

Corimbatichnus fernandezii: A Cluster of Fossil Bee Cells from the Late Cretaceous-Early Tertiary of Uruguay

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Corimbatichnus fernandezii n.igen, n. isp. is a cluster of fossil bee cells from the Uruguayan Late Cretaceous-early Tertiary Asencio Formation. It is composed of rows of small excavated cells contained in paleosol peds. Cells have inner surfaces somewhat rough and are closed with loose material. Separation among cells is very thin, and the cells are orientated uniformly, showing a great economy of space as in some halictine constructions. *Corimbatichnus* can be distinguished from *Rosellichnus* and *Uruguay* by its convex face, excavated cells and the spatial arrangement of them.

Keywords: Bee cells, Halictinae, Asencio Formation, Late Cretaceous-early Tertiary, Uruguay

INTRODUCTION

Recently, Genise and Bown (1996) described the only two known types of clusters of fossil bee cells, one being, *Rosellichnus* from the Tertiary of Argentina and the Arab Emirates, and the other, *Uruguay*, described originally by Roselli (1938) from the Late Cretaceous-early Tertiary Asencio Formation of Uruguay. In this paper, we describe a third ichnogenus, occurring in the Asencio Formation, where we have undertaken extensive research over the last several years to review Roselli's work and to study new fossil insect nests. The new trace fossil is very different morphologically from those described previ-

ously, particularly with respect to the arrangement of cells, which show a high economy of space as in some halictid "combs" (*sensu* Sakagami and Michener, 1962).

GEOLOGIC AND STRATIGRAPHIC SETTING

The trace fossils are present within the extended Late Cretaceous-early Tertiary outcrops from western Uruguay in southern South America. The geographic location of the quarries can be consulted in previous papers of this series (Genise and Bown, 1996; Genise and Laza, 1998) The age, stratigraphic position and other aspects of the outcrops that bear the fossil nests is still matter of discussion (Genise and Bown, 1996; Veroslavsky and Martínez, 1996; González et al., 1998; Pazos et al., 1998). The trace fossils occur in tiered paleosols developed in the Palacio Member of the Asencio Formation, about 20 m of ferruginous quartz sandstones that occur between the subjacent Cretaceous Mercedes Formation and the Oligocene Fray Bentos Formation. The age of this member is still controversial because of the complete absence of plant or animal remains.

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SYSTEMATIC ICHNOLOGY

Corimbatichnus n. igen

Etymology

Derived from the Latin *Corymbiatus*, meaning clustered, and from the Greek *Ichnos* meaning trace.

Type ichnospecies

Corimbatichnus fernandezi, type and only known ichnospecies

Diagnosis

Cluster of elongated cells, having rounded rears and flat tops, excavated in paleosol peds. Cells are devoid of discrete walls, they have inner surfaces somewhat rough and loosely packed closures. Cell entrances open in a convex face of the ped and they are arranged in rows and columns. Cells in each row are orientated with their axes parallel and inclined with respect to the convex face. The arrangement of cells result in thin intercellular separations. Some peds may contain two different clusters, in which case the cells of one are orientated to form a "V" with respect to the other. Clusters are vertically orientated, having horizontal and inclined cells.

Remarks

Corimbatichnus can be distinguished from *Uruguay* and *Rosellichnus* by the absence of constructed walls, the arrangement of cells and the convex aspect of the face containing the cell entrances.

Corimbatichnus fernandezi in. isp.

Etymology

Dedicated to Wilfredo Fernández, curator of the collection of fossil insect nests housed at the Museo Lucas Roselli from Nueva Palmira, field

assistant of the late Lucas Roselli and an invaluable collaborator in our recent field trips.

Holotype

Museo "Francisco Lucas Roselli" (Nueva Palmira, Uruguay) N° 727 (Maldonado Quarry, Genise-Bown col., 2-1994)

Hypodigm

Paratypes: Museo "Francisco Lucas Roselli" (MLR, Nueva Palmira, Uruguay) N° 732 (Espiga Quarry, Genise col., 5-1994) and N° 735 (Espiga Quarry, Verde col., 10-1995) and Museo Argentino de Ciencias Naturales Laboratorio de Icnología, (MACN-LI, Buenos Aires, Argentina) N° 611, 616, 618 and 619 (Maldonado Quarry, Genise col., 2-1995, 10-1996 and 9-1997). *Other material examined*: fourteen small fragments of combs (MLR N° 734 and MACN-LI N° 612, 613, 614, 615, 617, 620/628).

Type locality and Occurrence

Palacio Member of the Asencio Formation (Late Cretaceous-early Tertiary). Maldonado and Espiga quarries near the town of Nueva Palmira and Estancia Media Agua near the town of Palmitas.

Diagnosis

Only known ichnospecies, same as for the ichnogenus.

Description

The clusters of excavated cells occur in paleosol peds, which usually contain a more or less complete cluster plus several cells from another. Cells show a partially smoothed inner surface, in which it is possible to recognize coarse grains of the soil material protruding inside the chamber (Fig. 2 D). The cells show rounded cross-sections, without a distinct flat floor, indicating that they have radial symmetry. The rear ends are round and the cells show a constriction or neck near the top, which in some cases is filled with

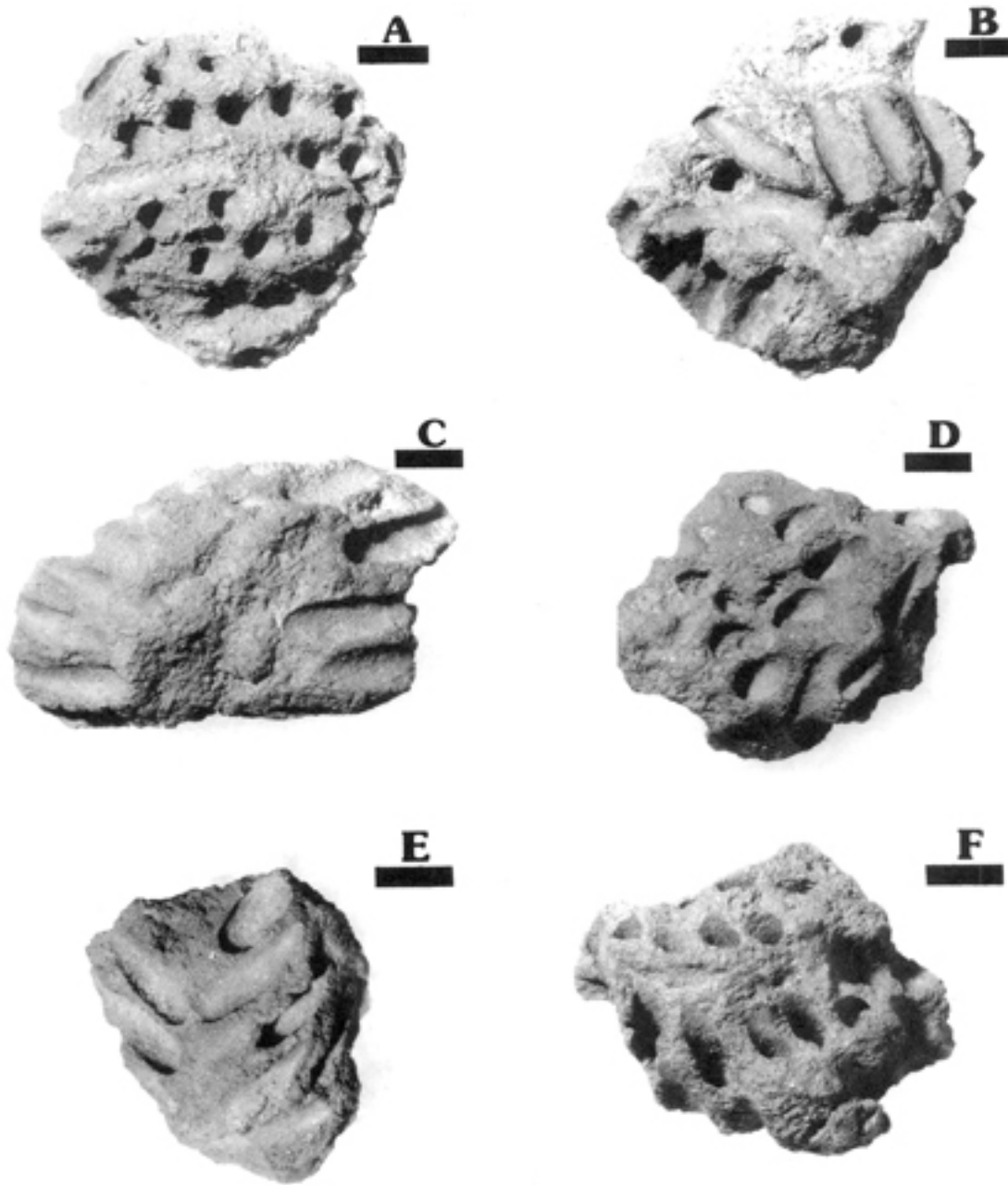


FIGURE 1 *Corimbaticinus fernandesi*. (A) Holotype, front. (B) Holotype, back. (C) Paratype (MLR N° 732) showing the arrangement in "V" of the two combs in the same ped. (D) Paratype (MLR N° 732) front view of one comb. (E) Paratype (MACN-LI N° 616) showing the arrangement of the combs in the ped. (F) Paratype (MACN-LI N° 616) front view of one comb. Scale bar: 1 cm

soil material. No spirally designed cap can be recognized in any cell, suggesting that the soil

material filling the neck was the original closure of the cell. Cells do not show discrete walls. Only

one incomplete cell of a fragment, at its posterior end, shows a distinct wall 0.5 mm thick slightly separated from the chamber wall (Fig. 2 C). This wall is constructed from a finer material but it is

impossible to ascertain if it represents a distinct lining produced by the original constructor of the trace or a superimposed structure of another species of parasite or inquiline.

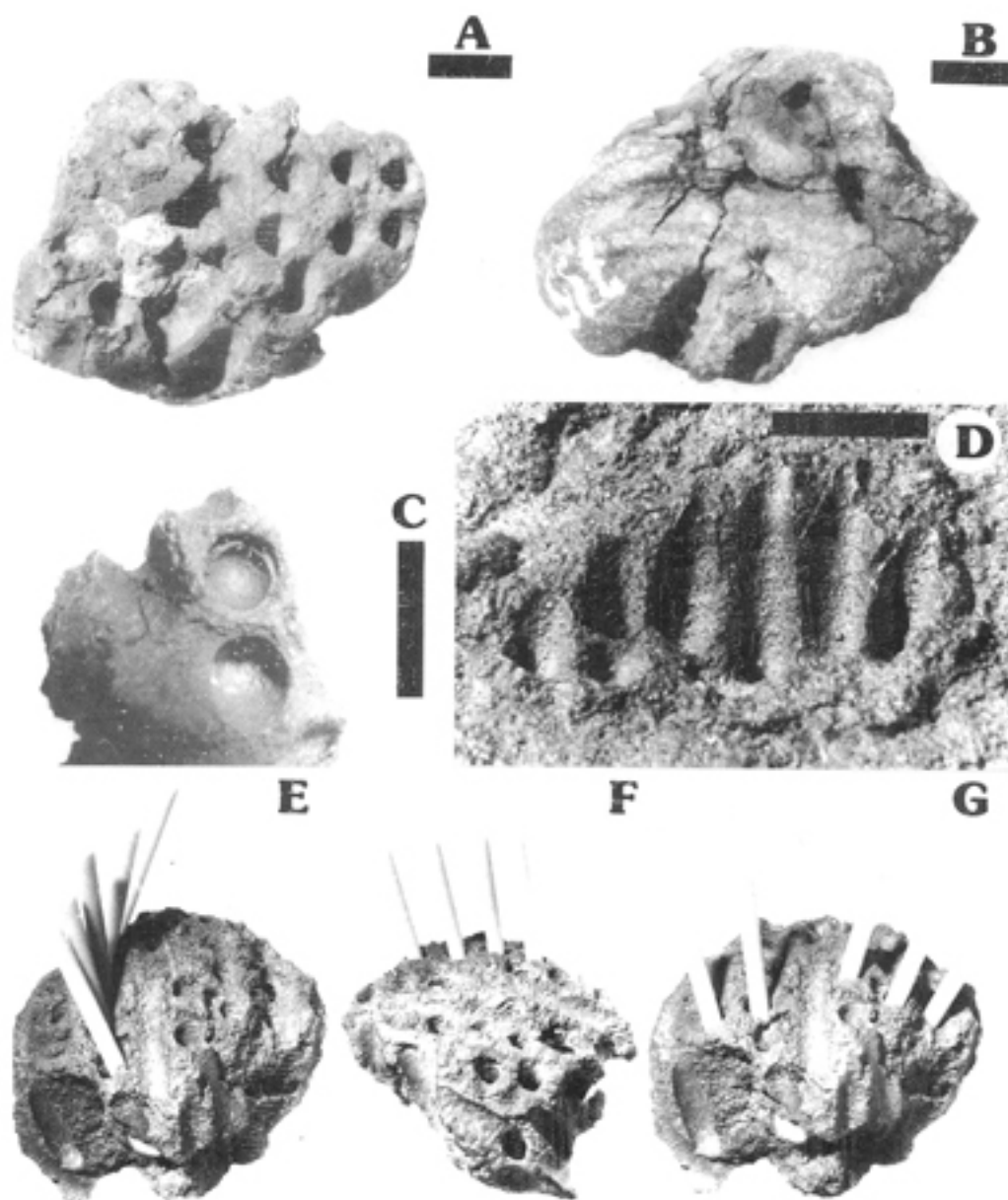


FIGURE 2 *Corimbaticinus fernandezi*. (A) Paratype (MLR N° 735) front view. (B) Paratype (MLR N° 735) back view. (C) Fragment showing an incomplete cell with a lining. (D) Fragment showing the inner surface of cells. (E), (F) and (G) Holotype in which sticks show the inclination of cells in an arched row, a straight row and transverse cross-section respectively

Peds containing the most complete clusters have a more or less flattened cubic design. Measurements range from 34 mm to 55 mm in length, from 26.8 mm to 34 mm in width and from 20 mm to 33 mm in height. In the best preserved specimens the cell length ranges from 14 mm to 19 mm. (mean: 17 mm, N=24); the cell maximum diameter ranges from 3.5 mm to 4.7 mm (mean: 4.09 mm, N=29); and the cell entrance diameter ranges from 2.6 mm to 3.2 mm (mean: 2.93 mm., N=20). In the best preserved samples, the number of cells ranges from 22 to 44 and may be disposed in one or two groups. To thoroughly reconstruct the entire morphology of the trace and to interpret the trace maker behavior it is necessary to integrate the descriptions of several of the most complete specimens found. No single example displays the complete morphology of a mature cluster.

The holotype (Fig. 1 A, B) shows a convex surface where the cell entrances can be located in an imaginary grid composed of rows (x axis) and columns (y axis). It is possible to distinguish 8 rows of cell entrances located in concave channels surrounded by two ridges. The longest row bears 7 cells. In each row (x axis) the cells are orientated uniformly, with their longitudinal axes parallel to each other and all of them at an angle of 110° with respect to the tangent of the arch formed by the convex face of the ped (Figs. 2 F, 4 B). It is also possible to observe that in the longest row, the longitudinal axis of the first cell is rotated about 30° with respect to the last one (seventh) in a hypothetical z axis (Figs. 2 E, 4 A). Columns of cells are more difficult to define; they can be recognized at two angles (60° or 120°) with respect to the rows (x axis). The angle results from the displacement of the rows in such a way that the cells of one row are excavated over the intercellular space of the neighboring rows. This comb-like arrangement is not perfect; the cells do not lay just in the middle of the intercellular space of the neighboring rows. In such inclined columns, the cells are equally orientated with their longitudinal axes parallel

to each other (Fig. 4 D). But also, it is difficult to unequivocally follow a column because of the curvature of the ped and imperfections of the design. When sectioned specimens in a y - z plane perpendicular to the rows of cells, indicate that the longitudinal axes are convergent downwards (Figs. 2 G, 4 C). Probably, the trace is constructed by the successive addition of rows and thus these can be better defined than the columns, which are not the direct result of the building behavior but a secondary consequence of it. The channels which define the rows appear to be the remains of the tunnels where the cells were excavated from. The missing half of the tunnel would have been in the surrounding paleosol (cf. *Ellipsoideichnus*; Genise and Hazeldine, 1998a). The back part of this cluster shows the remains of at least four cells clearly belonging to another one excavated at a very different angle to those described above. The longitudinal axes of these cells are almost parallel to the y axis of the grid and so at an almost right angle with the longitudinal axes of the cells of the former group.

Specimen N° 616 (MACN-LI) (Fig. 1 E, F) shows the arrangement of two groups of cells in the same ped. The best preserved group is composed of five incomplete rows of cells, which display the same disposition described previously (Fig. 1 F). The second group is composed of the remains of four rows of incomplete cells. The broken extremes of the ped show the cells of both groups orientated with their longitudinal axes forming a "V" (Fig. 1 E). At one extreme, the axes are orientated almost at a right angle and the rear ends of the cells of both groups are separated by thin spaces, whereas at the other, angles may reach 140° and some interspaces are larger. Specimen N° 732 (MLR) also shows clearly the presence of two groups of cells in the same ped at an angle of 140° - 150° (Fig. 1 C, D). The ped in the upper part of the "V" is broken, but it is possible to recognize three very incomplete cells orientated upwards, which are not clearly related to any of the two groups. One

possibility is that both groups of cells were separated by a hiatus; the other possibility is that both were connected by additional rows of cells. In a way, the broken extremes of a ped show a section in the y - z plane perpendicular to the rows, and even in the same group of cells the longitudinal axes show a convergent array as described previously.

Specimen N° 735 (MLR) comprises 6 rows of cells repeating the same arrangement (Fig. 2 A, B). A second group of cells is indicated only by the remains of one cell orientated at a right angle with respect to the group. In this specimen a groove is preserved in the back part (Fig. 2 B), and this may represent the trace of a root where the ped would be attached like other fossil nests of this formation (cf. *Uruguay*, Genise and Bown, 1996; *Monesichnus*, Genise and Laza, 1998).

The other specimens examined show the same morphology or are very fragmentary. Most were found as isolated clasts, broken or weathered, on the floor of the quarries. In most cases it is impossible to distinguish unequivocally if these specimens with few cells represent youngest stages of combs, which would permit study of the development of the whole structure. Others occur in individual peds of the blocky subhorizon of the paleosol. In many cases these peds may be rotated and weathered (González et al, 1998) precluding any conclusion with respect to the original position of the trace in the soil as well as its complete morphology.

Corimbatichnus sp.
View 1: 100%

DISCUSSION AND CONCLUSIONS

Corimbatichnus fernandezi poses several problems for discussion; among others, the reconstruction of the architecture of the whole trace, its comb-like architecture, the original position in the paleosol and the identity of the trace maker.

All the specimens examined show the same arrangement of cells. Two groups excavated in the same ped are orientated in the form of a "V". This orientation leaves no doubt about the origi-

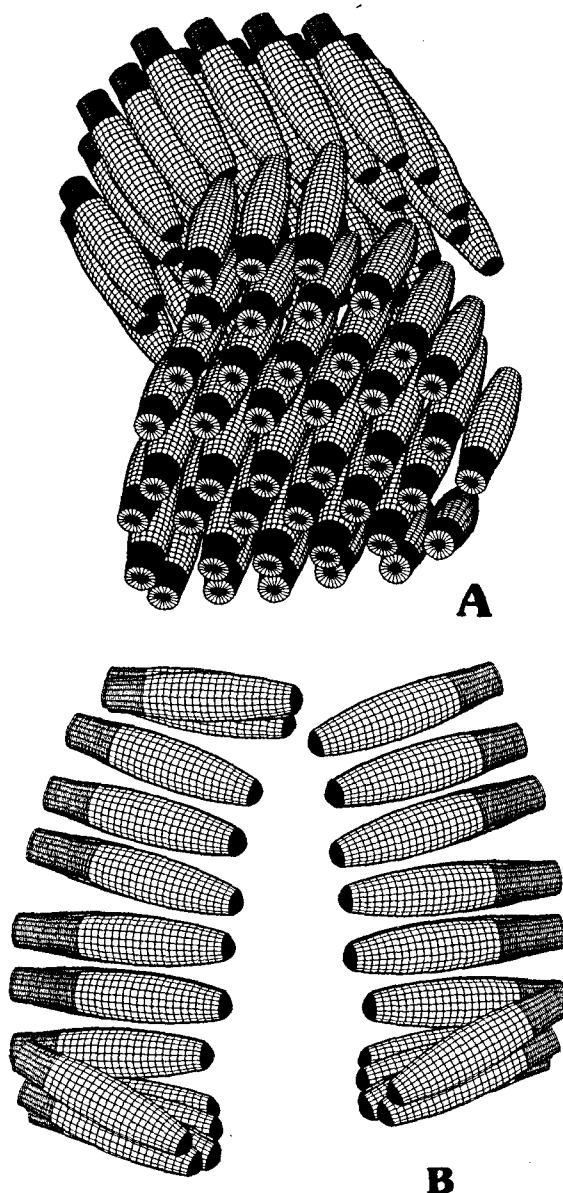


FIGURE 3 3D reconstruction of *C. fernandezi* showing (A) the general aspect and (B) a cross-section of the ped showing the arrangement of the cells

nal position of the ped and the cells in the soil. Bee cells may be vertical, inclined or horizontal but usually the posterior ends are orientated downwards to avoid the spilling of provisions. Hence, the only possible position of *C. fernandezi*

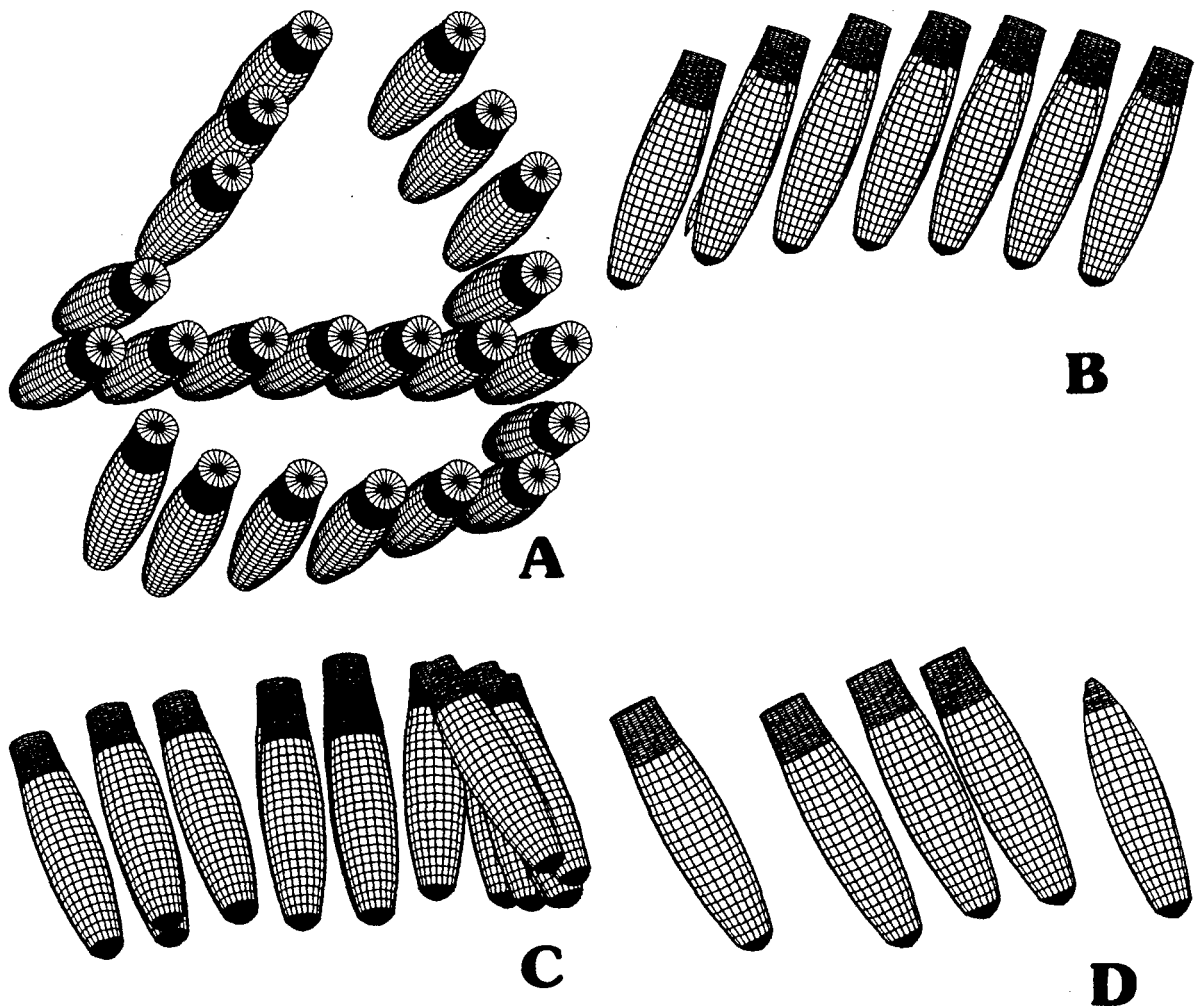


FIGURE 4 3D reconstruction of *C. fernandezi*. (A) Front view of a comb in which some cells were removed to show particular features. Note the rotation of the longitudinal axes of the cells in the row below. (B) Cells inclined uniformly in a row. (C) Divergence of cells in a cross-section of the comb perpendicular to the rows. (D) Cells inclined uniformly in a column (120° from a row)

in which no cell would be orientated bottom upwards is that of a "V", being each group of cells vertically orientated on both sides of the ped (Fig. 3 A, B). In each group, cells are orientated uniformly and they are separated by thin walls; the two requisites that Sakagami and Michener (1962) proposed to consider a group of cells of a halictine as a true "comb". For these authors, the combs represented the most effi-

cient way to achieve space economy and they could be excavated in a ped or constructed inside a cavity previously performed by the bee. In more recent papers on halictine architecture (Eickwort and Sakagami, 1979; Engel, 1998), combs are no longer distinguished from other clusters. It is impossible to ascertain to date if both clusters of a ped were originally connected by additional rows of cells, in which case the

complete morphology of *C. fernandezii* would be that of a single cluster excavated in a ped.

The convex surface of the clusters indicates that they were surrounded by a cavity constructed previously by the bee. Sakagami and Michener (1962) compared different nest patterns in halictinae from the standpoint of space economy. Some of them may be illustrated using the clusters of fossil bee cells described from the same Asencio Formation (Fig. 5). In the first instars of the series, the cells open directly into the main burrow, resulting in clusters having cells with close entrances and divergent bottoms (Fig. 5 A). In these clusters the face where the cells open is concave because it reflects the outline of the tunnel wall. In addition, there is little space economy because of the misuse of interspaces among the bottoms of the cells. Such is the case of the ichnogenus *Uruguay*. A second stage in this series is exemplified by *Rosellichnus*: the frontal face of the cluster is flat, reflecting the existence of a previous cavity from where to excavate the cells (Fig. 5 B). Nevertheless, in *Rosellichnus* the interspaces among cells is still considerable. *Corimbatichnus* shows a convex frontal surface, revealing that a cavity was also previously excavated, but additionally it shows the most efficient inclination of cells in terms of space economy. When the cells are excavated from a convex surface, large spaces among cells are necessary to avoid bottom overlapping, if the longitudinal axes are coincident with the radius of the curvature (Fig. 5 C). Economy of space is only achieved if the cells are excavated at a particular angle with respect to this curvature, as in *Corimbatichnus* (Fig. 5 D). Although efficient, this architecture is limited in terms of cluster expansion: the addition of more cells in the row is possible as far as cell bottoms begin to overlap (Fig. 5 E). To avoid this overlap a possible solution is to make use of the 3D space by coiling the cell row to form a helix, as in *Ellipsoideichnus* (Fig. 5 F).

The identity of the trace maker is in little doubt and, in addition, contributes to the pale-

ontological record of the family. Clusters surrounded by a cavity, with few exceptions, are performed by Halictinae, the sweat bees (Sakagami and Michener, 1962). Other features of *Corimbatichnus fernandezii* also confirm these constructors. A distinctly constricted neck as in cells of *C. fernandezii* is characteristic of cells of sweat bees. In contrast, the bilateral symmetry of halictinae cells is not present in cells of *C. fernandezii*, which seem to be radially symmetrical. The absence of a spiral closure, typical of most bee cells, is also common in halictinae cells. These bees close the cells with a permeable, loose, tampon-like closure according to Sakagami and Michener (1962), similar to that found in *C. fernandezii*. Another exception to a common bee cell feature, the absence of a smooth inner lining, can be explained in terms of halictinae architecture. With some exceptions, most sweat bees excavate cells in sandy soils and then line them with different materials: clay or fine wood particles, plus a secreted waxlike substance. The rough inner surface of *C. fernandezii* may indicate that the smooth inner lining had yet not been performed, that it was not preserved or that, as in some Australian species that nest in sandy soils, such linings were not constructed at all (Sakagami and Michener, 1962). Because in most bees the smoothing of the inner surface of the cells is simultaneous with its construction, the absence of this smoothed surface in cells of *C. fernandezii* may be other evidence of the halictinae origin of this trace fossil.

Engel (1996) found that the known older halictids came from Eocene-Oligocene deposits, but based on phylogenetic evidence, this author, estimated that the augochlorines should be 75–80 millions years old. Later, Engel (1998) proposed that these primitive augochlorines would have been semisocial species, constructing cell clusters in soils, and mentioned as physical evidence of this behavior the ichnogenus *Uruguay*. However, as discussed in previous papers (Genise and Bown, 1996; Genise and Hazeldine, 1998b), in spite of being clusters of cells, *Uruguay*

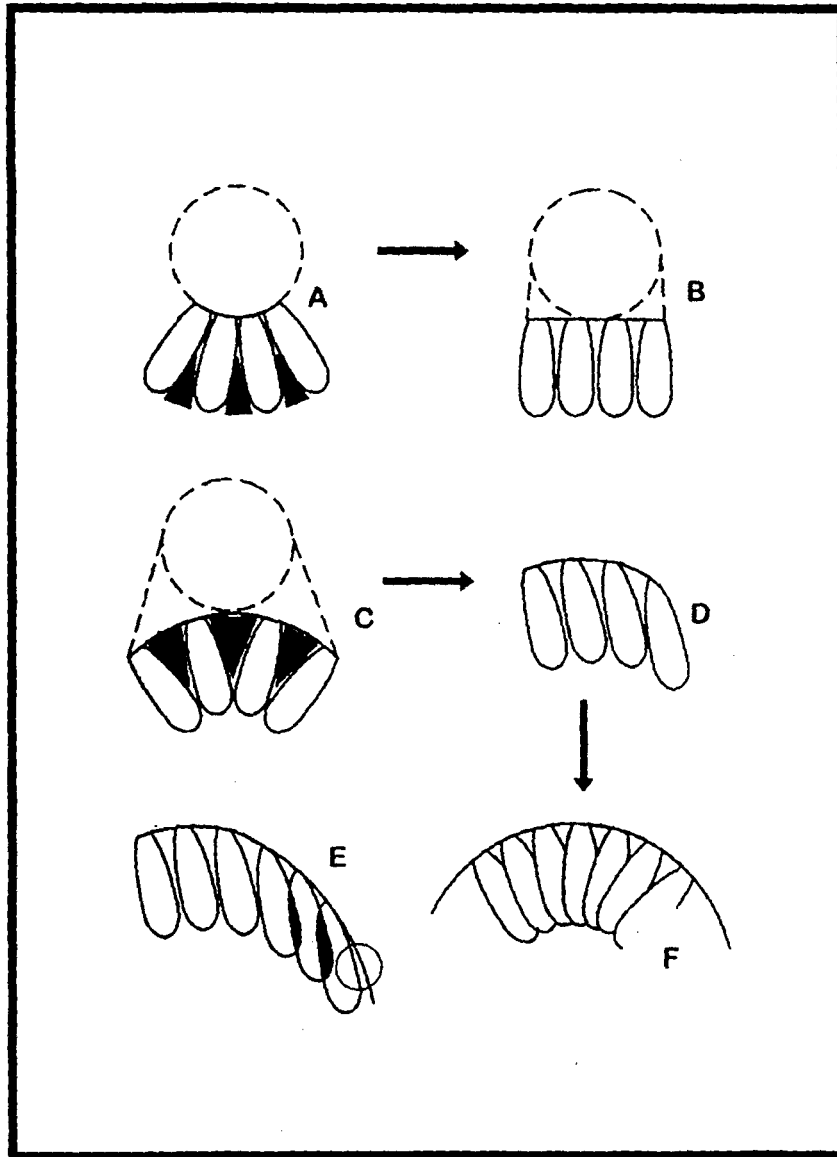


FIGURE 5 Different levels of space economy in clustered cells. (A) Black triangles show misused spaces between convergent cells (concave clusters). (B) The expansion of the tunnel results in a cluster having a flat face and more space economy. (C) Black triangles show misused spaces between divergent cells (convex clusters). (D) Cells inclined uniformly in a convex cluster avoid the space misuse. (E) In convex clusters the addition of cells in a row is limited by overlapping (black area) and the exhaustion of the free space (circle). (F) The helicoidal rows of cells avoid their overlapping.

cannot be attributed to sweat bees because of its size, thickened walls, spiral closures and other features. In contrast, the size, thin walls and other features of *C. fernandesi* closely resemble

those of halictinae clusters, and would represent definitively the pre-Oligocene evidence of these constructions.

Among halictines, constructions such as *C. fernandesi* are not restricted to a particular taxon (Sakagami and Michener, 1962; Eickwort and Sakagami, 1979). They are known in species of unrelated genera belonging to Augochlorini and Halictini, albeit Eickwort and Sakagami (1979) stated that clustering of cells is predominant in the neotropical Augochlorini and relatively uncommon in the cosmopolitan Halictini. The clusters of some of them are different from *Corimbatichnus* in having the cells vertically orientated (*Augochloropsis*, *Megommation*), divergent (*Paroxystoglossa*, and some *Caenaugochlora* and *Lasioglossum*), or in having flat or concave faces (some *Lasioglossum*, *Augochlorodes*, *Augochlorella*). According to the data compiled by these authors, vertical clusters are constructed by species of *Augochlorella*, *Halictillus*, *Corynura* s. str., *Paroxystoglossa*, *Augochlorodes* and *Pereirapis*. Another feature shown by *Corimbatichnus*, the existence of two opposite clusters in the same ped, is recorded exceptionally in the South American *Corynura cristata* and *Paroxystoglossa jocasta* (Sakagami and Michener, 1962). In summary, *Corimbatichnus* combines features exhibited by different clusters belonging to unrelated species of Halictinae, but without fitting in any of them in particular.

In this context it is difficult to speculate about the sociability of the constructor. Halictinae include solitary to primitively eusocial species, even belonging to the same genus (Michener, 1974). Eickwort and Sakagami (1979) concluded that among Augochlorini, the typical cluster-making halictines, semisocial behavior is common, whereas in Halictini larger eusocial societies are widespread. Later, Engel (1998) found that the semisocial condition would be a primitive condition for augochlorines. However, the fact is that simple nests are constructed by solitary species as well as social ones and, similarly, clusters belong indistinctly to solitary and social species (Sakagami and Michener, 1962).

C. fernandesi was probably constructed by a single species of bee as suggested by the similar

size of all the complete cells measured. Thus, this record adds another species of bee and another trace fossil to those previously documented from the Asencio Formation. These trace fossil associations are composed mainly of dung-beetle and bee nests, which are indicative of open herbaceous environments (Genise and Bown, 1994). Genise and Bown (1996) originally believed that the paleosols that bear the trace fossils in the Asencio Formation were oxisols that probably had developed under humid conditions, similar to those of tropical rain forests. However, recent studies (González et al., 1998) postulated that the structure of these paleosols more likely reflects soils of open environments, in agreement with the abundance of dung-beetle and bee nests.

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