

Ichnotaxonomy, Origin, and Paleoenvironment of Quaternary Insect Cells from Fuerteventura, Canary Islands, Spain

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ABSTRACT: On Fuerteventura, Canary Islands, micritic and silty to sandy insect cells are abundant, in well-exposed Quaternary terrestrial sediments and calcretes. Previous authors regarded these cells as hymenopteran in origin, referring them to the ichnogenus *Celliforma*. However, a new study of cell shape, cell wall thicknesses, cell lining, apertural closure, construction materials and cell aggregation and clustering, indicates that some of these fossils may be referable to the ichnogenus *Palmiraichnus* or an unnamed ichnogenus of the Celliformidae, attributed to bees. Other cells are referable to the ichnogenus *Rebuffoichnus*, considered to be coleopteran pupal cells. Similarities between this Quaternary assemblage and better-known Late Cretaceous to Early Tertiary insect cell assemblages from South America, support an earlier suggestion that the Fuerteventuran cell assemblages developed during periods of relatively increased rainfall in an overall semiarid paleoclimate.

KEY WORDS: Insect ichnofossils, ichnotaxonomy, trace-makers, paleoenvironment

Micritic and silty to sandy insect cells are abundant in Early or Middle to Late Pleistocene and Early Holocene eolian and fluvial sediments and calcretes well-exposed on Fuerteventura, Canary Islands. Although the published descriptions (Ellis and Ellis-Adam, 1993; Edwards and Meco, 2000; Alonso-Zarza and Silva, 2002) referred them to the ichnogenus *Celliforma* Brown, 1934, emended by Retallack, 1984, Genise (2000) only tentatively did so, proposing alternative origins such as coleopteran pupal chambers or lepidopteran cocoons. Any attribution to producers other than bees would be critical, considering published paleoclimatic inferences based on this previous assumption. Re-examination of specimens from Fuerteventura, including petrographic thin sections of cells, now provides new insights into their ichnotaxonomy, origin, and paleoenvironment.

Ichnotaxonomy

Although Ellis and Ellis-Adam (1993), Edwards and Meco (2000) and Alonso-Zarza and Silva (2002) referred the Fuerteventuran fossil cells to the ichnogenus *Celliforma*, this ichnogenus is inappropriate for entire thick-walled cells, detachable from their matrices. *Celliforma* exclusively comprises excavated cells with thin linings, preserved either as empty chambers in the matrix, or as detachable internal casts of the cell lumen (Genise, 2000). Ellis and Ellis-Adam (1993), and Alonso-Zarza and Silva (2002) recognized two cell types by reference to the mode of cementation of the constituent sand grains and the constructional materials respectively, but otherwise these cell types were similar in shape and other morphological characters. By contrast, the three cell types recognized by Edwards and Meco (2000) were based on shape, size, and wall thickness, thereby providing important clues for ichnotaxonomical identification.

Edwards and Meco's Type 1 cells are similar to those described by Ellis and Ellis-Adam (1993) and Alonso-Zarza and Silva (2002). They comprise specimens that are circular to oval in cross-section, with constructed walls, unthickened or slightly thickened at the distal end. Cell caps are strongly convex to low-conical and without an extension. These

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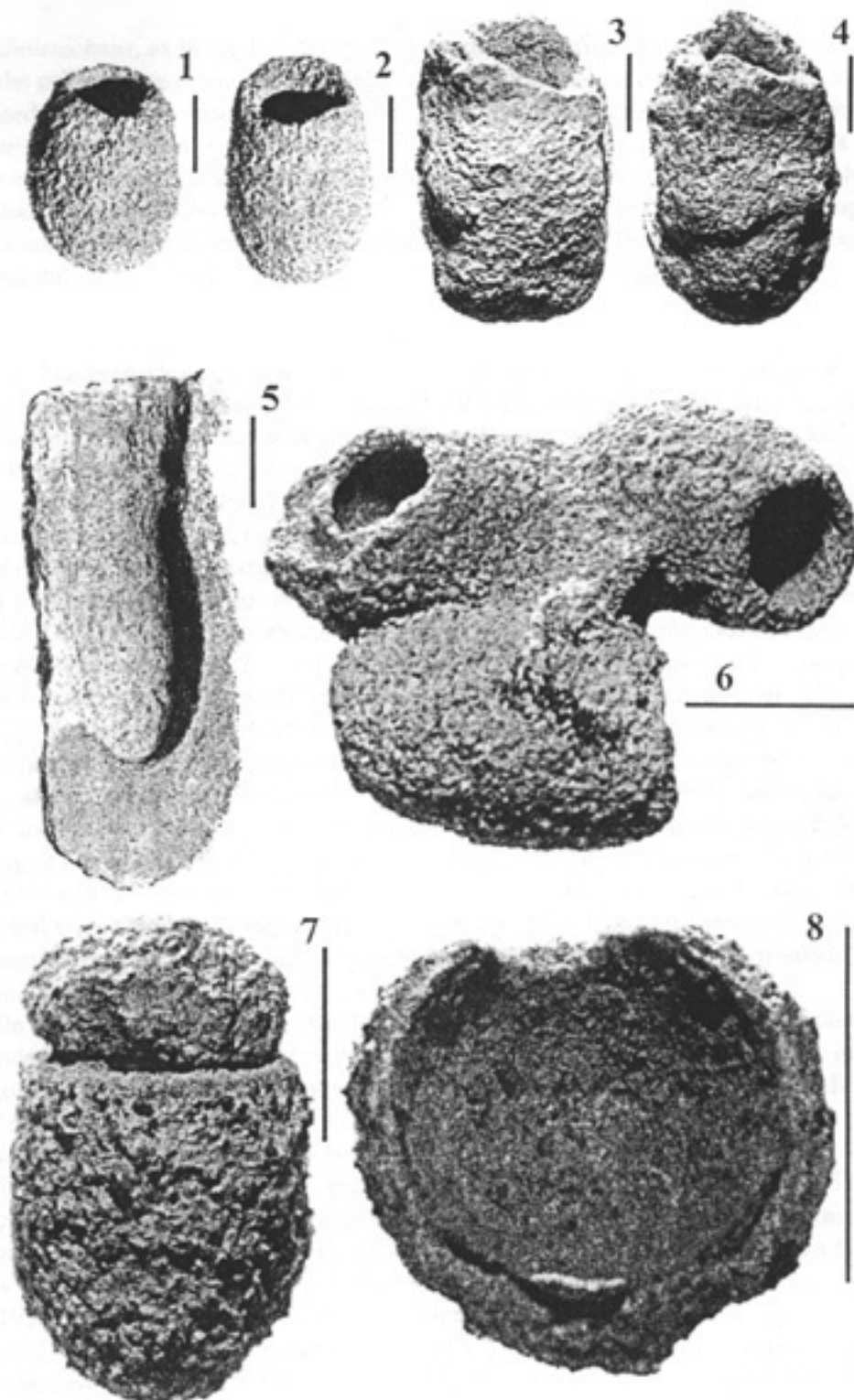
characteristics are critical for the ichnotaxonomic attribution of these trace fossils. The Celliformidae are characterized by the presence of rounded distal ends and flat or conical proximal (apertural) ends (Genise, 2000). Ellis and Ellis-Adam (1993) described their cells as truncate at the proximal end, with a flat to dome-shaped cap, which in most specimens is surrounded by a low rim.

Examination of newly acquired specimens, as well as those figured by Ellis and Ellis-Adam (1993, Figs. 1, 2, 4, 20) and by Alonso-Zarza and Silva (2002, Fig. 7), revealed that both ends of some cells are rounded, resulting in ovoid cells, while others are more asymmetrical. The origin of the latter poses three possibilities: (1) that cells were originally asymmetrical, having rounded bottoms and flat or conical tops as in Celliformidae; (2) that in open cells the emergence hole masked the actual outline of cells; or (3) that ovoid, open cells were reoccupied by another insect that made the flat or conical caps slightly below the emergence hole. Although Ellis and Ellis-Adam (1993) found little evidence for reoccupation of cells, it was confirmed by Edwards and Meco (2000), who reported the occurrence of a second cell wall and/or a closure within the lumen of some cells. It is difficult to ascertain the symmetry of open cells, which are the most abundant in the outcrops. Some have an unthickened wall around the apertural end (Edwards and Meco's Type 1), suggesting that the complete wall has an ovoid outline (Fig. 1); but others show a thickened wall suggesting that they were originally asymmetrical (Edwards and Meco's Type 2) (Fig. 2).

However, if the cells were originally asymmetrical, no ichnogenus is available for those with a rounded distal end and flat or conical proximal end, with constructed walls, and lacking an antechamber. Genise and Hazeldine (1998, p. 155) pointed out the need for a new ichnotaxon, distinguishable from *Palmiraichnus*, for cells of this kind from the Late Cretaceous-Early Tertiary Asencio Formation of Uruguay. However, if the cells are originally ovoid and the different proximal end is a result of reoccupation or adult emergence, the ichnogenus *Rebuffoichnus* (Roselli, 1987), attributed to coleopteran pupal cells (Genise *et al.*, 2002), should be considered. This ichnogenus was first described from the Late Cretaceous-Early Tertiary Asencio Formation in Uruguay, but it is also known from the Late Cretaceous of Argentina (Genise *et al.*, 2002). It has thick, constructed walls and a circular cross-section, like some of Edwards and Meco's Types 1 and 3 cells (Figs. 3, 4).

Edwards and Meco's Type 2, at least the cell illustrated in their fig. 7d and new material illustrated herein (Fig. 5), are referable to the ichnogenus *Palmiraichnus* Roselli, 1987, redescribed by Genise and Hazeldine (1998). The ichnogenus was first described from the Late Cretaceous to Early Tertiary Asencio Formation of Uruguay, but is also known from the Miocene of Argentina and Honduras, and the Pleistocene-Holocene of Australia (Genise, 2000). It has a thick constructed cell wall, especially thick at the distal end, and like some of the Edwards and Meco's specimens of Type 2 cells, it has an apertural extension. In *Palmiraichnus* this is present in all cells and is regarded as an antechamber, a common feature in cells of some groups of bees (Genise and Hazeldine, 1998). In contrast, it is rare among the Fuerteventuran specimens and was regarded by Edwards and Meco (2000) as an incomplete cell attached to an entire cell. Whatever the origin of this apertural extension, and despite the absence of the spiral closure and a polished inner lining characteristic of the ichnogenus, specimens included in Type 2, as well as that figured herein (Fig. 5), can be considered as poorly preserved examples of *Palmiraichnus*.

It is notable that *Palmiraichnus* shows similar micromorphological characteristics to Type 1 cells from a basaltic sand at Cañada Melián (Edwards and Meco, 2000, Fig. 8a,



Figs. 1-8. 1, a cell showing unthickened wall around the apertural end; 2, a cell showing thickened wall around the apertural end; 3, a cell attributable to *Rebuffoichnus*; 4, *Rebuffoichnus casamiquelai* from the Late Cretaceous Laguna Palacios Formation of Argentina; 5, a cell attributable to *Palmiraichnus*; 6, a cluster of cells; 7, a complete (and sectioned) cell showing the convex external aspect of the closure; 8, the inner aspect of the cell closure shown in Fig. 7.

b). In *Palmiraichnus*, as in the Fuerteventuran specimens, clastic grains in the innermost layer of the cell wall are orientated parallel to the cell lumen and the lumen is coated with fine-grained sediment (Genise and Hazeldine, 1998). Both characters are typical of insect constructions in soils and result from the rubbing of the pygidial plate or other parts of the body against the moistened cell wall (Genise and Poiré, 2000). These micromorphological characters, described originally in bee cells, are also present in coleopteran pupal chambers and probably in other insect constructions, resulting from physical processes originating through relatively simple behavior (Genise and Poiré, 2000).

Origin

While it has been shown that some of the fossil cells may be attributable either to *Palmiraichnus* or to an unnamed ichnogenus of the Celliformidae, there are important differences between these fossil cells and fossil and Recent solitary bee cells. In addition, the possibility that the fossil cells were made by more than one group of trace makers remains to be addressed. This will be done by reference to individual characteristics: spiral closure, cell lining, cell shape, construction materials, and cell aggregation and clustering.

Spiral closure: The spiral structure on the internal surface of the cell closure is perhaps the most important character to recognize fossil bee cells (Genise, 2000). It results from the inability of the bee to smooth the inner surface when making the closure, inwards from the outer rim (Stephen *et al.*, 1969). The spiral closure of cells is a plesiomorphic character for bees (J. G. Rozen, Jr., pers. comm.). Among the Fuerteventuran cells, all known caps have smooth inner surfaces (Ellis and Ellis-Adam, 1993; Edwards and Meco, 2000) as shown herein in fig. 8. Similarly, Alonso-Zarza and Silva (2002) did not find spiral closures, although incorrectly stating that Ellis and Ellis-Adam (1993) had done so. Edwards and Meco (2000) suggested that those associated with Type 1 cells resulted from smoothing of the inner surface late during cell construction, citing a statement by Stephen *et al.*, (1969, p. 97). However, in the latter instance, only the outer (earliest-formed) strips of the spiral were smoothed (Stephen *et al.*, 1969, fig. 272). Complete smoothing of the entire inner surface of the cap (Fig. 8) would more likely be performed from inside the cell by the larva, as for example in coleopteran pupal chambers.

Despite the many exceptions, particularly among halictines (Sakagami and Michener, 1962) and colletines (Stephen *et al.*, 1969), the absence of a spiral structure on the inner surface of fossil cell closures precludes unequivocal interpretation of the fossil cells as those of solitary bees.

Cell lining: The above differences between the fossil cells and typical solitary bee cells are reinforced by the absence in the cell lumen of a polished inner surface (Fig. 5). In Recent bee cells, this results from the application of glandular secretions preventing ingress of soil water and egress of liquid provisions (Cane, 1991; Rozen, Jr., pers. comm.). In fossil bee cells this lining can result in a polished, even glossy, inner surface (e.g., Genise and Bown, 1996, Fig. 6; Genise, 1999, Fig. 2D; Genise and Hazeldine, 1998, Fig. 1B). As with the cell closure, exceptions occur (Stephen *et al.*, 1969), and consequently the absence in the fossil cells of a polished inner surface only precludes their unequivocal attribution to bees. However, it may be noted that some fossil coleopteran pupal chambers exhibit the same smoothed, but not polished, inner walls (e.g., Lea, 1925; Retallack, 1984; Johnston *et al.*, 1996) as the Fuerteventuran fossil cells.

Cell shape: Shape is the third most important characteristic of Recent solitary bee cells that is also observable in fossil cells. The overall shape of the cell is strongly dependent on that of the cell closure. Those of Recent solitary bees are generally flat or conical and/or

bear a central nipple-like protuberance on their outer surface (Stephen *et al.*, 1969; J. G. Rozen, Jr., pers. comm.). As already noted, most of the fossil cells lack a cell closure, precluding direct observation of their general aspect. The fossil cell caps illustrated by Ellis and Ellis-Adam (1993, p. 162 and figs. 8–12) and Alonso-Zarza and Silva (2002, Fig. 7) are essentially flat to dome-shaped, whereas Edwards and Meco (2000) described them as weakly to strongly convex to low-conical, as shown herein in fig. 7. Open cells with thickened walls around the aperture (Edwards and Meco's Type 1) (Fig. 2) and those with a conical or flat cap surrounded by a raised rim resemble bee cells. However, as already discussed, the last two could be reoccupied cells. Other cells from Fuerteventura seem more symmetrical, ovoid in cross-section, and thick-walled, resembling coleopteran pupal chambers (e.g., Lea, 1925; Genise *et al.*, 2002) (Figs. 1, 3).

The presence of an apertural extension is another important morphological characteristic related to cell shape. It is common in cells of certain groups of bees (Houston, 1987; Rozen, 1992, 1993, 1994), but is also present in the ichnogenus *Teisseirei*, interpreted as a coleopteran pupal chamber (e.g., Melchor *et al.*, 2002). Even if the apertural extension resulted from the coalescence of neighboring cells, as suggested by Edwards and Meco (2000), it is nevertheless found in fossil bee cells (e.g., Melchor *et al.*, 2002) and coleopteran chambers (Genise and Laza, 1998; Genise, unpubl. data).

Cell shape is the most important characteristic suggesting a bee origin for some of the cells from Fuerteventura, a coleopteran origin for others and the possibility of reoccupation of cells by different trace makers. In addition, the range of sizes described by Ellis and Ellis-Adam (1993), and Edwards and Meco (2000) (Figs. 1, 3, 5) suggests that, despite their taxonomical affinities, more than one trace maker was involved.

Construction materials: A constructed wall is present in brood and pupal cells of different insect families other than bees and the similarities include micromorphological characters (Genise and Bown, 1994; Genise and Poiré, 2000; Genise *et al.*, 2002). Fossil cells from Fuerteventura that are attributable to solitary bees on the evidence of shape were assigned to the Anthophorini (Edwards and Meco, 2000). That this is the only Old World group that makes constructed cell walls, and cell wall thickness of less than 2 mm was used as a diagnostic character identifying some Type 1 cells with that group (J. G. Rozen, Jr., pers. comm., in Edwards and Meco, 2000). With reference to other cells from Fuerteventura, thickened distal-end walls are common in fossil bee cells of the ichnogenera *Uruguay* and *Palmiraichnus* (Genise and Hazeldine, 1998), and also in the Recent bee *Svastra obliqua* (Rozen, 1964). This suggests that the occurrence of this character does not exclude other bees as possible constructors. However, coleopteran pupal chambers included in the ichnogenera *Teisseirei* and *Rebuffoichnus* (Genise *et al.*, 2002; Melchor *et al.*, 2002) have thicker walls than those commonly present in bee cells and are more like some of the Fuerteventuran fossil cells.

Another important feature in Type 1 cells from the basaltic sand on Fuerteventura is that the inner two layers incorporate wind-blown marine bioclastic calcareous sand grains, as well as carbonate granules from weathered calcretes, rather than the basaltic sand matrix. Alonso-Zarza and Silva (2002) also found that cells were made with materials collected in nearby areas. Cell construction thus would have involved many journeys to and from the nesting site. Although this is a typical behavior of hymenopterans, particularly bees and wasps, bees that construct their cells rather than line excavated cavities, do not import material from other localities. Instead, they use material produced during the excavation process, such as the Emphorini (Hazeldine, 1997). The example of *Anthophora abrupta* mentioned by Edwards and Meco (2000) is atypical, because this species was

nesting in an adobe wall, not in soil (Norden, 1984). Although some burrowing halictines line their cells with clay-grade material, probably obtained from the burrow wall but possibly imported from elsewhere (Sakagami and Michener, 1962, p. 64), the clay lining is very thin and the cells of Halictinae are morphologically very different from the Fuerteventuran cells. In the few exceptions where imported material is definitely used to construct cells, as commonly is in megachilines, euglossines and some *Centris*, it is mostly plant material and secretions (Stephen *et al.*, 1969).

In conclusion, it is likely that those Fuerteventuran fossil cells that have two lithologically differing cell linings have no Recent analogues, unless re-lining of open cells was involved.

Cell aggregations and clusters: The Fuerteventuran fossil cells occur in tens of thousands, often in dense accumulations, in calcareous silts and sands and in some calcretes, within a succession of wind-blown sands and loesses, fluvial sands and calcretes (Edwards and Meco, 2000). The great abundance of these fossil cells is probably one of the reasons why authors identified them as hymenopteran in origin (references cited in Edwards and Meco, 2000). However, similar dense accumulations of fossil dung-beetle brood masses, wasp nests and coleopteran pupal chambers are also known (Genise *et al.*, 2000, and references therein). Some Fuerteventuran cells, resembling those of solitary bees, are grouped in clusters (Fig. 6), which is considered an important ichnotaxobase for Celliformidae (Genise, 2000). It is impossible to discern if a single individual constructed such clusters, or if they were produced by the coalescence of cells made by different individuals. The irregular orientation of cells suggests the latter possibility. However, such irregular clusters are known in Halictinae (Sakagami and Michener, 1962; Eickwort and Sakagami, 1979) and Apinae (Gutbier, 1916; J. G. Rozen, Jr., pers. comm.).

Paleoenvironment

Having attributed the fossil cells to bees, Ellis and Ellis-Adam (1993), Edwards and Meco (2000) and Alonso-Zarza and Silva (2002) consequently interpreted their presence as an indication of arid to semiarid conditions, supported by the presence of abundant arid-adapted land snails and calcretization of the sediments. However, whereas Ellis and Ellis-Adam (1993) favored an arid paleoclimate (average annual rainfall 150 mm or less), Edwards and Meco (2000), and earlier authors suggested that the bees nested during periods of increased rainfall (400–500 mm) in an overall semiarid to arid paleoclimate. Because solitary bees today are active in arid as well as semiarid regions (Michener, 1979), fossil bee cells cannot be used solely to determine rainfall, unless they are identifiable to a particular, ecologically restricted taxon. This is not possible for the Fuerteventuran fossil cells.

Paleoenvironmental inferences from trace fossils preferably should be based on the presence of more than one ichnogenus and trace maker. In the Fuerteventuran example, Celliformidae and *Rebuffoichnus*, the possible trace fossils present, are typical components of the *Coprinisphaera* ichnofacies, indicating open environments from steppes to savannas, dominated by low vegetation (Genise *et al.*, 2000). The possible environments envisaged by various authors for Fuerteventura range from drier to wetter conditions. These would have involved plant associations from sparse vegetation to desert scrub, all of which are consistent with the development of the *Coprinisphaera* ichnofacies.

The relative abundance of different ichnogenera, along with paleosol identification, to some extent may shed light on the different paleoclimates involved in the spectrum of plant associations considered within this ichnofacies. *Palmiraichnus* and *Rebuffoichnus* are abundant in Ultisols of the type locality, the Late Cretaceous to Early Tertiary Asencio

Formation of Uruguay, which developed under a temperate and humid climate (Gonzalez, 1999). Dense aggregations of *Rebuffoichnus* are present in Alfisols-Mollisols from the Late Cretaceous Laguna Palacios Formation of Chubut, Argentina, which developed under a subhumid to semiarid seasonal climate (Genise *et al.*, 2002).

These occurrences, documenting dense aggregations of insect trace fossils similar to those on Fuerteventura, support the suggestion by Edwards and Meco (2000), Alonso-Zarza and Silva (2002), and earlier authors, that nesting or pupation on Fuerteventura occurred during periods of relatively increased rainfall in an overall semiarid paleoclimate. Similar paleoclimatic variability was suggested independently by Coello *et al.* (1999), to explain sequential lithological variations in the late Pleistocene to early Holocene fill of a lava tube, in the north of the island.

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