CLEPTOPARASITISM AND DETRITIVORY IN DUNG BEETLE FOSSIL BROOD BALLS FROM PATAGONIA, ARGENTINA

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Abstract: Traces within traces is a new ichnological field that is meant to shed light on significative palaeoecological aspects. Dung beetle fossil brood balls (*Coprinisphaera* ispp.), from the Middle Eocene – Lower Miocene Sarmiento Formation of Patagonia, Argentina, show two different trace fossils excavated in its infillings and/or wall that reveal the presence and relationships among different components of past dung communities. *Tombownichnus pepei* n. isp. is represented by elongated pits, circular to elliptical in cross-section, occurring in the centre or beside ovoid mounds in the internal surface of the *Coprinisphaera* wall. These traces record the activity of cleptoparasites, such as other dung beetles or flies, whose larvae were probably carried passively with the dung for provisions. *Tombownichnus pepei* would

represent the pupation chambers excavated by full grown larvae in the *Coprinisphaera* wall after completing their development inside provisioned dung. The other trace fossil, *Lazaichnus fistulosus* is represented by circular to subcircular borings occurring in *Coprinisphaera* walls, in connection with an internal gallery in their infillings. Its connection also with meniscate burrows and chambers in the surrounding palaeosol attributable to aestivation chambers of earthworms revealed that these organisms would have been active cleptoparasites or detritivores in dung beetle fossil brood balls.

Key words: trace fossils, cleptoparasitism, detritivory, dung beetles, earthworms, Patagonia.

THERE are few records of traces within traces in the continental ichnofossil record. Most of them are holes, pits or galleries made in insect fossil nests or burrows in coprolites (Chin and Gill 1996; Mikuláš and Genise 2003; Chin 2007; and references therein). It is possible to recognize two types of traces within traces in the geological record. Traces that were constructed accidentally within or in contact to one another, and others where the co-occurrence is due to the interaction between two organisms that are biologically related. Examples of the former are exemplified by dung beetle traces accidentally crosscut by those of bees, cicadas and other beetles (Laza 2006; and references herein), whereas the latter may shed light on significant palaeobiological aspects of the producers. Most of these show different types of parasitism in which insects are the principal actors. Previous reports showed cases of cleptoparasitism between scarabs where provision burrows are crosscut by those of cleptoparasites; or cases of attack by parasitoids in insect nests (Chin and Gill 1996; Martin 2001; Mikuláš and Genise 2003; Genise and Cladera 2004). Mikuláš and Genise (2003) created two ichnogenera: *Tombownichnus,* to include holes and pits that occurred in constructed walls of fossil insect nests,

and *Lazaichnus* for holes in the wall connected with galleries in the fillings. They suggested that this type of trace fossil could be produced by parasitoids (i.e. organisms whose larvae develop as a parasite of the larva of the nest constructor until killing it), cleptoparasites (i.e. organisms that steal the provisions collected by others for the development of their own larvae) or detritivores (i.e. organisms whose larvae feed on the organic remains of nests).

This contribution shows traces occurring in dung beetle fossil brood balls, which can be attributed to cleptoparasites or detritivores. The objectives are: (1) to describe a new ichnospecies of *Tombownichnus* reflecting a potential case of cleptoparasitism; (2) to identify a possible producer of *L. fistulosus* in dung beetle fossil brood balls, which may involve cleptoparasitism or detritivory; and (3) to show palaeoecological aspects of the invertebrate community associated with dung beetle fossil brood balls.

GEOLOGICAL SETTING

The specimens studied here belong to the Sarmiento Formation, cropping out at Gran Barranca, Chubut

province, Argentina. The Sarmiento Formation is a Middle Eocene – Lower Miocene pyroclastic succession mostly known because of its abundant and diverse fossil vertebrates. The mammal assemblages (marsupials, xenarthrans, astrapotherians, notoungulates, primates and rodents) are considered the stratigraphic standards for the South America Land Mammal Ages (Ameghino 1906; Simpson 1940; Cifelli 1985). The Sarmiento Formation is broadly exposed in central and north Patagonia (Argentina), covering more than 200,000 km^2 and showing a relatively uniform lithology, characterized by chonites (mud and clay-size tuff), fine tuffs, bentonites and intraformational conglomerates (Mazzoni 1985). Likewise, the presence of palaeosols bearing trace fossils is another significant and well-known feature (Frenguelli 1938; Andreis *et al.* 1975; Spalletti and Mazzoni 1979; Bellosi and Genise 2004; Bellosi *et al.* in press). At the type locality, Gran Barranca, south of Chubut province, the Sarmiento Formation is divided into several members: Gran Barranca (Middle Eocene), Rosado (late Middle Eocene), Lower Puesto Almendra (Units 1 and 2, Upper Eocene), Vera (Uppermost Eocene – Lower Oligocene), Upper Puesto Almendra (Units 3 to 5, Oligocene) and Colhue-Huapi (Lower Miocene) (Madden and Bellosi in press). In the middle and the upper members there are numerous well-exposed palaeosols. The dominant parent material for the palaeosols is fine volcanic ash composed of rhyolitic-dacitic glass shards and subordinate plagioclase (andesine). Depositional scenarios included subaerial loessic plains (eolian deposits), ephemeral small lakes and incised fluvial valleys, developed in a subhumid to arid palaeoclimatic context (Bellosi in press). According to diagnostic features, recognized soil types are Andisol, Alfisol, Entisol, Aridisol and occasionally Vertisol (Bellosi and González in press). A characteristic feature of these palaeosols is well-preserved ichnofossils, particularly those of insects. The examined material came from Puesto Almendra and Colhue-Huapi Members. In this locality, Lower Puesto Almendra consists of conglomerate and sandstone, frequently moderately to poorly modified by pedogenesis. These deposits were accumulated in braided, probably ephemeral, fluvial channels (Bellosi in press). The Upper Puesto Almendra is formed by conglomerate, sandstone and pyroclastic mudstone, which in some cases are affected by pedogenesis. These facies record the sedimentation of a fluvial system in a deeply incised valley (Bellosi in press). The Colhue-Huapi member records a new episode of fluvial incision and aggradation. The lower and middle sections include fluvial channel deposits, tephric loessites and palaeosols with abundant mammal fossils. The upper section is composed of similar eolian deposits and calcareous poorly developed palaeosols (Bellosi in press).

SYSTEMATIC ICHNOLOGY

The material studied herein is housed in the Museo Paleontológico Egidio Feruglio, Colección de Icnología (MPEF-IC), Trelew, Chubut, Argentina; and in the Museo Argentino de Ciencias Naturales, Colección de Icnología (MACN-Icn), Buenos Aires, Argentina.

Tombownichnus Mikuláš and Genise, 2003

Diagnosis. Circular to subcircular passing borings (i.e. complete borings) or external or internal pits (i.e. incomplete borings) occurring in constructed linings of chambers made of agglutinated soil material. A single boring, despite its size, is not diagnostic for this ichnogenus, which can be identified only when more than one boring is present. If the chamber shows a single large boring and one or more smaller ones, the former should be considered as part of the substrate (i.e. the constructed chamber). On the contrary, a single external pit is diagnostic for this ichnogenus (emended from Mikuláš and Genise 2003).

Remarks. The diagnosis was emended to include pits that occur in the internal surface of the chamber lining. These types of traces within traces, which are compatible with the morphology represented by *Tombownichnus*, were not known at the time when Mikuláš and Genise (2003) defined the ichnogenus.

Tombownichnus pepei isp. nov.
Plate 1, figures 1–5; Text-figure 1A

Derivation of name. Dedicated to José 'Pepe' Laza, a pioneer of modern insect palaeoichnology, who discovered the type material of this ichnospecies as well as many other ichnological jewels during his 30 years of collection preparation and observation of *Coprinisphaera* specimens.

Holotype. One specimen (MACN-Icn 2346; Pl. 1, figs 1, 3) in a *Coprinisphaera* isp. (Laza col. MACN-Icn 2074) from Sierra de Talquino, Chubut province, Argentina (Sarmiento Formation).

Paratypes. Three specimens (MACN-Icn 2342, 2345 and 2355) in a *Coprinisphaera* isp. (Laza col. MACN-Icn 2074) from Sierra de Talquino, Chubut province, Argentina (Sarmiento Formation). One specimen (MPEF-IC 601) in a specimen of *Coprinisphaera murguiai* (MPEF-IC 600) from Gran Barranca, Chubut province, Argentina (Middle Eocene, Gran Barranca Member, Sarmiento Formation).

Material. Nineteen specimens (MACN-Icn 2342–2360), eight specimens (MACN-Icn, 2379–2386) and five specimens (MACN-Icn 2393–2397) in a *Coprinisphaera* isp. (Laza col. MACN-Icn 2074), a *Coprinisphaera ecuadoriensis* (Laza col. MACN-Icn

2300) and a *Coprinisphaera murguiai* (Laza col. MACN-Icn 2392), respectively, from Sierra de Talquino, Chubut province, Argentina (Sarmiento Formation). Seventy-five specimens (MPEF-IC 601–632, 639–648, 650–664 and MACN-Icn 2361–2378) in four specimens of *Coprinisphaera murguiai* (MPEF-IC 600, 638, 649 and MACN-Icn 1620), respectively, from Gran Barranca, Chubut province, Argentina (Middle Eocene – Oligocene, Gran Barranca and Puesto Almendra Members, Sarmiento Formation). Five specimens (MACN-Icn 2387–2391) in a *Coprinisphaera* isp. (MACN-Icn 1382) from Gran Barranca, Chubut province, Argentina (Upper Eocene, Puesto Almendra Member, Sarmiento Formation). One specimen (MPEF-IC 637) in a *Coprinisphaera murguiai* (MPEF-IC 636) from Gran Barranca, Chubut province, Argentina (Middle Eocene, Gran Barranca Member, Sarmiento Formation). One specimen (MPEF-IC 635) in a *Coprinisphaera ecuadoriensis* (MPEF-IC 634) from Gran Barranca, Chubut province, Argentina (Middle Eocene, Gran Barranca Member, Sarmiento Formation).

Diagnosis. *Tombownichnus* represented by an elongated pit, circular to elliptical in cross-section, occurring in the internal surface of the lining of *Coprinisphaera* specimens. The pits may occur in the centre or beside an ovoid mound.

Description. The holotype (MACN-Icn 2346) and other specimens (MACN-Icn 2342–2360, 2387–2391) occur in undetermined specimens of *Coprinisphaera* having no evidence of an emergence hole or egg chamber (Pl. 1, figs 1–3). The remaining specimens occur in the internal surface of the wall of *Coprinisphaera ecuadoriensis* or *Coprinisphaera murguiai*, respectively (Pl. 1, figs 4–5). In most cases, specimens are elongated with the long axis perpendicular, oblique or almost tangential to the wall surface. The few specimens that are hemispherical are interpreted as partly preserved ones. The pits range from 1 to 6.8 mm in length (n = 45), and those having circular cross-section from 2.2 to 4.6 mm in diameter (n = 19). In specimens having elliptical cross-section the long axis ranges from 2.6 to 5.3 mm and the short axis ranges from 2 to 4.1 mm (n = 26). The internal surface of the pit is smooth. In the most complete specimens the pit is opened in the centre or at one end of an elongated mound of material indistinguishable from that of the chamber wall (Pl. 1, fig. 3). The mound ranges from 1 to 4.4 mm in height, from 4.2 to 6.7 mm in length and from 4.1 to 4.9 mm wide (n = 14). Micromorphologically, the pit in cross-section shows the internal surface coated with a thin layer, 50–325 µ thick (Text-fig. 1A), and different in composition from the *Coprinisphaera* wall. The microstructure of this layer is microgranular and composed of non birefringent clay granules whose porosity is 10%. The coarse fraction, fine-sand to silt grain sized, is represented by very few volcanic glass shards, quartz and lithic fragments. The fine fraction is composed of abundant yellow and birefringent clay that coats the microgranules and fills the pores. The *Coprinisphaera* wall shows massive microstructure and the porosity is less than 1%. The coarse fraction is larger than in the lining (40%) and also contains plagioclase. The fine fraction shows brown, low birefringent clay, darkened by oxide (Text-fig. 1A).

Remarks. *Tombownichnus pepei* differs from *Tombownichnus parabolicus* in occurring in the internal surface of the wall of *Coprinisphaera* specimens. In addition many specimens show a mound, which is absent in *Tombownichnus parabolicus*.

Lazaichnus Mikuláš and Genise, 2003

Lazaichnus fistulosus Mikuláš and Genise, 2003
Plate 1, figures 6–7; Text-figure 1B–C

Material. Sixteen specimens (MPEF-IC 666, 668, 670, 672, 674, 676, 678, 680, 682, 684, 686, 688, 690 and 692, and MACN-Icn 2398 and 2399) occurring in 16 specimens of *Coprinisphaera* isp. (MPEF-IC 665, 667, 669, 671, 673, 675, 677, 679, 681, 683, 685, 687, 689 and 691, and MACN-Icn 1373 and 1605) from Gran Barranca, Chubut province, Argentina (Middle Eocene – Oligocene, Gran Barranca and Puesto Almendra Members, Sarmiento Formation).

Diagnosis. Circular to subcircular holes occurring in constructed walls of chambers made of agglutinated soil material, connected to an internal gallery in their infillings. A single hole connected with a single cavity, despite its size, is not diagnostic for this ichnogenus (Mikuláš and Genise 2003).

Description. The holes and galleries occur in walls and fillings, respectively, of weathered specimens of *Coprinisphaera* that lack diagnostic characters allowing identification to the ichnospecies level (Pl. 1, fig. 6). The holes in the wall and the gallery in the infillings show no particular arrangement and may be connected with a boxwork in the palaeosol (Pl. 1, fig. 7). Holes and burrows are circular to subcircular in cross-section. In circular ones the diameter ranges from 1.3 to 3.5 mm (n = 46), and in those that have subcircular cross-section, the long axis ranges from 2.9 to 3.5 mm and the short axis ranges from 2.2 to 2.5 mm (n = 4). Some of the burrows in the infillings have an enlargement at the end, whose section ranges from 5 to 6.4 mm in diameter (n = 4). Burrows show an internal lining with a smooth surface, and may be empty or filled. There are some *Coprinisphaera* specimens that show only meniscate and unpatterned burrows in the infillings (Pl. 1, figs 8–10), whereas other ones show only borings in the wall (Pl. 1, fig. 11). These traces, even when produced by the same organism, are not considered *L. fistulosus* because ichnotaxonomically they lack holes in the wall or internal gallery in the infillings respectively.

Micromorphologically, the *Coprinisphaera* filling shows a thin band of dark material, 25–50 µ thick (Text-fig. 1B), around the burrows composing the gallery. Short fragments of dark bands are also spread within the fillings. Each burrow has a thin lining of clay 25–75 µ thick (Text-fig. 1C). Observed with crossed nichols, the clay is yellow, optically oriented and birefringent (Text-fig. 1C). Burrow fillings are composed of volcanic glass shards, plagioclase and quartz, more porous than in the *Coprinisphaera*

fillings, and with irregularly deposited clay (Text-fig. 1C). The specimens of *L. fistulosus* are connected with a boxwork in the palaeosol showing meniscate fillings and chambers (Text-fig. 1D–E). Micromorphologically, the most complete meniscate burrow observed is 5.75 mm in length and ranges from 1.12 to 1.25 mm in diameter. Each menisci ranges from 125 to 175 μ in thickness and is composed of material similar to that of the palaeosol. Between successive menisci there is a clay layer that is yellow and birefringent observed with crossed nichols (Text-fig. 1D). The most complete chamber is ovoid with the long axis 3.62 mm and the short axis 2.75 mm (Text-fig. 1E). The internal surface of the chamber shows a clay lining that ranges from 75 to 500 μ in thickness. In some parts, the lining is composed of meniscate structures, 75 μ thick, which are oriented with the concavity toward the chamber lumen. The clay observed with crossed nichols in the lining and in the menisci is yellow, birefringent and shows optical orientation. The chamber is partially filled with palaeosol material and also with clay menisci, which have the same thickness and birefringence as those of the lining. Some of these menisci show a loose arrangement in a string, but the most of them are irregularly orientated into the cavity (Text-fig. 1E).

DISCUSSION

There are two types of traces within traces in the fossil record. The first type comprises traces that may crosscut others by chance or due to changes in palaeoenvironmental conditions. An example of the former may be galls occurring in fossil leaves partly consumed later by other insect (Wilf *et al.* 2005). In turn, the latter relationship involves an ichnotaxon crosscutting other after the establishment of new environmental conditions and it is a powerful tool for ichnofabric analyses (i.e. Taylor *et al.* 2003). The second type comprises traces made within other traces as a result of contemporaneous biological interactions, such as parasitism, cleptoparasitism and detritivory among others (Chin and Gill 1996; Martin 2001; Mikuláš and Genise 2003 and references therein). Both types of traces are recorded in dung beetle fossil brood

balls represented by specimens of *Coprinisphaera* (i.e. Laza 2006) from Middle Eocene – Oligocene beds of the Sarmiento Formation at Gran Barranca and Sierra de Talquino (Chubut, Argentina).

Laza (2006, fig. 5A–C, F), in his ichnotaxonomic review of *Coprinisphaera*, illustrated some cases of the first type. Bee cells are recorded in the fillings of *Coprinisphaera* (Laza 2006, fig. 5A) (Text-fig. 2A–B) as well as their remains in the outer surface of specimens (Text-fig. 2C) from the Middle Eocene – Lower Miocene Sarmiento Formation (Chubut, Argentina). In these cases, dung beetles were the first to construct their brood balls in the soil and later the bees dug their cells inside them. Large collections of *Coprinisphaera* at this locality (Sánchez *et al.* 2007) record a few specimens crosscut by bee cells, suggesting that this interaction records no changes in palaeo-environmental conditions favouring bees, but only accidental crosscutting probably due to the abundance of brood balls in soils. Other traces found in relation with dung beetle brood balls were feeding chambers of cicada nymphs (i.e. *Feoichnus challa* Krause *et al.* 2008) (Text-fig. 2D) from the Miocene Pinturas Formation (Santa Cruz, Argentina), *Teisseirei barattinia* (Text-fig. 2E), interpreted as beetle pupation chambers (Genise 2004) and undetermined burrows (Text-fig. 2F), both from the Middle Eocene – Lower Miocene Sarmiento Formation (Chubut, Argentina). Another case illustrated by Laza (2006, fig. 5C) was interpreted as possible insect eggs occurring inside a specimen of *Coprinisphaera* (Text-fig. 2G–H) from the Middle Eocene – Lower Miocene Sarmiento Formation (Chubut, Argentina). However, the structures closely resemble faecal pellets of rhizophagous coleopterans (Pl. 2, figs 1–2), whose burrows would have reached chambers of dung beetles by chance.

Traces within traces with palaeobiological meaning are poorly represented and analyzed in the ichnological literature. Some of them involve hymenopterans. The presence of complete and incomplete holes in walls of fossil

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EXPLANATION OF PLATE 1

Figs 1–11. *Tombownichnus* ispp. and *Lazaichnus fistulosus* occurring in specimens of *Coprinisphaera* ispp. 1, *Coprinisphaera* isp., MACN-Icn 2074, showing the holotype, MACN-Icn 2346 (white arrow) and some of the paratypes, MACN-Icn 2342, 2345 (black arrows) of *Tombownichnus pepei*. 2, *Coprinisphaera* isp., MACN-Icn 2074, showing one of the paratypes, MACN-Icn 2355 (black arrow), of *Tombownichnus pepei*. 3, Detail of the holotype, MACN-Icn 2346 (white arrow), and one paratype, MACN-Icn 2345 (black arrow). 4–5, *Coprinisphaera murguiai*, MPEF-IC 600, showing one of the paratypes, MPEF-IC 601 (black arrow) and a specimen of *Tombownichnus plenus*, MPEF-IC 633 (white arrow). 6, *Lazaichnus fistulosus*, MPEF-IC 688, occurring in a weathered specimen of *Coprinisphaera* isp., MPEF-IC 687. 7, *Coprinisphaera* isp., MACN-Icn 1589, with *L. fistulosus*, which is connected with a gallery excavated in the palaeosol (white arrow). 8, Specimen of *Coprinisphaera* isp., MPEF-IC 694, showing meniscate and unpatterned burrows in the infillings. 9, Detail of a meniscate burrow excavated in the *Coprinisphaera* infilling, MPEF-IC 694. 10–11, two specimens of *Coprinisphaera* isp., MACN-Icn 1605 and MPEF-IC 696, showing borings only in the infilling (10) or in the wall (11). Scale bars represent 1 cm.

PLATE 1
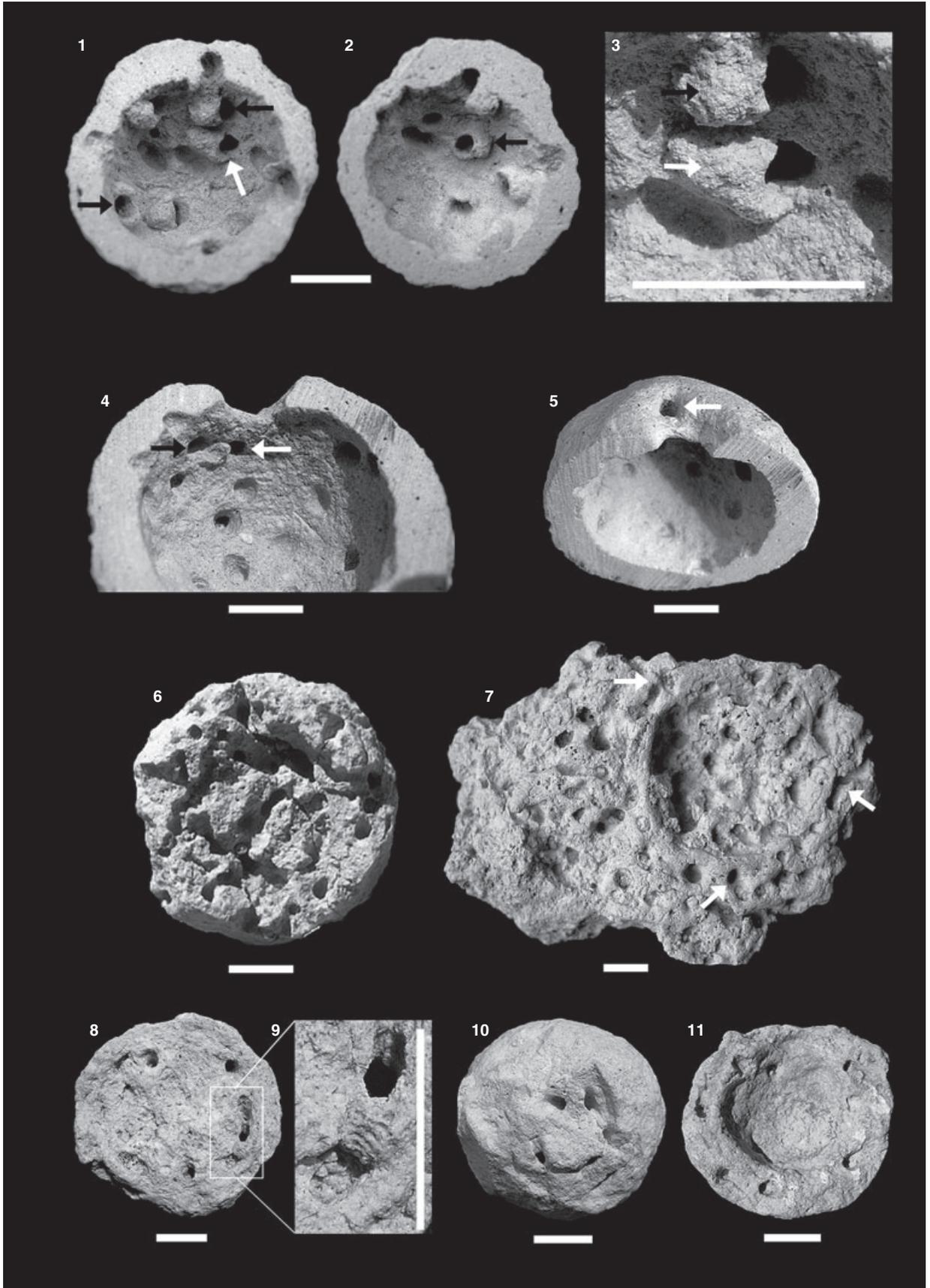
SÁNCHEZ and GENISE, *Tombownichnus, Lazaichnus fistulosus*

bee cells have been interpreted as the work of parasitoids, cleptoparasites or detritivores entering the cells from the outside, as suggested by the presence of incomplete perforations in the outer surface of the cell walls (i.e. Houston 1987; Ellis and Ellis-Adam 1993; Mikuláš and Genise 2003; Genise and Cladera 2004). Wasps were suggested as possible producers because some Mutillidae are known to attack larvae in their cell by digging through soil or boring through walls (Evans and Eberhard 1970). Bown *et al.* (1997), who studied wasp cocoons from the Paleocene–Eocene Claron and Colter Formations of Utah, is another possible example of wasp parasitoidism. They found smaller ovoid structures inside larger ones, which were interpreted as cocoons of parasitoid wasps inside other wasp cocoons. Martin (2001) mentioned examples of insect pupation cases from the Cretaceous Two Medicine Formation (USA), where he found burrows of small diameter connected with, or arising from, larger pupation cases. Considering the difference in size between burrows and cases, and the fact that modern parasitoids are typically smaller than their hosts, he concluded that parasitoids were the possible trace makers for small burrows.

Other examples involve trace fossils of dung beetles as those shown here. The oldest report belongs to Frenguelli (1938), who mentioned dung beetle fossil brood masses from the Oligocene of Patagonia with lateral holes, which were attributed to cleptoparasites. Brussaard (1987) interpreted large Holocene back-filling traces as constructed by geotrupines considering that they were crosscut by small back-filling traces, similar to those made by the cleptoparasitic scarab *Aphodius coenosus*. Chin and Gill (1996) described a herbivore dinosaur coprolite from the Cretaceous Two Medicine Formation (USA), which recorded a similar case of tiny burrows crosscutting larger ones. They suggested that paracoprid dung beetles created the tiny burrows and geotrupine beetles might have been responsible for the largest burrows. Mikuláš and Genise (2003) described holes and galleries occurring in the dung beetle fossil brood masses *Monesichnus ameghinoi* and holes in the walls of *Coprinisphaera isp.*, which were interpreted as structures made by cleptoparasites or detritivores.

These latter authors provided the first ichnotaxonomical treatment for traces made in insect chambers from palaeosols creating three new ichnotaxa for them: *Tombownichnus plenus*, *Tombownichnus parabolicus* and *L. fistulosus*. The new ichnospecies, *Tombownichnus pepei* is a well defined one since it is based on the internal location of pits, in contrast to the already known ichnospecies, which were based, respectively, on the external location of pits or the presence of full holes in the wall of the hosting trace fossil (Mikuláš and Genise 2003). Nevertheless, the examined material shows some morphological diversity. The holotype (Pl. 1, figs 1–3) and other specimens in the same brood ball occur beside or in the centre of an ovoid mound, which may be material removed from the pit bored in the chamber wall. This mound is absent in the other specimens. Some of the paratypes and other specimens examined (Pl. 1, figs 1–2) are elongated pits, circular to elliptical in cross-section, which have no mound and are more shallowly excavated. In any case, both mound-bearing and mound-less pits are present in the same completely closed specimen of *Coprinisphaera* suggesting that both might have been produced by the same organism.

Tombownichnus pepei can be interpreted as traces made by cleptoparasites. Cleptoparasitism is a common behaviour among insects in dung communities. Some species of dung beetles construct no nest and use the provisions stored by other species (Cambefort and Hanski 1991). These cleptoparasitic dung beetles belong to Aphodiinae and Scarabaeinae. There are two subguilds of cleptoparasites recognized by Cambefort (1991): cleptoparasites of dung beetles that roll balls and those of dung beetles that construct balls beneath dung pats. Among the Scarabaeinae, the smaller species, like those of *Cleptocaccobius*, are active cleptoparasites that attack scarabs when rolling a dung ball (Cambefort and Hanski 1991), whereas larger species of *Pedaria* and *Onthophagus* enter burrows containing tunnelers provisions (Halffter and Mathews 1966; Cambefort and Hanski 1991) or their brood balls (Halffter and Mathews 1966 and references therein). Aphodiinae includes some passive cleptoparasites, which are present in the dung pats and can be buried by tunnelers by chance

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EXPLANATION OF PLATE 2

Figs 1–7. Extant traces and analogues. 1, Burrows filled with faecal pellets of rhizophagous coleopteran larva (Formosa, Argentina). 2, Detail of faecal pellets and the larva (La Pampa, Argentina). 3, Fly perching on back of *Malagoniella* sp., while the ball is being buried (La Rioja, Argentina). 4, Larva of Sarcophagidae inside buried dung balls of *Malagoniella* sp. (La Rioja, Argentina). 5, Dungfly larva in horse dung pat (Ushuaia, Argentina). 6, Maggot of Sarcophagidae inside buried dung balls of *Malagoniella sp.* (La Rioja, Argentina). 7, Earthworm in horse dung pat (Ushuaia, Argentina). Scale bars represent 1 cm.

SÁNCHEZ and GENISE, traces in beetle brood balls

PLATE 2
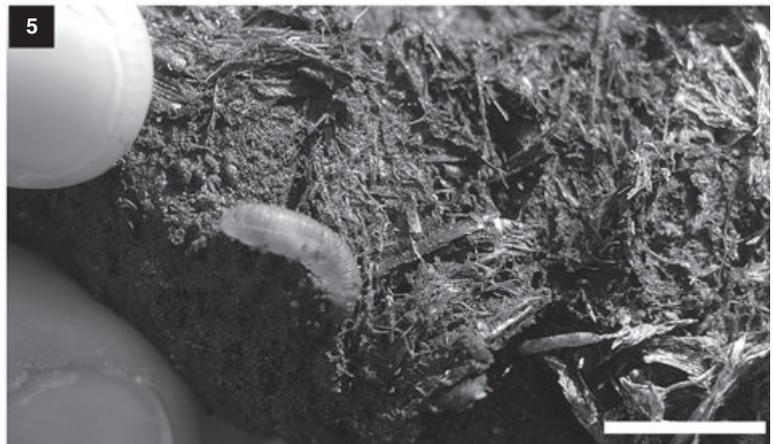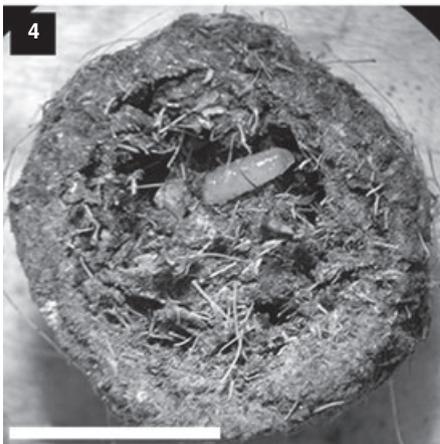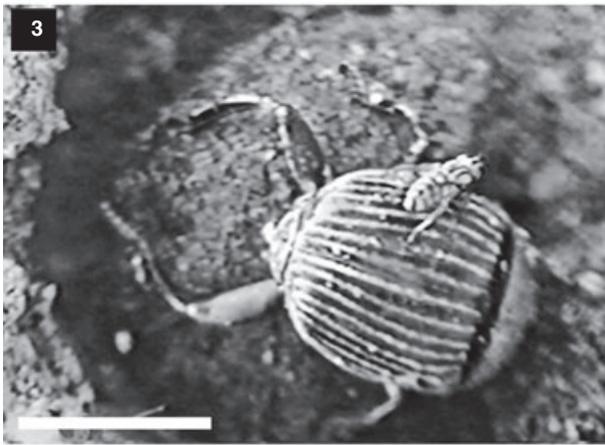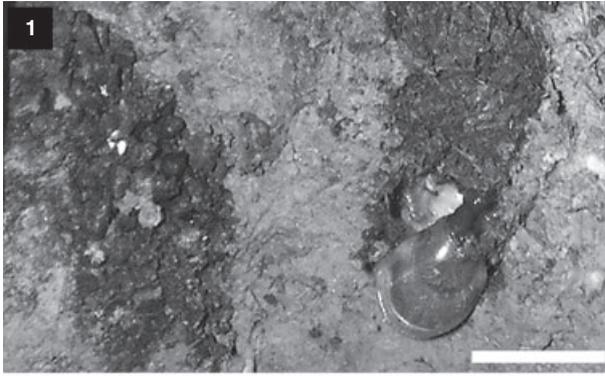
SÁNCHEZ and GENISE, traces in beetle brood balls
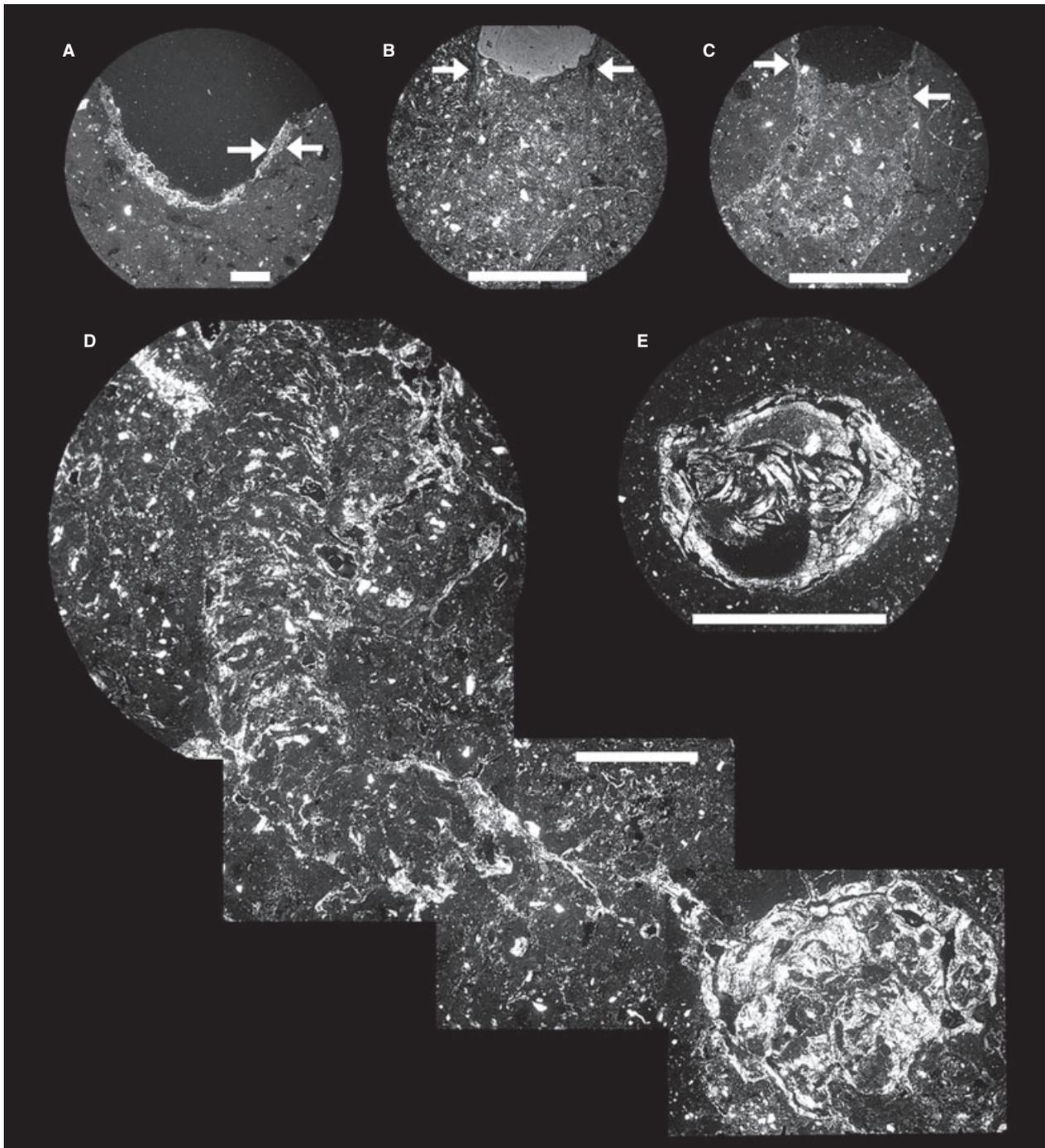
TEXT-FIG. 1. Micromorphology of A, *Tombownichnus pepei*; B–E, *Lazaichnus fistulosus*. A, Cross-section showing the thin layer of birefringent clay that coats the internal surface of the pit (white arrows) (crossed nichols), scale bar: 700 μm. B–C, Burrow excavated in the *Coprinisphaera* filling that shows a thin fringe of dark material (B, white arrows) around them, and a thin internal lining of birefringent clay (crossed nichols) (C, white arrows), scale bar: 2 mm. D, Burrow excavated in the palaeosol showing meniscate fillings with yellow and birefringent clay deposited between successive menisci (crossed nichols), connected with a chamber (*Castrichnus incolumis*), scale bar: 1.50 mm. E, *Castrichnus incolumis* showing birefringent clay lining composed of meniscate pellets, and filled with unpatterned palaeosol material and a string of birefringent clay menisci, scale bar: 2.75 mm.

with the provisions (Rougon and Rougon 1980; Cambefort and Hanski 1991). Others are active, such as *Aphodius rufipes*, whose third instar larva excavates burrows

to enter brood masses of *Geotrupes spiniger* (e.g. Klemperer 1980). Some species of Aphodiinae are obligate cleptoparasites, whereas others show a facultative clepto-
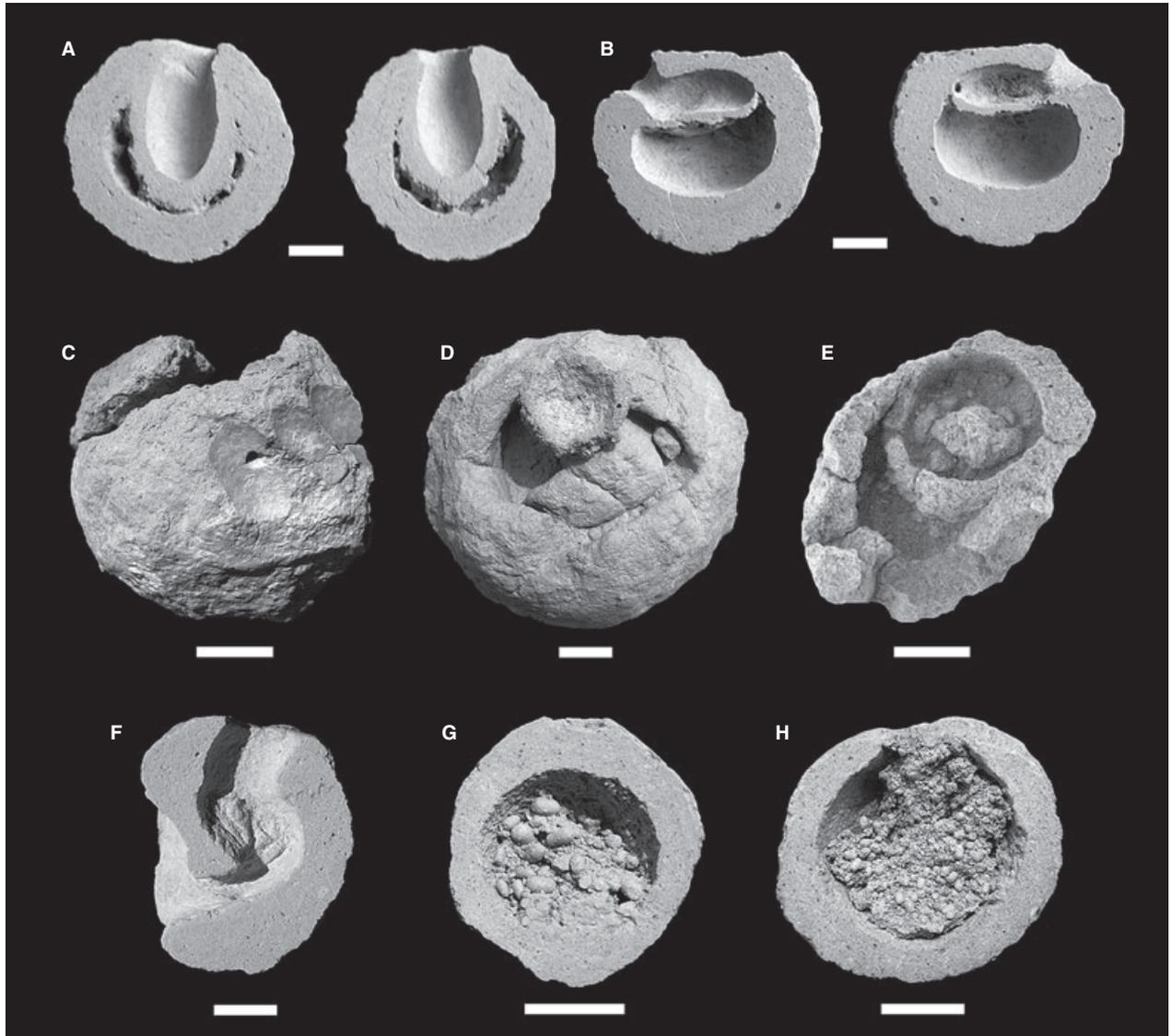
TEXT-FIG. 2. *Coprinisphaera* isp. crosscut by other trace fossils. A–B, MACN-Icn 2261 and 2128, bee cell in the filling. C, MPEF-IC 698, bee cell in the wall, outer surface. D, feeding chamber of cicada nymph, *Feoichnus challa* on the emergence hole. E, MPEF-IC 699, *Coprinisphaera* isp. inside *Teisseirei barattinia*, a beetle pupation chamber. F, MPEF-IC 700, an undetermined burrow excavated in the infilling. G–H, Possible faecal pellets of rhizophagous coleopterans filling the interior chamber. Scale bars represent 1 cm.

parasitism only during the dry season (Rougon and Rougon 1980; González-Megías and Sánchez-Piñero 2003). Both, Aphodiinae and Scarabaeinae may attack the same nest. A single *Heliocopris* nest contained five species of cleptoparasitic Scarabaeinae and two of Aphodiinae (Cambefort 1984).

Dungflies also show different degrees of cleptoparasitism (Halffter and Mathews 1966; Hanski 1991). Active cleptoparasitism is represented by some species of borborid flies that cling to the back of the beetle while it is rolling the ball, run or fly behind the rolling beetle (Halffter and Mathews 1966). Field observations at La Rioja, Argentina, revealed several species of flies flying around

balls being rolled or buried by *Malagoniella* sp. (Pl. 2, fig. 3). Material collected there, also revealed the presence of larvae and maggots of a species of Sarcophagidae inside buried balls previously used for making brood balls (Pl. 2, figs 4, 6). Passive cleptoparasitism may result from the presence of dungfly larva in dung pats (Pl. 2, fig. 5). Richter (1918) found brood pears of *Malagoniella violacea* attacked by *Tetanops sanguinipes*, an otitid fly, which caused the larva death by starving. He proposed that the adult beetle, by accident, carried the fly eggs along with the dung.

Tombownichnus pepei occurs in specimens of *Coprinisphaera* without evidence of any emergence hole of its con-

structor, suggesting cleptoparasitic activity that would have precluded, actively or passively, the development of the constructor's larva. The presence of cleptoparasites in the ball may be the result of two different circumstances. In one case, the trace maker could be an organism that was originally feeding in the dung pat and that was carried accidentally by a scarab with the piece of dung taken for provisioning the nest. This inferred passive cleptoparasitism is supported by the absence of holes in the specimen of *Coprinisphaera* bearing the holotype of *Tombownichnus pepei*. Cleptoparasites neither entered the ball actively, nor could they have left it after their emergence. In such cases, it can be inferred that the passive cleptoparasites, after completing their development, left the provisioned dung to pupate in the soil as if they were still in the dung pat. In turn, they found the soil chamber wall, where they excavated anyway the pupation chambers represented by *Tombownichnus pepei*. The emerged adults failed to leave the ball, as there are no openings to the exterior, suggesting that they have no tools to do that, which support the hypothesis of passive cleptoparasitism, even when other causes of death cannot be ruled out. On the other hand, other specimens of *Coprinisphaera* bearing *Tombownichnus pepei* show holes that could be used by cleptoparasites to leave or to enter the ball. One of the studied specimens shows both *Tombownichnus pepei* and *Tombownichnus plenus* (Pl. 1, figs 4–5). *Tombownichnus plenus* may represent the entrance or exit of a cleptoparasite, whereas *Tombownichnus pepei* may represent their pupation chambers in the case of the deeper specimens, or some intent to bore into the wall in the case of the shallower ones. Some dungflies pupate within the dung (Pl. 2, fig. 6); others pupate in the soil beneath the dung pats (Ferrar 1980) such as all Aphodiinae (Halffter and Edmonds 1982), and Scarabaeinae pupate inside brood chambers (Halffter and Edmonds 1982). Accordingly, *Tombownichnus pepei* was produced by soil-pupating flies or Aphodiinae.

Lazaichnus fistulosus was originally described by Mikuláš and Genise (2003) mostly from *Monesichnus ameghinoi*, a trace fossil interpreted as a dung beetle brood mass (Genise and Laza 1998). However, no suggestion about possible trace makers was proposed in those papers. The material described herein occurs in specimens of *Coprinisphaera* isp. from palaeosols of the Sarmiento Formation, at Gran Barranca, bearing a boxwork of burrows similar to that found in *Coprinisphaera* specimens. Bellosi et al. (2001) tentatively interpreted these trace fossils in the palaeosol as possible termite nests. Later, using micromorphological characters, Cosarinsky et al. (2005) demonstrated that these trace fossils definitely do not have a termite character and could have been made by other organisms. Some of the characters found in that contribution, such as burrow hypocoatings (dark bands, Text-fig. 1B) and intercalations of dark bands were found also

herein in the infillings of the *Coprinisphaera* specimens. The new data demonstrate that some characters in the boxwork occurring in the host palaeosol and in a specimen of *Coprinisphaera* (Text-fig. 1) are compatible with those of earthworm traces recently described by Verde et al. (2007). These earthworm trace fossils in palaeosols from the Late Pleistocene Sopas Formation (Uruguay) are represented by spherical aestivation chambers (*Castrichnus incolumis*) connected with *Taenidium serpentinum* in the palaeosol. The structures described herein for the palaeosol (Text-fig. 1D–E) are compatible with *Castrichnus incolumis* connected to meniscate burrows, suggesting that the earthworms could be the trace makers of these boxworks. This is further supported by the presence of lenticular pellets coating the internal surface of the chamber wall, and arranged in strings inside them (Verde et al. 2007) (Text-fig. 1E). These trace fossils in the palaeosol are connected to *L. fistulosus* occurring in specimens of *Coprinisphaera* (Pl. 1, fig. 7), suggesting the same trace maker for both the boxwork in the palaeosol and *L. fistulosus*. Earthworms are considered part of the dung community (Hanski 1991) (Pl. 2, fig. 7) and they have an important impact on pat disappearance and decomposition (Holter 1979; Hendriksen 1991). Morelli (pers. comm. 2007) found extant earthworms inside dung beetle brood balls, which destroy the provisions causing the egg or larva's death.

Earthworms producing *L. fistulosus* can be considered as active cleptoparasites or detritivores. The holes in the wall of the dung beetle brood balls are connected to the internal gallery, suggesting that they entered the balls actively seeking the provisioned dung. This refutes the possibility that the earthworms were passive cleptoparasites carried by chance from the dung pats. As the weathered and bioturbated condition of the balls precludes any inference about the adult scarab emergence, it is impossible to ascertain if earthworms feed on fresh provisioned dung (active cleptoparasitism) causing the egg or larva death, or if they entered emerged balls seeking remains of provisions (detritivores), or both. In one case it appears that earthworms utilized the *Coprinisphaera* emergence hole to enter or exit (Pl. 1, fig. 10), suggesting that they acted as detritivores.

CONCLUSIONS

1. The new ichnospecies, *Tombownichnus pepei*, represented by pits in the internal surface of the wall of Eocene–Oligocene dung beetle brood balls from Patagonia, records cleptoparasitism by other dung beetles or flies.
2. *Lazaichnus fistulosus*, occurring in *Coprinisphaera* specimens and connected with meniscate burrows and aestivation chambers in the surrounding palaeosol, revealed that

earthworms were active cleptoparasites or detritivores in Eocene–Oligocene dung beetle brood balls from Patagonia.

3. *Coprinisphaera* bearing *Tombownichnus pepei* and *L. fistulosus* represents a fossil example of a dung palaeocommunity provided by ichnology from rocks, in which body fossils are absent and comparable to extant analogues. It was composed of a brood ball constructor, which originated a food resource available for cleptoparasites or detritivores.

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