times and are not considered as a part of the trace fossil assemblage of the Cerro Azul Formation.

1. Introduction

Paleosol ichnofacies has been a field of active developments in the last years, especially after the proposal of the *Coprinisphaera* ichnofacies to distinguish insect-dominated trace fossil assemblages typical of herbaceous communities (Genise et al., 2000). Currently recognized paleosol ichnofacies also include the *Termitichnus* and *Celliforma*, and the recently proposed *Camborygma* ichnofacies, "rhizolith ichnofacies" and "vertebrate burrow ichnofacies" (Smith et al., 1993; Genise et al., 2000, 2010, in press; Melchor et al., 2012; Melchor, 2015). The *Termitichnus* ichnofacies is currently used to refer trace fossil associations dominated by termite nests, typical of closed forests, which are developed under warm and humid climate (Smith et al., 1993; Genise et al., 2000, 2010). The *Celliforma* ichnofacies was proposed for insect-dominated trace fossil assemblages from calcareous paleosols developed in terrestrial or palustrine settings. This ichnofacies is characterized by *Celliforma*, *Rebuffoichnus* and subordinate beetle trace fossils (including *Fictovichnus*), and by the absence of *Coprinisphaera* (Genise et al., 2010, 2013a, in press). In terrestrial settings, the latter ichnofacies indicates low plant coverage due to arid climate typical of desert scrubs and dry woodlands. The *Camborygma* ichnofacies has been recently proposed (Genise et al., in press) to refer to assemblages dominated by crayfish and earthworm trace fossils, indicative of paleosols with fluctuating, high water tables and distinctive of wetlands and swamps (see also Melchor et al., 2012). The "rhizolith ichnofacies" is typified by a dominance of root traces of different morphology and is suggestive of subaerial exposure (Melchor et al., 2012; Genise et al., in press). The "vertebrate burrow ichnofacies" is characterized by dominance of large tetrapod burrows that occur in well-drained calcareous paleosols developed in arid or semiarid climatic settings (Melchor et al., 2012; Melchor, 2015).

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In the original proposal of the *Coprinisphaera* ichnofacies (Genise et al., 2000), the late Miocene Cerro Azul Formation was considered as one of the examples of that ichnofacies. This assignation was based on a report by Laza (1982) about the presence of fossil ant nests, *Attaichnus kuenzelii* Laza, 1982, from the Salinas Grandes de Hidalgo locality and unpublished information on the presence of *Coprinisphaera* (Genise et al., 2000; table 2). From outcrops assigned to the Cerro Azul Formation in the west of Buenos Aires province, Laza (2006) described a cluster of fossil dung beetle brood balls within a cavity as the new ichnospecies *Quirogaichnus coniunctus*. The ichnoassemblage of the Cerro Azul Formation from the Salinas Grandes de Hidalgo locality was recently assessed by Genise et al. (2013c). These authors redescribed *A. kuenzelii* and the associated trace fossils, including large vertebrate burrows, rhizoliths, meniscate burrows, *Coprinisphaera* and bee trace fossils. Genise et al. (2013c) indicated that the poor cementation of *Coprinisphaera* specimens and presence of organic remains in the bee trace fossils they found suggested production by insects younger than late Miocene.

In this paper, we describe invertebrate trace fossils recovered from thirteen localities of the Cerro Azul Formation from a wider geographic coverage, which allows a more complete assessment of the ichnofauna of the unit. The purposes of this work are: 1) to infer the paleoenvironmental conditions during soil formation of the trace fossil bearing intervals of the unit, and 2) to compare the invertebrate ichnofauna of the Cerro Azul Formation with known paleosol ichnofacies.

2. Material and methods

A total of 52 trace fossil specimens were analyzed for this work, which are housed at the Paleontology Collection, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa (acronym GHUNLPam). Specimens were measured using a micrometer ocular in a binocular Leica MS5 microscope and a manual caliper. Photographs of trace fossils were taken with Nikon P90 and Nikon D3100 digital cameras.

The new findings of invertebrate trace fossils reported in this contribution belong to 13 localities from La Pampa province (Fig. 1). These localities are distributed in an area with a maximum latitudinal range of more than 300 km and more than 300 km in the E–W direction. The study localities are (Fig. 1): Caleufú (35° 41′ 37″S, 64° 40′ 08″W), Salinas Grandes de Hidalgo (37° 12′ 55″S, 63° 35′ 25″W), Telén (36° 15′ 15″S, 65° 30′48″W), Quehué (37° 04′ 01″S, 64° 42′ 02″W), Las Torrecitas (36° 24′ 51″S, 67° 14′ 37″W), Estancia La Malvina (36° 37′ 04″ S, 64° 19′ 52″W), Road 14 (36° 42′ 48″S, 64° 26′ 51″W), Punta de la Barda (37° 09′ 02″S, 67° 14′ 52″W), Bajo Giuliani (36° 42′ 55″S, 64° 17′ 55″ W), El Guanaco (36° 18′ 36″S, 64° 16′ 43′′W), Estancia Puerta Grande (36° 32′ 44″S, 67° 13′ 18″W), Puesto Luján (36° 50′ 28″S, 67° 20′ 56″ W), and Cerro El Morro (38° 42′ 37″S, 64° 05′ 12″W). At every locality, a standard sedimentologic log of the trace fossil bearing interval was measured (Fig. 2).

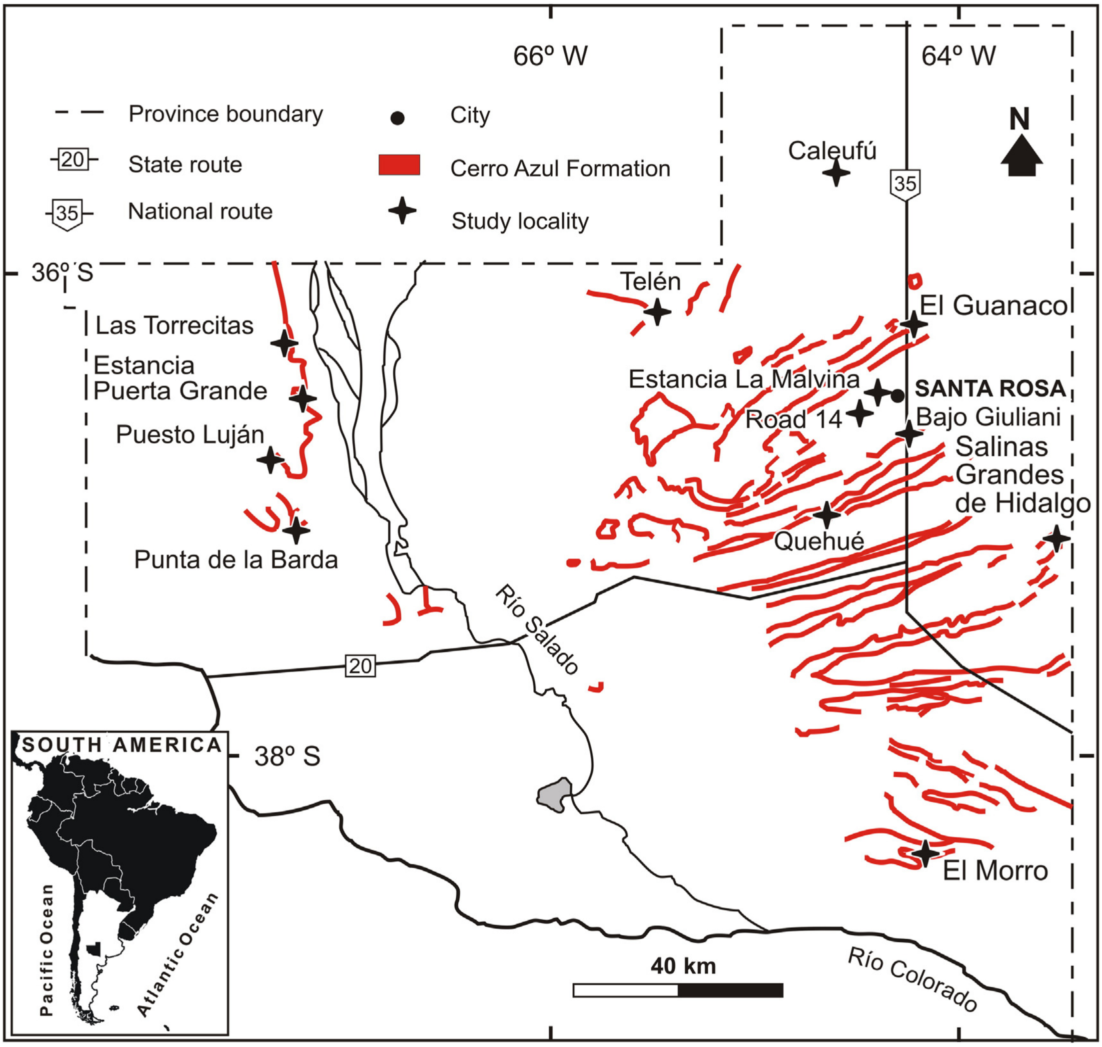

Fig. 1. Map of outcrops of the Cerro Azul Formation in La Pampa province showing the localities with trace fossils. Modified from Linares et al. (1980) and Visconti (2007).

3. Geological setting

The Cerro Azul outcrops are located in the northwestern, central, and eastern part of La Pampa province, Argentina (Visconti et al., 2010). The unit is characterized by a monotonous succession of loess containing paleosols (Fig. 2) that has been assigned to the late Miocene (Huayquerian Land Mammal age) essentially on the basis of its mammal remains (Montalvo and Casadío, 1988; Verzi

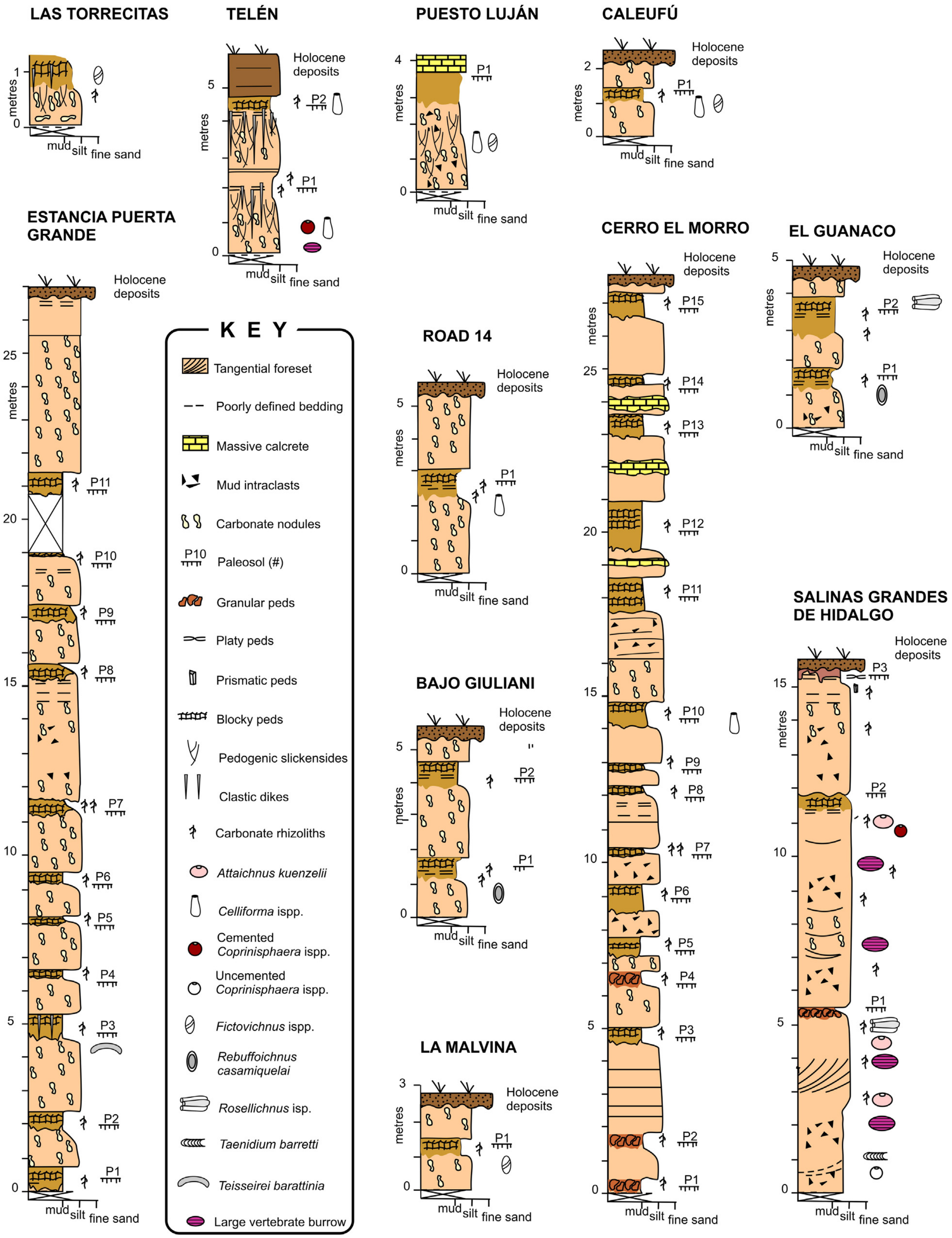

Fig. 2. Sedimentary logs from trace fossil bearing sections of the Cerro Azul Formation.

et al., 1999, 2003). In particular, the formation is considered as representing the interval between 10 and 5.7 Ma (Visconti et al., 2010). The maximum exposed thickness in outcrop is 54 m, although the unit reaches about 180 m in the subsurface (Visconti et al., 2010). The formation is essentially composed of structureless, light brown (5YR 6/4), pale reddish brown (10R 5/4) or grayish orange pink (5YR 7/2), sandy siltstones and fine-grained sandstones, showing moderate selection.

4. Paleosol description

4.1. Paleosols with vertic features

Paleosol profiles from the northwestern sector of the study area (Telén, Las Torrecitas and Estancia Puerta Grande localities, Fig. 1) display clastic dikes and slickensides. The examples from Las Torrecitas and Telén are described below.

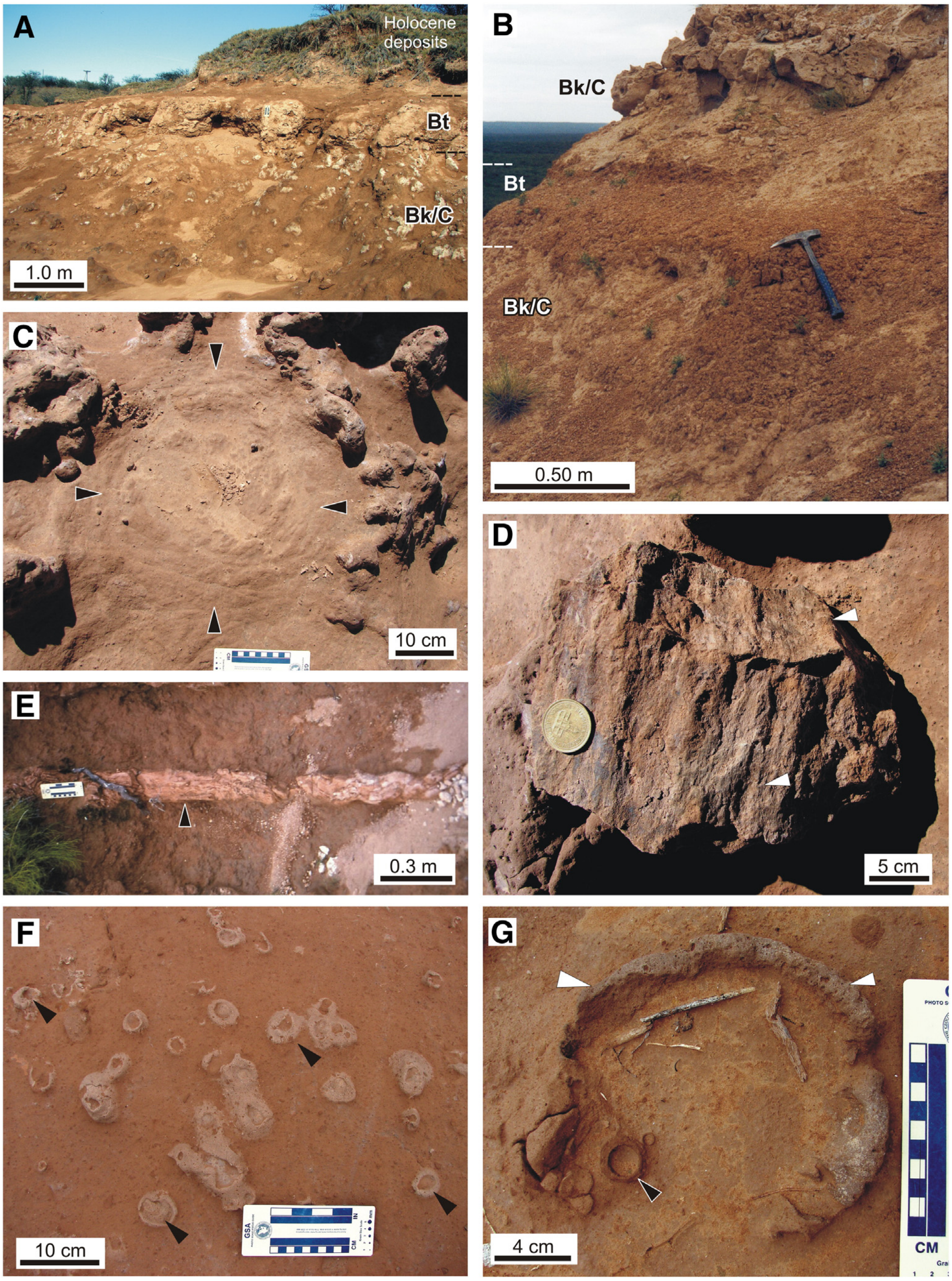

Fig. 3. Field views of paleosols and trace fossils of the Cerro Azul Formation. (A) Uppermost calcic vertisol from Telén locality. Bt: argillic horizon, Bk/C: calcic horizon transitional to parent material. (B) Paleosols from the Cerro El Morro locality showing an upper argillic horizon (Bt) and a lower calcic horizon (Bk/C). (C) Plan view of concentric, curved, nearly vertical planes corresponding to nested slickensides with a tridimensional conical arrangement. Calcic vertisol from Telén. (D) Block of siltstone with pedogenic slickensides from a calcic vertisol of Telén. Arrows points to intersecting striated surfaces of slickensides. (E) Plan view of nearly vertical clastic dike (arrow) from a vertisol of Estancia Puerta Grande. (F) Plan view exposure of cross-section of medium-sized rhizoliths (some arrowed) from Salinas Grandes de Hidalgo locality. (G) Plan view of an eroded and cemented *Attaichnus kuenzelii*(white arrows) containing an uncemented *Coprinisphaera* specimen (black arrow). Salinas Grandes de Hidalgo locality.

The lowermost paleosol from Las Torrecitas is composed of two horizons (Fig. 2). The upper 0.70 m thick horizon (compared with a Bt horizon) is composed of light brown (5YR 6/4) clayey siltstone with 5–15 mm wide blocky peds and scarce vertical, 30 mm wide, clastic dikes. The lower 0.25 m of this upper horizon contains 10 mm wide vertical calcareous rhizoliths and calcareous concretions with a vertical habit. The lower 0.50 m thick horizon (Bk) is composed of grayish orange pink (5YR 7/2) massive siltstone with sparse slickensides and horizontal calcareous concretions that tend to merge.

The 6 m thick section from Telén (Figs. 2, 3A) exhibits well-developed vertic soil features (Montalvo et al., 2008). It is composed of carbonate-cemented grayish orange pink (5YR 7/2) siltstones and fine-grained sandstones. The most conspicuous features of the paleosols include heterogeneous micrite cementation, pedogenic slickensides and clastic dikes (Fig. 3C–E). Two stacked paleosol profiles were recognized, which are 1.7 (lower) and 1.9 m thick (upper), and show poor horizonation. Carbonate cementation is more abundant in the lower horizon of both paleosols (Bk horizon) with calcareous rhizoliths and concretions that have a dominantly subvertical arrangement (up to 15 cm long and 5 cm diameter) and scarce calcareous nodules (1 a 2 cm in diameter). *Coprinisphaera* ispp. specimens were recovered from the lower horizon of the lowermost paleosol. In contrast the upper paleosol profile has a second uppermost clayey horizon (Bt), which is 0.30 m thick and exhibit fine prismatic peds and *Celliforma* isp. Pedogenic slickensides compose curved, striated and clayey surfaces with a circular roughly concentric arrangement in plan view and a conical 3-D pattern (Fig. 3C–D). These structures are 0.2 to 0.7 m in diameter and 1 m in depth. Clastic dikes are 1 to 7 cm thick, subvertical and filled by two to four pairs of symmetrical muddy laminae of contrasting grain size and color (Fig. 3E). The depth to the Bk horizon for paleosols with vertic features from the three localities averages 0.49 m (range = 0.3 −0.9 m, n = 11).

4.2. Paleosols lacking vertic features

Macroscopic features of the remaining paleosols are very similar in the studied localities and in most of the Cerro Azul Formation outcrops (Visconti et al., 2010). Paleosol profiles are composed of two horizons (Fig. 3B). The upper horizon is a clayey siltstone that is distinguished by the presence of subangular blocky or prismatic peds (the latter only in the Cerro El Morro locality) and a darker color (5YR 6/4) than the underlying horizon. Carbonates are absent except for the local occurrence of 1 to 2 mm wide carbonate rhizoliths. This upper horizon can be compared with a Bt horizon and its thickness averages 0.57 m (range = 0.30 −1.30 m, n = 19). The thicker Bt horizons were measured in the middle part of the Cerro El Morro section (Fig. 2).

The lower horizon is characterized by lighter colored (5YR 7/2), siltstone to fine-grained sandstone with pervasive carbonate cementation, both in the form of nodules and rhizoliths (Fig. 3B). Rhizoliths are small to medium sized and commonly 1–30 mm in diameter (Fig. 3F). Much of the diameter of the larger rhizoliths are product of concretionary growth of carbonate around former roots. The lower horizon can be up to more than 5 m thick and contain remains of primary sedimentary structures, like tangential cross-bedding or horizontal bedding, as seen in the Salinas Grandes de Hidalgo section (Fig. 2). Mud intraclasts are common. The remains of primary sedimentary structures and carbonate cementation suggest comparison with a Bk or Bk/C horizon. The trace fossils described in this paper were mostly recovered from these horizons.

4.3. Micromorphologic description of paleosols

Analized paleosol samples are characterized by an apedal microestructure with a predominantly porphyric distribution (Bullock et al., 1985). Basic components in the coarse fraction (silt-sized) are dominantly volcanic rock fragments, some quartz, plagioclase and scarce heavy minerals (hyperstene, augite, hornblende, opaque minerals). The fine fraction is mainly clay-sized material. The groundmass is undifferentiated to weakly stipple-speckled (Telén, El Guanaco) and crystallitic b-fabric (Bajo Giuliani, Road 14). Aggregates are scarce, some of them with a striated fabric. The pattern of vugs is in channel and chamber, suggesting root and faunal activity, respectively. Pedofeatures include clay hypocoatings in voids, grains and aggregates. Limpid clay coatings are found commonly in the Telén and El Guanaco samples. Dusty clay coatings were found in the Bajo Giuliani and Road 14 samples. Impregnative Fe–Mn nodules were recorded in samples from all localities. They were recorded in aggregates, vugs and grains, with digitate boundaries and ameboidal forms. Calcitic (micritic) coatings, hypocoatings, and impregnative nodules are common in the Bajo Giuliani and Road 14 samples.

5. Systematic ichnology

Ichnofamily Celliformidae Genise, 2000
Ichnogenus *Celliforma* Brown, 1934
Celliforma germanica Brown, 1935
Fig. 4A
Material: GHUNLPam 18711 from Caleufú,
Description: Elongate internal mold of tear-shaped chamber with a smooth surface and a neck in the apical end. Cell length is 17.3 mm, maximum diameter is 7.4 mm, and wall thickness is 0.15 mm.
Remarks: Although the apical portion is partially missing, the presence of a constriction is a diagnostic feature that suggest assignation to *C. germanica*. Other features that distinguish this specimen from *C. rosellii* are a smaller size and a thinner wall (Genise and Bown, 1994; Genise, 2000; Melchor et al., 2002). Cell shape is characteristic of the Halictinae (Genise, 2000).

Celliforma cf. *rosellii* Genise and Bown, 1994
Fig. 4B–C
Material: GHUNLPam 18717 from El Guanaco, 18718 from Road 14, 18783 from Puesto Luján, and 18789 from Cerro El Morro.
Description: Detached, barrel-shaped to cylindrical internal molds of chambers, with the lower end rounded and the upper end truncated. No antechamber was observed and all specimens display remains of a very thin wall. Cell length ranges from 21.3 to 22.9 mm and maximum diameter from 10.2 mm to 13.0 mm. GHUNLPam 18717 (Fig. 4B, C) shows a truncated apex and its surface has two 3 mm wide circular depressions (Fig. 4C), and the preserved wall thickness is 0.45 mm. Specimen GHUNLPam 18718 is included in a calcareous concretion and the apex is broken by an oblique fracture, wall thickness is 0.6 mm. In GHUNLPam 18783 the apex is broken and a sealed fracture produces a subdued step in the middle of the cell. Thickness of preserved wall is 0.45 mm. GHUNLPam 18789 is barrel-shaped and 11.2 mm wide and 19.8 of maximum preserved length.
Remarks: These specimens are compared with *C. rosellii* because of the cylindrical to barrel-shaped form and similar size to the type material (Genise and Bown, 1994). Their poor preservation precludes identification of diagnostic features of the apex, which would allow a more precise assignation.

Celliforma isp.
Fig. 4D, E
Material: GHUNLPam 14471 and 18775 from Telén and 18788 from Cerro El Morro.
Description: GHUNLPam 18775 (Fig. 4D, E) is composed of two parallel internal molds of tear-shaped to cylindrical chambers, arranged about 7 mm apart, hosted in massive siltstone and capped by a thin mudstone laminae (Fig. 4E). Both cells are cut by a healed fracture that produces a displacement of about 1 mm. The length of one of the cells is 22.0 mm and the width cannot be measured due to the fracture. The cells are arranged with the long axis parallel to the mudstone laminae in the same piece of rock, suggesting a subhorizontal arrangement of the

cells. GHUNLPam 14471 and 18788 are smaller (6 mm and 7.2 mm in diameter, respectively), although the complete length is unknown because the apical end is embedded in the host rock (maximum preserved length is 12.5 mm).

Remarks: The incomplete preservation of these specimens precludes a definite specific assignation. The laminated mudstone of specimen GHUNLPam 18775 is only found in the formation as fill of vertebrate burrows (Genise et al., 2013c), thus suggesting that the cells may have been constructed in the filling sediments of a large and open burrow of vertebrate origin. The fracture that cuts the specimens may be linked to trampling during the filling of the vertebrate burrow, as the facture does not affect the laminated mudstone.

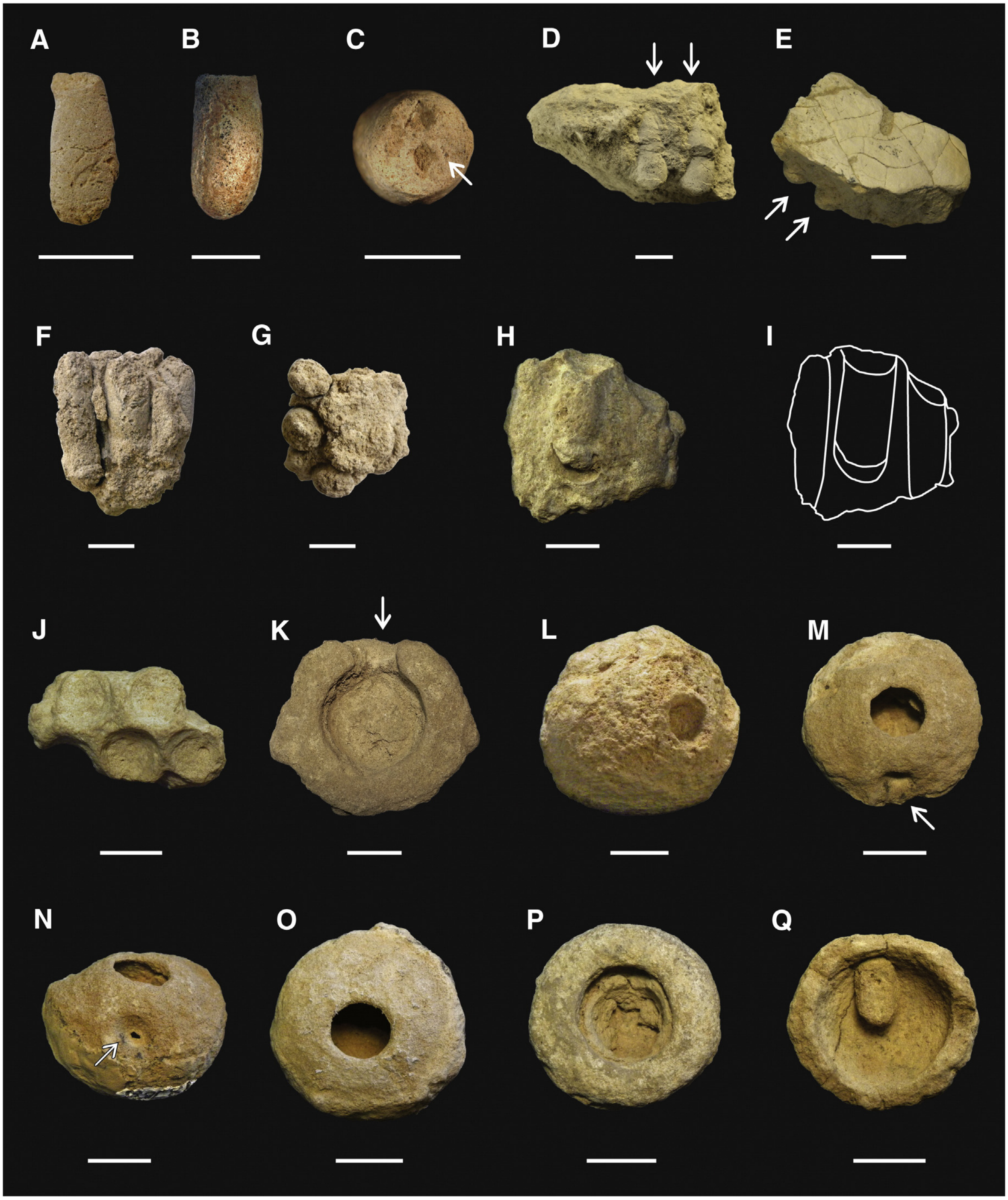

Fig. 4. Trace fossils from the Cerro Azul Formation. (A) *Celliforma germanica* (GHUNLPam 18711). (B) and (C) Lateral and apical view of *Celliforma* cf. *roselli* (GHUNLPam 18717), the arrow in C indicates one of the two depressions in the apical end. (D) and (E) Two specimens of *Celliforma* isp. (arrowed) in ventral and dorsal view (GHUNLPam 18775). Note cells broken by a fracture in D and laminated mudstone with an unidentified burrow in E. (F) and (G) Lateral and distal view of *Rosellichnus* isp. (GHUNLPam 18716). (H), (I) and (J) Lateral view, diagram and apical view of *Rosellichnus* isp. (GHUNLPam 18777). (K) Uncemented *Coprinisphaera lazai* (GHUNLPam 18629). The upper part of the chamber has been eroded. The arrow points to the accessory lateral hole. (L) *Coprinisphaera lazai* (GHUNLPam 18765) with accessory lateral hole. (M) and (N) Dorsal and lateral view of *Coprinisphaera lazai* (GHUNLPam 18768) showing the accessory lateral hole (arrows). (O) *Coprinisphaera murguiai* (GHUNLPam 18767). (P) *Coprinisphaera murguiai* (GHUNLPam 18636). (Q) *Coprinisphaera* isp. (GHUNLPam 18477) showing an ellipsoidal structure within the chamber fill. Scale bar: 10 mm.

Ichnogenus *Rosellichnus* Genise and Bown, 1996
Rosellichnus isp.
Fig. 4F–K
Material: GHUNLPam 18716 from El Guanaco, and 18776 (a plaster cast) and 18777 from Salinas Grandes de Hidalgo.
Description: GHUNLPam 18716 is the most complete specimen and is composed of a cluster of five parallel nearly cylindrical cells arranged in three rows, plus external molds of other two adjacent cells suggesting the existence of a fourth row (Fig. 4F, G). This specimen was not found in situ. Each cell is an internal mold of a chamber showing a smooth surface, a very thin wall (0.15 mm thick) and rounded lower end. The maximum length of the most complete cell is 32.8 mm, and the diameter ranges between 9.65 and 10.65 mm ($n = 3$).

The specimen GHUNLPam 18777 (Fig. 4H–J), also not found in situ, is a cluster of four cells arranged in two rows with a very thin wall (0.45 mm thick). The maximum length of the most complete cell is 32 mm and its maximum diameter is 12.4 mm.

The field specimen corresponding to the cast GHUNLPam 18776 was arranged sub-horizontally (Fig. 4K). The cluster is composed of seven cells apparently composing three rows showing a thin lining (0.45 mm thick). Measured cell length is 28.4 and 29.1 mm ($n = 2$) and maximum diameter is 10.8 and 11.8 mm ($n = 2$).
Remarks: The parallel arrangement of cells in the cluster distinguishes *Rosellichnus* from *Uruguay*. In the latter ichnogenus the bottoms of cells are divergent and the upper part of the cluster is concave (Genise and Bown, 1996). Although larger than the type material of *Rosellichnus arabicus* Genise and Bown, 1996; GHUNLPam 18716 is comparable with that ichnospecies in the number of rows and presence of a thin wall. The poor preservation (GHUNLPam 18777) and incompleteness (GHUNLPam 18776) of the remaining specimens preclude a definite ichnospecific assignation. The specimens described herein are larger and display a greater number of rows than *Rosellichnus* isp. from the early Eocene calcareous paleosols of the Gran Salitral Formation, southwestern La Pampa province, Argentina (see Melchor et al., 2002).

Ichnofamily Coprinisphaeridae Genise, 2004
Ichnogenus *Coprinisphaera* Sauer, 1955
Coprinisphaera lazai Sánchez et al., 2013
Fig. 4K–N
Material: GHUNLPam 18629 and 18706 from Salinas Grandes de Hidalgo, and 18765, 18768 and 18769 from Telén.
Description: Spherical to hemispherical (incomplete) chamber fills with diameters ranging from 29.1 to 34.6 mm ($n = 4$) and wall thickness between 6.7 and 8.2 mm ($n = 2$). The specimens display an accessory circular lateral hole with diameter ranging from 4.7 and 7 mm. The circular emergence hole is present in all specimens except in GHUNLPam 18765.
The assignment of the following specimens is tentative due to their poor preservation; GHUNLPam 18629, 18706, and 18769. GHUNLPam 18629 is a hemisphere that shows a lateral notch, considered as relict of the egg chamber. GHUNLPam 18706 is also a hemisphere but the lateral chamber is almost complete adjacent to the external margin of the wall. GHUNLPam 18769 is a spherical structure broken in two parts, showing the emergence hole and another larger lateral hole that may belong to the secondary chamber typical of the ichnotaxon. Most of the specimens from Telén are cemented by carbonate and impregnated by Mn oxides, whereas those from Salinas Grandes de Hidalgo and a single specimen from Telén (GHUNLPam 18769) are compact but lack cementation and manganese impregnation. In addition, some of the uncemented specimens of *Coprinisphaera* from Salinas Grandes de Hidalgo lie within strongly cemented and partially eroded *A. kuenzelii* (Fig. 3G).

Remarks: These specimens are assigned to *C. lazai* because of the presence of an accessory lateral hole, interpreted as the base of the egg chamber. In addition, GHUNLPam 18768 displays a small subcircular hole connecting the egg chamber with the main chamber (Fig. 4N). The absence of an emergence hole in GHUNLPam 18765 suggests that an adult has not emerged from the nest. Uncemented specimens and those lying within *A. kuenzelii* are considered younger than the cemented trace fossils from the formation. The isolation of the egg chamber from the provisions in *Coprinisphaera*, as found in the described specimens, is a feature found in necrophagous dung beetles (Cantil et al., 2013).

Coprinisphaera murguiai (Roselli, 1939)
Fig. 4O, P
Material: GHUNLPam 18475, 18478, 18636, 18766, 18767 and 18772 from Telén; 18628 from Salinas Grandes de Hidalgo, and 18787 from Quehué.
Description: These specimens are well-preserved spherical chamber fills with a relatively thick wall. They exhibit an emergence hole and no secondary chamber, some specimens are empty and other exhibit a massive fill. The maximum diameter of the chamber ranges from 22.8 to 31.2 mm ($n = 9$); wall thickness is between 5.1 and 11.5 mm ($n = 8$) and the diameter of the emergence hole is between 11.9 and 8.8 mm ($n = 4$). The fill of GHUNLPam 18636 displays remains of a thin constructed wall. The specimens from Telén are cemented by carbonate and impregnated by manganese oxides, whereas those from Salinas Grandes de Hidalgo are compact but lack cementation.

Remarks: We follow the ichnotaxonomy proposed by Sánchez et al. (2013). The features that suggest assignation of these isolated chamber fills to *C. murguiai* include: spherical to subspherical shape, thick wall, presence of an emergence hole, a passive fill and absence of a secondary chamber. The remains of a thin constructed wall in GHUNLPam 18636 may correspond to the pupal chamber of the producer (Laza, 2006). Although very rare, Zunino (2013) found remains of an adult dung beetle (a new species of *Phanaeus*) in a specimen of *C. murguai* from the Cangahua of Ecuador. Most *Coprinisphaera* ichnospecies (including *C. murguiai*) are considered brood balls of coprophagous dung beetles (Genise et al., 2000; Cantil et al., 2013).

Coprinisphaera isp.
Fig. 4Q
Material: GHUNLPam 18635, 18764, 18771, 18773, 18774, 18476, 18477 and 18479 from Telén; and 14498, 18627, 18707 and 18747 from Salinas Grandes de Hidalgo.
Description: Incomplete subspherical chamber fills with a thick wall (5.05–10.85 mm, $n = 12$) and no preserved emergence hole. The structure is empty or filled by massive sediment similar to the hosting rock. The interior of GHUNLPam 18477 display an ellipsoidal structure (9.5 mm long by 5.7 mm wide) attached to the chamber wall and a distal rounded end. The specimens from Telén are cemented by carbonate and impregnated by manganse oxides, whereas those from Salinas Grandes de Hidalgo are compact but lack cementation
Remarks: These specimens have diagnostic features of *Coprinisphaera*, including a subspherical shape and a thick constructed wall, but their incomplete preservation precludes an ichnospecific assigment. The subellipsoidal structure found inside the chamber of GHUNLPam 18477 can be interpreted as the egg chamber or another trace within *Coprinisphaera* that may be contemporaneous or postdate it (Laza, 2006). This ellipsoidal structure is not comparable with *Tombownichnus* or *Lazaichnus* (Mikuláš and Genise, 2003; Sánchez and Genise, 2009).

Ichnogenus *Rebuffoichnus* Roselli, 1987
Rebuffoichnus casamiquelai Roselli, 1987
Fig. 5A–B
Material: GHUNLPam 18720 from Bajo Giuliani, 18721 from Punta de la Barda, and 18778 from El Guanaco.
Description: Subovoid, empty isolated chambers with a thick wall, the internal surface of the chamber is smooth and the external is irregular.

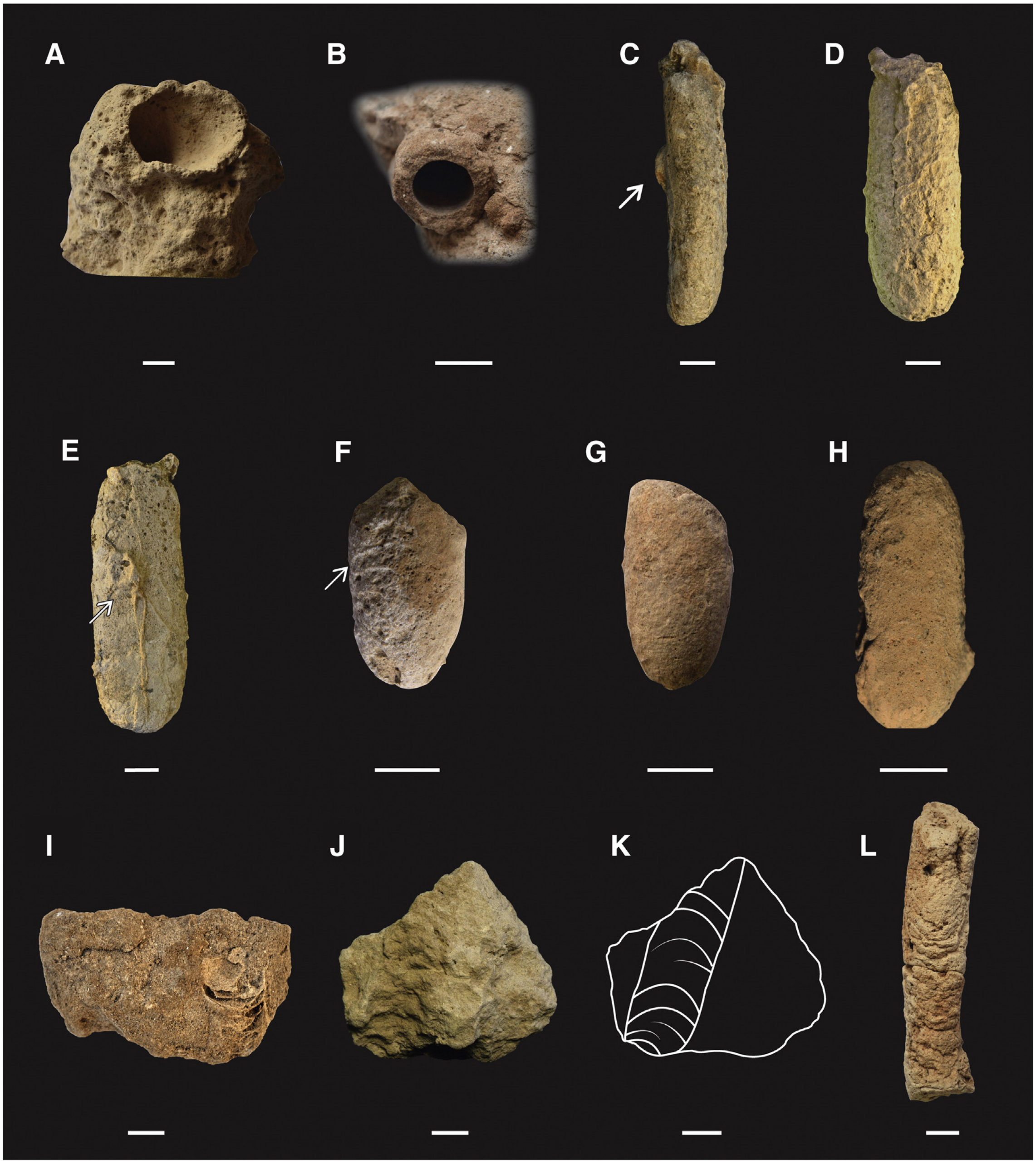

Fig. 5. Trace fossils from the Cerro Azul Formation (continued). (A) *Rebuffoichnus casamiquelai* (GHUNLPam 18720). (B) *Rebuffoichnus casamiquelai* (GHUNLPam 18721). (C), (D) and (E) Lateral, dorsal and ventral view of *Teisseirei barattinia* (GHUNLPam 18781). Arrows point to the subcircular protuberance. (F) *Fictovichnus* cf. *sciuttoi* (GHUNLPam 18713) showing the surface texture (arrowed). (G) *Fictovichnus* cf. *sciuttoi* (GHUNLPam 18719). (H) *Fictovichnus* cf. *sciuttoi* (GHUNLPam 18782/2). (I) Block of sediment with *Taenidium barretti* (GHUNLPam 18710). (J) and (K) Block of sediment with *Taenidium barretti* (GHUNLPam 18715) and interpretative drawing, respectively. (L) Cylindrical burrow fill (GHUNLPam 18722) showing the pseudomenisci. Scale bar: 10 mm.

The internal cavity is ellipsoidal with a circular transverse section. The chamber length is 24 mm (only measured in GHUNLPam 18778), the maximum internal diameter ranges between 17.50 and 35.50 mm (n = 3). The wall thickness is variable within the specimens except for GHUNLPam 18721, and the maximum wall thickness range is 4.20–8.20 mm (n = 3). The preserved depth of the chamber is 48.15 and 17.45 mm (n = 2). GHUNLPam 18721 displays submillimetre shallow pits in the internal surface of the wall.

Remarks: We follow the recent proposal by Alonso-Zarza et al. (2014) to distinguish elliptical to ovoid chambers with thick discrete wall under *Rebuffoichnus* Roselli, 1987, whereas similar forms lacking a thick discrete wall visible to the unaided eye are assigned to *Fictovichnus* Johnston et al, 1996. Accordingly, the known valid ichnospecies of *Rebuffoichnus* includes *R. casamiquelai* Roselli, 1987 and *R. guanche* Genise et al., 2013a. The described specimens show diagnostic features of *R. casamiquelai* including a sub-ovoid structure, thick wall with uneven external and smooth internal surface, and ovoid chamber with circular cross-section (Genise, 2004). *Rebuffoichnus casamiquelai* is attributed to pupation chambers of Curculionidae (Johnston et al., 1996; Genise et al., 2002; Alonso-Zarza et al., 2014), because of the finding of its producer in a single specimen from Australia (Lea, 1925).

Ichnogenus *Teisseirei* Roselli, 1939
Teisseirei barattinia Roselli, 1939
Fig. 5C–E

Material: GHUNLPam 18781 from Estancia Puerta Grande.

Description: Isolated chamber fill, subovoid to elongated, slightly arched longitudinally, with a depressed transverse section. One end is rounded and the other is a truncated antechamber, separated of the remaining part of the structure by a marked constriction. The convex chamber surface displays a reticulate texture. The concave surface is smooth and exhibits a 9.1 mm wide and 4.40 mm high subcircular protuberance (Fig. 5C, D). Total length is 79.60 mm, maximum diameter is 26.15 mm, minimum diameter (constriction) is 19.5 mm, and maximum height is 17.05 mm. The partially preserved antechamber is 3 mm long, 20 mm wide and 12.1 mm deep.

Remarks: The diagnostic features of *T. barattinia* observed in this specimen are: a depressed cross-section, slight longitudinal arching, the surface texture and the presence of an antechamber (Melchor et al., 2002; Genise, 2004). The described protuberance has not been previously mentioned for the ichnospecies and its origin is unknown. The specimen is considerably longer and wider (more than 35%) than the specimens with antechamber from the early Eocene Gran Salitral Formation (Melchor et al., 2002, fig. 12 D) and from the early Eocene Asencio Formation (Genise et al., 2013b, fig. 1F). Although previously considered a coleopteran pupation chamber (Genise, 2004), neoichnological observations (Genise et al., 2013b) suggested that *T. barattinia* is the pupation chamber of a sphinx moth (Lepidoptera, Sphingidae). The reticulated texture is interpreted as the imprints of the true legs of the larva of the producer (Genise et al., 2013b). Modern moth pupation chambers are shallowly emplaced in soils and the presence of *T. barattinia* was proposed as a good indicator of the upper horizons of paleosols (Genise et al., 2013b).

Ichnofamily Pallichnidae Genise, 2004
Ichnogenus *Fictovichnus* Johnston et al., 1996
Fictovichnus cf. *sciuttoi* (Genise et al., 2007)
Fig. 5F–H

Material: GHUNLPam 18713 from Estancia La Malvina; 18719, 18784, and 18785 from Las Torrecitas; and 18782/2 from Puesto Luján.

Description: Internal mold of ovoid chambers that can exhibit a truncated end. Some specimens display a thin constructed wall with a helicoidal surface texture composed of subtle ridges arranged transverse to the long axis of the chamber (Fig. 5F). Chamber cross-section from oval (difference between major and minor diameter up to 2 mm) to circular. The complete specimen (GHUNLPam 18782/2) is 40.10 mm long and 15.50 mm wide. The truncated specimens have a preserved length of 32.7–39.0 mm ($n = 5$) and the maximum diameter is 13.5–21.5 mm ($n = 7$).

Remarks: These specimens display the diagnostic features of *F. sciuttoi*, including the ovoid shape of the chambers, presence of a thin constructed wall that, in one specimen, exhibits the typical helicoidal surface texture (Genise et al., 2007; Alonso-Zarza et al., 2014). These chambers have a slightly oval transverse section. *Fictovichnus sciuttoi* was interpreted as cocoons made by aculeate wasps (Genise et al., 2007). The truncated end was interpreted as result of emergence of the adult and a complete chamber would indicate a failed cocoon (Genise et al., 2007).

Fictovichnus isp.

Material: GHUNLPam 18712 from Caleufú, 18714/1 and 18714/2 from Estancia La Malvina, and 18782/1 from Puesto Luján.

Description: Ellipsoidal chamber fills and broken chambers with part of the filling sediments and rough exterior surface. Maximum diameter is 14.80–19.00 mm ($n = 3$) and length is 30.60 and 31.60 mm ($n = 2$).

Remarks: These specimens display features of *Fictovichnus*, including the ellipsoidal shape, a rough external surface (Johnston et al., 1996; Alonso-Zarza et al., 2014), but their poor preservation does not allow an ichnospecific assignation.

Ichnofamily indeterminate
Taenidium Heer, 1877
Taenidium barretti (Bradshaw, 1981)
Fig. 5I–K

Material: GHUNLPam 18710 and five additional field specimens from Salinas Grandes de Hidalgo, and 18715 from Punta de la Barda.

Description: GHUNLPam 18710 is an unlined, slightly curved, cylindrical meniscate burrow with horizontal to oblique orientation. The fill is composed of arched, densely packed menisci (average meniscus thickness is 2 mm). Burrow width is 17.45 mm and the preserved length is 20 mm.

GHUNLPam 18715 is a slightly curved meniscate burrow, the menisci are less arcuate and thicker than in the previous specimen (average meniscus thickness 4.4 mm). The preserved length is 57.4 mm and the burrow width is 16 mm.

Remarks: In this work, we follow the revision of *Taenidium* by Keighley and Pickerill (1994). The analyzed specimens are assigned to *T. barretti* because of its meniscate filling and absence of wall and burrow branching.

Cylindrical burrow fills
Fig. 5L

Material: GHUNLPam 18722 and 18779 from El Guanaco.

Description: GHUNLPam 18722 is a sinuous, cylindrical burrow fill with rough external surface showing thin arched striations resembling menisci in part of the surface (here named as pseudomenisci) and submillimetre cylindrical grooves parallel to the surface. This specimen was found detached from the hosting rock. Preserved length is 95.4 mm and maximum width is 22 mm. GHUNLPam 18779 is a curved, cylindrical, structureless burrow fill with rough surface. Surface texture in the form of rounded mounds and irregularly distributed small pits. Preserved length is 118.0 mm and maximum width is 22.4 mm.

Remarks: The lack of true menisci precludes the comparison of GHUNLPam 18722 with *Taenidium*. Although specimen GHUNLPam 18779 is massive, the diameter is similar to the pseudomeniscate specimen (GHUNLPam 18722). Submillimetre cylindrical grooves parallel to the surface are interpreted as rootlet traces.

6. Discussion

6.1. Paleoenvironmental conditions during deposition and paleosol formation

Thick, monotonous, massive continental successions of siltstone showing moderate to good sorting are typical of loess deposits, whose dominantly eolian origin is well established (e.g., Johnson, 1989; Pye, 1995; Chan, 1999). The presence of pedogenic calcite is indicative of well-drained soil profiles in sub-humid, semi-arid, and arid climates with low rainfall (less than 800 mm/yr) and high evapotranspiration (see review in Sheldon and Tabor, 2009). For the studied paleosols, a quantitative approximation to the annual precipitation during soil formation can be obtained from the empirical relation between precipitation and depth to the nodular carbonate (Bk) horizon (Retallack, 1994, 2005). The average depth to the Bk horizon is slightly smaller for the paleosol with vertic features than for the remaining paleosols (0.49 m and 0.57 m, respectively), and the average depth for all analyzed paleosols is 0.54 m. The estimate for mean annual precipitation using the relationship by Retallack (2005) is 449 ± 147 mm.

The paleosols from the localities Telén, Estancia Puerta Grande and Las Torrecitas display many diagnostic features of vertisols (Fig. 3C–E), including a thick homogeneous profile, pedogenic slickensides, and deeply penetrating clastic dikes (Retallack, 1990; Parrish, 1998; Montalvo et al., 2008). Vertisols are excellent indicators of warm climate with seasonal rainfall and are mainly found in flat landscapes, located near gentle slopes (Retallack, 1990). The presence of a calcic horizon in the paleosols from Telén, Estancia Puerta Grande and Las Torrecitas suggest that they are calcic vertisols, which are linked to strongly seasonal and semi-arid climates (Parrish, 1998).

The presence of a Bt horizon and blocky or prismatic peds in the remaining paleosols suggest that they can be compared with mollisols (Visconti, 2007). Fe–Mn oxides commonly accumulate in soils with seasonal waterlogging (Fanning and Fanning, 1989), although these paleosols do not exhibit hydromorphic features.

Some paleoenvironmental constraints can also be derived from the composition of the mammal fauna, and the stable isotopic composition of enamel teeth and paleosol carbonates. Vertebrate remains of the Cerro Azul Formation, mainly notoungulates and rodents, suggest that these sediments were deposited in open landscapes like steppes or herbaceous plains (Montalvo et al., 2008). Carbon isotope composition from late Miocene herbivorous enamel teeth from Salinas Grandes de Hidalgo and nearby localities indicates a dominance of C3 plants (MacFadden et al., 1996). Concordantly, carbon isotopic composition from paleosol carbonates for the Cerro Azul Formation has values that suggest a vertical (temporal) change from mixed C3/C4 plants to C3 plants (Visconti, 2007; Visconti et al., 2012). Both isotopic proxies are in agreement and suggest a dominance of C3 plants in lowland areas of the latitude of the study localities, which are favored in climates with cool growing season (Ehleringer et al., 1997).

6.2. Comparison with paleosol ichnofacies

Invertebrate trace fossils from the Cerro Azul Formation appear with low abundance and diversity at each locality. The distribution of trace fossils is summarized in Table 1 and Fig. 6. *Coprinisphaera* specimens were recorded only in three localities: Salinas Grandes de Hidalgo (7 specimens), Telén (17 specimens), and Quehué (1 specimen). All *Coprinisphaera* specimens from the first locality (Fig. 4K) and one from the second locality (GHUNLPam 18769) are not cemented by carbonate and/or impregnated by manganese, as typical for the remaining trace fossils of the unit (Table 1). Genise et al. (2013c) already noted this contrasting preservation of trace fossils from one locality of the unit and argued that the producers of uncemented *Coprinisphaera* were younger than late Miocene. The presence of uncemented *Coprinisphaera* within eroded and cemented specimen of *A. kuenzelii* (Fig. 3G) is also evidence for co-occurrence of trace fossils with different taphonomic history. The most likely explanation is that the uncemented trace fossils were produced in post-Miocene paleosols overlying the Cerro Azul Formation (Genise et al., 2013c). As dung beetle brood balls contain a high concentration of organic matter, if of late Miocene age, they must be strongly cemented as the remaining trace fossils that originally contained organic matter (rhizoliths and ant nests). This inference can be extended to the uncemented specimens described herein (Table 1) and they are not further considered as part of the late Miocene Cerro Azul ichnofauna.

Most of the studied localities yielded either Celliformidae (*Celliforma*, *Rosellichnus*) alone or combined with *Fictovichnus* or *Rebuffoichnus*, and *Teisseirei* was recorded in a single locality (Table 1, Fig. 6). The dominance of the insect trace fossils *Celliforma*, *Rosellichnus*, *Fictovichnus*, and *Rebuffoichnus*, plus the presence of *Teisseirei* and absence of *Coprinisphaera* in these localities is indicative of the *Celliforma* ichnofacies (Genise et al., 2010, in press; Alonso-Zarza et al., 2014). This assignation is in agreement with the occurrence of these trace fossils in paleosols with a calcic horizon, as typical of several examples of the *Celliforma* ichnofacies (Genise et al., 2010, in press). The mentioned trace fossils can be linked to bees (*Celliforma* and *Rosellichnus*), wasps (*Fictovichnus*), beetles (*Rebuffoichnus*) and sphinx moths (*Teisseirei*). Most of the associated trace fossils, including *T. barretti*, large vertebrate burrows, cylindrical burrow fills, and rhizoliths, can also be accommodated within the *Celliforma* ichnofacies, although they are not diagnostic. *Taenidium barretti* and other small meniscate burrows has been cited as an accessory component of several ichnofacies (see Melchor et al., 2012), however, its presence is not diagnostic of any ichnofacies. *Attaichnus kuenzelii* is only recorded in the Salinas Grandes de Hidalgo locality and has not been considered previously as composing the *Celliforma* ichnofacies. This ichnospecies is currently interpreted as fungus-growing nest of Attini developed under a temperate climate (Genise et al., 2013c). Genise et al. (2013c) noted the presence of Poaceae phytoliths in *A. kuenzelii* and hosting rocks, suggesting the presence of grasses at Salinas Grandes de Hidalgo during the late Miocene. In this paper, the trace fossil assemblage from the later locality is provisionally considered as belonging within the *Celliforma* ichnofacies because of the associated cemented *Rosellichnus* specimens. In addition, the inferred producers of *A. kuenzelii* can be found today in temperate semi-arid climates of Argentina (e.g., Farji Brener and Ruggiero, 1994) where calcareous soils are being developed, which suggest that this ichnospecies match the main features of the *Celliforma* ichnofacies. The *Celliforma* ichnofacies has been linked (Genise et al., 2010) to plant formations known as scrubland and woodland after Mueller-Dombois and Ellenberg (1980). The ichnofacies is thought to indicate well drained soils with low vegetation cover where hymenopterans can nest, and scarcity of grasses and other available food for herbivores as reflected by the absence of the ichnogenus *Coprinisphaera* (Genise et al., 2010). Rhizoliths from the Cerro Azul Formation are commonly between 1 and 30 mm wide (Fig. 3F) and no large rhizoliths attributable

Table 1
Distribution of trace fossils by locality.

Ichnotaxa/locality	TE	LT	PG	CA	EG	LM	BG	R14	QU	SG	EM	PL	PB
Celliforma germanica				X									
Celliforma cf. *rosellii*					X			X				X	
Celliforma isp.	X										X		
Fictovichnus cf. *sciuttoi*		X				X						X	
Fictovichnus isp.				X		X						X	
Rosellichnus isp.					X					X			
Rebuffoichnus casamiquelai					X		X						X
Teisseirei barattinia			X										
Coprinisphaera lazai[a]	X									X			
Coprinisphaera lazai	X												
Coprinisphaera murguiai[a]										X			
Coprinisphaera murguiai	X								X				
Coprinisphaera isp.[a]										X			
Coprinisphaera isp.	X												
Attaichnus kuenzelii										X			
Taenidium barretti										X			X
Vertebrate burrow	X									X			
Cylindrical burrow fills					X								

TE: Telén, LT: Las Torrecitas, PG: Estancia Puerta Grande, CA: Caleufú, EG: El Guanaco, LM: Estancia La Malvina, BG: Bajo Giuliani, R14: Road 14, QU: Quehué, SG: Salinas Grandes de Hidalgo, EM: Cerro El Morro, PL: Puesto Luján, PB: Punta de la Barda.

[a] Indicates uncemented specimens.

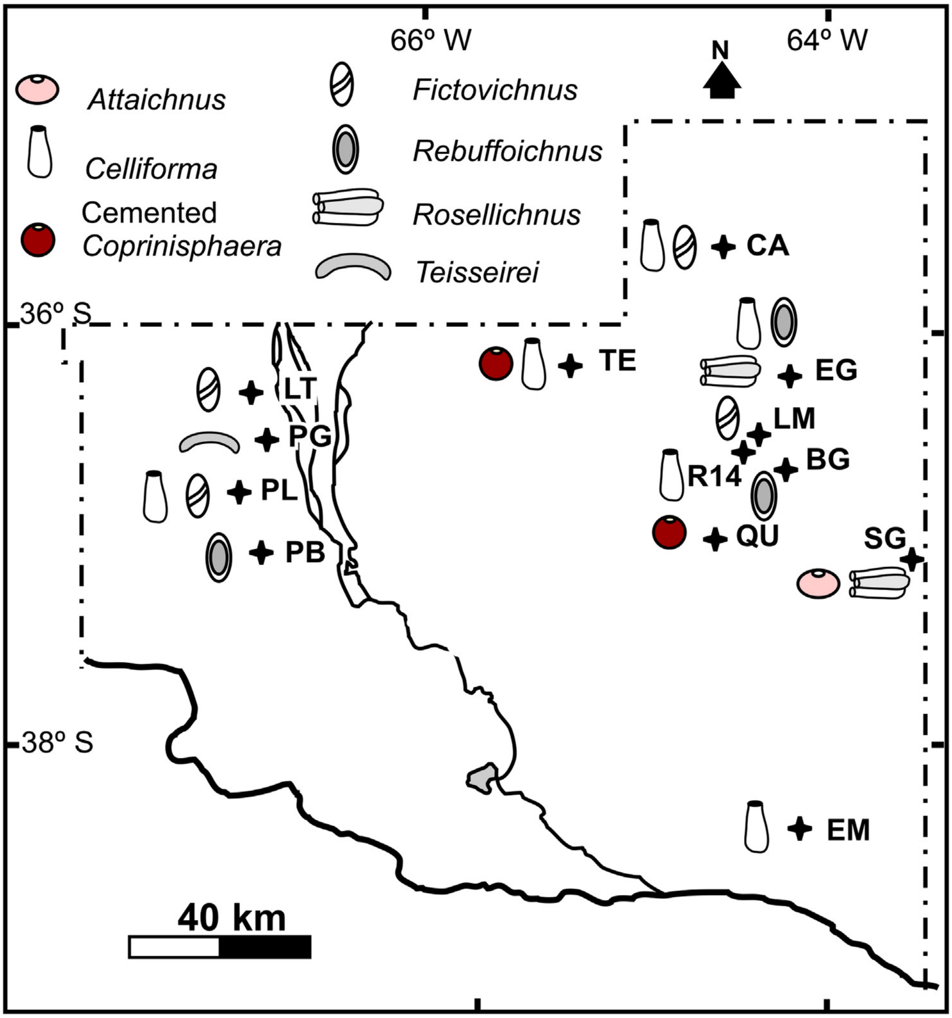

Fig. 6. Map of La Pampa province showing the distribution of late Miocene insect trace fossils of the Cerro Azul Formation. TE: Telén, LT: Las Torrecitas, PG: Estancia Puerta Grande, CA: Caleufú, EG: El Guanaco, LM: Estancia La Malvina, BG: Bajo Giuliani, R14: Road 14, QU: Quehué, SG: Salinas Grandes de Hidalgo, EM: Cerro El Morro, PL: Puesto Luján, PB: Punta de la Barda.

to trees has been recorded. As these rhizoliths are largely concretionary, the diameter of the precursor roots was smaller than that of the structure. In consequence, the example of the *Celliforma* ichnofacies from the Cerro Azul Formation was probably developed in scrublands.

The occurrence of two of the *Celliforma* isp. specimens from Telén (Fig. 4D–E) is noteworthy as they are associated with laminated mudstone from the floor of a vertebrate burrow fill and display a sealed fracture that may be related to vertebrate trampling. This is an unusual example of fossil bee cells probably constructed within an open vertebrate burrow.

The trace fossil assemblage containing abundant cemented *Coprinishaera* ispp. associated to *Celliforma* isp. from Telén and a single isolated specimen of *C. murguiai* from Quehué (Table 1 and Fig. 6), can be provisionally assigned to the *Coprinisphaera* ichnofacies. This ichnofacies reflects paleosols developed under herbaceous communities and suggest wetter climatic conditions than the *Celliforma* ichnofacies (Genise et al., 2000, 2010). This contrasting trace fossil assemblage cannot be correlated with differences in the depth to the Bk horizon of paleosols (and inferred mean annual precipitation) between Telén and Quehué (*Coprinisphaera* ichnofacies) and the remaining localities (assigned to the *Celliforma* ichnofacies). The occurrence of trace fossils comparable with the *Celliforma* and *Coprinisphaera* ichnofacies in the Cerro Azul Formation can be linked to stratigraphic or paleoenvironmental factors. The correlation of outcrops of the Cerro Azul Formation is hampered by the monotonous lithology, reduced thickness and patchy distribution of exposed sections, and poor lateral continuity of individual paleosols. In consequence, it is difficult to decide if the trace fossil bearing intervals of the different localities are correlative or not. An alternative explanation is that, although potentially correlative, the trace fossil bearing intervals represent subtle differences in the paleonvironmental conditions. The available information is insufficient to decide between both explanations.

7. Conclusions

Sedimentological and paleosol features of the trace fossil-bearing intervals of the late Miocene Cerro Azul Formation suggest eolian deposition of silt-sized particles in a flat landscape, under semi-arid and seasonal climatic conditions. Annual precipitation during soil formation is estimated approximately at 450 mm/yr (standard error is 147 mm/yr), as inferred from the depth to the Bk horizon. Calcic vertisols recorded in northwestern localities suggest strongly seasonal and semi-arid climates. The remaining paleosols can be compared with mollisols developed under a seasonal climate. The paleoclimatic information derived from the mammal fauna also support the inference of open landscapes and stable isotopic composition of teeth enamel and paleosol carbonates point to dominance of C3 plants that require a seasonal climate.

Uncemented *Coprinisphaera* ispp. from Salinas Grandes de Hidalgo and Telén are not considered as part of the trace fossil assemblage of the Cerro Azul Formation, instead they must postdate late Miocene paleosols.

The trace fossil assemblage of the Cerro Azul Formation is of low diversity and abundance and dominated by insect trace fossils including *Celliforma*, *Rosellichnus*, *Fictovichnus*, *Rebuffoichnus* and *Teisseirei*. This dominant ichnologic composition (in 11 of the 13 studied localities) is compared with the *Celliforma* ichnofacies, typical of well-drained calcareous paleosols developed under low vegetation coverage. The reduced size of associated rhizoliths suggests that the vegetation was dominated by scrubs with minor participation of herbaceous plants.

Two localities (Telén and Quehué) containing cemented (i.e., late Miocene) *Coprinisphaera* are provisionally compared with the homonymous ichnofacies, suggesting herbaceous communities and wetter climatic conditions. With the available information it is not possible to decide if the trace fossil assemblages representing the local *Coprinisphaera* ichnofacies associated with the dominant *Celliforma* ichnofacies belong to different stratigraphc intervals or represent local paleoenvironmental conditions.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.palaeo.2015.11.036. These data include a Google map of the most important areas described in this article.

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