geologica**acta**

Traces within traces: holes, pits and galleries in walls and fillings of insect trace fossils in paleosols

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─┤ A B S T R A C T ├─

Fossil insect nests with constructed walls (ichnogenera *Uruguay* ROSELLI 1938, *Palmiraichnus* ROSELLI 1987, *Rosellichnus* GENISE and BOWN 1996), as well as fossil brood masses from dung beetles (*Monesichnus* ROSELLI 1987) often display pits or galleries made by inquilines, parasitoids, cleptoparasites and scavengers, which develop and/or feed inside them. Some of these "traces within traces" can be distinguished, using morphologic criteria, as separate ichnotaxa. *Tombownichnus* n. igen. is represented by circular to subcircular holes or paraboloid external pits occurring in discrete walls of chambers made of agglutinated soil material. *T. plenus* n. isp. consists of a complete perforation, mostly cylindrical in longitudinal section, which pierces whole thickness of the cell wall. *Tombownichnus parabolicus* n. isp. includes incomplete perforations, i.e. pits, parabolic, conic or subcylindrical in longitudinal section, on the external surface of the chamber wall. *Lazaichnus fistulosus* n. igen., n. isp. is composed of circular to subcircular holes occurring in constructed walls of chambers made of agglutinated soil material, which are connected to an internal gallery in their infillings. The trace fossils described herein may be the first formal records of this hitherto neglected but promising field of ichnologic research.

KEYWORDS | Composite specimens. Holes. Pits. Galleries. Insect trace fossils. Ichnotaxonomy.

INTRODUCTION

In recent years much evidence has accumulated on holes and pits in walls of fossil insect nests (Houston, 1987; Ellis and Ellis-Adam, 1993; Genise and Bown, 1996; Genise and Hazeldine, 1998; Genise and Laza, 1998; Edwards and Meco, 2000). This evidence records the presence of a recurrent fact in modern insect nests: they house not only their constructors, but also a complete spectrum of inquilines, parasitoids, cleptoparasites and scavengers, which develop and/or feed inside them

(Halffter and Matthews, 1966; Evans and Eberhard, 1970; Fritz and Genise, 1980). Each component of this particular assemblage makes their own traces in the nests. They are commonly feeding galleries, emergence holes and/or finished or unfinished entrance holes, resulting in traces within traces. This represents a particular, almost ignored and fruitful case of "composite specimens" (Pickerill, 1994). As such, they record distinct behaviours of different trace makers that are reflected in distinct morphologies, a situation that deserves formal ichnotaxonomical treatment (Bromley, 1996).

The presence of perforations or pits is directly related to the presence of constructional walling (*sensu* Bromley, 1990). Fossil bee cells having discrete (constructed) walls belong to the ichnogenera *Uruguay* ROSELLI 1938, *Palmiraichnus* ROSELLI 1987 and *Rosellichnus* GENISE and BOWN 1996. They are represented by drop-shaped to flask-shaped structures, some of which form clusters (Genise and Bown, 1996; Genise and Hazeldine, 1998; Genise, 2000a). Many specimens belonging to these ichnogenera lack cell closures or have circular holes in them, which may be the result of different behaviours and producers. Emergence of adult offspring of the cell's constructor is the most obvious possibility, but also emergence or penetration of parasitoids, cleptoparasites and scavengers may result in similar traces. Lateral holes penetrating cell walls were reported by Houston (1987), Ellis and Ellis-Adam (1993), Genise and Bown (1996), and Genise and Hazeldine (1998). Ellis and Ellis-Adam (1993) reported incomplete perforations, i.e. pits, made from outside towards the cell chamber.

Fossil dung-beetle brood masses pose a similar case. Genise and Laza (1998) redescribed the ichnogenus *Monesichnus* ROSELLI 1987, concluding that this trace fossil resulted from the activity of the constructor, a dung beetle, and a cleptoparasite. The latter made an internal gallery system and lateral emergence holes. In that paper, the authors also reviewed previous data on fossil dung beetle brood masses having lateral holes (Frenguelli, 1938).

In the above-mentioned examples, the walls may display two kinds of holes: one made by the constructor and the other by parasites. However, in the former case, even when the species is the same, the individual that made the emergence hole was not that which constructed the nest, and these traces may be regarded as composites. Consequently, an emergence hole can be considered as a different trace, resulting from the distinct behaviour of a different individual of the same species that constructed the nest. On the other hand, in the case of *Teisseirei* and *Rebuffoichnus*, which are pupal chambers, the constructor of the chamber is supposed to be the same specimen that perforates the emergence hole, although in a different stage of development. Therefore, in these cases neither the hole can be treated as a trace within a trace, nor the structures as composite specimens. Definitively, these perforations belong to the original traces, which will show the most complete morphology when they bear these emergence holes.

The above-stated situation poses a problem of form and function, and a complicated challenge for ichnotaxonomy. The main aims of this paper are to describe the holes, to discuss their form and function and their possible trace makers and finally, to outline the possibilities of ichnotaxonomy in addressing this particular problem.

Setting of the studied material

The material considered for description and interpretation in the present paper comes from numerous localities. Some data mentioned and/or re-interpreted herein have been obtained merely from literary sources (the Pliocene insect traces from Tchad; Duringer et al. 2000a, 2000b). The material studied in detail comes from the five following stratigraphic units: Late Cretaceous Laguna Palacios Formation, Sarmiento, Chubut, Argentina (A on Fig. 1); Late Cretaceous-Early Tertiary Asencio Formation, Nueva Palmira, Uruguay (B on Fig. 1); Eocene-Miocene Sarmiento Formation, Bryn Gwyn, Chubut, Argentina (C on Fig. 1); Pliocene Vorohue Formation, Necochea, Buenos Aires, Argentina (D on Fig. 1); and Pleistocene to Holocene sands of the Fuerteventura, Canary Islands, Spain (Fig. 2). All the mentioned
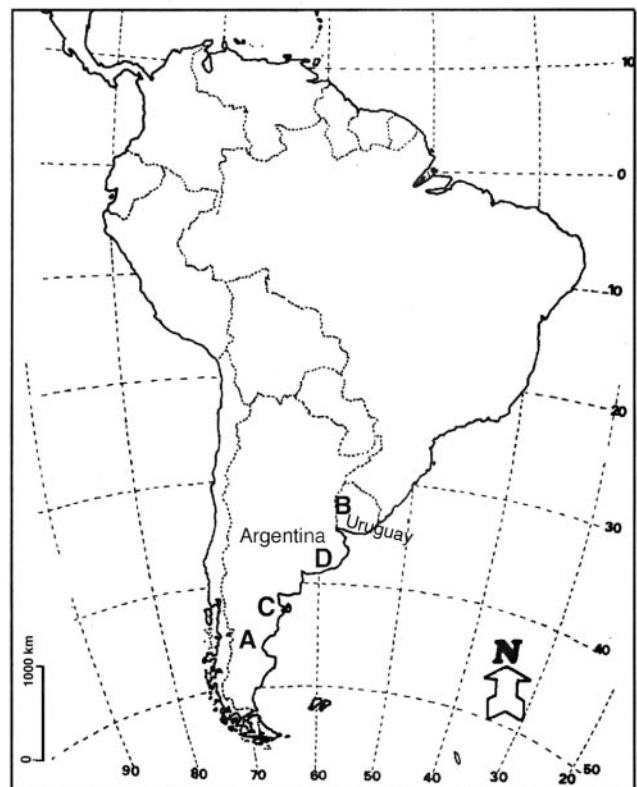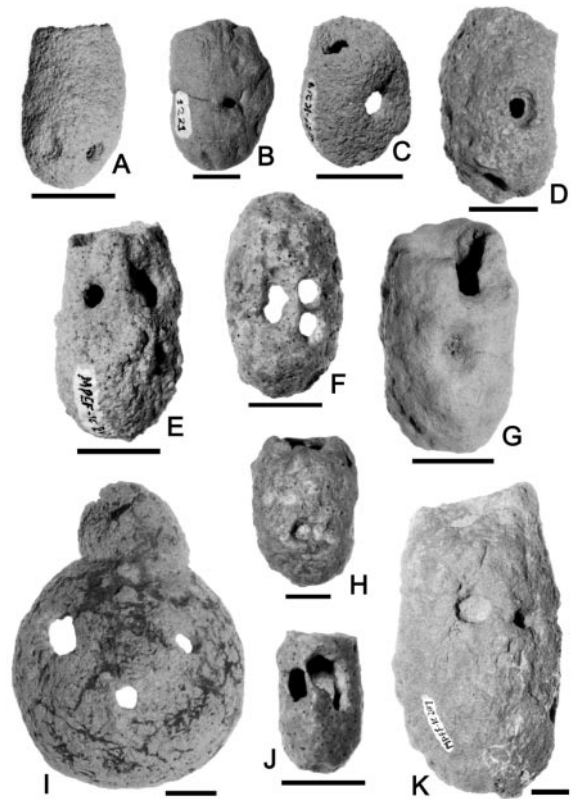

FIGURE 1 | Sketch map of South America showing the location of stratigraphic units bearing the described insect trace fossils. A: Late Cretaceous Laguna Palacios Formation, Sarmiento, Chubut, Argentina; B: Late Cretaceous-Early Tertiary Asencio Formation, Nueva Palmira, Uruguay; C: Eocene-Miocene Sarmiento Formation, Bryn Gwyn, Chubut, Argentina; D: Pliocene Vorohue Formation, Necochea, Buenos Aires, Argentina.

units represent terrestrial deposits, whose ichnofabric consists of trace fossils of bees, wasps, ants, beetles, termites and other insects; meniscate burrows and rhizoliths may also occur. Such trace fossil associations were recently defined as the *Coprinisphaera* Ichnofacies (Genise et al., 2000). This ichnofacies ranges from the Late Cretaceous to the Recent, and characterises paleosols developed in paleoecosystems of herbaceous communities. These herbaceous communities range from dry and cold to humid and warm climates. A dominance of hymenopterous traces may indicate drier conditions, whereas the presence of termite nests would indicate more humid climate. The respective paleosols developed in various depositional systems subject to subaerial exposure, such as alluvial plains, desiccated floodplains, crevassee splays or vegetated eolian environments (Genise et al., 2000).
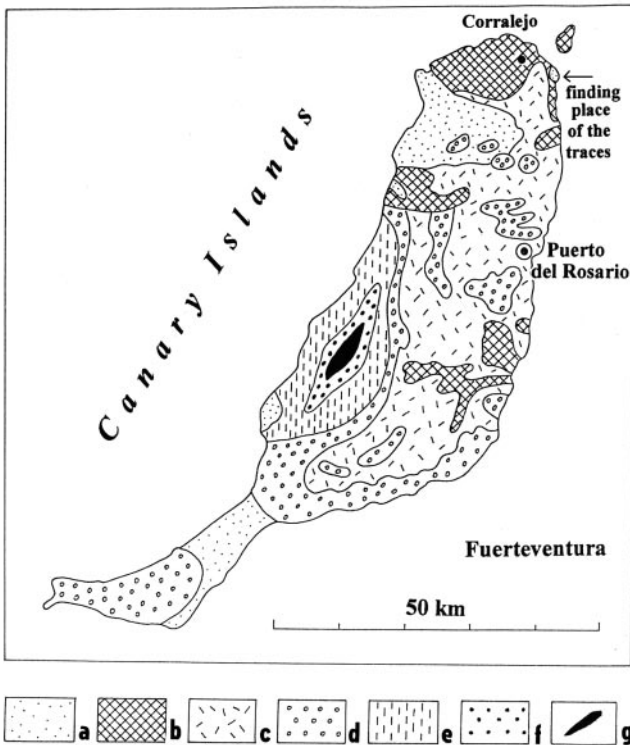
SYSTEMATIC ICHNOLOGY

ICHNOGENUS *Tombownichnus* **n. igen.**
Figures 3A to 3K, 4A and 4B, and 5A to 5D

FIGURE 2 | **Geological sketch of the Fuerteventura Island, Canary Archipelago, Spain. Corralejo Dunes corresponds to the finding place of the traces. a: Pleistocene to Holocene moving and consolidated sands; b: Quaternary (?Holocene) basalts; c: Quaternary (?Pleistocene) basalts; d: Pliocene basalts; e: pre-Pliocene basalts; f: Miocene rhyolites and gabbros; g: Miocene syenites and microsyenites.**

FIGURE 3 | **Figs. 3A to 3F, 3I and 3J:** *Tombownichnus plenus* n. igen., n. isp. A) Holotype (Museo Paleontológico Egidio Feruglio, Colección de Icnología, abbreviated MPEF-IC 230) - the specimen on right side of a cell of *Rebuffoichnus*? isp. (MPEF-IC 221). ?Pleistocene, Fuerteventura, Canary Islands. B) One specimen (MACN-LI 1666) occurring in *Rebuffoichnus casamiquelai,* Late Cretaceous, Laguna Palacios Formation, Sarmiento, Chubut province, Argentina. Museo Argentino de Ciencias Naturales, Laboratorio de Icnología (MACN-LI) 1221, nat. size. C) One specimen (MPEF-IC 240) in a cell of *Rebuffoichnus*? (MPEF-IC 219). ?Pleistocene, Fuerteventura, Canary Islands. D) two specimens (MPEF-IC 234-235) in a cell of *Rebuffoichnus*? (MPEF-IC 218). ?Pleistocene, Corralejo, Fuerteventura, Canary Islands. E) Paratypes, two specimens (MPEF-IC 231-232) in a cell of *Rebuffoichnus*? (MPEF-IC 213). ?Pleistocene, Corralejo, Fuerteventura, Canary Islands. F) Four specimens (MPEF-IC 237-240) in a cell of *Rebuffoichnus*? (MPEF-IC 212). ?Pleistocene, Fuerteventura, Canary Islands. I) Three specimens occurring in *Coprinisphaera* isp. (Museo Municipal de Mar del Plata "Lorenzo Scaglia, MMP 4046). Pliocene, Vorohué Formation, (Las Grutas, Necochea, Buenos Aires province, Argentina. J) Two specimens (MPEF-IC 243-244) in a cell of *Rebuffoichnus*? (MPEF-IC 220). ?Pleistocene, Fuerteventura, Canary Islands. Figs. 3A, 3G, 3H, 3K: *Tombownichnus parabolicus* n. igen., n. isp. A) The specimen on left side of a cell of *Rebuffoichnus*? isp. (MPEF-IC 221). ?Pleistocene, Fuerteventura, Canary Islands. G) One specimen (MPEF-IC 248) in a cell of *Rebuffoichnus*? (MPEF-IC 217). ?Pleistocene, Fuerteventura, Canary Islands. H) One specimen (MPEF-IC 248) in a cell of *Rebuffoichnus*? (MPEF-IC 215); ?Pleistocene, Fuerteventura, Canary Islands. K) Three specimens (MPEF-IC 249-251) in *Teisseirei barattinia* (MPEF-IC 209). Eocene-Miocene, Sarmiento Formation, Bryn Gwyn, Chubut province, Argentina. Scale bars = 1 cm.

Etymology

The ichnogenus is dedicated to Thomas M. Bown, a pioneer of modern insect paleoichnology.

Type ichnospecies

Tombownichnus plenus n. isp.

Diagnosis

Circular to subcircular holes, or paraboloid external pits occurring in discrete (constructed) walls of chambers made of agglutinated soil material. A single hole, despite its size, is not diagnostic for this ichnogenus, which can be identi-

fied only when more than one hole is present. If the chamber shows a single large hole 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.

Comments

This ichnogenus is comparable with others based on single perforations (*Oichnus* BROMLEY 1981; see below in Discussion), but it occurs in a distinct substrate: walls of insect constructions in paleosols. The presence of a single hole, even when it was a small one, more comparable to those of parasites than those of the constructor, is not enough to recognise the presence of this ichnogenus. Size of holes is potentially a character subject to a continuous range of values, which in many cases would preclude a sharp distinction between emergence holes of the constructor and those made by parasites. On the other hand, when more than one hole is present in the same chamber, it is common to find a single large hole and one or more of smaller size. In this case the large one is only useful to recognise the presence of *Tombownichnus*, but it should be considered as part of the substrate. In contrast, the presence of a single external pit, despite its size, is very
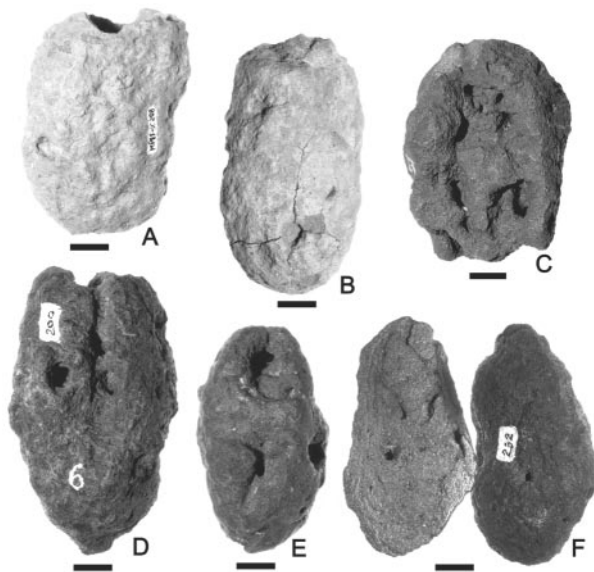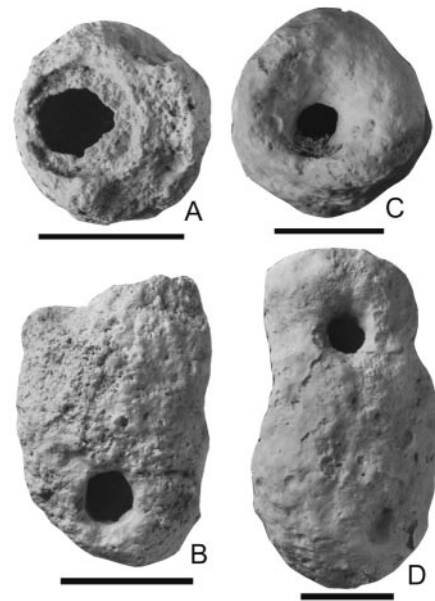

FIGURE 4 | Figs. 4A and 4B: *Tombownichnus parabolicus* n. igen., n. isp. A) Paratype, one specimen (MPEF-IC 246) in *Teisseirei barattinia* (MPEF-IC 208). Eocene-Miocene, Sarmiento Formation, Bryn Gwyn, Chubut province, Argentina. B) Two specimens (MPEF-IC 251-252) occurring in *Teisseirei barattinia* (MPEF-IC 210). Eocene-Miocene, Sarmiento Formation, Bryn Gwyn, Chubut province, Argentina. Figs. 4C to 4F: *Lazaichnus fistulosus* n. igen., n. isp. C) One gallery system (MACN-LI 1629) occurring in *Monesichnus ameghinoi* (MACN-LI 205). Late Cretaceous-Early Tertiary, Asencio Formation, Uruguay. D) Gallery system (MACN-LI 1627) occurring in *Monesichnus ameghinoi* (MACN-LI 200). Late Cretaceous-Early Tertiary, Asencio Formation, Uruguay. E) Gallery system (MACN-LI 1626) occurring in *Monesichnus ameghinoi* (MACN-LI 191). Late Cretaceous-Early Tertiary, Asencio Formation, Uruguay. F) Holotype, one specimen (MACN-LI 1625) in *Monesichnus ameghinoi* (MACN-LI 232) illustrated by Genise and Laza (1998, figure 5) as specimen 56, for which seriate tomographic images are provided therein. The specimen of *M. ameghinoi* is sectioned in two halves that show part of the gallery connected to external holes. Late Cretaceous-Early Tertiary, Asencio Formation, Uruguay. Scale bars = 1 cm.

FIGURE 5 | Figs. 5A and 5B: *Tombownichnus plenus* n. igen., n. isp.; specimens NM T 02766 b (A) and NM T 02766 c (B) in a cell of *Rebuffoichnus*? (NM T 02766 a). The specimen penetrating the cell closure (A) is larger than that made from lateral side (B). ?Pleistocene, Corralejo, Fuerteventura, Canary Islands. Figs. 5C and 5D: *Tombownichnus plenus* n. igen., n. isp.; specimens NM T 02767 b (C) and NM T 02767 c (D) in a cell of *Rebuffoichnus*? (NM T 02767 a). The specimen penetrating the cell closure (C) shows the same diameter as that on the lateral side (D). ?Pleistocene, Corralejo, Fuerteventura, Canary Islands. Scale bars = 1 cm.

diagnostic, because being excavated from the outside, it can never be misidentified as the constructor's emergence hole.

Tombownichnus plenus n. isp.
Figures 3A to 3F, 3J and 3K, and 5A to 5D

1987 "Smaller lateral holes", Houston, p. 95, fig. 2.
1993 "One or more additional perforations", Ellis and Ellis-Adam, p. 163, figs 5, 7-12.
1996 "Tiny holes in the lateral walls", Genise and Bown, pp. 204/207, figs 4 A, B and 5 C.
1998 "Lateral holes", Genise and Hazeldine, p. 154.
2000 "Irregular holes in lateral walls", Edwards and Meco, p. 179.
2000 Duringer et al. 2000, fig 3C?

Etymology

From Latin: *plenus* = full, complete.

Diagnosis

Tombownichnus represented by a complete perforation, mostly cylindrical in longitudinal section, which pierces the full thickness of the wall.

Type material

Holotype: One specimen (MPEF-IC 230) in a cell (*Rebuffoichnus*?), from the ?Pleistocene of Fuerteventura, Canary Islands, Spain (Museo Paleontológico Egidio Feruglio, Colección de Icnología, MPEF-IC 221). Paratypes: Three specimens (MPEF-IC 231-233) in a cell (*Rebuffoichnus*?) from the ?Pleistocene of Corralejo, Fuerteventura, Canary Islands (MPEF-IC 213); three specimens (MPEF-IC 234-236) in a cell (*Rebuffoichnus*?) from Corralejo, Fuerteventura, Canary Islands (MPEF-IC 218).

Material studied

Eight specimens (MPEF-IC 237-244) in three cells (*Rebuffoichnus*?) from the ?Pleistocene of Fuerteventura, Canary Islands (MPEF-IC 212, 219, 220). Three specimens (National Museum, Prague, abbreviated NM, No T 02766 b-d) in a cell (*Rebuffoichnus*?) from the ?Pleistocene of Corralejo, Fuerteventura, Canary Islands (NM T 02766 a); two specimens (NM T 02767 b-c) in a cell (*Rebuffoichnus*?) from Corralejo, Fuerteventura, Canary Islands (NM T 02767 a). Three specimens occurring in a *Coprinisphaera* sample from the Pliocene Vorohué Formation, Las Grutas, Necochea, Buenos Aires province, Argentina (Museo Municipal de Mar del Plata "Lorenzo Scaglia, MMP 4046). One perforation (*?T. plenus* n.igen.; MACN-LI 1666) occurring in *Rebuffoichnus casamiquelai* from the Late Cretaceous Laguna Palacios Formation,

Sarmiento, Chubut province, Argentina (Museo Argentino de Ciencias Naturales, Laboratorio de Icnología, MACN-LI 1221). Sixteen specimens (MACN-LI 1636-1651) occurring in 10 samples of *Palmiraichnus castellanosi* from the Late Cretaceous-Early Tertiary Asencio Formation from Uruguay (MACN-LI 624-627, 632, 637, 712, 720, 726 and 1158). Thirteen specimens (MACN-LI 1652-1664) in 6 samples of *Uruguay rivasi* (MACN-LI 235, 264, 266, 267, 278, and 290) from the Late Cretaceous-Early Tertiary Asencio Formation from Uruguay.

Previous and present descriptions of the material

The specimens from the Canary Islands occur in fossil insect chambers from calcareous sandstones of Fuerteventura and Lanzarote described by Ellis and Ellis-Adam (1993) and Edwards and Meco (2000). These authors attributed them to bees. However, more recently, Genise (2000a) and Genise and Edwards (2003), also considered the possibility of attributing them to coleopteran pupal chambers. According to Ellis and Ellis-Adam (1993), of the 240 cells measured by them, 190 had perforated caps. Many cells have one or more additional perforations, mostly in the sides; while 141 cells measured have no perforation, 62 have a single lateral opening, 31 have two openings, 3 have three openings, 2 cells have four openings, and one cell has six lateral openings. Edwards and Meco (2000) stated that most preserved caps have a roughly circular hole, 7-8 mm or less in diameter and that many cells from two localities also have similar circular and much larger irregular holes in the lateral walls. The new material studied for this paper shows rounded to somewhat irregular perforations 2.5 mm to 7 mm in diameter, near the rear ends, at the equators and near the closures. The number of specimens of *T. plenus* n. isp. in the collected samples ranges from 2 to 5. The holes are either paraboloid in shape (similarly as the naticid boring *Oichnus paraboloides* BROMLEY 1981) or roughly cylindrical, slightly modified by weathering. Two specimens of *T. plenus* n. isp. are coalescent, resembling the figure «8» (MPEF-IC 239 and 240). Some of them have an external larger diameter and an internal smaller one, which is then surrounded by a rim (MPEF-IC 234 - 236 in MPEF-IC 218).

Other specimens of *T. plenus* n. isp. occur in samples of the ichnogenera *Uruguay* and *Palmiraichnus,* redescribed by Genise and Bown (1996) and Genise and Hazeldine (1998) from the Late Cretaceous-Early Tertiary Asencio Formation of Uruguay. Among the specimens described by these authors, holes in lateral positions are from 1 mm to 3 mm in diameter and thereby differ in diameter from the size of presumed constructors of cells; they are probably emergence or penetration holes of parasitoids, cleptoparasites or scavengers. Houston (1987) attributed small lateral holes in *Palmiraichnus bedfordi*

from the Pleistocene of Australia to the emergence of parasites, and larger lateral holes to the emergence of bees. However, he recognised that such lateral emergence is atypical of bees. The new material examined shows that in clusters of *Uruguay rivasi* from the Late Cretaceous-Early Tertiary Asencio Formation from Uruguay there is, in average, one perforation per individual cell, and up to four holes in a cluster. Diameters range from 2 to 3 mm (N= 13), and in all cases holes are located at the base of the cells. In *Uruguay auroranormae* (GENISE and BOWN 1996, figures 4 A and B), three specimens of *T. plenus* n. isp. are also located at the base of cells. In cells of *Palmiraichnus*, up to three *T. plenus* n. isp. per cell are located indistinctly at the base or at the equator of cells (N = 10). Diameters range from 1 to 5 mm (N = 16), those of 2 mm being the most frequent (7 of 16).

The only specimen of *Coprinisphaera* isp. studied that shows the presence of *T. plenus* n. isp. is rare, because it comprises the provision chamber below a smaller egg chamber. The holes may originally have been connected to an internal gallery, but the infilling of the chamber and consequently the possible gallery is absent. The morphology of these trace fossils is compatible with that of *Tombownichnus plenus* n. isp. Holes are 3, 4 and 6 mm in diameter respectively and are located approximately at the equator of the ball, displaying a triangular distribution. Probably a similar case was figured by Duringer et al. (2000, figure 3C), from the Pliocene of Tchad. Their specimens are hollow balls in which it is possible to recognise external, although somewhat irregular holes.

Remarks

One specimen of *Rebuffoichnus casamiquelai* from the Late Cretaceous Laguna Palacios Formation of Argentina bears a single 2 mm in diameter perforation located at the equator. However, the single perforation (though differing from the size of the presumed constructor) cannot be considered diagnostic for *T. plenus* n. isp.

Nesting chambers, which lack a discrete wall construction, represented by the ichnogenus *Celliforma* BROWN 1934, may present a specific problem. Even those examples studied (e.g. from Dětaň; Oligocene, Czech Republic; Mikuláš et al., 2002), may show regular rounded spots on the otherwise smooth unlined wall. When preserved as natural casts, the specimens of *Celliforma* from Dětaň may have rounded protuberances (Fig. 6). Such structures may record the activity of inquilines, parasitoids, cleptoparasites or scavengers. However, many other types of subsequent bioturbation (e.g. root penetration) may have produced similar structures. Therefore, we consider these structures unsuitable for taxonomic treatment.

Tombownichnus parabolicus n. isp.
Figures 3A, 3G, 3H, 3K, and 4A and 4B

? 1993 Ellis and Ellis-Adam, fig. 6 top.
1996 Genise and Bown, fig. 5C.

Etymology

After the parabolic shape of the traces.

Diagnosis

Tombownichnus n. igen. includes pits, parabolic, conic or subcylindrical in longitudinal section, on the external surface of the chamber wall.

Type material

Holotype: One specimen (MPEF-IC 245) in a cell (*Rebuffoichnus*?) from Fuerteventura, Canary Islands, Spain (Museo Paleontológico Egidio Feruglio, Colección de Icnología, MPEF-IC 221) Paratype: One specimen (MPEF-IC 246) in *Teisseirei barattinia* from the Eocene-Miocene Sarmiento Formation (Bryn Gwyn, Chubut province, Argentina, MPEF-IC 208).

Material studied

One specimen (MACN-LI 1665) in one sample of *Uruguay rivasi* (MACN-LI 250) from the Late Cretaceous-Early Tertiary Asencio Formation from Uruguay. Two specimens (MPEF-IC 247-248) in two cells (*Rebuffoichnus*?) from Fuerteventura, Canary Islands, Spain (MPEF-IC 215 and 217). One specimen (National
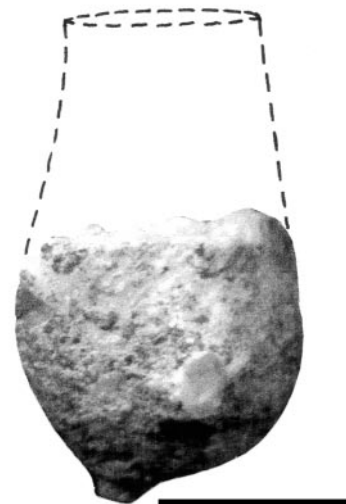

FIGURE 6 | *Celliforma* isp., natural cast with two rounded protuberances (NM P 01231). Oligocene, Dětaň locality, Czech Republic. Scale bar = 5 mm.

Museum, Prague, abbreviated NM, No T 02766 e) in a cell (*Rebuffoichnus*?) from Corralejo, Fuerteventura, Canary Islands, Fuerteventura, Spain (NM T 02766 a). Four specimens (MPEF-IC 249-252) occurring in *Teisseirei barattinia* from the Eocene-Miocene Sarmiento Formation (Bryn Gwyn, Chubut province, Argentina, MPEF-IC 209 and 210).

Description

In the chambers from Fuerteventura, as well as in *Uruguay* (Late Cretaceous-Early Tertiary Asencio Formation, Uruguay)*,* specimens of *T. parabolicus* n. isp. occur altogether with completed circular holes, i.e. *T. plenus* n. isp. and in addition, the diameters of both ichnospecies are similar. This fact strongly suggests that both ichnospecies correspond in many cases to two different stages of penetration by the same parasites or scavengers from the outside of the cells. One specimen of *T. parabolicus* n. isp. in *Uruguay rivasi* is located laterally at the equator of the cell and is 3 mm in diameter. Genise and Bown (1996, figure 5C) have illustrated a row of specimens of *T. parabolicus* n. isp. at the equator of cells in a cluster of *Uruguay auroranormae*. In chambers from Fuerteventura, *T. parabolicus* are lateral as well as basal and range from 3 to 6 mm in diameter. In *Teisseirei barattinia*, specimens range from 4 mm to 7 mm occupying basal to equatorial positions.

Remarks

Ellis and Ellis-Adam (1993) concluded that all lateral perforations in the chambers from Fuerteventura were probably made from the outside, regarding its conical shape and larger external diameter. The differences in mean size between the cell cap and the lateral perforations suggested to these authors that the constructor of the chambers did not make the lateral perforations. They proposed that the perforations were made by members of one of the three main groups of parasitoids of bees: Meloidae, Bombyliidae, or Mutillidae. Most parasitoids and cleptoparasites emerge and enter the cell through the entrance, either when it is still open, or by piercing the cap (Evans and Eberhard, 1970). Incomplete perforations in fossil cells evidence that they were made from the outside inwards. This indicates that parasitoids, (e.g. velvet ants, Mutillidae), or predators (ground beetles, Carabidae), which enter cells by digging through the soil are the most probable trace makers (Evans and Eberhard, 1970). In addition, some kind of scavenger, seeking the remains of provisions or larvae, should also be considered. Probably the completed holes, particularly those in lateral positions, may be attributed to the same producers.

ICHNOGENUS *Lazaichnus* n. igen.
Figures 4C to 4F

Etymology

Dedicated to José H. Laza, one of the pioneers of modern insect paleoichnology and to his permanent research on dung-beetle trace fossils.

Type ichnospecies

Lazaichnus fistulosus n. isp.

Diagnosis

Circular to sub circular 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.

Comments

The ichnogenus is hardly comparable with any other regarding its occurrence in insect chambers with infillings. It is readily distinguishable from *Tombownichnus* n.igen. because of the different substrate: *Lazaichnus* n.igen occurs in chambers preserving their infillings (i.e. dung-beetle brood masses), in which the internal gallery was made. *Tombownichnus* n.igen occurs mostly in chambers which lack infillings (i.e. fossil bee cells and coleopteran pupal chambers). Nevertheless, the latter can also occur in dung-beetle chambers lacking infillings, and lacking the internal gallery, as shown herein.

The presence of a single hole connected to a single cavity, even when it is small Genise and Cladera, 1995, figure 5F, centre), is not diagnostic for this ichnogenus, because size of holes and cavities is potentially a character subject to a continuous range of values. As in *Tombownichnus* n.igen, this would preclude a sharp distinction between emergence holes of the constructor and those made by parasites. On the other hand, a large emergence hole of the constructor is unlikely in *Lazaichnus* n.igen. because the full development of the constructor is usually incompatible with the presence of cleptoparasites or parasites.

Lazaichnus fistulosus n. isp.
Figures 4C to 4F

1938 "Vari piu piccoli perforazioni" "Orificio piu piccolo", Frenguelli, pp.82 and 87.
1998 "Gallery system inside the active filling", Genise and Laza, p. 218, figs 3, 4 and 5B.
2000 Duringer et al., 2000b, fig 3A, upper right.
2000 Duringer et al., 2000a, p. 266.

Etymology

From the Latin *fistula* = tube, pipe.

Diagnosis

Only known ichnospecies, the same as for the ichnogenus.

Holotype

One specimen (MACN-LI 1625) in *Monesichnus ameghinoi* from the Late Cretaceous-Early Tertiary Asencio Formation from Uruguay (MACN-LI 232) illustrated by Genise and Laza (1998, figure 5) as specimen 56, from which seriate tomographic images are provided therein. Presently the specimen of *M. ameghinoi* is sectioned in two halves that show part of the gallery connected to external holes.

Material studied

10 specimens (MACN-LI 1626-1635) occurring in *Monesichnus ameghinoi* (MACN-LI 191, 200, 204, 205, 210, 213, 228, and 928-930) from the Late Cretaceous-Early Tertiary Asencio Formation from Uruguay. Some were illustrated by Genise and Laza (1998, figures 3 and 4).

Description

Detailed descriptions of these traces were provided and illustrated by Genise and Laza (1998) in their review of *Monesichnus ameghinoi*. The external holes range in number from 3 to 17 per specimen of *M. ameghinoi* (N = 10), and from 1 mm to 5 mm in diameter (N = 66), of which the most frequent are from 2 mm to 3 mm (43 of 66). Holes are located indistinctly on medial and apical sectors of the wall. Galleries connected to holes are concealed in entire specimens and difficult to trace in sectioned or broken ones. Hence it is difficult to determine if each hole is connected to an individual gallery or if all holes are connected to a single entire gallery. Seriate tomographic images of the specimen of *M. ameghinoi* (Genise and Laza, 1998, figure 5), bearing the holotype of *L. fistulosus* n. isp. (MACN-LI 1625), show apparently a single system composed of horizontal and inclined tunnels connected with the exterior by holes (Genise and Laza, 1998). In *M. ameghinoi* (MACN-LI 205) it can be seen that different holes are connected to the same gallery.

Remarks

Duringer et al., (2000b), describing fossil dung-beetle brood masses from the Pliocene of Tchad, illustrated entire sandstone balls showing small perforations and in one case a tunnel system connecting them (their figure 3C, particularly the specimen in the upper right corner). Duringer et al. (in press) documented the presence of termite constructions inside some of these balls, which would constitute a particular case to analyse ichnotaxonomically. Because of the morphology of these constructions is incompatible with *Lazaichnus* n. igen. and their internal structure is unknown, the holes in the entire balls illustrated in Duringer et al. (2000b, figure 3A) are only included herein tentatively.

DISCUSSION

A perforation of a hard or firm envelop covering softer material is a recurring trace produced by numerous animal activities. These activities may be related to predation, as in naticid gastropods that perforate different mollusc shells (Bromley, 1981); or as in microscopic borers in foraminifer conchs (Nielsen, 1999). Similar holes also occur in very different substrates, such as plant remains (seeds, nuts, fruit stones, and spores), where they have been also named *Carporichnus* and *Lamniporichnus* respectively, providing that the holes were connected or otherwise with internal cavities (Scott et al. 1992, Genise, 1995; Mikuláš et al., 1998). Holes and holes plus galleries in soil-walled chambers (i.e. *Tombownichnus plenus* n. isp. and *Lazaichnus fistulosus* n. isp.) are morphologically identical to *Lamniporichnus* Mikuláš et al. (1998) and *Carporichnus* Genise (1995), but differ in substrate: fruit stones in *Lamniporichnus* and *Carporichnus* vs. agglutinated soil particles in *Tombownichnus* n. igen. and *Lazaichnus* n. igen. In this sense, the different morphologies of traces recorded herein demonstrate the importance of insect trace fossils as a particular substrate for the development of other traces, and their value as additional substrate ichnotaxobases.

Insect trace fossils pose very particular problems for classical ichnology itself (Genise et al., 2000; Genise, 2000b). As stated previously, in many cases, insect nests house constructors, but also inquilines, parasitoids, cleptoparasites and scavengers (Fritz and Genise, 1980). Each one commonly produces feeding galleries and/or emergence holes. These traces deserve a formal ichnotaxonomical treatment because they represent: 1) traces within traces (composite specimens of Pickerill, 1994); 2) a very different behaviour from that of the constructor, reflected in a very different trace; and 3) the work of different tracemakers. The original purpose of this paper was to deal only with traces produced by inquilines, parasitoids, cleptoparasites and scavengers, leaving aside those of the species that produced the nest. However, this approach resulted to be very difficult, considering the different facts analysed below.

Emergence holes from parasites can also be located at the cell closure and the only difference with that produced by the constructor would be the size of the hole. Size is not a good ichnotaxobase for separating ichnospecies and, moreover, it is clear from some known specimens (Ellis and Ellis-Adam, 1993, figure 12) that it would be impossible to use it. In many cases the simple morphology of the holes precludes differentiation between traces produced by the offspring of the cell constructor and those of parasites (Ellis and Ellis-Adam, 1993, figure 10 and 12). If the size of perforations differs substantially from the mean size of cell caps, the trace maker will probably be a different species from the constructor. However, the ratio cell cap diameter/perforation diameter will probably be a continuum and it cannot be considered a valid ichnotaxobase.

At this point, the dilemma would be if the emergence holes made by the constructor of the cells should be included together with those of the parasites in a single new ichnotaxon, or if the whole group of traces should be left without ichnological treatment. There are two reasons for the first alternative: 1) the lack of ichnotaxonomic treatment would probably result in a total lack of ichnological treatment, with the consequent loss of valuable information; and 2) in the case of emergence holes from brood cells, the constructor of the cells is not the same one that emerges from them, since both individuals clearly display a very different behaviour. Different individuals of the same species that produced different traces should be included in different ichnotaxa; this is a well-known and accepted principle of ichnology (Bromley, 1990, 1996). However, such an ichnotaxonomic treatment would present a new problem. In *Teisseirei* and *Rebuffoichnus* the chamber and the emergence holes are made by the same individual. This fact clearly weakens the main argument that all possible holes are made by individuals other than the constructors.

How would it be possible to define new ichnotaxa, while avoiding all references to the interpretation of the trace that bears it, and restricting its definition to a morphological ground?. At first, there is no reason to avoid the creation of a new ichnotaxon, *Tombownichnus parabolicus* n. isp. for incomplete holes made from the outside of a cell. These clearly show a distinct morphology reflecting a particular behaviour and, in addition, they represent with certainty the work of a trace maker different from the constructor. The morphology of unfinished holes is quite different from completed ones and the difference can be easily considered a valid ichnotaxobase.

The distinction between complete holes made by the constructor or its offspring from those made by other organisms is not always possible. However, commonly it can be inferred from the presence of more than one hole

in the cell wall. The number of holes (i.e. two or more) is a valid, morphological ichnotaxobase, allowing recognition of the ichnogenus *Tombownichnus* n. igen. In turn, this reflects the necessary presence of other organisms apart from the constructor. Brood masses or cells are only made to shelter one offspring and they will show only one emergence hole, unless other producers were involved. Similarly, the connection of these holes with a gallery system burrowed in the infilling should be considered as a distinct morphology, herein named *Lazaichnus fistulosus* n.isp.

CONCLUDING REMARKS

The trace fossils described here may be the first formal records of a future field of ichnological research, which may bring its own palaeobiologic, palaeoecologic and palaeoenvironmental consequences. The presence of inquilines, parasitoids, cleptoparasites and scavengers is a well-known and recurrent fact in modern insect nests, resulting in a large number of distinct traces. These traces develop on other traces, insect brood masses and cells, and on pupal chambers, which in turn constitute a very distinct kind of substrate. As such, it deserves its own ichnotaxonomical framework, which up to date had not been established. In addition, these traces within traces potentially are one of the most important cases of composite specimens.

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