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A new earthworm trace fossil from paleosols: Aestivation chambers from the Late Pleistocene Sopas Formation of Uruguay

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Abstract

A new ichnotaxon, attributed to earthworm aestivation chambers, is described from paleosols of the Sopas Formation (Upper Pleistocene) of northern Uruguay. This ichnofossil consists of a spherical chamber with a constructed wall of imbricated faecal pellets and a filling of rounded to meniscate pellets arranged in winding strings. The strings may also be connected to specimens of *Taenidium serpentinum* in the paleosol, resulting in a compound trace fossil. *Castrichnus incolumis* igen. et isp. nov. is interpreted as an earthworm aestivation chamber based on its morphological similarity to the chambers produced by extant earthworms. As such, *C. incolumis* is considered an indicator of subaerial exposure, and also of seasonal climate. *C. incolumis* is the second trace fossil that can be attributed with certainty to earthworms. In addition, the *Castrichnus*–*T. serpentinum* compound specimens indicate that in paleosols, earthworms can be the producers of *T. serpentinum.* Aestivation chambers would represent a new ethological category.

Keywords: Trace fossils; Earthworm aestivation chambers; Paleosols; Seasonal climate; Pleistocene; Uruguay

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1. Introduction

In the ichnological literature, the great majority of invertebrate trace fossils in paleosols, particularly the chambered ones, are attributed to insects (Genise, 2004). Despite earthworms being as abundant as insects in Recent soils, only the trace fossil *Edaphichnium lumbricatum* Bown and Kraus, 1983 has been assigned to the former until now. This was based on the presence of elliptical faecal pellets having a high carbonate content, inside tubular burrows. A new ichnotaxon, *Castrichnus incolumis* igen. et isp. nov., which can be attributed to earthworm aestivation chambers, is described herein for the first time from the Late Pleistocene Sopas Formation of Uruguay. The identification of the trace maker was possible due to the complex morphology of the trace fossil, which is similar to that shown by aestivation chambers of modern earthworms. Accordingly, this new, chambered trace fossil in paleosols, the first not attributed to insects, is also an indicator of seasonal climate. The earthworm aestivation chambers were found in the paleosols associated with other trace fossils, such as *Taenidium*

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serpentinum Heer, 1877, rhizoliths and mammal caves. The interconnection of some specimens of *C. incolumis* with *T. serpentinum* indicates in turn, that in paleosols, the latter can be attributed to earthworms as well.

2. Geological setting

The Sopas Formation outcrops in the northern region of Uruguay in Tacuarembó, Salto and Artigas Counties. The trace fossils analyzed herein come from paleosols developed on fluvial deposits assigned to the Sopas Formation, including the former Mataojo and Sopas formations of Antón (1975) (see Ubilla et al., 2004 for a detailed description and discussion of the terminology of the lithostratigraphic units), outcropping in Arroyo Sopas (31°15′S–57°00′W), Paso del Potrero (31°25′S–56°54′W) and Ofelia Piegas (31°33′S–56°47′W) at Salto County, and Arroyo Malo (32°03′S–56°07′W) at Tacuarembó County (Fig. 1). Throughout the formation, these deposits consist of conglomerates that can reach 1 m thickness, with clasts up to 20 cm in diameter (Fig. 2). The conglomeratic levels are capped by massive brownish mudstones reaching an average thickness of 2.5 m, which in some places include gravel size clasts. The thickness of these two facies is highly variable. Some relicts of primary sedimentary structures in the muddy facies and slump structures in the uppermost part were apparent. Levels with carbonate concretions are also present at the top of these lithologies.

In some outcrops the mudstone bears a rich fossil assemblage composed of terrestrial and aquatic vertebrates, fresh water molluscs and trace fossils. These body fossils are also present in the conglomerates.

In the uppermost levels, fine grained sandstone bodies of centimetre thickness are found intercalated with the muddy facies, showing lenticular geometry and ripples. Earthworm trace fossils and rhizoliths are abundant in most of the muddy facies (Fig. 3).

The sub-aquatic origin of the deposits is also confirmed, in some localities, by the presence of fresh water molluscs, fishes and other aquatic or amphibious vertebrates in the same levels that bear the trace fossils (*e.g.* at Arroyo Malo). At the other studied localities, Arroyo Sopas, Paso del Potrero and Ofelia Piegas, the sub-aquatic origin of the deposit is not so obvious because of the obliteration of the original structures due to strong pedogenesis (*cf.* Ubilla et al., 2004).

The stratigraphic logs of Arroyo Sopas and Arroyo Malo are illustrated in Fig. 2. Sedimentary logs of the other localities, Paso del Potrero and Ofelia Piegas, are not included here due to their poor vertical and horizontal exposure respectively.

The age of the Sopas Formation, based on its fossil mammals, is considered Late Pleistocene, Lujanian

Fig. 1. Geographic location of ichnofossiliferous outcrops of the Sopas Formation in the northern region of Uruguay. (A) Arroyo Sopas. (B) Paso del Potrero. (C) Ofelia Piegas (Salto County). (D) Arroyo Malo (Tacuarembó County).

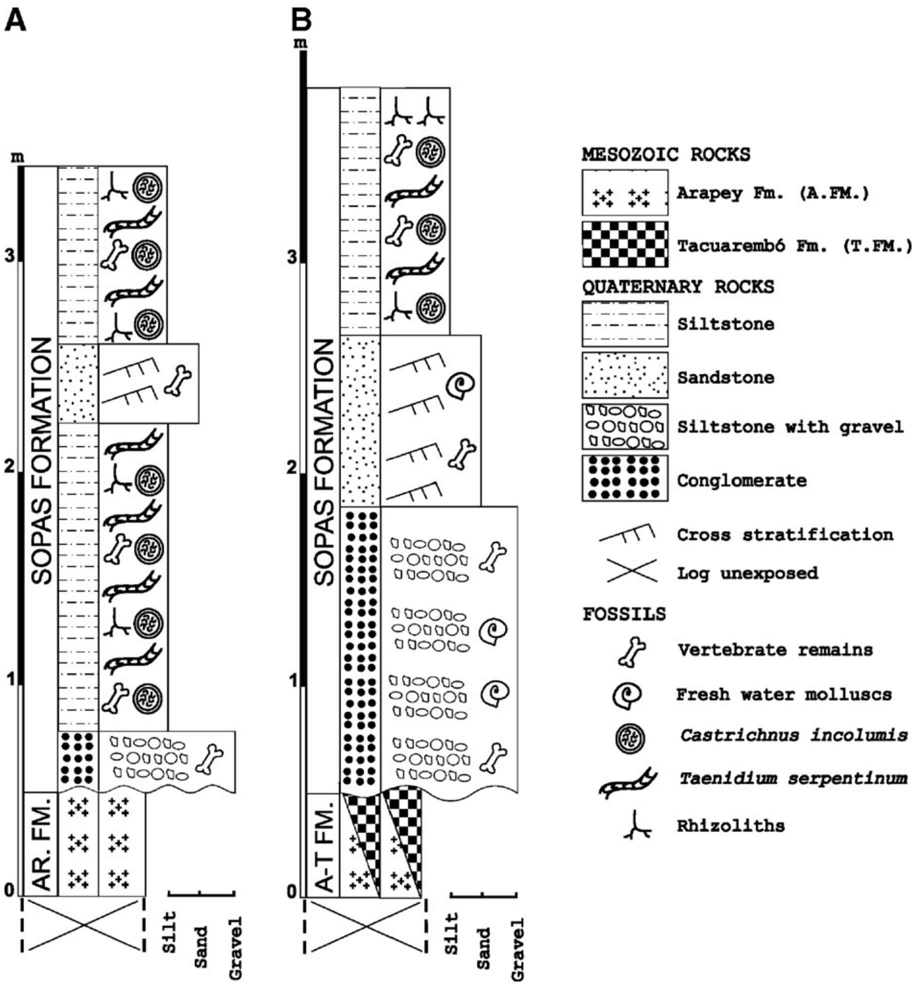

Fig. 2. Stratigraphical logs of two exposures of the Sopas Formation bearing *Castrichnus incolumis* igen. et isp. nov. (A) Arroyo Sopas. (B) Arroyo Malo.

Stage (Ubilla, 1996; Ubilla et al., 2004). Radiometric datings of ^{14}C (>45 ka BP) and TL/OSL (58.3 ± 7.4 ka BP) for the Arroyo Malo locality support the age based on mammals, as well as the TL/OSL (43.5 ± 3.6 ka BP) for Arroyo Sopas and ^{14}C (>45 ka BP) age for Sarandı stream, near Arroyo Sopas (Ubilla et al., 2004).

3. The fossil assemblage of the Sopas Formation

3.1. Body fossils

Mammals are by far the best known body fossils of the Sopas Formation, because of their diversity and abundance. The South American native Order Xenarthra is the best documented, with the highest number of species recorded in the unit. Other orders such as Carnivora, Rodentia, Litopterna, Notoungulata, Proboscidea, Perissodactyla, and Artiodactyla are also present (Ubilla et al., 2004). Apart from mammals, other groups of vertebrates such as fishes, reptiles and birds have also been found in this unit, although recorded by a few species (Ubilla et al., 2004). The vertebrates mentioned above were found in a wide variety of lithological facies within the unit, but the silty facies is the richest. Fresh water molluscs are also a conspicuous component of the body fossil assemblages in many outcrops of the Sopas Formation (Martínez and Rojas, 2004). Amongst the several species of molluscs recorded, the bivalves *Neocorbicula limosa* and *Diplodon peraeformis* are the most abundant, but a great number of gastropod and other bivalve species are also present.

With respect to the localities treated here, both Arroyo Sopas and Arroyo Malo have a wide variety of vertebrates, whereas the molluscs are present only in Arroyo Malo (Ubilla et al., 2004; Martínez and Rojas, 2004). The faunas of the other localities (Paso del

Potrero and Ofelia Piegas) are poorly known, probably because of their deficient exposure.

3.2. Trace fossils

Previous records of invertebrate trace fossils in the Sopas Formation are restricted to some short communications in scientific meetings without detailed morphological descriptions (Verde et al., 1998; Verde, 1999; Verde et al., 2002, 2004). Vertebrate ichnofossils are also present, represented by only two specimens of carnivore coprolites (Verde and Ubilla, 2002), and probable mammal caves (MV and MU, personal observation, 2003).

Invertebrate trace fossils of the Sopas Formation are abundant in the silty facies at four localities: Arroyo Sopas, Paso del Potrero, Ofelia Piegas (at Salto County) and Arroyo Malo (at Tacuarembó County). In many outcrops, this facies is totally bioturbated. Its ichnofabric is dominated by *T. serpentinum*, described in the following section. Vertical and horizontal rhizoliths and small stumps are also present, reaching high densities in the uppermost part of the silts (Fig. 3A).

Finally, the other ichnofossils associated with *T. serpentinum* are the earthworm aestivation chambers described below. In the four localities of the Sopas Formation treated here, the earthworm aestivation chambers are conspicuous elements of the ichnofabrics, because of their size and abundance.

4. Systematic palaeontology

The specimens described below are deposited at the Colección Paleontológica del Departamento de Evolución de Cuencas, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay (FCDP).

Castrichnus igen. nov.
Etymology: From the Latin, *castra aestiva*, a fort or encampment put up for use during summer or warm weather by the Roman legions.
Type ichnospecies: C. incolumis isp. nov., type and only known ichnospecies.
Diagnosis: Spherical to slightly ovoid chambers preserved in full relief with multilayered wall composed of imbricated pellets. Knobby external surface texture, that results from rounded protruding pellets. Internal surface has flattened pellets with concentrically arranged rims around a central longitudinal ridge. Chamber filling composed of rounded to meniscate pellets arranged in winding strings, which may pierce the wall.
Remarks: The overall shape of this trace fossil – particularly when the pelleted filling is not preserved – resembles the ichnogenus *Coprinisphaera* Sauer, 1955 (dung beetle brood balls). However, there are some important differences between the two. *Castrichnus* shows a multilayered wall constructed with pellets showing distinct external and internal surface textures

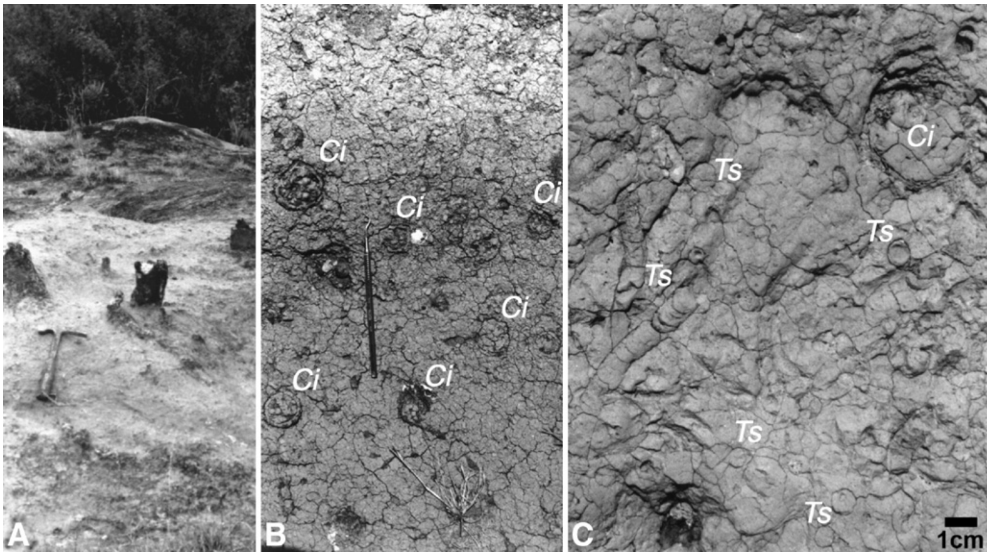

Fig. 3. Exposure of the Sopas Fm. at Arroyo Sopas. (A) Stumps in the silty facies; hammer is 28 cm long. (B and C) Close up of bedding planes showing the high density of trace fossils. (B) *Castrichnus incolumis* (*Ci*); needle is 14 cm long. (C) *C. incolumis* (*Ci*) and *Taenidium serpentinum* (*Ts*).

that is lacking in *Coprinisphaera*, and also an active fill composed of strings of pellets in some cases curled into a ball, in contrast with the passive fillings of the latter. On the other hand, the small secondary chambers and emergence holes of *Coprinisphaera* (Laza, in press) are lacking in *Castrichnus*.

C. incolumis isp. nov.
Figs. 3B–C and 4A–H.
1998 *Coprinisphaera* Verde et al. p. 31.
1999 "cámaras de letargo de lombrices" Verde, p. 35.
2002 "cámaras de estivación de lombrices" Verde et al., p. 87.
2004 "earthworm aestivation chambers" Verde et al., p. 81.

Etymology: From the Latin, *incolumis*: uninjured, safe, scatheless, unharmed, due to the function of the structure for protection of the trace maker.

Holotype: A complete specimen broken in the upper part, which shows the active fillings and multilayered wall, FCDP 4241, Fig. 4A–B.

Paratypes: Four almost complete specimens showing active fillings and wall structure and textures, FCDP 4242, Fig. 4C; FCDP 4243, Fig. 4D; FCDP 4244; FCDP 4245, Fig. 4E.

Diagnosis: The same as for the ichnogenus.

Description: The holotype, FCDP No. 4241 is an ovoid chamber 30.33 × 28.00 mm in diameter (Fig. 4A). The wall is multilayered, 2.75 mm thick, having at least four layers, each one composed of imbricate pellets. Externally, the wall has a knobby surface because of the presence of ball-shaped pellets, 2 mm in diameter, whereas internally the pellets are flattened and show concentric rims (Fig. 4B). The filling consists of larger, rounded pellets 5.4 mm in diameter, arranged in a string curled into a ball (Fig. 4A). Some of the pellets are compressed against others, composing a meniscate string as seen in cross section. Paratype FCDP No. 4242 is ovoid, 35.5 × 31.0 mm in diameter, the multilayered wall is 2.9 mm thick, external pellets and those of the fillings are 2 mm and 7.2 mm in diameter respectively (Fig. 4C). Paratype FCDP No. 4243 is subspherical, 30.9 mm in diameter and the wall is 2.6 mm thick (Fig. 4D). External pellets and those of the fillings are 2 mm and 6.9 mm in diameter respectively. The pellets are more distinguishable in that part of the string that pierces the wall. Paratype FCDP No. 4244 is subspherical, 37.3 mm in diameter and the wall is 4.1 mm thick. External pellets and those of the fillings are 2 mm and 6.3 mm in diameter respectively. Those pellets in the part of the string that pierces the wall are darker than the inner ones. The pellet boundaries are locally hard to distinguish. Paratype FCDP No. 4245 is sub-spherical, 28.10 mm in diameter and the wall is 3.1 mm thick (Fig. 4E). External pellets and those of the fillings are 2 mm and 7.04 mm in diameter respectively. The arrangement of the filling in a string is not clear except for the part where the chamber wall is pierced.

Other material examined shows the following range in sizes: maximum external diameter of chambers: 21–43 mm ($n = 58$; mean = 30.91; $S.D.^2 = 23.46$; S.D. = 4.84); wall thickness: 1.4–4.1 mm ($n = 67$; mean = 2.62; $S.D.^2 = 0.46$; S.D. = 0.68).

The inner surface of the wall observed in several broken specimens shows a recurrent pattern in each pellet comprising up to three subcircular concentric rims, frequently with a central, transversal ridge probably produced by the anus of the earthworm (Fig. 4G–H). At least three of the studied specimens show a string of pellets, protruding through the wall (Fig. 4D–E). The concavity of pellets indicates that these pellets were produced while the tracemaker was leaving the chamber. The complete string would have been made while the producer was leaving the chamber, while burrowing the soil around it. A specimen shows pellets of different, darker material, than that of the chamber, indicating that it reached a different layer in the soil while emerging upwards. The winding would probably reproduce the rolled up position of earthworms inside chambers to avoid desiccation, and the pellets show the different positions of the anus while the producer excavated its way out into the soil (Fig. 4I).

The string of pellets resembles a meniscate burrow, or *T. serpentinum*, however they are deposited inside the empty chamber and thus, it is not a true excavation. When the string pierces the wall, continuing into the paleosol, this meniscate burrow can be assigned to *T. serpentinum*, which occurs very commonly in the same levels as *Castrichnus*. This fact suggests that the *Castrichnus* tracemaker and the *T. serpentinum* tracemaker are the same. Meniscate burrows in paleosols have been attributed to insects (Frey et al., 1984; Retallack, 2001; O'Geen and Busacca, 2001), and also to earthworms (Bown and Kraus, 1983; Fitzpatrick, 1984; Verde, 1999). The association of *Castrichnus* with *T. serpentinum* indicates that also earthworms are potential producers for meniscate burrows in paleosols.

The similarity of the overall shape of this trace fossil – particularly when the pelleted filling is not preserved – to the ichnogenus *Coprinisphaera* led Verde et al. (1998) to include the material in this ichnogenus. Later in short contributions, Verde (1999) and Verde et al. (2002, 2004), based on new data on the filling of these structures, stressed the probable earthworm origin of

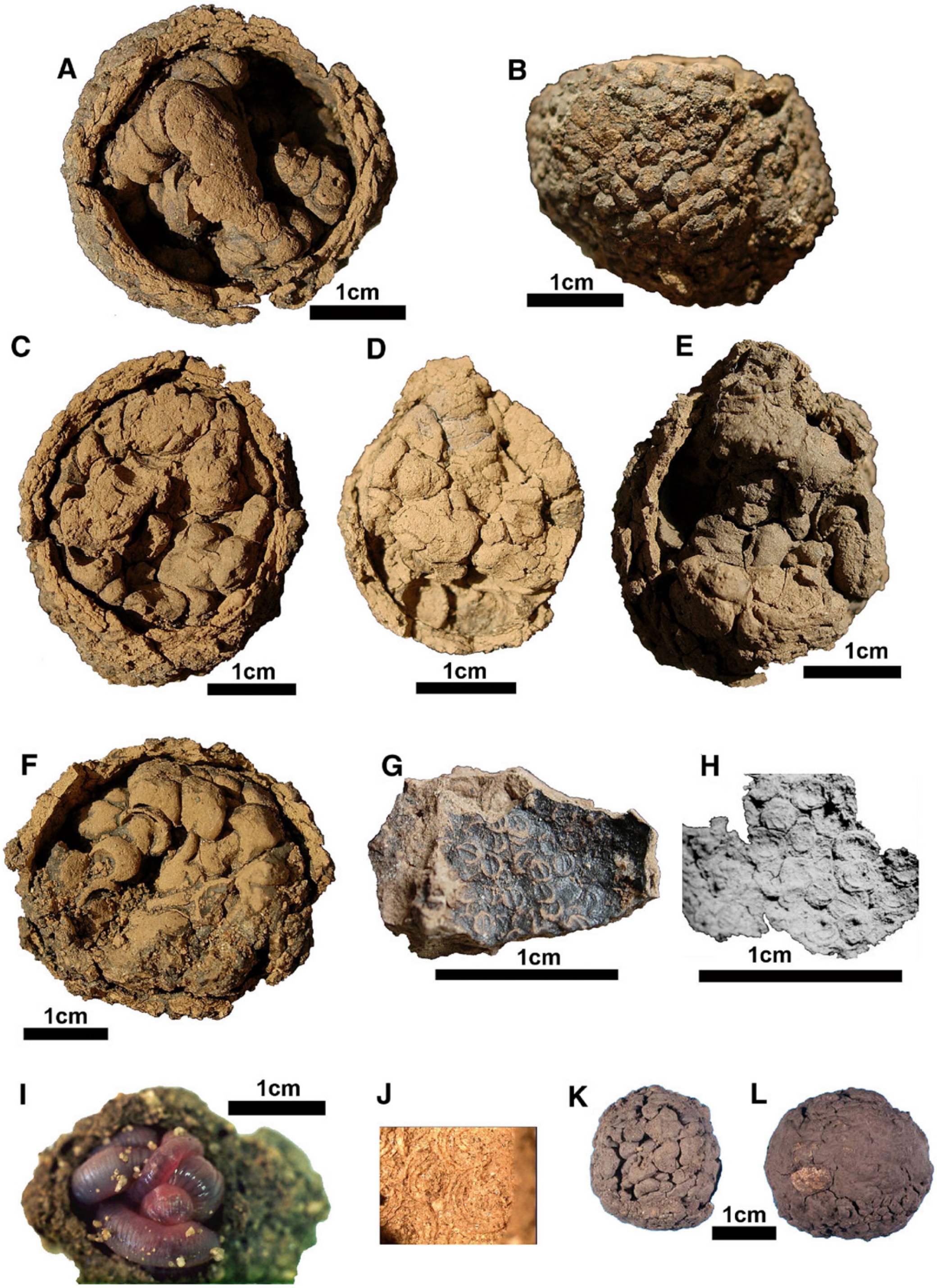

Fig. 4. (A–H) *Castrichnus incolumis*. (A–B) Holotype FCDP No. 4241, (A) horizontal section showing wall and filling structure and (B) lateral view showing external wall texture. (C) Paratype FCDP No. 4242 horizontal section showing wall and filling. (D) Paratype FCDP No. 4243 horizontal section where a meniscate string breaks the wall outwards. (E) Paratype FCDP No. 4245. (F) FCDP No. 4249, horizontal section with rounded pellets from the filling. (G–H) Detail of the internal texture of wall. (I–J) *Hormogaster elisae* aestivation chambers. (I) Chamber with earthworm inside. (J) Internal detail of wall texture (photos courtesy of Díaz Cosín and Ruiz Gil). (K–L) *Martiodrilus heterostichon* aestivation chambers. (K) Broken specimen showing pelleted wall and filling. (L) External view of the pelleted wall (photos courtesy of Alexander Feijoo). (A–H) From the Arroyo Sopas locality, Sopas Fm. (I–J) Recent specimens from Spain. (K–L) Recent specimens from Spain.

these trace fossils as a more probable hypothesis. *Castrichnus* is interpreted as an earthworm aestivation chamber on the basis of comparisons with extant earthworm traces, the walls of which are also composed of pellets. This structure of the wall can be recognized in modern aestivation chambers of *Martiodrilus heterostichon* (Glossosscolecidae) externally (Fig. 4K–L) where the pellets are rounded and small in comparison with those of the fillings as in *Castrichnus*, and also in those of *Hormogaster elisae* (Hormogastridae) internally, where the flattened pellets show concentric rims as in *Castrichnus* (Díaz Cosín, personal communication 2004 to MV) (Fig. 4J). The texture of concentric rims could be reproduced in the laboratory using a pastry bag loaded with soft mud. The rims were more pronounced when the mud was extruded almost in contact with the substrate, rhythmically, and with increasing pressure. The central structure was produced when the flow was interrupted (Fig. 5).

These observations suggest that for the chamber lining earthworms use soft faecal material applied with the anus almost in contact with the wall, rhythmically and with some pressure. The central structure, which in contrast to this reconstruction is generally a ridge, would reflect the interruption of the defaecation.

Jiménez et al. (2000) described the *M. heterostichon* chambers as discrete structures that could be separated completely from the rest of the soil, covered with a clay and mucus coating. The same authors stated that the construction of these chambers involved clay particle selection by the animal, deposited in a complete globe in which it enclosed itself. They also mentioned that the earthworms, when emerging from the chambers, defaecated within the chamber and also within the emergence burrow while moving upward in the soil. Another reference of the fillings of chambers of extant earthworms (*Aporrectodea caliginosa*) that parallels *C. incolumis* is that of Lee (1985). This author described them as chambers filled with humus-stained casts originated in the excavation of vertical burrows made by the earthworm when they abandon the resting stage and move back close to the surface in autumn.

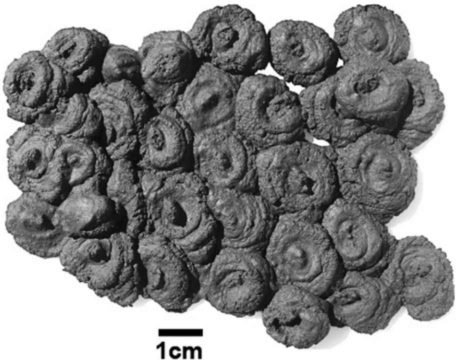

Fig. 5. Artificial mud pellets produced in laboratory showing concentric rims and central structure.

Ichnogenus *Taenidium* Heer, 1877.
Type ichnospecies. *T. serpentinum* Heer, 1877.
Diagnosis: Variably oriented, unwalled, straight, winding, curved, or sinuous, essentially cylindrical, meniscate backfilled trace fossils. Secondary successive branching may occur, but true branching is absent (after Keighley and Pickerill, 1994).

T. serpentinum Heer, 1877.
Fig. 3C.
Description: Sinuous to nearly straight *Taenidium* with well-spaced arcuate menisci, distance between menisci equal to or slightly less than burrow diameter. External moulds may exhibit slight smooth annulation corresponding to menisci. Boundary sharp. Branching not recorded. Filling homogeneous with the same aspect than the enclosing rock. Diameter may vary between 0.4 and 0.75 cm.
Remarks: Some specimens of *C. incolumis* show a prolongation of the internal meniscate string of pellets as a meniscate burrow in the enclosing paleosol, comparable to the co-occurring abundant specimens of *T. serpentinum* (Fig. 4D–E). This morphology implies that *Castrichnus* with *Taenidium* elements is a compound trace fossil produced by the same tracemaker (Pickerill, 1994). In addition, they do not represent only a sudden change in the behaviour of the producer, as in classical examples of other invertebrate ichnofossils (Pickerill, 1994), because the chamber walls are constructed before the aestivation season, whereas the meniscate structures, namely the *Castrichnus* filling plus the *T. serpentinum*, are formed after it. The meniscate string of pellets breaks the wall of *Castrichnus* and, taking into account the concave-outward orientation of the menisci, it can be inferred that the compound trace fossil records the abandonment of the chamber by the earthworm after aestivation.

5. Significance of *C. incolumis*

C. incolumis, interpreted herein as earthworm aestivation chambers, provides evidence for the presence of paleosols that originated where water was originally confined to films on the surface of soil aggregates or was held in pore spaces, and where the relative humidity of air-filled spaces was 100% or slightly less (Lee, 1985). In waterlogged soils, most earthworms cannot survive, whereas in those that are periodically subjected to a seasonally strong dry period, they construct aestivation chambers (Jiménez et al., 2000), as those represented by *C. incolumis* described herein.

Lee (1985) distinguished three types of earthworm burrows: (1) rather vertical burrows made by anecic species (Bouché, 1972) that feed on surface litter; (2) horizontal burrows made by endogeic species (Bouché, 1972) that feed on organic matter in subsurface soil horizons; and (3) more or less vertical burrows connected with roughly spherical chambers, where earthworms retreat to enter a resting state during dry or cold seasons. *C. incolumis* in combination with *T. serpentinum* represents the latter type. Particular examples of these aestivation chambers are produced today by *H. elisae*, *M. heterostichon* and *A. caliginosa* in soils where seasonal variation is marked (Lee, 1985; Jiménez et al., 2000; Díaz Cosín, personal communication 2004 to MV). *A. caliginosa* burrows down in the soil up to 40 cm and then constructs chambers in which the earthworm rolls up to avoid desiccation during the summer (Lee, 1985). In this context the abundance of *C. incolumis* suggests the presence of a seasonal climate during the pedogenesis of the deposits belonging to the Sopas Formation. Independent evidence supporting this hypothesis is the presence of fossils from the migratory anseriform *Chloephaga picta* (Magellan goose) (Ubilla et al., 2004; Tambussi et al., 2005), which today only reaches the southern coastal region of Uruguay during the austral winter.

Most chambered trace fossils described from paleosols are nests or pupal chambers of insects (Genise, 2004). Both types are placed in distinct ethological categories: calichnia for insect nests (Genise and Bown, 1994), and pupichnia (Genise et al., in press). Aestivation chambers are not contemplated in any of these or other established ethological categories at present. Another ichnogenus created for aestivation chambers of amphibians, *Torridorefugium* (Hembree et al., 2005), and aestivation chambers of lungfishes (Voorhies, 1975), can be grouped with *Castrichnus*, according to the function of these structures. Recognition of further cases would encourage the discussion about the advisability of the creation of a new ethological category for these, such as aestivichnia, or whether they should remain as distinct subset of domichnia.

6. Concluding remarks

- *C. incolumis* is a new ichnotaxon interpreted as a fossil earthworm aestivation chamber based on its morphological similarity to aestivation chambers made by extant earthworms.
- *C. incolumis* is the second trace fossil that can be attributed to earthworms with certainty, along with the already known *E. lumbricatum*.
- Specimens of *C. incolumis* containing *T. serpentinum* suggest that the latter ichnotaxon, where it occurs in paleosols, can be the product of earthworms, although its simple morphology precludes the exclusion of other producers.
- *C. incolumis*, being an earthworm aestivation chamber, is an indicator of seasonal climate and well aerated soils, the presence of which can be inferred for the Sopas Formation.

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