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Fossil brood cells of solitary bees on Fuerteventura and Lanzarote, Canary Islands (Hymenoptera: Apoidea)

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Abstract: Large numbers of ichnofossils, presumably brood cells of Anthophoridae, are described from areas of calcareous sand dunes on Fuerteventura and Lanzarote. They are taxonomically associated with *Eucera*, rather than *Anthophora*, because of the presumed nest architecture, as far as this could be deduced from the structure of the cells. A comparison is made with published records of similar fossils, mostly placed in the ichnogenus *Celliforma*. The fossils are assumed to have been deposited under climatic conditions comparable to the present ones. Numerous perforations in the walls of the cells and unopened cells are indicative of a preimaginal mortality, due to predation and fungal attacks, of $\pm 47\%$. The sites are under severe recreational pressure.

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Introduction

On the two eastern islands of the Canary Archipelago we came across large numbers of presumably fossilised bee cells. They are mostly found, blown out of their sandy matrix, scattered on the surface together with a multitude of subfossil shells of terrestrial molluscs. As it turned out, they are hardly mentioned in the entomological literature, but are known to geologists as *Anthophora* nests. As we will argue below, this identification may need to be reconsidered.

The material on which the present note is based is deposited in the Zoological Museum (Institute of Taxonomic Zoology), Amsterdam. All comes from Corralejo, in the north of Fuerteventura.

The sites

The two eastern islands Lanzarote and Fuerteventura stand rather apart in the Canary Archipelago (Báez et al., 1983). Both have with certainty had a land connection with the African mainland (Rothe, 1964, 1986; Stock, 1990) and seem to be geologically much older than the western islands; Fuerteventura in particular has a large central area of Lower Creta-

ceous age (Rothe, 1986). The eastern position of the islands brings them under the strong influence of the Saharan climate of Africa (only a good 100 km away). Finally, both islands are relatively low, which makes that the amount of rainfall they receive is only one half to one third of that of the other islands (Fernandopullé, 1976; Petit-Maire et al., 1987).

On both islands the cells were found in sandy areas. The "sand" referred to in this note actually consists of very fine debris of mollusc shells and sea urchin spines; it is light in colour (contrary to lava sand) and contains small but variable quantities of fine red-brown dust of Saharan origin. The localities on Lanzarote lie in the area called "El Jable" in the north-western part of the island, roughly between the villages of Tinajo, Teguisse and La Caleta. For Fuerteventura we are referring to the dune area in the north of the island, near the small town of Corralejo, alternatively indicated on the maps as "Jable del Moro" or "Reserva Natural las Dunas".

The vegetation consists of isolated shrubs of *Launaea arborescens* (Batt.) Murb. and *Ononis natrix* L.; *Cyperus capitatus* Vand. (= *C.*

kalli (Forssk.) Murb.), *Heliotropium ramosissimum* (Lehm.) DC, *Lotus lancerottensis* Webb & Berth., *Euphorbia paralias* L. and *Androcymbium psammophilum* Svent. are typical herbs in these sparse and arid vegetations. There are almost no stones of any size, which implies, among other things, that where the vegetation cover is disturbed, the wind can freely carry off large quantities of the dry and loose sand. Large stretches consist of mobile sand, devoid of any vegetation (fig. 15).

Looking at the general aspect of the terrain and of the vegetation, one may expect to find the cells also in the dune area (or what is left of it) in the south of Gran Canaria (Maspalomas). We did not find them there, but we have been there only once. Rothe (1986) mentions these cells from the Istmo de la Pared between the mainland of Fuerteventura and the Jandía peninsula to the south, and from the Barranco de los Molinos (west coast of Fuerteventura, due south-west of Casillas del Angel). Petit-Maire et al. (1987) mention them additionally from El Quemado, approximately 10 km south-west of Corralejo.

Description of the cells

The cells are made of the same calcareous sand in which they are found; there is a varying admixture of brown dust, and usually a few black grains of lava sand can be discerned as well. The outer surface usually is rather regular and smooth, the inner surface is perfectly smooth; we could find no trace of lining.

In many cells the sand grains are fairly loosely cemented; we will refer to them as cells of the "sandy" type (e.g. figs 1, 3, 4, 10).

In other cells the sand particles are almost completely coalesced; at the same time the outer surface is smooth, almost varnished, yellow-brown and pocked by numerous shallow dimples (figs 2, 7, 11). We assume that these latter cells, that somewhat remind of peanut pods, have been exposed at the surface for a long time. Small quantities of water (from the scant rain and less rare dew) would have led to the change of structure of the calcareous mat-

ter, and mechanical effects (ablation by wind drifted sand) would have caused the polishing and the surface dimples.

The hardness of the cells varies: some of the sandy type can be destroyed with little effort by squeezing them between thumb and finger; others, in particular the ones of the peanut type are hard as pebbles.

The cells are oval in general outline. The ones of the sandy type are on average 24.6 ± 0.40 (SE) mm long and 16.5 ± 0.23 mm wide; those of the peanut type are somewhat smaller: $22.9 \pm 0.30 \times 15.0 \pm 0.16$ mm (fig. 13). Length, width and length/width ratio of the two types differ significantly (t-test, $N = 238$, $p = 0.003$, < 0.001 and 0.016 , respectively). The thickness of the wall varies (the sides are thickest); it has only been measured on a few damaged specimens, and ranges from 2-4 and 1-2 mm in the sandy and peanut type cells, respectively.

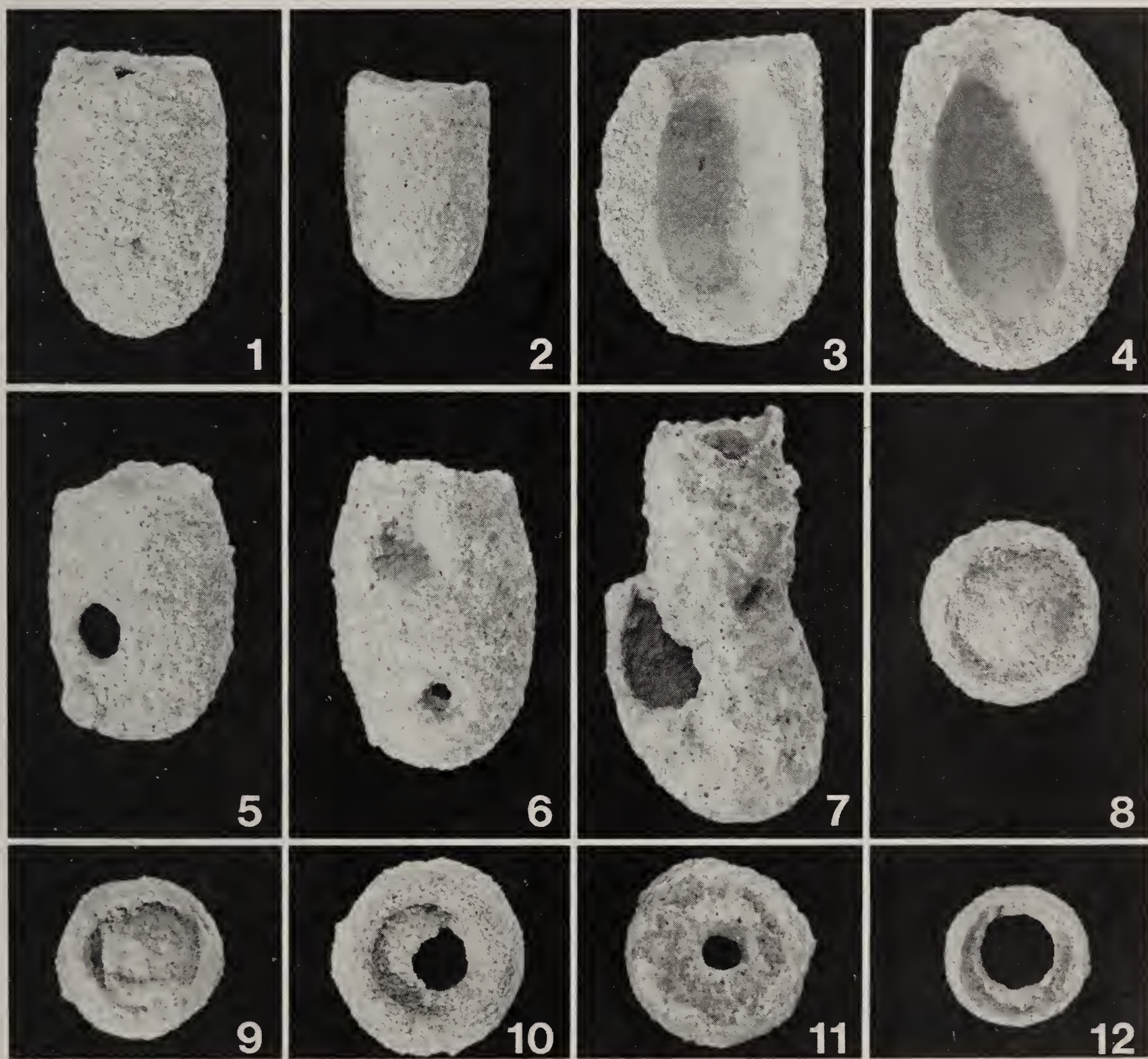
At one pole the cell is truncated, and closed with a cap that mostly is surrounded by a low rim (figs 8-9). Intact caps are flat to dome-shaped; the inner side usually is smooth; we did not notice a spiral sculpture on either side.

Out of the 240 cells we measured, 190 had a clear perforation in the cap (figs 10-12); in the remaining cells sometimes the condition of the fossil did not permit to see an eventual hole, but in the very most cases the cap was really not perforated. The mean diameter of this apical opening, when present, is 6.9 ± 0.1 mm; figure 14a shows the distribution.

The cells usually seem to have been used only once; in a few instances there was a double rim, but these probably are complications caused by many generations of cells having been made consecutively on the same place. Most cells are single; a few odd cells are laterally fused.

In rare cases we noted a part of a cell wall to cross the open space within another cell (fig. 7), suggesting that cell walls can be constructed without the guiding support of a cavity wall.

Quite often the cells have one or more additional perforations, mostly in the sides (figs 5, 6). Table 1 gives their number and frequency,



Figs 1-12. Fossil brood cells. 1, a cell of the "sandy" type; 2, a cell of the "peanut" type; 3, 4, interior and wall structure of two cells; 5, cell with a large lateral opening; 6, cell with a small lateral opening (note the conical shape of the opening); 7, a double cell; 8, 9, intact cell caps; 10, 11, 12, perforated cell caps. All from Fuerteventura; printed at actual size.

Table 1. Frequency of cells with lateral perforations

number of lateral openings	number of cells
0	141
1	62
2	31
3	3
4	2
5	0
6	1

and the distribution of their sizes is shown in figure 14b. Their diameter is often distinctly larger at the outer side of the wall than at the inner side (the latter is given in the table). This suggests that these additional perforations have been made by an animal coming from outside of the cell.

Field relations

The majority of the cells are found blown out of the loose sand, in numbers that often exceed 10 per m² (figs 15-18). Cells of the two types are sometimes found mixed, but generally patches yield only either type. Most of the time the cells are accompanied by shells of terrestrial gastropods. These shells are generally rather worn

and pale and may be considered subfossil. A characteristic element among these shells is *Rumina decollata* (Linnaeus); Petit-Maire et al. (1987) identified also *Hemicycla glasiana* (Shuttleworth) and several *Helicella* species. A photograph, also from Fuerteventura, of such an assemblage can be found in Machado (1976).

With little effort we found places where the process of outblowing was in progress, and where the cells still were half covered by sand. Yet, it seems probable that the position of these cells was not original either, but that their arrangement has resulted from a previous cycle of outblowing and sedimentation. The cells were not placed in a recognisable orientation or pattern; there was no sign of stratification within the deposition.

In El Jable on Lanzarote we discovered a small barranco (erosion gully) of about four meters deep, cutting through a layer of at least two meters that almost completely consisted of such cells (figs 21-22). Again there was no recognisable orientation of the cells, and their position seemed secondary.

A similar situation was discovered in the littoral zone of Fuerteventura, near Corralejo (more precisely: just in front of the surf school "Waikiki Beach"). Here we found a red-brown fossil bank of at least 15 m² that was composed of hardly anything but cells (figs 19-20). The thickness of the bank could not be established. Like in the Lanzarote deposition just mentioned, the cells were of the "sandy" type; understandably they were strongly worn.

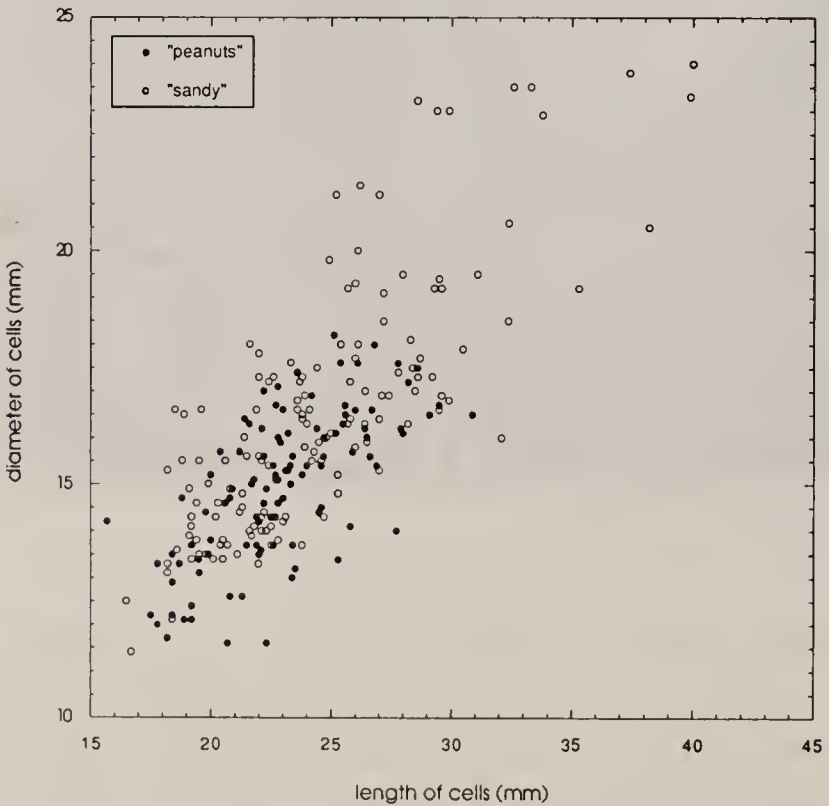


Fig. 13. Scatter diagram of lengths and widths of the cells, segregated into "sandy" and "peanut" type. All cells are from Fuerteventura.

Petit-Maire et al. (1987), at three localities, studied several outcrops of cells and shells intercalated between strata of sand of one or more meters. Because they specifically mention that in all instances the cells occurred in a separate layer immediately below a layer of shells, it is very probable that these cells were in a primary position. They found one such formation in Jandía (dated 9,800 ± 140 years before present), two at Corralejo (of which the basal one was dated 15,000 ± 200 before present) and another two at El Quemado (of which the lower one yielded an age of > 30,000 before

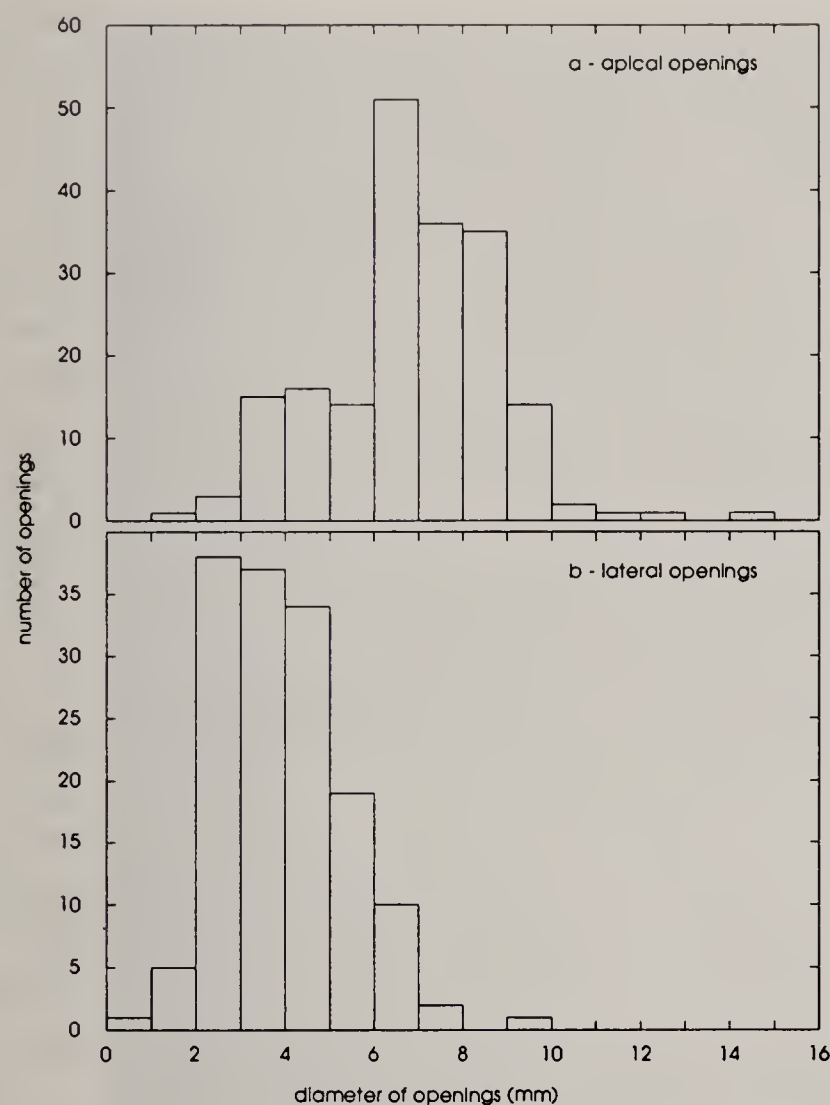


Fig. 14. Histogram of the diameter of the cell openings. a (top), apical openings; b (bottom), lateral openings. All cells are from Fuerteventura.

present). From the scale of their schematic drawing, a thickness of approximately 15 cm can be inferred for the cell-bearing layers in all cases.

Identification

No doubt these cells are insect-made. The more surprisingly that we did not find a reference to these cells in the extensive bibliography of the entomological literature of the Canary Islands by Machado (1987).

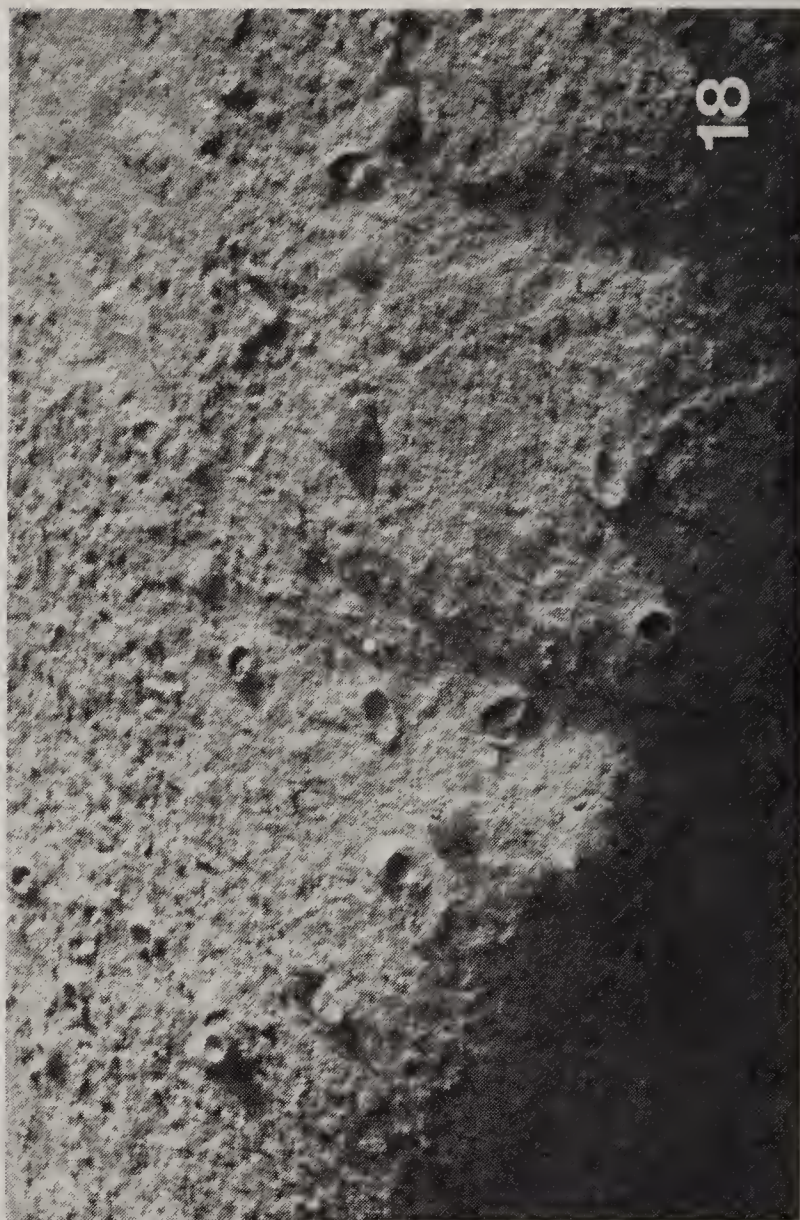
Despite the differences in shape and texture, we think that the cells all are the work of the same species, or at least genus. Their regular outer surface indicated that they have been formed within the soil, not freely attached to a plant or rock face. Moreover, we assume that the material of the cell has not been brought from elsewhere. We come to this assumption because the material of the cells is not constant,

because there is no indication in the structure of the wall that it has been put into place piecemeal, and because the texture of the material suggests that, even if moistened, it would not easily be transported. That nevertheless the wall of a cell is both hard and well-defined to the outside is best explained by assuming that the maker imbibed the walls with some, possibly proteinaceous, liquid. There might be three, not necessarily mutually exclusive, reasons to do that: 1) to consolidate the loose soil material (if indeed this was as dry and loose then as it is now), 2) to harden the wall in order to prevent predator intrusion, and 3) to keep the contents of the cell from leaking out. Finally, because the tremendous number of cells, it might be conjectured that the maker was very common, and possibly colonial, even though it is probable the cells have been accumulated over a long period.

The obvious guess as to the maker of these cells is some solitary bee. However, no reference to comparable cells is made in the monograph of fossil bees by Zeuner & Manning (1976); neither are they mentioned in the checklists of the bees of the Canary Islands by Lieftinck (1954), Báez & Ortega (1978) or Herrera Hernández & Pérez-Iñigo (1985). Perhaps the only reference in the entomological literature to these structures is made by Machado (1976), who adds a personal communication of T. Bravo who had observed "Antophora making this type of nest with mud near Orotava (Tenerife)".

In geological literature concerning the Canary Islands (Báez & Bacallado, 1984; Rothe, 1986; Petit-Maire et al., 1987) they are mentioned indeed, and referred to the Anthophoridae genus *Anthophora*. Like Machado (1976), the first two papers refer back to Bravo (1954, 1964) as the source of the identification; Petit-Maire et al. do not document their identification.

The library of the Netherlands' National Museum of Natural History (Leiden) possesses a partial photocopy of Bravo's rare book, and his reference to the cells is short enough to cite in full: "Entre los Icneumóni-



Figs 15-18. Field relations. 15, dune landscape with blown-out brood cells; 16, 17, details; 18, cells, not necessarily in primary position, being blown out. All Fuerteventura, Dunas.

dos, llamados vulgarmente enterradores, se encuentran algunas especies útiles para la agricultura, ya que ponen sus huevos en orugas inmovilizadas que entierran cuidadosamente. También se encuentran algunas *Anthophoras*, que ponen sus huevos en las ootecas de las cucarachas, destruyéndolas. Estos beneficios insectos apenas son notadas o en su caso destruidos. Entre las hormigas . . .” (“Among the Ichneumonidae, popularly called grave-diggers, some species are met that are beneficial to agriculture, in that they place their eggs on caterpillars that they have immobilised, and bury them carefully. We also meet some *Anthophoras*, who lay their eggs in the ootheca of cockroaches, destroying them thereby. These beneficial insects are hardly noted unless when their cases are broken. Among the ants . . .”). Without willing to give an opinion on Mr. Bravo’s professional qualifications, we feel that he cannot be regarded a qualified entomologist, and that it would not be justified to base an identification on his testimony alone.

On the basis of the checklists of bees from the Canary Islands of Lieftinck (1958) and Báez & Ortega (1978), the following genera are possible candidates as makers of the cells, because they both occur in the archipelago and are known to make nests in the soil (brood parasites of course are excluded too): *Colletes* (Colletidae), *Andrena* and *Panurgus* (Andrenidae), *Halictus* s.l., *Nomioides* and *Dufourea* (Halictidae), *Melitta* (Melittidae), and *Anthophora*, (together with the related genera *Amegilla* and *Heliophila*) and *Eucera*, with its relative *Tetralonia* (Anthophoridae).

Looking in this list for a genus that contains species that are both common and relatively large, and basing ourselves on our own limited experience, *Anthophora*, with *Anthophora aluaudi* Pérez¹, and *Andrena*, with *Andrena savignyi* Spinola would seem the most promising. Both are fairly large (± 12 mm) and, were very common during our visit to Fuerteventura

(February, 1992), occurring in all kinds of available habitats, including the sites where we found the fossil brood cells. Unfortunately, we have not been able to dig out nests of any, although we found that *Andrena savignyi* breeds in colonies. (*A. savignyi* is not on the lists of Lieftinck and Báez & Ortega, but was recorded from most islands by Warncke, 1968).

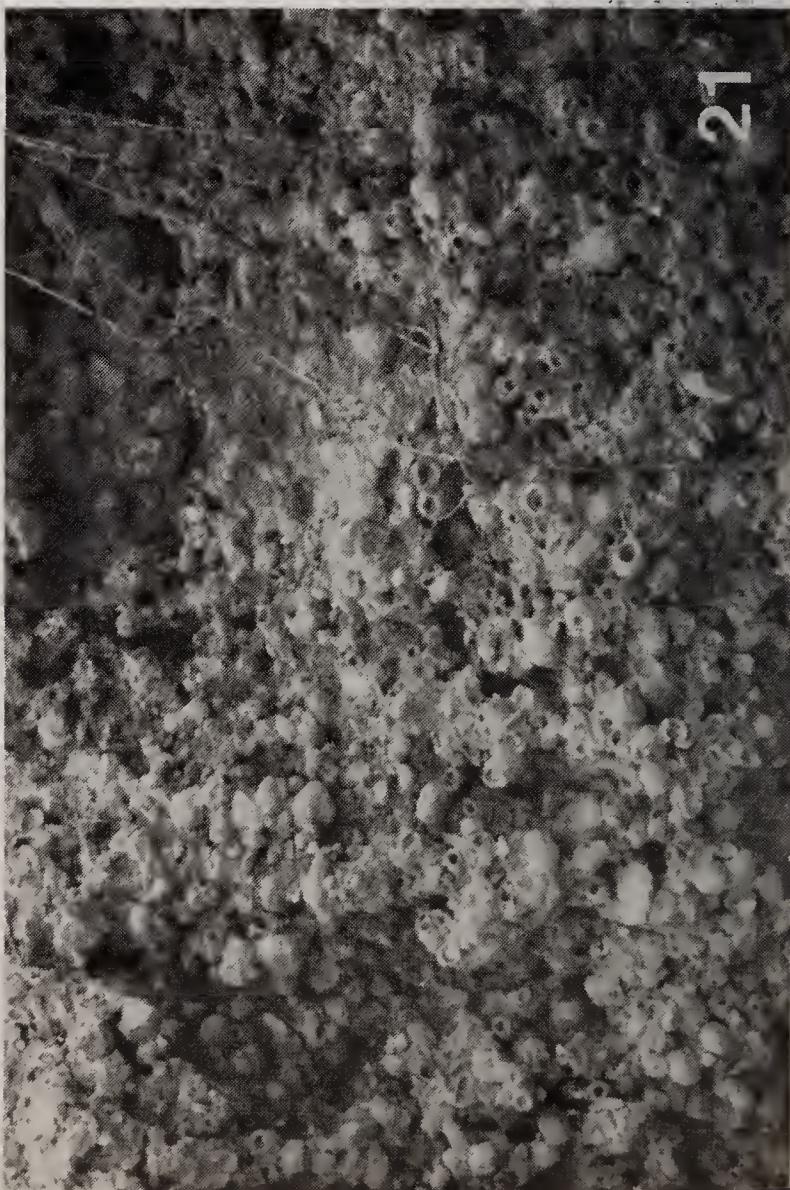
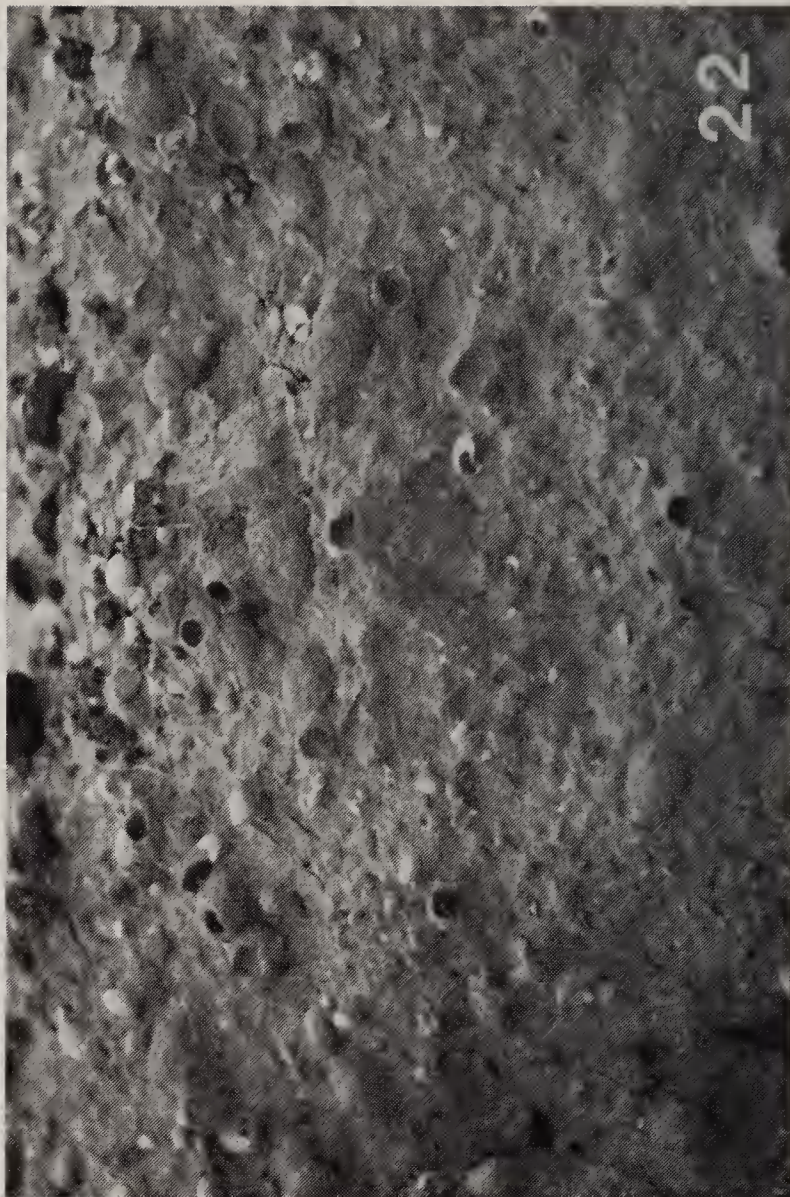
Anthophoridae tend to provide their larvae with food that contains much more nectar than is usual in solitary bees (Westrich, 1989), which may explain the compact and leak-proof cell walls that they construct. As a matter of fact, from several sources one gathers the impression that the cell walls of Anthophoridae are stronger and more enduring than those of other families; Orison (1922), Linsley (1958) and Torchio & Trostle (1986) for instance mention that Anthophoridae cells can be removed intact from the soil. Many Anthophoridae start with the excavation of a gallery, and subsequently construct one or more cells within this space, using soil scraped from the walls of the entrance tunnel of the nest. These cells are constructed more or less independently of the enclosing cavity (Malyshev, 1928; Michener & Lange, 1958).

Anthophora, and perhaps all genera of its family, line the interior of their brood cells with a waxy secrete and Westrich (1989) describes that in *A. acervorum* (Linnaeus) this secretion is produced in such quantity that it is possible to wash off the soil from the cell, leaving a fragile “egg shell”. It may be that this waxy substance makes *Anthophora* cells more prone to fossilisation.

Although this is rarely stated explicitly in the literature, Colletidae, Andrenidae and Melittidae cells have a less compact wall (Malyshev, 1926, 1936). Cells of Halictidae tend to be aggregated, in connection with the semisociality in this family.

On the basis of this, it seems probable that the cells are the work of a member of the Anthophoridae. The Canarian cells have a good general resemblance to brood cells of Anthophoridae, like *Anthophora acervorum*, *A. crinipes* Smith and *A. plagiata* (Illiger)

¹ Dr. Westrich informed us that he has a paper in print with the description of two more *Anthophora* species from Fuerteventura.



Figs 19-22. Field relations. 19, rock outcrop on beach, composed of fossil cells (the light formation in the foreground; the dark rocks in the background are lava debris); 20, detail; 21, vertical wall of a gully cutting through a massive layer of cells; 22, soil surface adjacent to the gully of fig. 21. 19-20, Fuerteventura, Corralejo; 21-22, Lanzarote, El Jable.

(Grozdanic & Vasic, 1965), *A. abrupta* Say (Rau, 1929; Norden, 1984), *A. occidentalis* Cresson (Hobbs et al., 1961) and species of *Diadasia* (Linsley & MacSwain, 1957; Eickwort et al., 1977), *Melitoma* (Linsley et al., 1980) and *Tetralonia* (Malyshev, 1930).

Many species of Anthophoridae continue the main tunnel of their nest by a fragile turret of some cm length, that usually is more or less curved and often has a longitudinal fissure (e.g., Malyshev, 1936; Linsley, MacSwain & Michener, 1980; Westrich, 1989). Nothing of the like was found by us.

Within the Anthophoridae, two types of nest architecture can be encountered (Michener & Lange, 1958). In the first type the main shaft gives off a few lateral burrows, from which branch off a number of short tunnels, each of which terminates in a single cell. The second type again shows a main shaft with some side burrows, but in this case the cells lie within the lateral burrows; working backwards from the tip of a side burrow the bee fills it with a linear series of cells (Malyshev, 1936; Linsley, 1958; Westrich, 1989; O'Toole & Raw, 1991). Although the two types are not always clearly separated, as in the case of *Anthophora urbana* Cresson, described by Torchio & Trostle (1986), it is possible to place genera like *Eucera* and *Tetralonia* in the first group (Höppner, 1901), and *Anthophora*, *Amegilla*, and *Melitoma* in the second (Cardale, 1968).

An arrangement of brood cells like in the second type would imply that an emerging bee, after having perforated the cap of its cell, often must pass one or more proximal cells on its way to the main shaft. One would expect therefore to find many cells having their distal wall perforated by the emerging occupant of the neighbouring cell. This was actually observed by Cardale (1968) in *Amegilla*.

As a matter of fact, many of the cells we found do have perforations additional to the apical one, but the large majority of these additional perforations are in the side, rather than in the distal wall of the cells. Moreover, most of them are quite small (fig. 14a, b). We conclude there-

fore that these openings have not been made by emerging bees and that the cells are not constructed by a bee genus attributable to the second type. The additional perforations must be the work of predators.

Our best estimate of the maker of the brood cells therefore is an anthophorid of the genus *Eucera* or a closely related genus, like *Tetralonia*. Both genera are known to occur on Fuerteventura and Lanzarote.

Discussion

Other fossil cells

There is a superficial resemblance to the pupal cases made by the Australian curculionid genus *Leptopius*, described (as *Leptops*) by Lea (1925). These, however, are much larger, up to 7 cm, and the subapical position of their large opening makes them resemble a wooden shoe.

References to fossil brood cells of bees in literature are uncommon (Frenguelli, 1938a, 1938b, 1939; Zeuner & Manning, 1976; Boucot, 1990; Buckland & Coope, 1991). They are mostly brought together in the ichnogenus *Celliforma* Brown (1934, 1935). Schlüter (1984) was of the opinion that all of these, except the material described by Sauer & Schremmer (1969) from the Upper Miocene of Germany, were made by wasps (possibly *Sceliphron*, Sphecidae), rather than bees. Houston (1987), however, recognised in the ichnospecies *Celliforma septata* and *C. bedfordi*, both described by Zeuner & Manning, the cells of a bee of the Australian endemic family Stenotritidae from the Pleistocene of South Australia. These cells are rather large (4-7 cm), more or less tubular and have a characteristic plug that fills about half of the cell.

Celliforma germanica Brown (1935), based on a fossil burrow from the Oligocene of Württemberg, and doubtfully associated with *Anthophora*, is described as having a waist-like constriction and otherwise is too old to be associated with the present material. *Celliforma* sp. indet. of Buxton (1932) consists of

tubular burrows in and on natural chalk in Israel and attributed by Buxton to *Osmia* or *Anthophora*, and dated "not later than King Solomon"; the description makes one rather think of a nest of *Sceliphron*.

Celliforma ficoides, that was described by Retallack (1984) from the Oligocene of Wyoming and is figured again in Retallack (1990), has a rather variable shape but seems not to overlap with the Canarian material; it is tentatively associated by its author with Halictidae cells. There is a rather close similarity, however, between our material and brood cells of solitary bees described and figured by Ritchie (1987) from the Pliocene of Tanzania.

Anketell & Ghellali (1984) discovered numerous cells in situ in the Jeffara flood plain in Libya, which they attribute to *Xylocopa*. Most *Xylocopa*-species are wood-nesting (like *X. virginica* Linnaeus with which they compare their material) but there exist a few ground-nesting species, like the south-east European *X. olivieri* Lepeletier (Malyshev, 1931). A photograph shows three serially aligned cells; this could also point to an *Anthophora*-like bee, but the cell walls are not well differentiated from the surrounding matrix.

Climatological conjectures

Irrespective of their precise identification, these fossils provide an indication of both the pollination system of the vegetation and the climate at the time of their construction.

Long-tongued bees (viz. Anthophoridae) obviously have played a major role in the ecosystem.

Solitary bees are most numerous, both in number of individuals and of species, under warm and semiarid conditions, roughly like locally exists nowadays (Malyshev, 1936; Linsley, 1958; Michener, 1979; Messer, 1985; Petanidou & Ellis, in press). Bravo (1954, 1964), having observed his *Anthophora* at La Orotava (situated above Puerto, in the north of Tenerife, which has a relatively moist climate), interpreted the occurrence of their remains on the eastern islands as an indication that until recently these islands had a climate similar to

that of the north of Tenerife. This conclusion, that is taken up by Machado (1976), is precisely the opposite of what we believe.

Likewise, Petit-Maire et al. (1987) think that the strata with mollusc shells and bee cells are indicative of relatively moist periods when the pluviosity was sufficient to maintain a closed, albeit sparse and drought-adapted vegetation; these relatively moist periods were separated by dry phases characterised by aeolian sedimentation. However, even at present (considered a dry phase), the landscape offers a mosaic of moving sand, devoid of vegetation, and patches with a vegetation as we described above. Because the shells-cells bearing strata found by Petit-Maire et al. have been only partly dated, they cannot be correlated with certainty with each other or with the humid phases of the Sahara, as is done by these authors.

Preimaginal mortality

As noted above, the perforations in the walls of the cells are probably made from the outside. The differences in mean size between the emergence opening in the cell cap and the lateral perforations suggests that generally the lateral perforations have not been made or used by emerging bees, forcing their way out of their own cell, up to the main tunnel of the nest. It is rather more probable that they have been made by members of one of the three main groups of predators of larval bees (exclusive of brood parasites): It is rather more probable that they have been made by members of one of the three main groups of predators of larval bees (exclusive of brood parasites): Meloidae, Bombyliidae, and Mutillidae. All three have been observed on Fuerteventura; as a matter of fact we collected several bees carrying Meloidae larvae, and witnessed Bombyliidae in their characteristic random oviposition behaviour. Both Meloidae larvae (Pinto & Selander, 1970; Mayer & Johansen, 1978) and Bombyliidae larvae (Torchio & Trostle, 1986; Packer, 1988) have been reported to feed on several cells in succession, which implies the making of several entrance holes per predator larva; Meloidae even

seem to have a preference for Anthophoridae. Adult mutillid females are described to inspect a number of cells, and to oviposit only on fully grown bee larvae (Gauld & Bolten, 1988); seemingly the larva completes its development on a single bee larva.

Whichever predator group is responsible for the lateral perforations, it is difficult to explain the large number of cells with more than one lateral opening. Perhaps many must be regarded as exploratory openings, to inspect the condition of the interior.

If, on the basis of figure 14a, a diameter of the apical opening of 6-9 mm is considered a regular size for a bee to leave its cell, then one may assume that a hole of less than 4 mm is an indication of a predator attack. The number of cells with at least one of the lateral openings < 4.0 mm is 58; of the remaining cells 18 have an apical opening < 4.0 mm. As a conservative estimate, and assuming that a predator attack is fatal in every case, one may conclude therefore that 76 cells, or 32%, have fallen prey to preimaginal predation. Of the remaining, "un-attacked" cells, 37 were either closed or – in a few cases only – their apical opening could not be studied, which indicates that the total preimaginal mortality is higher by about 15% because of fungal attacks. To this figure still the mortality caused by brood parasitism should be added; brood parasites essentially do nothing else but sneak in another egg, which should leave no trace in the cell structure. A preimaginal mortality of this level is not particularly exceptional. For example, Linsley et al. (1980) and Packer (1988) mention levels of mortality ranging from 7 to 92%. The level of mortality may vary with time, but tends to be higher in old and dense colonies (D. Yanega, personal communication).

We realise that this note raises more questions than it answers. Most of the answers should come both from a study of the breeding biology of the Canarian bees and from a detailed study of undisturbed fossil strata. This requires someone with a shovel, and more muscles than we have.

We must end this note in a tone of concern, because the sight of countless fossils strewn

over the sand is a threatened phenomenon. They are crushed in large numbers, not only under the feet of visitors afoot but are destroyed (together with the beauty of the landscape) by joy riding with fancy jeeps.

Acknowledgements

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