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The Ichnofamily Celliformidae for *Celliforma* and Allied Ichnogenera

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This contribution undertakes a comprehensive revision, lacking until now, of all the ichnotaxa attributed to fossil bee cells, one of the most common traces in paleosols. These ichnotaxa are morphologically related to *Celliforma* and consequently grouped herein in the new ichnofamily Celliformidae. Two new ichnogenera are formulated, *Cellicalichnus* igen. nov., for several ichnospecies previously included in *Celliforma*, and a new ichnospecies, *C. chubutensis* isp. nov., belonging to this ichnofamily, and *Brownichnus* igen. nov., for the ichnospecies *favosites*, which is not morphologically related to *Celliforma*. The ichnogenera included in this ichnofamily involve traces in which *Celliforma*, the most simple trace of the group, is part of their structure. *Palmiraichnus* is akin to *Celliforma* with antechambers and discrete walls. *Uruguay*, *Corimbatichnus* and *Rosellichnus* are clusters composed of adjacent rows of *Celliforma*, or *Palmiraichnus*-like cells. *Ellipsoideichnus* and *Cellicalichnus* are different arrangements of *Celliforma*-like cells attached to tunnels.

Celliformidae are based on the morphology of the traces, all of them comprising cells, groups of cells and cells attached to tunnels. As such, its component ichnotaxa are based exclusively on morphological ichnotaxobases, which, in turn, were evaluated and selected with respect to the nest architecture of the trace makers, the bees. This paper analyzes some procedures and clues (i.e. behavioral homologies) that may be used to select the proper taxobases to erect ichnotaxa when the identity of the trace makers is known, as in this study case.

Keywords: Celliformidae, *Celliforma*, allied ichnogenera, bee traces

INTRODUCTION

Fossil bee cells are one of the most common trace fossils in paleosols; however, a comprehensive treatment of their ichnotaxonomy has, until now, been lacking. Rivas (1900) was the first to mention a fossil insect nest in a paleosol which, incidentally, was a bee nest. Shortly after, Schütze (1907) was the first to describe and illustrate a fossil bee cell. However, it was Brown (1934, 1935) who, almost thirty years later, formally described and named the first fossil bee cells, erecting the ichnogenus *Celliforma* to include them. In the same decade, Frenguelli (1930, 1938, 1939) mentioned fossil bee cells (*"nidos de véspidos"*) from the Tertiary of Uruguay and Argentina, and Roselli (1938) described and named the ichnogenus *Uruguay* for clusters of fossil bee cells. Almost fifty years later, Roselli (1987) described and named two other ichnogenera for fossil bee cells: *Palmiraichnus* and *Ellipsoideichnus*. During this interim, many authors described, and in some cases named, several ichnospecies of *Celliforma* (e.g., Brown, 1941; Sauer and Schremmer, 1969; Retallack, 1984; Ritchie, 1987). More recently, several new ichnogenera for fossil bee cells have been described and redescribed (Genise and Bown, 1996; Genise and Hazeldine, 1998a, b; Genise and Verde, in press)

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and new ichnospecies attributed to *Celliforma* described and named (e.g., Ducreux et al., 1988; Genise and Bown, 1994; Thackray, 1994; Elliott and Nations, 1998; Domínguez and Coca, 1998).

As a result of the publication of this information, the ichnotaxonomy of fossil bee cells at present shows some well-defined ichnogenera, each including few ichnospecies, namely *Palmiraichnus, Uruguay, Ellipsoideichnus, Rosellichnus,* and *Corimbatichnus* and a remaining one, *Celliforma,* that comprises many named and unnamed trace fossils, several of them incorrectly assigned to this ichnogenus. Many authors followed the original proposal of Brown (1935) who believed *Celliforma* "to include all fossil fillings of chambers purporting to have been made originally by unknown mining Hymenoptera", a non-morphological definition that was not supported later by other authors (Retallack, 1984; Genise and Bown, 1996). The necessity and problems for a review of *Celliforma* have been suggested elsewhere (Retallack, 1984; Genise and Bown, 1994; Elliott and Nations, 1998; Genise and Hazeldine, 1998b). The present revision follows the direction of previous papers in considering that although a thorough revision of *Celliforma* is at present very difficult, an advance can be accomplished by redefining the limits of this ichnogenus and distinguish those ichnospecies that do not appropriately belong within it (Genise and Hazeldine, 1998b).

The purpose of the present contribution is, therefore, to enumerate and redefine where necessary all the ichnotaxa corresponding to fossil bee cells, all of which are morphologically related to *Celliforma* and consequently attributed herein to the new ichnofamily Celliformidae. Two new ichnogenera are proposed: *Cellicalichnus* igen. nov. belonging to this ichnofamily, for some ichnospecies previously included in *Celliforma,* and *Brownichnus* igen. nov., which is not included within this ichnofamily. *Brownichnus*is is proposed to include the ichnospecies *favosites* Brown (1941) attributed to a wasp comb and originally included in *Celliforma.*

SYSTEMATIC ICHNOLOGY

Type ichnogenus

Celliforma Brown 1934.

Diagnosis

Group of ichnogenera related morphologically to Celliforma. In all cases these ichnogenera involve traces in which *Celliforma,* the most simple trace of the group, comprising chambers or their internal molds of different shapes (subcylindrical, tear, flask, urn, vase, barrel); having one end rounded and the other either truncated or capped by a spiral closure, is part of their structure. *Palmiraichnus* is similar to *Celliforma* with antechambers and discrete walls. *Uruguay, Corimbatichnus* and *Rosellichnus* are clusters composed of adjacent rows of *Celliforma or Palmiraichnus*-like cells. *Ellipsoideichnus* and *Cellicalichnus* igen. nov. are different arrangements of *Celliforma*-like cells attached to tunnels.

Key to separate the ichnogenera of *Celliformidae*

1.-	Isolated cells	2
	Cells in clusters or attached to tunnels	3
2.-	Cells having antechambers and discrete walls	*Palmiraichnus* Roselli
	Cells preserved as casts or chambers lacking a discrete wall and antechambers	*Celliforma* Brown

3.-	Clusters composed of adjacent rows of cells	4
	Cells attached to tunnels	6
4.-	Cells having discrete, constructed walls	5
	Cells lacking discrete walls, entrance of cells on a convex surface	*Corimbatichnus* Genise and Verde
5.-	Entrances of cells on a concave surface	*Uruguay* Roselli
	Entrances of cells on a flat surface	*Rosellichnus* Genise and Bown
6.-	Cells attached to a helicoidal tunnel	*Ellipsoideichnus* Roselli
	Cells attached to straight or curved tunnels	*Cellicalichnus* igen. nov.

Cellicalichnus igen. nov.

Figs. 1 A, B, 2

Etymology

From the Latin *cella* meaning cell, and the Greek *kalos* and *ichnos* meaning nest and trace respectively.

Type ichnospecies

dakotensis (Elliott and Nations 1998)

Diagnosis

Rows or whorls of tear-shaped or ellipsoidal cells attached by means of short necks to main tunnels.

Comments

The other ichnogenus in which cells are attached to a tunnel is *Ellipsoideichnus* Roselli 1987, which has a very distinct aspect because of the helicoidal design of the tunnel and the presence of a pair of opposite cells in each whorl of the helix (Fig. 1 C).

The ichnogenus comprises three known ichnospecies, formerly attributed to *Celliforma,* and a new one described herein. The morphology of these trace fossils involving cells (*Celliforma*) related to tunnels is far more complex and largely exceeds the diagnosis of *Celliforma,* which even in the broad definition of Brown (1935) is restricted to single chambers. *Celliforma* represents cells, whereas *Cellicalichnus,* nests or parts of them.

Hasiotis and Demko (1996, p. 366, fig. 9A, B) briefly described, from the Jurassic Morrison Formation (USA) under the name of *Celliforma spirifer,* a supposed bee nest whose idealized reconstruction comprised cells attached directly to tunnels, the typical morphology of *Cellicalichnus* ichnospecies. However, this and other important findings of Triassic traces composed of cells, in petrified wood and paleosols, communicated at different meetings by these authors (e.g., Hasiotis et al., 1995), would require detailed and formal descriptions, still pending, to be properly interpreted and incorporated into the ichnotaxonomical framework. Moreover, if they were true bee nests, they would change our present knowledge on the origin and coevolution of angiosperms and bees.

Ichnospecies included

ficoides Retallack 1984 (Late Oligocene, Brule Formation, USA)

habari Thackray 1994 (Miocene, Hiwegi Formation, Kenya)

dakotensis Elliott and Nations 1998 (Late Cretaceous, Dakota Formation, USA)

chubutensis isp. nov. (Late Cretaceous, Laguna Palacios Formation, Argentina)

Ichnotaxobases

Ichnogeneric taxobases: Cells attached to tunnels by means of short laterals or necks. Tunnel design. *Ichnospecific taxobases:* Arrangement of

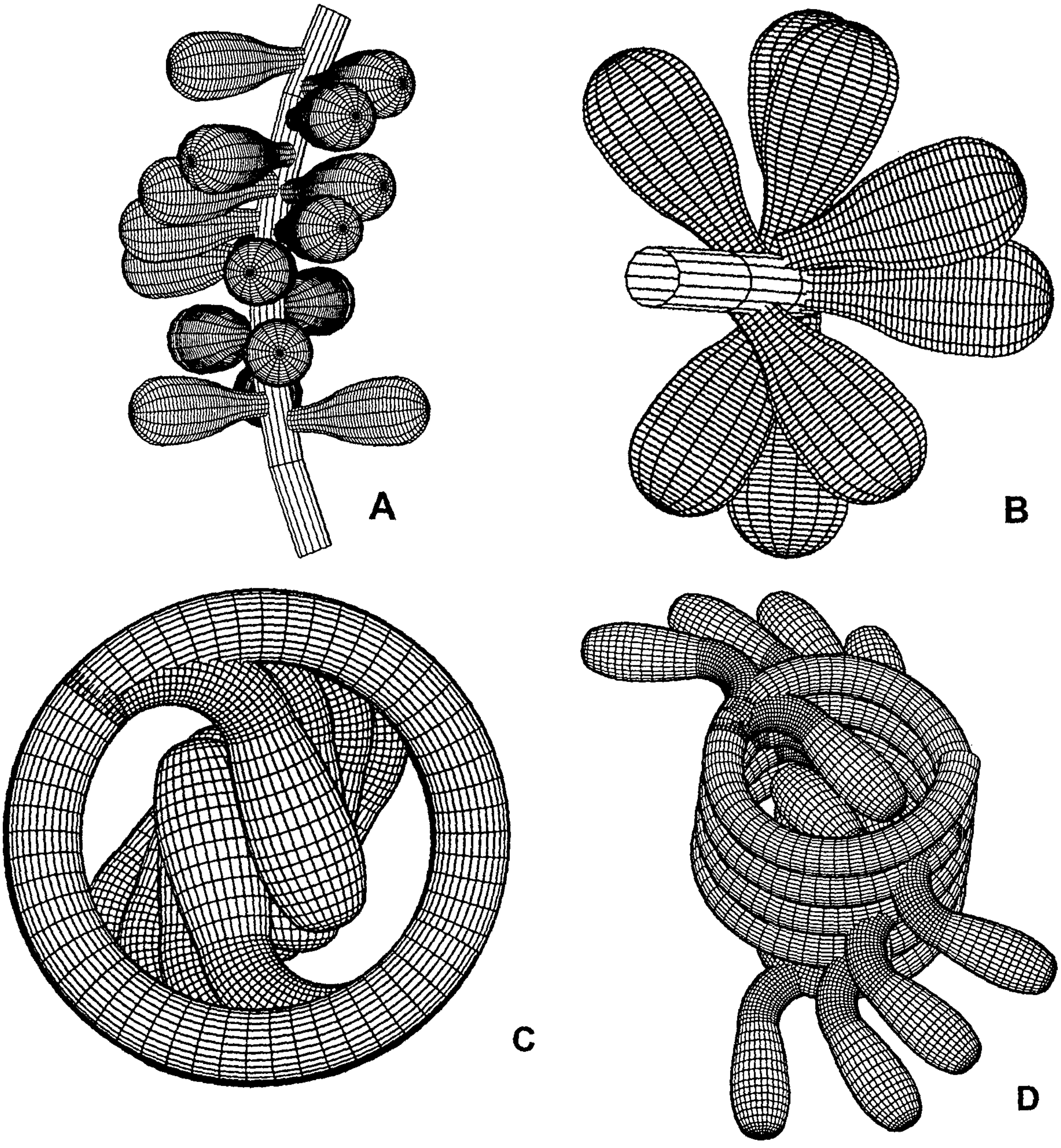

FIGURE 1 A, and B, *Cellicalichnus chubutensis* isp. nov. C, *Ellipsoideichnus meyeri* Roselli. D, a possible reconstruction of *E. meyeri*, which predicts the existence of an opposite row of cells in the unknown exterior part of the tunnel

cells, presence or absence of short laterals, orientation and curvature of tunnels.

The importance of these ichnotaxobases was evaluated in terms of morphology, and additionally considering that they represent the common nest architecture of a monophyletic group of bees. This procedure was proposed by Genise and Hazeldine (1998b) in redefining the ichnoge-

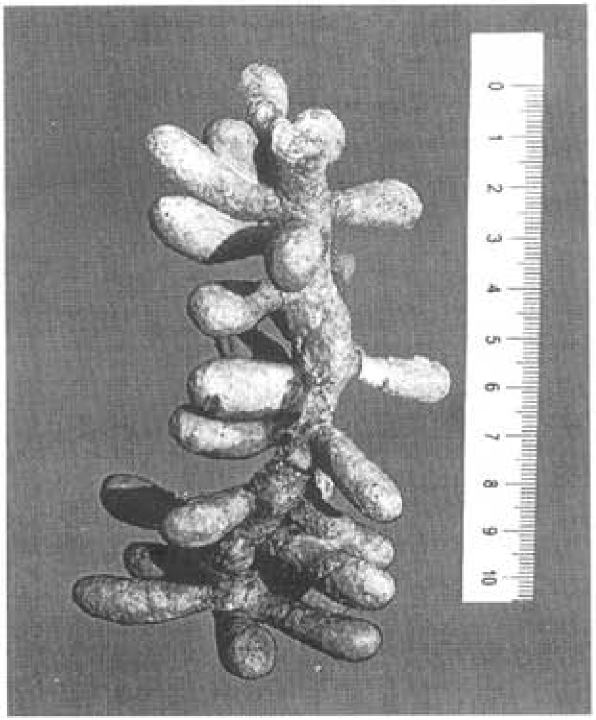

FIGURE 2 Holotype of *Cellicalichnus chubutensis*. Scale bar 10 cm

nus *Palmiraichnus*, and is compatible with the statement that inferences about the producers can help to select appropriate ichnotaxobases (Rindsberg, 1999) (see Discussion).

Possible trace makers

Halictinae, particularly Halictini.

Cellicalichnus chubutensis **isp. nov.**
Figs. 1 A, B, 2

Etymology

From the Chubut province, Patagonia, Argentina.

Holotype

A specimen comprising part of a tunnel having whorls of cells attached to it. Deposited at the Universidad Nacional de la Patagonia S.J. Bosco (UNPSJB IC N° 11) (Fig. 2).

Paratypes

Four specimens similar to the holotype deposited at the Universidad Nacional de la Patagonia S. J. Bosco (UNPSJB IC N° 12 and N° 13), in the collections of the Laboratorio de Icnología (Museo Argentino de Ciencias Naturales) (MACN-LI N° 1088) and at the Museo Desiderio Torres from Sarmiento (Chubut) (MDT N° 542).

Examined material

The types, isolated cells and other specimens, not collected but observed in the field.

Type locality and age

The observed material was from the upper member of the Laguna Palacios Formation (Late Cretaceous), Cañadon Puerta del Diablo (S 45°31, W 69°46), Sarmiento Departament, Chubut province, Argentina.

Diagnosis

Whorls of tear-shaped cells attached directly to sloping to subvertical, moderately curved tunnels (Figs. 1 A, B, 2).

Comments

C. chubutensis differs from *C. dakotensis* in lacking horizontal tunnels with opposite rows of cells, from *C. ficoides* in having the cells grouped in whorls and arising directly from the vertical tunnels and from *C. habari* in having subvertical to sloping tunnels with whorls of cells instead of horizontal tunnels with cells arranged in opposite pairs. The most complex morphology in the group is shown by *C. dakotensis*, which combines, in the same structure, the horizontal tunnels with paired cells of *C. habari* and the whorls of cells attached to vertical tunnels of *C. chubutensis*.

Description

Remains of nests, composed of infilled casts of sloping tunnels bearing cells, covered by a more resistant, thin, brownish layer, were located in a paleosol, mostly composed of moderately bioturbated, mainly by small roots, whitish volcanic ash. (Genise et al., 1999). Nests were located in close proximity to each other (less than 30 cm). The upper parts of tunnels were truncated by erosion and their lower extremities continued downwards inside the rock. They could not be removed completely, and so their actual length and complete design remain unknown. The length of the excavated tunnels ranges from 113 mm to 165 mm and the diameter from 9 mm to 11 mm; they are curved and penetrate the soil at different angles (45° to 85°). Cells are subhorizontal, tear-shaped, and they are attached directly to the tunnels by means of a neck, which may represent a part of the cells or a short lateral tunnel. Distinction between a true neck or a short lateral tunnel is at present impossible because of the nature of preservation, which precludes any speculation on the precise position of the cell closure. Cells radiate in all directions from the tunnels and in most cases they are arranged in closely packed whorls (Figs. 1 A, B, 2). The length of cells ranges from 15 mm to 30.4 mm (X= 25.55 mm; N= 144); the maximum diameter ranges from 6.4 mm to 13.9 mm (X= 11.09; N= 144) and the diameter of the neck ranges from 4 mm to 8.3 mm (X= 6.49 mm; N= 101). There were hundreds of detached cells in the loose material weathered from the outcrop; these isolated cells could be attributed to *Celliforma germanica* Brown 1935 but they also closely resemble the detached cells included in *Celliforma ficoides* by Retallack (1984).

Celliforma Brown 1934
Figs. 3 A

Type ichnospecies

Celliforma spirifer Brown 1934

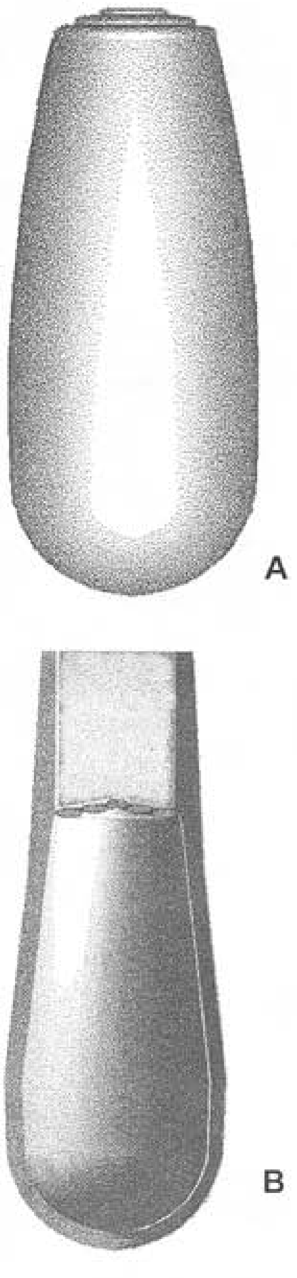

FIGURE 3 A, *Celliforma spirifer* Brown. B, longitudinal section of *Palmiraichnus castellanosi* Roselli showing the discrete wall and the antechamber

Diagnosis

Chambers or internal molds of chambers of different shapes (subcylindrical, tear, flask, urn, vase, barrel); having one end rounded and the other either truncated or capped by a flat or conical closure, bearing spiral grooves on its inner surface; walls polished and having a smooth lining (modified from Retallack, 1984).

Comments

In the present study, *Celliforma* is restricted to isolated chambers or molds (Fig. 3 A). Traces composed of *Celliforma* and antechambers, constructed walls, or other cells or tunnels are included in other ichnogenera. Even so, the remaining ichnospecies attributed to *Celliforma* that have already been described, named or retained in open nomenclature, constitute a difficult ichnotaxonomical problem to solve that has commonly produced the repetition of long comparative notes each time a new ichnospecies has been described (i.e., Retallack, 1984; Genise and Bown, 1994; Elliott and Nations, 1998). Some of the problems with respect to the ichnotaxonomy of *Celliforma* are related to the difficulties in examination of the large number of traces described from different regions (Genise and Hazeldine, 1998b), particularly the numerous types described by Sauer and Schremmer (1969) and Ritchie (1987). Other problems are related to the different criteria utilized by authors to describe and name ichnospecies. In summary, it is necessary to examine comparatively all the described trace fossils, named or not, and reduce the ichnospecies to the smallest possible number, avoiding unnecessary description of new ichnospecies until such comprehensive comparison is accomplished.

Ichnospecies and trace fossils included

spirifer Brown 1934 (Late Eocene, Bridger Formation, USA)

nuda Brown 1934 (Early Miocene, Tampa Formation, USA)

germanica Brown 1935 (Oligocene, Germany)

"Nidos de véspidos" (two types) Frenguelli, 1930, 1938; Martínez et al., 1997 (Paleocene, Mercedes Formation(?), Uruguay)

"Nidos de véspidos" (one type) Frenguelli, 1939 (Late Oligocene, unnamed formation, Argentina)

"Fossile Insekten-Bauten" (five types) Sauer and Schremmer, 1969 (Late Miocene, unnamed formation, Germany)

"Nidos de Véspidos" Pascual and Bondesio, 1981 (Late Miocene, Paso de las Carretas Formation, Argentina)

"Signos de Apidae" Laza, 1986 a, b (Eocene, Oligocene, Miocene and Pliocene of different localities and formations of Argentina)

"Bee brood cell fossils" (several types) Ritchie, 1987 (Pliocene, Laetoli Formation, Tanzania)

arvernensis Ducreux et al., 1988 (Late Eocene, unnamed formation, France)

"Fossil brood cells" Ellis and Ellis-Adam, 1993 (unnamed formation, Spain)

Celliforma sp. Bown et al., 1997 (Paleocene, Claron Formation, USA)

Ichnotaxobases

Ichnogeneric taxobases: Isolation of cells. Absence of antechambers and discrete walls. No connection with tunnels. *Ichnospecific taxobases*: Shape, cell closure.

The quite simple structure of these traces reduces the spectrum of available taxobases to differentiate ichnospecies (Fig. 3 A). However, almost every author dealing with *Celliforma* has created a new ichnospecies or left the material in open nomenclature. Frequently, it is possible to distinguish different sizes and different shapes of cells between the material coming from a single locality, and, as such, these characters are good indicators of the trace maker's diversity. However, ichnotaxonomically, on a global scale, and considering the large number of specimens that are continuously being discovered, it is highly likely that in all probability, the discontinuities in the size dispersion will be masked by new findings and the extremely different outlines from barrel-shaped to tear-shaped will be connected by a spectrum of intermediate shapes. An ichnotaxonomy erected on these features is currently in use but in all probability it will become redundant in the near future. For instance, all tear-shaped cells (Frenguelli, 1930, 1938; Martínez et al., 1997) can now be included in *germanica,* the oval-shaped in *spirifer* and the subcylindrical in *nuda,* a simple scheme proposed by Brown (1935) utilized to elaborate the key presented by Genise and Bown (1994). However, that key is becoming increasingly equivocal when confronted with new material discovered in recent years. It seems probable that *nuda* (Brown, 1934), *roselli* (Genise and Bown, 1994) and some of the unnamed species of Frenguelli (1930, 1938, 1939), Sauer and Schremmer (1969), Ritchie (1987), Martínez et al. (1997) and Bown et al. (1997) will result in all likelihood in synonyms of *spirifer* (Brown, 1934).

The fossil cells described by Ellis and Ellis-Adams (1993) are uncommon in having discrete walls, no antechamber, no smooth lining and closure without spiral design. For this reason, they are only tentatively included in *Celliforma,* following the original assignment, but other alternatives as coleopteran pupal chambers or lepidopteran cocoons, should not be disregarded.

The value as an ichnotaxobase of the presence or absence of a spiral closure has already been discussed (i.e., Retallack, 1984; Houston, 1987; Genise and Bown, 1994; Genise and Verde, in press). Bees are the only hymenopterans that construct spiral closures in their cells, and such a construction is widespread in almost all their groups (Rozen, pers. comm.); therefore, it is assumed that a cell having smooth lining and a spiral closure is a bee cell. However, there are some groups of bees that secondarily have lost this behavior (i.e., halictines, Sakagami and Michener, 1962), coincidentally, the trace makers of *Corimbatichnus* and *Cellicalichnus.* Furthermore, even when present as a specific behavioral trait, the preservation of a spiral closure in a fossil bee cell depends on different factors; for example, the success of the larvae to reach maturity and emerge from the cell as an adult (Zeuner and Manning, 1976; Retallack, 1984; Houston, 1987). In summary, the spiral closure, in combination with the smooth lining are the only traits to identify unequivocally a cell as a bee cell, but for ichnotaxonomical purposes the importance of their presence is relative. However, when present, the spiral closures can yield important information on the trace maker, because different groups of bees construct them in different ways.

Possible trace makers

A great diversity of digging bees may be the trace makers of *Celliforma.* There is almost no way to positively relate any ichnospecies to a particular taxon of bees.

Defined as such, *Celliforma* therefore includes traces of unrelated groups of bees. One exception could be *germanica* Brown (1935) whose tear-shaped outline resembles halictine cells.

Corimbatichnus Genise and Verde
Figs. 4 D, E

Type ichnospecies

Corimbatichnus fernandezi Genise and Verde (in press)

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 apparently closures made of soil material. Cell entrances are open in a convex face of the ped and they can be 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 results 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 (Genise and Verde, in press) (Fig. 4 D, E).

Comments

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

Ichnospecies included

fernandezi Genise and Verde (in press) (Late Cretaceous-early Tertiary, Asencio Formation, Uruguay).

Ichnotaxobases

Ichnogeneric taxobases: Clustered condition of cells. Cell wall, cell arrangement. Convexity of the cluster. *Ichnospecific taxobases*: Only one known ichnospecies.

Possible trace makers

Halictinae, probably Augochlorini.

Ellipsoideichnus Roselli 1987

Figs. 1 C, D

Type ichnospecies

Ellipsoideichnus meyeri Roselli 1987

Diagnosis

Helicoidal tunnel, having attached in the internal part of the helix two opposite cells per whorl. Each cell is attached by means of a short, elbowed, lateral tunnel (Fig. 1 C).

Comments

E. meyeri was redescribed and reconstructed in 3D by computer by Genise and Hazeldine (1998a) who stated that it was probably constructed by a bee but that there was no extant or fossil insect trace comparable to it. However, in spite of the different external aspect of the ichnospecies of *Ellipsoideichnus* and *Cellicalichnus* there are some similarities that relate both ichnogenera. In both cases the *bauplan* is based on cells attached by short laterals or necks to tunnels. Coiling a *Cellicalichnus* or unwinding an *Ellipsoideichnus* would result in a similar trace, particularly if it is presumed that an opposite row of cells would have been attached to the unknown half of the helicoidal tunnel of *Ellipsoideichnus* (Fig. 1 D).

Ichnospecies included

meyeri Roselli 1987 (Late Cretaceous-early Tertiary, Asencio Formation, Uruguay).

Ichnotaxobases

Ichnogeneric taxobases: Cell attachment to tunnels. Cell arrangement. Helicoidal tunnel. *Ichnospecific taxobases*: Only one known ichnospecies.

Possible trace makers

Bees of unknown taxa. Its relationship with *Cellicalichnus* would suggest halictines.

Palmiraichnus Roselli 1987

Figs. 3 B

Type ichnospecies

Palmiraichnus castellanosi (Roselli 1938)

Diagnosis

Discrete structures, ovoid to subcylindrical, straight or slightly curved, having one end rounded and the other truncated or concave. Internally they are composed of an ovoid chamber having a smooth surface and ending in a spiral cap, which is preceded by an antechamber that may be empty or filled with sediments packed or not in concave septa (Genise and Hazeldine, 1998b) (Fig. 3 B).

Comments

Differs from *Celliforma*, the other ichnogenus for isolated cells, in having an antechamber and a discrete wall surrounding both the antechamber and the chamber.

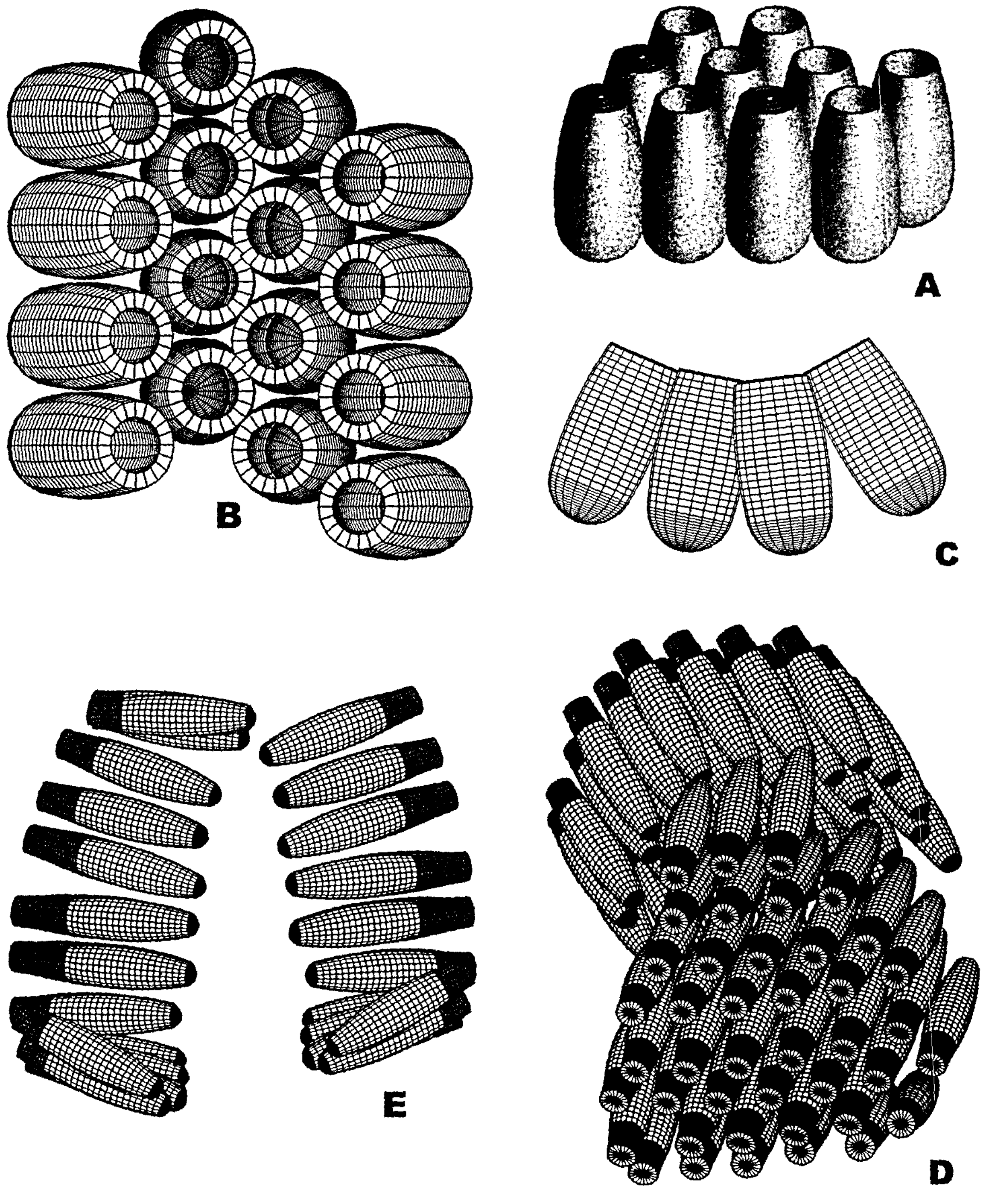

FIGURE 4 A, *Rosellichnus arabicus* Genise and Bown. B, *Uruguay auroranormae* Roselli. C, cross-section of *U. auroranormae* showing the arrangement of cells that originate from the concave top face of the cluster. D, *Corimbatichnus fernandezi* Genise and Verde. E, Section of *C. fernandezi* showing the arrangement of cells

Ichnospecies included

castellanosi (Roselli 1938) (Late Cretaceous-early Tertiary, Asencio Formation, Uruguay)

pinturensis (Genise and Bown 1994) (Early Miocene, Pinturas Formation, Argentina)

bedfordi (Zeuner and Manning 1976) (Pleistocene and Holocene, Bridgewater Formation, Australia).

gomezi (Dominguez Alonso and Coca Abia 1998) n. comb. (Miocene, El Periodista Formation, Honduras). From the original description and illustrations, this ichnospecies is indistinguishable from *castellanosi*, but without seeing the material it would be risky to propose the synonymy herein.

Ichnotaxobases

Ichnogeneric taxobases: Isolation of cells. Presence of antechambers and discrete walls. Chamber closure. *Ichnospecific taxobases*: Thickness of rear ends. Presence or absence of septa in the antechamber closure. Micromorphology of the wall.

P. bedfordi is the unique ichnospecies having the antechamber fillings packed in one or more concave septa, whereas *P. castellanosi* can be distinguished from *P. pinturensis* because of the micromorphology of its walls composed of distinct layers of soil material (Genise and Hazeldine, 1998b).

Possible trace makers

Bees of the subfamiliy Oxaeinae. Cells closely resemble those of *Protoxaea gloriosa.*

Rosellichnus Genise and Bown 1996
Fig. 4 A

Type ichnospecies

Rosellichnus patagonicus Genise and Bown 1996

Diagnosis

Group of ovoid cells having distinct walls with smooth inner surfaces. Bottoms of cells are rounded whereas the tops are flat and opened. Cells have parallel axes, and therefore the upper part of the cluster is flat. Cells are arranged in a layer of several rows with bottoms and tops at the same level, forming a comb (Genise and Bown, 1996) (Fig. 4 A).

Comments

Rosellichnus differs from *Uruguay* and *Corimbatichnus*, the other two ichnogenera for clusters of cells, in having parallel cells and the upper part of the cluster flat. It differs also from *Corimbatichnus* in having cells with discrete walls and large intercellular spaces.

Ichnospecies included

patagonicus Genise and Bown 1996 (Late Miocene, Collón-Curá Formation, Argentina) *arabicus* Genise and Bown 1996 (Late Miocene-late Pleistocene, Baynunah and unnamed formation respectively, United Arab Emirates)

Ichnotaxobases

Ichnogeneric taxobases: Clustering of cells. Cell wall and arrangement. Cluster shape. *Ichnospecific taxobases*: Number of cell rows. Cell size. Wall thickness.

R. patagonicus is composed of only two rows of large cells, whereas, *R. arabicus* consists of 4–5 rows of smaller cells, having thinner walls. In all probability the ichnospecific taxobases require additional review. A third ichnospecies that can be distinguished by the shape of its cells is currently under study.

Possible trace makers

Unknown group of bees. The Asiatic material could be assigned tentatively to Nomiinae, a halictid subfamily. The third ichnospecies under study may be attributed to Halictinae.

Uruguay Roselli 1938
Fig. 4 B, C

Type ichnospecies

Uruguay auroranormae Roselli 1938

Diagnosis

Group of ovoid cells having distinct walls with smooth inner surfaces. Bottoms of cells are round whereas the tops are flat and may be open or closed with a spiral cap. Bottoms of cells divergent, causing the upper part of the cluster to be concave. Cells are arranged so as to form a layer of several rows with bottoms and tops at the same level, like a comb (Genise and Bown, 1996) (Fig. 4 B).

Comments

Uruguay differs from *Rosellichnus* and *Corimbatichnus*, the other two ichnogenera for clusters of cells, in having divergent cells and the upper part of the cluster concave. It also differs from *Corimbatichnus* in having cells with discrete walls and large intercellular spaces.

Ichnospecies included

auroranormae Roselli 1938 (Late Cretaceous-early Tertiary, Asencio Formation, Uruguay)

rivasi Roselli 1987 (Late Cretaceous-early Tertiary, Asencio Formation, Uruguay)

Ichnotaxobases

Ichnogeneric taxobases: Clustering of cells. Cell arrangement and wall. Cluster shape. *Ichnospecific taxobases*: Number of cell rows. Cell shape.

Both ichnospecies were separated by Roselli (1987) based on the number of cell rows, a criterion later revalidated by Genise and Bown (1996). However, based on new material collected from the type locality, it was stated that the morphological diversity of the ichnogenus is higher than it was previously suspected (Cilla, 1999). New ichnospecific taxobases to separate and interpret the different new morphological types are currently under study.

Possible trace makers

Genise and Bown (1996) discarded the Halictinae, which commonly construct clusters of cells, as possible constructors, but failed to propose another group of bees. Later, Genise and Hazeldine (1998b) found a close similarity between *Palmiraichnus* and the individual cells of *Uruguay*, postulating a close relationship between both traces and trace makers. Thus, the Oxaeinae, a small family of bees, having most of its species behaviorally unstudied, is a possible group of producers.

Ichnofamily indet.

Brownichnus igen. nov.

Etymology

Dedicated to Roland W. Brown, author of the ichnogenus *Celliforma* and the ichnospecies included here in this new ichnogenus.

Type ichnospecies

Brownichnus favosites (Brown 1941), type and only known ichnospecies.

Diagnosis

Combs composed of a regular hexagonal array of dome-shaped cocoons. Domes are parallel to the center of the comb and more divergent toward the margin. The interspace among domes is small and it increases toward the rear of the comb. (modified from Wenzel, 1990).

Comments

The morphology of this trace fossil is not comparable with any other described insect trace fossil. Differences with *Celliforma* are not only related to the comb-like shape but also to the dome-shaped structures, which originate from cocoons and not from cells (Wenzel, 1990). The significant morphological differences preclude its inclusion in the ichnofamily Celliformidae. Previously, different authors have stated the necessity of the creation of a new ichnogenus to include *favosites* (Retallack, 1984; Genise and Bown, 1994; Elliott and Nations, 1998).

Ichnospecies included

favosites Brown 1941 (Late Cretaceous, unnamed formation, USA)

Ichnotaxobases

Ichnogeneric taxobases: Shape and comb-like arrangement of cocoons. *Ichnospecific taxobases*: Only one known ichnospecies.

Possible trace makers

A social wasp, possibly, Polistinae (Wenzel, 1990).

Brownichnus favorites (Brown, 1941)

Celliforma favosites Brown, 1941a, p. 54

Celliforma favosites Bequaert and Carpenter, 1941, p. 50

Celliforma favosites Brown, 1941b, p. 105

Celliforma favosites Retallack, 1984, p. 586

Celliforma favosites Wenzel, 1990, p. 21

Celliforma favosites Genise and Bown, 1994, p. 112

Celliforma favosites Elliott and Nations, 1998, p. 249

Celliforma favosites Genise and Hazeldine, 1998b, p. 162

Type locality and age

Late Cretaceous deposits (unnamed formation) from Gunlock, Utah, USA.

Diagnosis

Only known ichnospecies, same as for the ichnogenus.

Comments

In the past, this ichnospecies prompted many discussions on its affinities and preservation (Bequaert and Carpenter, 1941; Brown, 1941b), which continued until Wenzel (1990) confirmed the social wasp origin of this trace.

DISCUSSION

There are essentially two important issues to discuss with respect to Celliformidae; first, many of its ichnogenera have been defined from the Late Cretaceous-early Tertiary Asencio Formation of Uruguay, in southern South America, and second, the criteria utilized to elaborate the ichnotaxonomical hierarchy of the trace fossils, bee cells and nests, included in this ichnofamily.

The reasons to explain the origin of many traces in the same formation are several and have been partially commented on elsewhere (Genise and Bown, 1995, 1996). The Asencio Formation bears one of the most diversified, well-preserved and abundant assemblages of bee and dung-beetle fossil nests yet studied from anywhere in the world. It occurs in stacked paleosols that extend for kilometers in western Uruguay. The preservation of the trace fossils has been favored by complex diagenetic processes in which impregnation with iron, silica and carbonate has allowed the conservation of the most delicate traces and a long repertoire of micromorphological details. Finally, the pioneering work of Roselli (1938, 1987), who correctly described and named *Uruguay*, *Palmiraichnus* and *Ellipsoideichnus*, and deposited the types in the collection of the Museo de Nueva Palmira, encouraged recent studies to review his work and resulted, for example, in the discovery of a new ichnogenus of bee trace fossil, *Corimbatichnus* (Genise and Verde, in press).

The ichnotaxonomy of fossil bee traces proposed herein follows two of the recommendations of the recent Workshop on Ichnotaxonomy (Rindsberg, 1999) that encouraged the use of ichnofamilies and that stated that inferences with respect to producers can assist in the selection of meaningful ichnotaxobases. In the last several years, insect ichnologists have been producing a large amount of information, which in part does not accord with some of the traditional concepts and classifications of ichnology based mostly upon marine traces. Ethological, ichnofacial and morphological classifications of trace fossils, among others, as well as several of the ichnological principles (Bromley, 1990), require a re-evaluation given the more recent information obtained from continental trace fossils (Genise, 1999). One of the most important differences between most insect fossil nests, like those of bees, and most marine traces is the possibility to attribute the former to particular taxa, because the same nest is always constructed by the same species of insect and viceversa. The advantage of knowing the identity of the trace makers for ichnotaxonomical purposes is that it may add more objective criteria to evaluate the importance of the morphological taxobases selected for erecting ichnogenera and ichnospecies (Genise and Hazeldine, 1998b). The ichnofamily Celliformidae is based on the morphology of the traces included in *Celliforma* and allied ichnogenera, all of them being cells, groups of cells and cells attached to tunnels. This ichnofamily, as well as the newly erected ichnogenus, are based exclusively on morphological ichnotaxobases, which, in turn, were evaluated and selected with consideration of the nest architecture of the trace makers, the bees.

Bromley (1990) recognized that one of the problems of ichnotaxonomy was the subjectiveness in evaluating the relative significance of the behavioral traits reflected by the morphology of traces. However, when traces can be assigned to definite taxa having known phylogenies, the relative significance of these traits can be evaluated more objectively in terms of behavioral homologies. Similar complex morphologies are the result of similar complex behaviors, which, being displayed by monophyletic taxa, can be considered as behavioral homologies (Wenzel, 1992). For instance, cells having smooth linings and spiral closures are, to our present knowledge, constructed exclusively by bees. Hence, these structures, which are complex enough to satisfy the criterion of homology and which are present in a monophyletic taxon, the Apidae, are reflecting a behavioral homology. Morphological traits like these, present in a group of trace fossils belonging to a monophyletic group of trace makers, should be selected as ichnofamily or ichnogeneric taxobases, whereas, morphological traits reflecting only specific behavioral autapomorphies of trace makers should be retained as taxobases for ichnospecies.

The ichnofamily Celliformidae is based on cells and related structures that can be attributed to bees. In evaluating the importance of the morphological taxobases utilized to erect the ichnofamily, the fact that these type of cells represent a behavioral homology of bees played an important role. An opposite criterion, only partially used until now, has been to include all these traces in the single ichnogenus *Celliforma*. However, this procedure has resulted in the inclusion of a large amount of morphological diversity in a single ichnotaxon, producing a consequent loss of ichnological information and the erection of an inconsistent ichnotaxonomical hierarchy. When it is possible to consult a comprehensive (but always insufficient) picture of the trace maker's architecture, it is possible to envisage the future of the ichnotaxonomy of their trace fossils, even when most of them are still to be found and described. This insight of the "trace fossils to come" given by the knowledge of the behavioral (architectonic) diversity of modern taxa provides a powerful clue in selecting the proper taxobases to erect ichnotaxa. The selection of subjective ichnotaxobases would potentially result in the collapse of the whole ichnotaxonomy of the group.

In redefining the ichnogenus *Palmiraichnus*, Genise and Hazeldine (1998b) considered that antechambers and discrete walls of these bee cells were important morphological traits that reflected behavioral patterns which justified its separation from *Celliforma*. In addition, it was important to know that these type of cells are presently constructed by a monophyletic group of bees so as to select these ichnotaxobases for ichnogeneric separation. Similarly, the erection of *Cellicalichnus* is based on the morphology of its ichnospecies, represented by cells attached directly, by means of short necks, to tunnels. In the evaluation of the importance of the ichnotaxobases to erect this new ichnogenus, it was considered that this architecture represents a behavioral homology only present in some monophyletic taxa of halictines. A parameter to corroborate the value of the ichnotaxobases selected for the creation of a new ichnogenus is the discovery of new ichnospecies that share these characters. After the redefinition of the ichnogenus *Palmiraichnus* by Genise and Hazeldine (1998b) a new ichnospecies was found in Honduras (Domínguez and Coca, 1998). A new ichnospecies of *Rosellichnus* is currently under study three years after the formulation of this ichnogenus (Genise and Bown, 1996). Since the description of the first ichnospecies of *Cellicalichnus, C. ficoides* (Retallack, 1984), three new related ichnospecies have been discovered (Thackray, 1994; Elliott and Nations, 1998; and herein).

In the long term it is conceivable an ichnotaxonomy of insect fossil nests in which ichnogenera will reflect behavioral diversity at the generic level of trace makers, whereas ichnospecies will reflect specific behavioral traits. On the other hand, following Bromley's (1990) statement that the basis of the name should be "the morphology of the specimen as an expression of animal behavior", it may be predictable to formulate an ichnotaxonomy more linked to knowledge of the behavioral diversity of the trace makers. Additionally, as proposed by Genise and Hazeldine (1998b), trace fossils that can be related to known extant traces provide the physical evidence to complete and improve our knowledge of the trace maker's phylogeny and behavioral evolution.

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