Teisseirei barattinia Roselli 1939: the first sphinx moth trace fossil from palaeosols, and its distinct type of wall

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LETHAIA

The trace fossil *Teisseirei barattinia*, found in Cenozoic formations of Uruguay and Argentina, is an elongated chamber recognizable by its depressed cross-section, antechamber, and its multi-layered lining with an inner surface texture composed of densely packed sub-rectangular to sub-triangular pits. Our recent behavioural observations on larval and pupal stages of Sphingidae (Lepidoptera), particularly on *Manduca rustica*, suggest that *Teisseirei barattinia* is the pupation chamber of a sphinx moth. Last instar larvae of *Manduca rustica*, *Eumorpha anchemolus* and *E. labruscae* were placed in terraria to observe their burrowing behaviour and to recover pupation chambers. Chambers show depressed or plane convex cross-sections as *T. barattinia*. The internal surface texture of walls is also similar to that of *T. barattinia*. The same pattern could be obtained experimentally by pressing the true legs of *Manduca rustica* larva against plasticine. The multi-layered wall structure, shown by *T. barattinia*, is a new type of lining for insect trace fossils in palaeosols that result from soil packing combined with discharges of abundant liquid excretion by soft-bodied larvae, as in the case of *Manduca rustica*. *T. barattinia* is the first trace fossil documented in palaeosols attributed to sphinx moths and supported by macro and micromorphological comparisons with extant pupation chambers. The shallow emplacement of moth pupation chambers in soils suggests that *T. barattinia* would be a good indicator of palaeosol upper horizons. □ *Multi-layered wall, palaeopedological significance, pupation chambers, sphinx moth, Teisseirei barattinia.*

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In his pioneering work, Francisco Lucas Roselli described (amongst other ichnotaxa from the Early Eocene Asencio Formation of Uruguay) the ichnogenus *Teisseirei* and its unique ichnospecies, *Teisseirei barattinia*. Long and complicated taxonomic names are a signature of Roselli, who usually dedicated ichnotaxa to colleagues and friends. In this case, it was named for Auguste Teisseire, a French amateur palaeontologist, who was probably the first to observe these structures (Teisseire 1927), and for Luis Barattini, the Director of the National Oceanographic Museum of Uruguay at that time. Roselli (1939) suggested that *Teisseirei* represented the work of hymenopterans, although in 1987, he placed *Teisseirei* amongst coleopteran (Scarabaeidae) trace fossils, and the taxon was later tentatively considered as a coleopteran pupation chamber (Genise 2004). *T. barattinia* remained as another rare trace fossil described by Roselli only known from its original locality until recently, when it was also found in Cenozoic localities of Argentina (Genise & Zelich 2001; Melchor *et al.*

2002; Bellosi & Genise 2004; Scasso & Bellosi 2004; Bellosi *et al.* 2010).

Considering that some representatives of Lepidoptera pupate in soils (Roach & Campbell 1983; Bouyer *et al.* 2004; Jump *et al.* 2006; Pinault *et al.* 2007), one of us (JLF) started larval rearings at laboratory to obtain pupation chambers. The first behavioural observations and chambers obtained in laboratory suggested that *T. barattinia* could be a Sphingidae pupation chamber (Farina *et al.* 2010). This hypothesis could also explain the origin of the distinct type of lining and internal surface texture shown by *Teisseirei barattinia*. There is a record of possible fossil pupation chambers of Saturniidae from France (Kuntz 2012).

The aims of this contribution are: (1) to demonstrate that *T. barattinia* is a sphinx moth pupation chamber, the first described from palaeosols; (2) to describe and interpret a new type of lining for insect trace fossils in palaeosols; and (3) to introduce *T. barattinia* as a possible indicator of palaeosol uppermost horizons.

Materials and methods

Teisseirei barattinia

Two ichnotaxonomical reviews of *Teisseirei* have been accomplished recently. Melchor *et al.* (2002) and Genise (2004) redescribed *Teisseirei,* including materials from Entre Ríos, Chubut and La Pampa provinces from Argentina and Uruguay. Accordingly, it will not be presented herein other review or geological settings, which were included in those contributions and also in Genise *et al.* (2004), Bellosi & Genise (2004), Bellosi *et al.* (2010) and Scasso & Bellosi (2004). The amended diagnosis of both the ichnogenus and its only ichnospecies was given by Genise (2004): elongated, sub-cylindrical, horizontal to sub-horizontal structures, depressed all along its length, having elliptical cross-section and a multi-layered wall. A circular aperture located at one end, may be preceded by a rounded, non-depressed antechamber, separated from the main chamber by a constriction. The opposite end is rounded and blind. The internal surface of the chamber may bear densely packed, short, sub-rectangular to sub-triangular pits, covering the entire surface (Fig. 1A–K).

Teisseirei barattinia occurs in palaeosols from different Cenozoic ages in at least four lithological units of southern South America. The original record corresponds to the Early Eocene Asencio Formation of Uruguay (Roselli 1939). This unit is characterized by its stacked ultisols, developed on siliciclastic deposits, bearing diverse and abundant insect ichnoassemblages at many geographic localities of
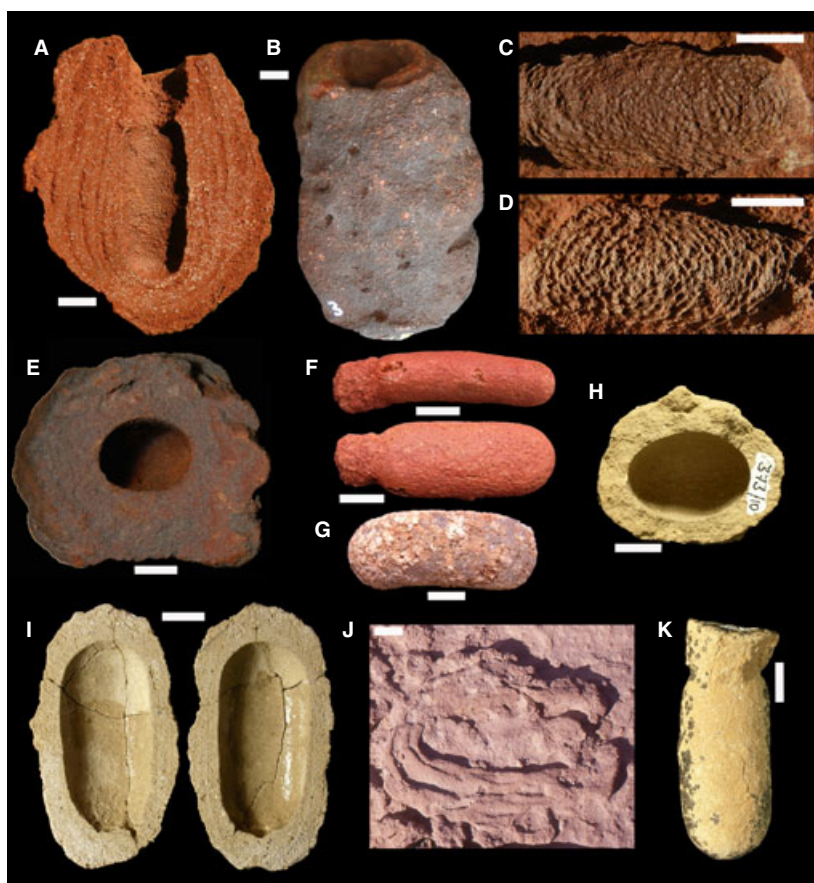

Fig. 1. Teisseirei barattinia. A–F, specimens from the Asencio Formation of Uruguay and Puerto Unzué Formation of Argentina. G, specimen from the Gran Salitral Formation of Argentina. H–K, specimens from the Sarmiento Formation of Argentina. A, longitudinal section showing chamber, antechamber and multi-layered wall (FCDPI 5001). B, external aspect of a specimen preserving a thick wall (MACN-Icn 2440). C, internal sculpture composed of packed pits that follow the curvature of chamber at margins and are more transverse or lack orientation at the centre of the floor (FCDPI 5028). D, internal sculpture showing a more concentric, elliptical arrangement of pits (FCDPI 5024). E, cross-section. Compare the width/height ratio with C (FCDPI 5747). F, internal cast of chamber and antechamber in lateral and plan view. Note the sculpture (MACN-Icn 908). G, internal cast of chamber resembling a 'ladyfinger' (MACN-Icn 1306). H, cross-section. Note the discrete, thinner, sharply defined wall in comparison with A, B and E (MPEF-IC 373/10). I, longitudinal section showing the two halves. Note slightly arched sides of internal chamber and well defined, thin wall (MPEF-IC 372/15). J, field picture of an uncollected specimen of a weathered longitudinal section showing thick multi-layered wall. K, internal cast of chamber and antechamber (MPEF-IC 511). Scale bars = 1 cm.

south-western and central Uruguay (Bellosi *et al.* 2004; Genise *et al.* 2004). The second record is from the Early Eocene Puerto Unzué Formation of Colón, Entre Ríos province, Argentina, which is a lateral extension of the Asencio Formation of Uruguay (Genise & Zelich 2001). In both formations, the material mostly comprises specimens whose discrete wall is not easily observable, looking merely as excavations *in situ* or as loose, poorly shaped, gross concretions on the floor of outcrops (Fig. 1A, B, E). Some of these specimens show a multi-layered wall when naturally weathered or sectioned (Fig. 1A), which had already been observed by Roselli (1939, 1987). The antechamber (Fig. 1A, F) and the internal sculpture of the wall (Fig. 1C, D) are usually well preserved. A few specimens show a thinner, better-defined discrete wall. Internal casts, which look like small 'ladyfingers', are also common (Fig. 1F). Depressed cross-sections showing different width/height ratios are also common (Fig. 1E, F). A third record came from the Early Eocene Gran Salitral Formation of La Pampa province, Argentina (Melchor *et al.* 2002), where *T. barattinia* occurs in palaeosols developed on palustrine carbonates. At Gran Salitral, *T. barattinia* is mostly preserved as internal casts (Fig. 1G). The fourth record was reported from the middle Eocene–lower Miocene pyroclastic palaeosols of the Sarmiento Formation, at two different localities, Gran Barranca and Bryn Gwyn, in Chubut Province, Argentina (Bellosi & Genise 2004; Scasso & Bellosi 2004; Bellosi *et al.* 2010). Oppositely to those from Uruguay, Entre Ríos and La Pampa (all Early Eocene in age), most specimens from Chubut, which are younger (Oligocene–Miocene), show a well-defined discrete wall (Fig. 1H, I). In contrast, antechambers and the internal surface pattern of pit depressions are represented only in few specimens (Fig. 1K). Less common are specimens preserving a thick multi-layered wall (Fig. 1J) and internal casts (Fig. 1K).

Differences between older, northern localities from younger, southern ones are considered to be mostly taphonomical, although different species of producers should be clearly involved considering the different localities and ages of outcrops. In addition, longitudinal section shows more parallel sides in the older (Uruguay, Entre Rios and La Pampa) specimens (Fig. 1A, F, G) and slightly arched sides in some of the younger ones (Chubut) (Fig. 1I). In any case, a sharp ichnotaxonomical distinction between northern and southern localities is impossible by now. Examined material is housed in the following collections: Colección de Icnología del Museo Argentino de Ciencias Naturales, Buenos Aires (MACN-Icn); Museo Paleontológico Egidio Feru-

glio, Trelew, Chubut, Argentina (MPEF-Ic); and Colección Paleontológica de la Facultad de Ciencias, Montevideo, Uruguay (FCDPI).

Moth rearing and documenting methods

Different families of moths have representatives that pupate in soils, such as Geometridae, Noctuidae, Sphingidae and Saturnidae (Roach & Campbell 1983; Bouyer *et al.* 2004; Jump *et al.* 2006; Pinault *et al.* 2007). Sphinx moths, particularly *Manduca rustica* and *Eumorpha labruscae* were used as modern analogues for behavioural observations and for obtaining pupation chambers due to their availability at Mar del Plata (Buenos Aires province, Argentina), where rearing and laboratory observations were mostly conducted (Fig. 2A, C). Incomplete chambers of *Manduca diffissa* and *Eumorpha analis* from the same locality were also useful to check the shape of other sphinx moth pupation chambers (Fig. 2B, D). In addition, one pupation chamber of *Eumorpha anchemolus* was also obtained and studied at Montevideo, Uruguay.

At Mar del Plata, the larvae of *Manduca rustica* (Fig. 3A) feed on privets (*Ligustrum* spp., Oleaceae), cedron (*Aloysia triphylla*, Verbenaceae) and *Buddleja thyrsoides* (Scrophulariaceae). Larvae of *Eumorpha analis* (Fig. 3B) and *E. labruscae* (Fig. 3C) feed on vines (*Vitis sp.*, Vitaceae) and larvae of *Manduca diffissa* (Fig. 3D) feed on tomato (*Solanum lycopersicum*, Solanaceae). The larvae of these species are commonly found in the field while remaining motionless on branches, back down, with the anterior part of the body curved in the typical sphinx position. This immobility, along with the particular colour pattern, make these larvae very cryptic amongst leaves and branches (Fig. 3A). Last instar larvae leave plants and move to the soil to pupate, or in some cases, they just drop to the ground. At this moment, some larvae change dorsal colour from greenish, more similar to leaves to a darker colour more similar to the soil (Fig. 3F).

Mature larvae, collected on plants, were reared in terraria or on fresh branches with leaves maintained in containers with water up to their full development (Fig. 3D). Last instar larvae, obtained in laboratory or field, were located in two types of terraria to obtain pupation chambers: mobile ones for allowing easily handling and transportation, filled with soil or sand up to 20 cm from the bottom, or plastic mesh cages partially buried in ground up to 30 cm, for providing the larvae with a more natural environment for pupating (Fig. 3E). Both procedures were successful for obtaining pupation chambers of *Manduca rustica* and *Eumorpha labruscae*, which
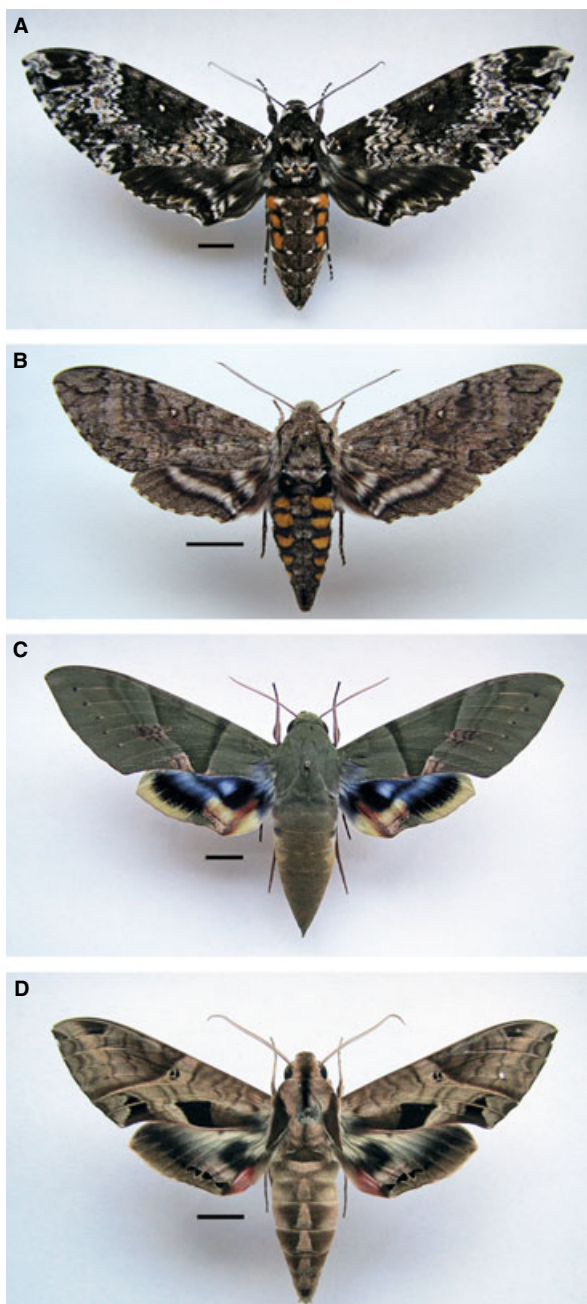
Fig. 2. Adult moths (Sphingidae). A, *Manduca rustica.* B, *Manduca diffissa.* C, *Eumorpha labruscae.* D, *Eumorpha analis.* Scale bars = 1 cm.

were then removed from the terraria for description, measuring and obtaining plaster casts. The pupation chamber of *Eumorpha anchemolus* was obtained in a mobile terrarium.

The burrowing behaviour of a larva of *Manduca rustica* in a mesh cage, burying itself in ground, was recorded on video. One of the mobile terrariums containing a 4-day-buried larva was carried to the Instituto Radiológico of Mar del Plata for X-ray

observation and recording below ground with an equipment of VHS digital radiology with radioscopy Philips DuoDiagnostic.

Results

The shape and wall of Teisseirei barattinia

One of the most distinctive characters of this ichnospecies is its depressed, elliptical outline resulting from the comparatively lower height in contrast to the lateral widening of the chamber. Specimens from the Asencio Formation of Uruguay and the Puerto Unzué Formation of Argentina are as follows: 2.5–6.6 cm long (*n*: 90); 1.1–3 cm wide (*n*: 83); and 0.75–2.34 cm high (*n*: 87). Specimens from the Gran Salitral Formation of La Pampa, Argentina are: 1.9–5.5 cm long (*n*: 56); 1.3–2.4 cm wide (*n*: 56); and, 0.9–1.7 cm high (*n*: 29). Specimens from the Sarmiento Formation of Chubut, Argentina are as follows: 2.7–9 cm long (*n*: 80); 1.27–4.9 cm wide (*n*: 136); and 0.8–3 cm high (*n*: 102). An exceptionally large specimen from this formation at Gran Barranca measured in the field was 11.5 cm long and 7 cm wide. The width/height ratio is 1.3–1.6 (*n*: 214) in all localities, which gives *T. barattinia* its distinct elliptical cross-section.

The multi-layered structure of *T. barattinia* wall can be observed with the naked eye in weathered specimens at the outcrops (Fig. 1J) or in sawn sections (Fig. 1A). In these specimens, layers of more weathered material alternate with others more cemented ones. Thin sections of specimens of both localities show that the more cemented layers contain a higher concentration of iron oxide, whereas the less cemented ones are less oxidized. The internal surface texture of the wall, which is mostly observable in the Uruguayan material, shows a pattern of densely packed, sub-triangular to sub-rectangular pits that cover the entire surface. When a clear pattern can be recognized, in the floor and roof, the orientation is transversal if they are rectangular, whereas on the lateral sides and ends of the chamber, they are mostly arranged with their long axes subparallel to the wall following its curvature (Fig. 1C). In some cases, pits with their long axes following chamber curvature cover most of the floor composing a more concentric, elliptical pattern (Fig. 1D).

Behaviour and pupation chambers of sphinx moths

One larva of *Manduca rustica* was observed while burying itself by peristaltic movements of the
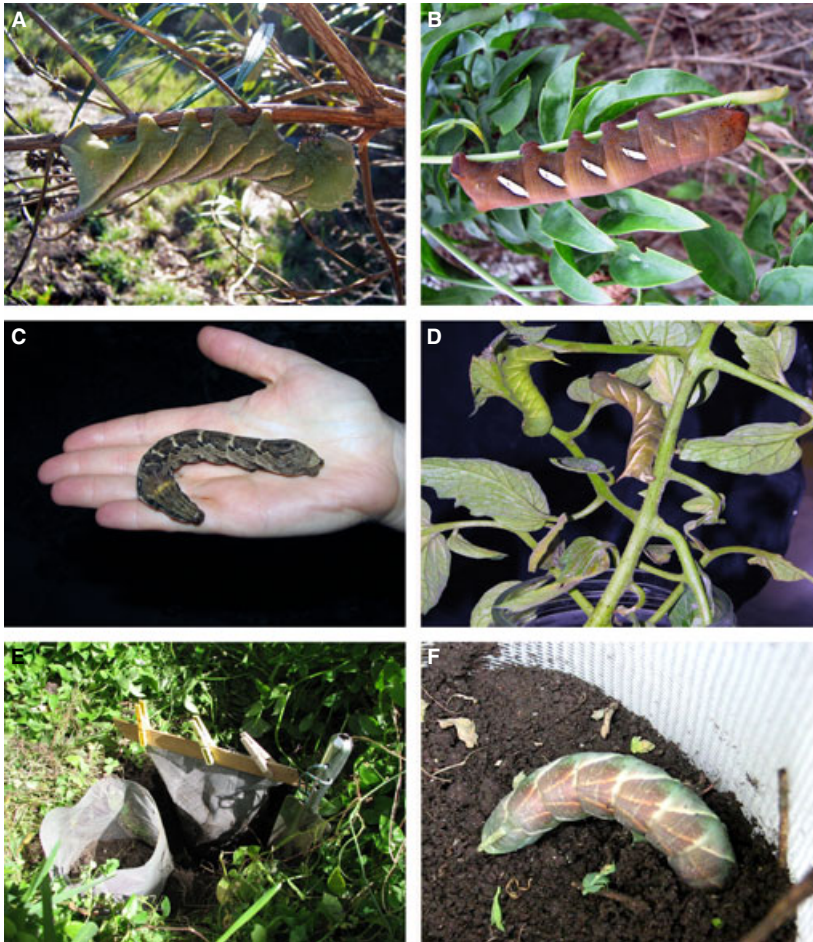
Fig. 3. Sphinx moth larvae. A, *Manduca rustica*. Larva diameter: 15 mm. B, *Eumorpha analis*. Larva diameter: 15 mm. C, *Eumorpha labruscae*. Larva diameter: 15 mm. D, two larvae of *Manduca diffissa* reared in branches maintained in a container with water. Larvae diameter: 12 mm. E, two plastic mesh cages partially buried in ground containing pupae. F, a picture captured from video showing *Manduca rustica* burrowing in a mesh cage. Compare with A the dorsal change of colour. Larva diameter: 18 mm.

anterior part of the body for penetrating the soil aided by the anchorage of its posterior part (Fig. 3F; http://www.youtube.com/watch?v=IDsey86cl38&feature=youtu.be). The participation of its short legs or mandibles in this digging process could not be confirmed. When post-feeding larvae like this are placed in clean recipients deprived of soil material, they discharge abundant liquid excretion in the recipient. If soil is not added, they pupate anyway but usually fail to become an adult. Before or during soil penetration, the observed *Manduca rustica* larva discharges no liquid excretion, which consequently took place during chamber excavation enabling soil softening and packing. The larvae, when taken with the hand, are capable of arching their body strongly to both sides with fast lateral movements, adopting C shapes. These movements were also recorded on X-ray video for the 4-day-buried larva illustrated in Figure 3A (Fig. 4A, B; http://www.youtube.com/watch?v=JcjHtghdBq4&feature=youtu.be). If applied slowly and with pressure against moistened walls, these movements may also contribute to chamber enlargement. The legs would be probably applied

against wall at the end of the process, so as to leave the densely packed pits.

All the pupation chambers examined (*n*: 7) showed a shallow horizontal to sub-horizontal location, with the uppermost part inclined upwards and up to 2 cm below surface (Fig. 4B). A plaster cast of one specimen, excavated by the larva illustrated in Figure 3F and the video, showed that the chamber had flat floor and an arched and slanting roof that reached its maximum height at the extreme near the soil surface (Fig. 4E). The uppermost part, the hatch, which points upward, shows a hemispheric outline (Fig. 4D, E). Chambers, which show depressed or plane convex cross-sections, are enlarged in comparison with pupae (Fig. 4D; 5B, C). This enlargement is noticeable because chambers are 2–3 cm wider and higher than pupae (1.5–2 cm in diameter). Chambers are as follows: 7–9.5 cm long (*n*: 7), 3.4–4.2 cm wide (*n*: 7) and 3.5–4 cm high at its middle section (*n*: 4) (Fig. 5A, B, C). The cast is 2 cm high at its rear, 3.9 cm at its middle section and 4.4 cm at the hatch (Fig. 4C, D, E).

Fig. 4. Manduca rustica chambers. A, plan view taken from the X-ray video record. Note the dark inner lining and larva forming a C. B, lateral view (inclined) taken from the X-ray video record. Note the hatch on top and the dark inner lining. Larva is arched forming a U. This chamber was excavated by the larva illustrated in Figure 3A. C–E, plaster cast of the chamber excavated by the larva illustrated in Figure 3F and video. C, plan view, compare with A. D, posterior view. Note the flat floor and arched roof composing a depressed cross-section. Dotted line shows the hatch protruding above the outline. E, lateral view. Dotted line shows the protruding hatch. Scale bars = 1 cm.
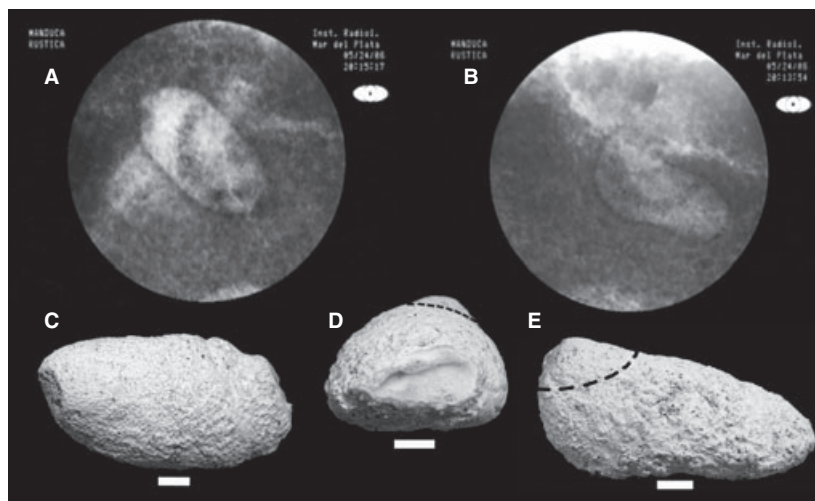
At the time of extracting the chambers from the terraria, it was noted that the substrate surrounding the chamber was consolidated compared with the more outlying, loose one. However, this consolidated rind of soil around the chamber, 0.7–1.2 cm wide (*n*: 6), could not be removed easily or distinguished sharply from the remaining substrate (Fig. 5B). A chamber excavated in sand shows a darker layer in the internal part of the wall (Fig. 5D). Thin sections of a chamber excavated in soil show that in the consolidated rind around the chamber, the packing of material is high (Fig. 5E), which probably results from the pressure produced by the larvae against the soil to enlarge the chamber. It is also possible to distinguish at least three concentrical discontinuities marked by darker layers composed of organic matter and oxides, and/or alignments of voids (Fig. 5E). The latter are probably the result of dehydration of the structure once removed from soil.

In contrast to the blurred external surface wall, the inner surface is sharply defined, showing a pattern of sub-triangular to sub-rectangular pits, with their long axes at right to nearly right angles to the long axis of the chamber. The pits are densely packed in rows that seem to radiate from a mid-line of the roof (Fig. 5F, G). Individual sub-triangular to sub-rectangular pits were obtained by pressing the larval true legs (Fig. 5H) against plasticine (Fig. 5I). In contrast, buccal apparatus, prolegs, anal shield and horn produced no such marks.

Discussion

Sphinx moth chambers show striking similarities with *Teisseirei barattinia*, which leave few doubts about its origin. The former are horizontal to sub-horizontal enlarged structures in width and height, which largely exceed pupae diameter, showing flat floors and depressed cross-sections (Fig. 4D; 5A, B, C). These large chambers compared to the size of the pupa may reflect the loss of nearly 40% of the larval weight due to discharges of liquid excretions for constructing the chamber (Reinecke *et al.* 1980). Chamber size probably fits better the body of the larvae, their true producers, which are then 30–40% larger than the pupae. However, chambers are also larger than larvae suggesting that the particular digging behaviour of these larvae is mostly responsible for the production of these elliptical chambers in cross-section. The depressed cross-section is the main diagnostic ichnotaxobase of *T. barattinia* (Fig. 1E, F, H) in contrast to other pupation chambers recorded from palaeosols showing rounded cross-sections, which probably better reflect the diameter of the occupants (Genise 2004). Longitudinal section of Patagonian specimens, which have more arched sides in contrast to parallel sides shown by northern specimens, is also similar to that of sphinx moth chambers (Figs 1A, C, F, I; 4C; 5A, C). Beyond the orientation, longitudinal and cross-section, the sculpture on the internal surface of the wall composed of densely packed, sub-rectangular to sub-triangular pits is also unique for insect trace fossils, and very similar in both, moth pupation chambers and *T. barattinia* (Figs 1C, D; 5F, G). Such pits were obtained experimentally by pressing true legs of *Manduca rustica* (Sphingidae) larvae against a plastic surface (Fig. 5H, I). The multi-layered arrangement of wall is also similar in both structures, even when due to diagenetic and weathering processes the layers are more evident in fossil examples (Fig. 1A, J) than in modern ones (Fig. 5A–E). The differences in: (1)
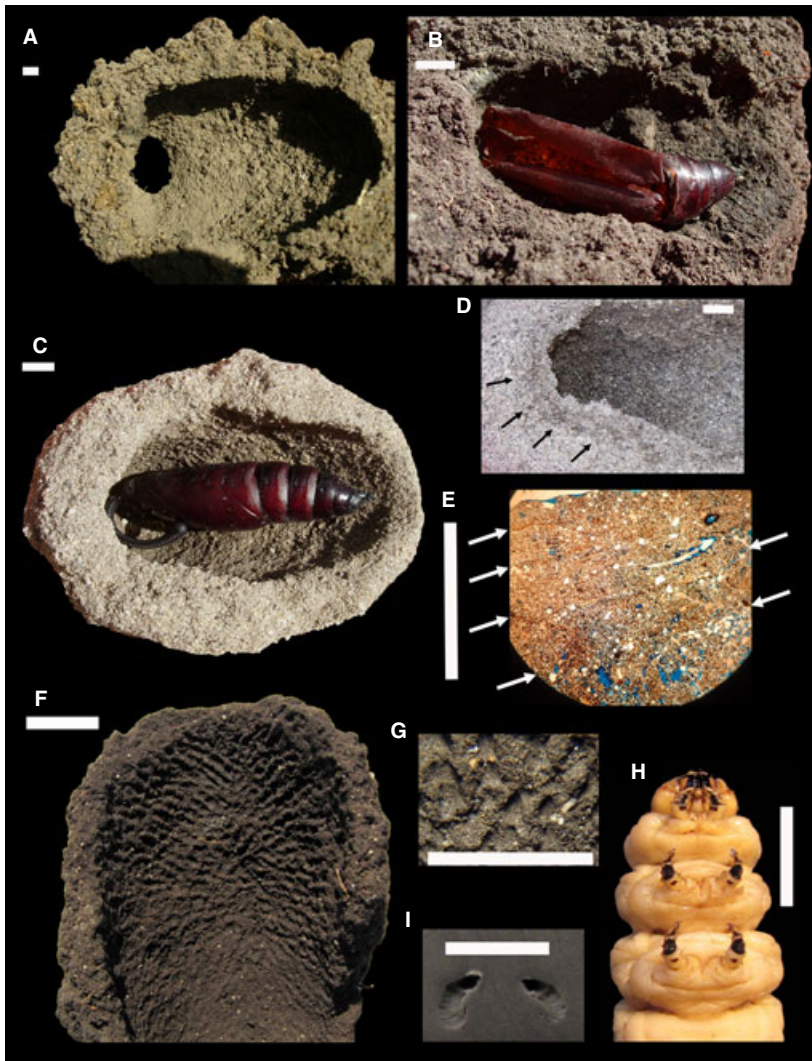
Fig. 5. Sphinx pupation chambers. A, pupation chamber of *Eumorpha anchemolus*. B, pupation chamber excavated by the larvae of *Eumorpha labruscae* illustrated in Figure 3C, which contained remains of the pupa when extracted from a terrarium. C–F, pupation chambers of *Manduca rustica*. C, pupation chamber made in pure sand a containing pupa. D, detail of C showing the innermost part of the wall darkened (arrows). E, thin section of an earthern chamber wall. Arrows show thin, darker layers of organic matter, oxides and aligned voids (at right). The arrows at the base of the picture show the boundary between the compacted wall and the soil. F, inner surface showing the pattern of densely packed pits. Note that rows of pits radiate from a central area. G, detail of sub-triangular pits. H, larva of *Manduca rustica* showing the shape of the true legs. I, cast of anterior true legs in plasticine. Scale bars = 1 cm.

tangential sections: roof parallel to floor in *Teisseirei* in contrast to roof inclined in *Manduca* chamber; (2) apical rounded antechamber in *Teisseirei* in contrast to sub-apical, hemispherical hatch in *Manduca* chamber; and (3) orientation of pits are expectable from phylogenetically related, but distinct producers.

Manduca and *Eumorpha* pupation chambers were located superficially in terraria, as in most cases recorded from moth pupation chambers (i.e. Tuskes & Emmel 1981; Roach & Campbell 1983; Villanueva 1998; Bouyer *et al.* 2004; Pinault *et al.* 2007), suggesting that *T. barattinia,* if constructed by a moth, would not have been located deep in the soil, and accordingly would be an indicator of palaeosol uppermost horizons. The shallow position of moth pupation chambers is probably related to adult emergence. Adult moths have no specialized appendages for hard digging, and the scales that cover the whole body would be severely damaged by

friction during emergence if chambers were emplaced deeply in soils. In contrast, Jump *et al.* (2006) believe that pupation of at least some moths may take place deep in the soil to avoid sun heat and fires, as reported for one species of Saturnidae by Ande (2004). The hatch, which can be easily separated from the chamber as a skullcap, may be detached when the emergent adult pushes outwards for emerging, serving as a door and also as a shield to avoid friction against soil. In addition, soil compaction and humidity were mentioned as controls in successful moth emergence (Roach & Campbell 1983; Osborne 1995). Murray & Zalucki (1990) demonstrated that the maintenance of silk-lined, pupation burrows excavated by larvae was critical for adult emergence. Reinecke *et al.* (1980) mentioned a discharge of liquid meconium to soften the soil and facilitate emergence in *Manduca sexta*. Despite their different shape, the hatch of sphinx pupation chambers could be comparable in function

with the antechambers of *T. barattinia*. In the latter, the antechamber would be the remains of the pupation burrow filled originally with loose soil to aid later in the emergence.

Genise (2004) analysed the different type of walls found in insect trace fossils in palaeosols, calling the attention of the ambiguous meaning that has colloquially the term 'wall' beyond its ichnological use and the complexity that insect-made walls can reach. As recognized by Bromley (1996) in its most simple meaning, a wall is the boundary between the trace lumen and the matrix. Such a bidimensional wall is present in all trace fossils despite its subsequent modifications. For insect traces, one of the most common modifications is the presence of a lining of fine material (dust films of Bromley), which insects may achieve by three methods: (1) addition of organic (faecal or regurgitated) material producing organic linings as in many termites (Noirot 1970; Grassé 1984) or some ants (Genise & Farina 2011); (2) addition of clay material brought from somewhere else as in some hymenopterans (Sakagami & Michener 1962); and (3) probably the most common one, concentration of fine material by fluidization (Genise & Poiré 2000; Genise 2004). Organic, clay and fluidized linings share in common that they are made with fine, well-sorted material, and that they are relatively thin, and mostly undetachable from the boundary wall. Another different type of lining, called the constructional wall by Bromley (1996) and Genise (2004) is that made with unsorted soil material, producing mostly relatively thick linings easily removable from the boundary wall. The producer insects can leave distinct sculptures on both sides of these three-dimensional linings, which are mostly constructed by the addition of pellets. Pellets can be recognized micromorphologically in trace fossils as distinct layers (Genise & Hazeldine 1998; Genise 2004). Pelletal linings should be distinguished from free-standing walls constructed by some termites: linings, no matter the thickness, are always constructed against a wall, whereas free-standing walls are constructed in an empty space inside a chamber. As warned by Genise (2004), insect constructions are still more complex than this oversimplification and different types of walls and linings can be included in the same trace fossil. Despite this diversity, in most of these cases, organic, clay or pelletal linings and free-standing walls are produced by insects using rigid appendages and mouthparts adapted for digging, moulding and transportation of material.

In contrast, the case of soft-bodied moth larvae is completely different, as they use abundant liquid excretions for softening and packing soil along with body pressure against walls. Accordingly, the lining that they produce is a new type to add to those mentioned before, namely, organic, clay, fluidized and pelletal linings. The name 'multi-layered lining' is used here to define this new type of modification of the boundary wall. Both, sphinx pupation chambers and *Teisseirei barattinia* show a relatively thick multi-layered lining that results from the modification of the surrounding soil. The disproportionate width that this lining reaches in some cases (Fig. 1A, J) in comparison with the chamber suggests also that producers should have no direct interaction at least with the distal layers of this envelope. Yet the surrounding soil is clearly modified. How is it possible? *Teisseirei* multi-layered wall structure may be the result of burrowing by soft-bodied larvae that pack the surrounding soil by body movements and pressure aided by the release in successive discharges of abundant liquid excretions as proposed herein for *Manduca rustica*. Reinecke *et al.* (1980) distinguished several behaviours and developmental stages for *Manduca sexta* post-feeding larvae. These authors described that the larvae excreted a clear fluid in several discharges over a period of 28 hours and that larvae burrowing in soil use this liquid to dampen and pack the surrounding soil to make the pupation chamber. This packing is documented herein for chambers of *Manduca rustica* (Fig. 5E). Accordingly, each discharge of organic-rich liquid secretion would produce the oxidation and concentration of iron in the reduction/oxidation front boundary as observed herein for *Manduca rustica* (Fig. 5E) and in ferruginous concretions, rhizoliths and palaeorhizospheres (Chan *et al.* 2007; Genise *et al.* 2011). These layers are the most consolidated ones observed herein (Fig. 1A, J) because of the cementation produced by iron oxide. They produce a concentric pattern because of the centrifugal migration of the reduction/oxidation front boundary as in iron concretions (Chan *et al.* 2007) and ferruginous palaeorhizospheres (Genise *et al.* 2011), probably each rim produced by a different excretion discharge. This digging behaviour of sphinx moth larvae, documented herein for *Manduca rustica*, explains multi-layered lining of both sphinx pupation chambers and *Teisseirei barattinia*.

Conclusions

A number of conclusions can be drawn from this study.

- *Teisseirei barattinia* is attributed to moth pupation chambers according to its horizontal to

sub-horizontal orientation, depressed cross-section, multi-layered lining and its inner surface texture composed of densely packed, sub-rectangular to sub-triangular pits.

- *Teisseirei barattinia* is the first trace fossil documented in palaeosols attributed to sphinx moths, which is supported by macro and micromorphological comparisons with extant pupation chambers.

- Moth pupation chambers are located near soil surface to aid in the emergence of fragile adults provided with little digging ability. Consequently, *Teisseirei barattinia* would be an indicator of uppermost horizons in palaeosols.

- Antechamber of *Teisseirei barattinia* and the hatch of *Manduca rustica* pupation chambers would be devices to aid in adult emergence as well.

- *Teisseirei barattinia* shows a new type of lining for insect trace fossils in palaeosols, called herein *multi-layered lining*, composed of multiple oxidized layers that would result from the packing of the surrounding soil aided by multiple discharges of liquid excretions during chamber excavation.

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