FOSSIL BROOD CELLS OF STENOTRITID BEES (HYMENOPTERA: APOIDEA) FROM THE PLEISTOCENE OF SOUTH AUSTRALIA

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Summary


Calcareaous fossils from the west coast of Eyre Peninsula, South Australia, previously recognized correctly as petrified brood cells of burrowing bees and denoted by the ichnospecies names Celliforma bedfordi and C. septata by Zeuner & Manning (1976), are assigned to the bee family Stenotritidae. Notes are provided on a fossil site and samples from it are described, figured and discussed.

KEY WORDS: fossils, brood cells, stenotritid bees, Pleistocene, South Australia.

Introduction

The fossils forming the subject of this paper were first described by Zeuner & Manning (1976) who recognized them as the petrified brood cells of burrowing bees but could not identify them further. Instead, they referred them to the ichnogenus Celliforma recognizing two ichnospesies C. bedfordi and C. septata. Zeuner and Manning's specimens were collected from "coastal travertine and consolidated dune-rock" of Pleistocene or Sub-Recent age at Venus Bay on the west coast of Eyre Peninsula, South Australia, and are lodged in the British Museum of Natural History. Their description of the fossils contains some confusing errors and these are dealt with later.

Additional specimens of the fossils from the west coast of South Australia were located in the South Australian Museum (registered numbers SAM P24877-82). They were collected by A. Crooks from "5 ml [miles] east of Rocky Point", Guided by directions from this collector, I was able to locate a bed of the fossils in coastal cliffs 0.5 km west of Scott Point (32°01'S, 132°23'E) and about 6 km west of Fowlers Bay. I observed the form and distribution of the fossils and obtained samples for the Western Australian Museum (registered nos. WAM 86.723-86.730) on 7 January 1985.

Recent studies of stenotritid bee nests (Houston 1984; Houston & Thorp 1984) have revealed several features which distinguish stenotritid brood cells from those of other bees. These same features characterise the fossils known as Celliforma septata and C. bedfordi and are the basis of my contention that the fossils are a legacy of the nesting activities of stenotritid bees.

Observations

Description of fossil site

The geological terminology employed here follows Flint (1986). 1

The bed of fossils found near Scott Point is located in an embayment of the coastal cliffs and forms a band about 20 cm high and approximately 30 m long in the cliff face (Fig. 1). The fossil band rests on a hard calcrete shelf that rises gently at each side and beneath this are three other calcrete shelves separated by soft aeolian calcarenite. The fossil band appears to be situated in the lowest horizon of a fossil colluvial soil about 1 m high. Three horizons are evident: (1) an upper zone of brown silt about 30-40 cm high (presumably the original surface); (2) a middle zone of calcrete breccia; and (3) a lower zone of pale yellow clayey calcareous aeolianite in which the fossils are embedded. Above this fossil soil is deep white aeolianite capped by calcrete and on this are recent aeolian dunes (suffering deflation).

The fossil brood cells are very numerous and occur densely packed, some being welded together or to the calcrete basement. All are horizontal or subhorizontal.

Searches nearby located only a small number of other brood cells welded to a lower calcrete shelf.

Description of fossils

Loose fossils from the Scott Point site (Fig. 2) measure 40-70 mm in length and 17-20 mm in diameter. Usually they are slightly curved, rounded at one end and truncated or concave at the other. Within the rounded end of each is a somewhat ovoidal chamber (either empty or soil-filled) measuring 13 mm in maximum diameter and, when plugged, 28 mm in maximum length. When not plugged, the chamber is continuous with a cylindrical burrow which extends to the truncate

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Fig. 1. Fossil site west of Scott Point (background). Fossiliferous horizon in upper Bridgewater Formation is arrowed.

Fig. 2. Loose fossils from upper Bridgewater Formation west of Scott Point. Holes in the specimens on the right were probably made by emergence of a parasite (upper) and a bee occupant (lower). (WAM 86.723-86.726).
end. The cemented wall of the chamber varies from 2-7 mm in thickness and while variably rough externally it is quite smooth internally (Figs 2, 3).

Many of the fossils are sealed with a complex closure. In the neck of each chamber is a plug about 10 mm long, the inner face of which usually exhibits an inverted conical spiral pattern and the outer face being smoothly concave. Between this and the truncate end may be 4-8 thin concave cemented partitions, 3-4 mm apart. The spaces between them are solidly filled with fine soil and gravel particles up to 5 mm across.

Other fossils lack the plugs and partitions and are uniformly filled with soil and gravel. Many specimens with intact closures had a lateral hole 9-10 mm in diameter about 30 mm from the rounded end while a few had smaller holes in a similar position (Fig. 2).

Amongst the S. Aust. Museum specimens are some that are embedded in a solid calcrite rock matrix (e.g. P24879 and P24882) and which are evidently older than those described above. Nevertheless, they clearly show the series of concave partitions in the chamber access burrows and their internal dimensions match those of free fossils (Fig. 5).

Discussion

An uncritical observer could easily confuse the fossils described here with other more common kinds of fossils derived from the pupal cases of Coleoptera, in particular the large weevils, *Leptopius* spp. These were described and figured by Lea (1925) and are distinguishable by their more ovoidal form (both externally and internally), the absence of a chamber closure, and usually by their larger diameter.

That the fossils described here are the petrified brood cells of a stenotritid bee can scarcely be
doubted in view of their close resemblances to the brood cells of extant species. Diagnostic features of stenotritid cells (Houston & Thorp 1984) which are observable in the fossils are: (1) built-in walls of cell chamber continuous with those of access burrow; (2) cell plug with concave spiral pattern on inner face, outer face smooth and concave; (3) access burrow sealed with one or more concave cemented partitions; (4) gravel particles included in soil-filling between plug and partitions; and (5) cells more or less horizontally oriented.

Only two genera of Stenotritidae, Stenotritus and Ctenocolletes, are recognized and our present knowledge of stenotritid nest architecture provides no means of distinguishing the brood cells of these two taxa. However, adults of Ctenocolletes are larger on average than those of Stenotritus and, since the internal dimensions of the fossil cells marginally exceed those of the largest known Ctenocolletes cells (C. nicholsoni (Cockerell); unpublished personal observations), it seems more probable that they are derived from the constructions of a Ctenocolletes species. Were that species to be extant, it would most probably be C. fulvus (1976) Houston, the only stenotritid known to inhabit the country fringing the Great Australian Bight. Unfortunately, nests of this species are unknown. One of the extraordinary features of the fossils is the high number of concave septa occurring in the cell closures (up to eight of them). Three is the maximum number observed in the closures of extant Stenotritidae (Houston & Thorp 1984).

Although Zeuner & Manning (1976) recognize two ichnospecies of fossil cells from Venus Bay, there is no reason to suppose that more than one bee species was involved in their making. Celliforma bedfordi was distinguished by the cell plug having a concave spiral pattern on its inner face (absent in C. septata). The spiral pattern would be typical of cells which remained undisturbed after closure (presumably when occupants had died). The closure of cells from which adults had emerged would be modified or destroyed as the occupants burrowed out.

Retallack (1984) likened C. bedfordi and C. septata to the earthen brood cells of living Melittida and Philothrix bees (Anthophoridae) but the resemblances are few and are far surpassed by those of stenotritid brood cells.

The stenotritid fossils occur in rocks forming part of the Bridgewater Formation which was laid down during the middle Pleistocene (Flint 1986).1 Fossils occurring in the lower part of this formation (those embedded in solid calcite) are of uncertain age but possibly as old as 700 000 years while those from the upper part (the separable or only slightly fused fossils) may be up to 100 000 years old (R. B. Flint, personal communication).

I consider the fossil bed in the upper Bridgewater Formation near Scott Point to represent a perennial nesting site where hundreds of female bees over numerous generations had nested gregariously (but individually) in colluvial soil filling a limestone swale. Stenotritids burrow into level ground and construct brood cells at the lower ends of the shafts. They cement the earthen walls of the cells and the access burrows with some secretion so that they are quite durable constructions which may remain for years. There must be a tendency for lime to be deposited in the walls of the cells at a greater rate than in the surrounding soil. Thus they become calcified first as separate entities, then gradually fused to one another, then finally encased in a solid calcite matrix.

Because of the high frequency of unperforated closures amongst the specimens examined it must be supposed that either there was a high mortality rate amongst immatures or that emerging adults bypassed the closures. Evidence for the latter possibility occurred in the many specimens with a large lateral hole in near proximity to the cell plug (Fig. 2). However, such lateral emergence is so far unknown amongst extant Stenotritidae and is atypical of bees generally; emergence usually occurs via the old access burrows and involving demolition of the closures.

Comment

The following corrections are made to Zeuner & Manning (1976). Page 205: Under "Remarks" for C. bedfordi, the second sentence should be restructured to make it clear that the whole fossils are "some 6-7 cm long by 2 cm in diameter", not the septate cross walls.

Registration number for paratype of C. septata should be In. 31433 (not 34133). Caption for Plate 1, Fig. 9, should read Paratype (not Holotype).

Plate 1 figure numbers should be altered as follows: 6 to 9, 7 to 6, and 9 to 7.

Caption for Plate 2, Fig. 1, should read Holotype (not Paratype).

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References


