

A SOCIAL WASP'S NEST FROM THE
CRETACEOUS PERIOD, UTAH, USA, AND ITS
BIOGEOGRAPHICAL SIGNIFICANCE*

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INTRODUCTION

Nearly a half century ago, Brown (1941a) described *celliforma favosites*, a fossil wasp nest recovered in 1936 from undifferentiated Cretaceous deposits of Utah, USA (37° 20'N, 133° 40'W). Bequaert and Carpenter (1941), authorities on social wasps and insect fossils, respectively, disputed the identity of this specimen. Likely due to the sterling reputation Bequaert and Carpenter each had earned among their peers, Brown's opinion has been ignored by later workers reviewing the fossil record of social insects (eg. Burnham 1978). The purpose of my note is to argue *Celliforma favosites* is indeed a legitimate fossil of a social wasp's nest. Such status increases the known age of social behavior in wasps from Oligocene to at least 63 million years.

THE FOSSIL

The fossil is contained in the center of an irregular ironstone nodule. The primary face of the split nodule measures about 17 cm by 9.5 cm and presents about 214 dome-shaped projections arranged in regular hexagonal array (Fig. 1a); the other face (secondary) is lined with shallow cavities corresponding to the ends of the domes. The domes are mostly parallel in the center of the nodule, but more divergent toward the margin (Fig. 1b). There is a region on one end of the secondary face where five or six irregularly arranged domes appear to be folded back and point inward obliquely toward the other domes on the primary face. The domes vary in cross section from round and about 4 mm across to rather oval. Neighboring domes are not always the same height and are separated

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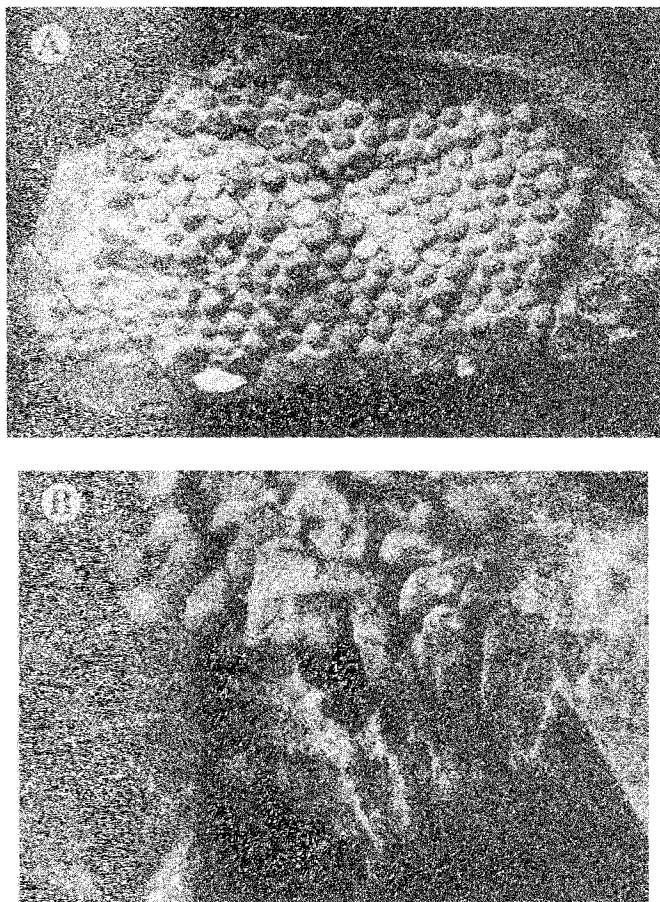


Figure 1. *Celliforma favosites*. A. Primary face of split nodule showing cells and intervening matrix viewed from above. B. Cells revealed in side view by fracture in upper left of Fig. 1a, showing domed ends, domes widely separated at the comb back (upper region) and drawing nearer each other at the comb face (lower region).

from each other by 1–2 mm in the plane of the fracture. Examining domes exposed in side view reveal that they are about 20 mm in height. They are much closer to each other toward the external surface of the nodule, the spacing between them becoming imperceptibly thin. Also, as the domes draw closer together the walls of the domes become angular rather than smoothly curved.

The matrix between the domes is likely an extension of the secondary face, originally fitting over the domes like a glove over fingers. It is composed of both fine and coarse sand, beige to rusty-brown in color. Some domes represent extensions of the harder, darker, ironstone exterior of the nodule while other domes are of the same material as the matrix between domes, giving the fossil a mottled appearance (Fig. 1a). The domes and the intervening matrix are separated only by very fine faults ringing the domes, sometimes with a fine, white, mineral layer marking the fault.

Bequaert and Carpenter (1941) rejected this fossil as a specimen of a vespid nest on several grounds, four of which seem to be major points. They found it incredible that a paper nest could survive long enough to be fossilized. The cell bottoms in combs of Recent social Vespidae are flattened and angular, not dome-shaped. The separation between domes is far too large to represent paper walls between vespid cells. The fossil is very much older than any other remnant of a social insect known at that time. Brown (1941b) defended his position in a six page rebuttal that corrected several errors in his opponents' characterization of the fossil, but that is not worth repeating here. Rather, I will propose a process by which an ordinary social vespid nest could become like the fossil in question, an idea Brown (1941b) touched upon.

I propose that the domes were produced by mud and sand conforming to a mold provided by the silk cocoons rather than the paper cells of the brood comb. In any species that typically spins long cocoons that protrude from the open end of the paper cell, larvae inevitably stick silk to neighboring cocoons during the spinning process. Such cocoons will remain united despite loss of the original carton backing. Because they are united on the face side of the comb as opposed to the back side, the closed ends of the silk domes are free to drift apart to distances far wider than if they were still bound by the paper comb. Most of the cocoons should still be close together at their open ends and their walls more angular. This trait is seen in the fossil (Fig. 1b and above).

The specimen shown in Figure 2 was created from a mature and undamaged *Polistes annularis* nest by soaking it in water and closing it in a plastic bag with soil and forest litter, complete with arthropods, for ten weeks, then brushing away the decayed paper with a probe and a toothbrush. While not completely natural, the process reproduces what might happen if a fallen nest were washed into a turbid, sandy stream after a period in the litter. Compare the nest in Fig. 2 with the fossil in Fig. 1. I saw many nests decay naturally over years during my study of architecture in *Polistes annularis* (Wenzel 1989), and the artificially produced specimen shown here is typical of these. Combs of *Dolichovespula* species rot similarly, but the Old World polistine genera (*Belonogaster*, *Ropalidia*, *Parapolybia*, and *Polybioides*) would not produce such uniform domes since none of them have a cocoon that remains intact at the bottom of the cell (Wenzel 1990).

Since silk is relatively tough and resistant to decay, such cocoons filled with sand or mud probably could lie buried in a stream bed long enough to allow fossilization to begin. Even if a nest is folded back upon itself, as suggested by a few marginal cells in the fossil (above), the silk pieces might still remain together rather than break loose to be lost, unlike the wax comb of a social bee nest. Thus, this fossil is a rather convincing preservation of a rotten wasp nest. It is worth noting that an arboreal silk nest of the ant *Oecophylla* from 30 mybp is so well preserved that even the soft grub-like larvae are clearly distinguishable (Wilson and Taylor 1964).

Finally, although Bequaert and Carpenter (1941) adopted a conservative attitude that was appropriate for the day, it is no longer radical to assert that social wasps date from the Cretaceous. We now have ants (Wilson et al. 1967) and social bees (Michener and Grimaldi 1988) from the Cretaceous period. Several genera of solitary vespids of the Euparagiinae and a new subfamily are known from lower Cretaceous deposits (Rasnitsyn 1975, Carpenter and Rasnitsyn [in prep]).

After questioning the identity of this specimen, Bequaert and Carpenter (1941) proposed that *C. favosites* might be properly placed with another Cretaceous fossil, *Uruguay auroranormai* (Roselli 1939), which resembles the nest of an halictid bee (for example, see Eickwort and Sakagami 1979, Figs 1-7). I do not think *C.*

favosites resembles an halictid nest and agree with Zeuner and Manning (1976) who found this suggestion "far fetched".

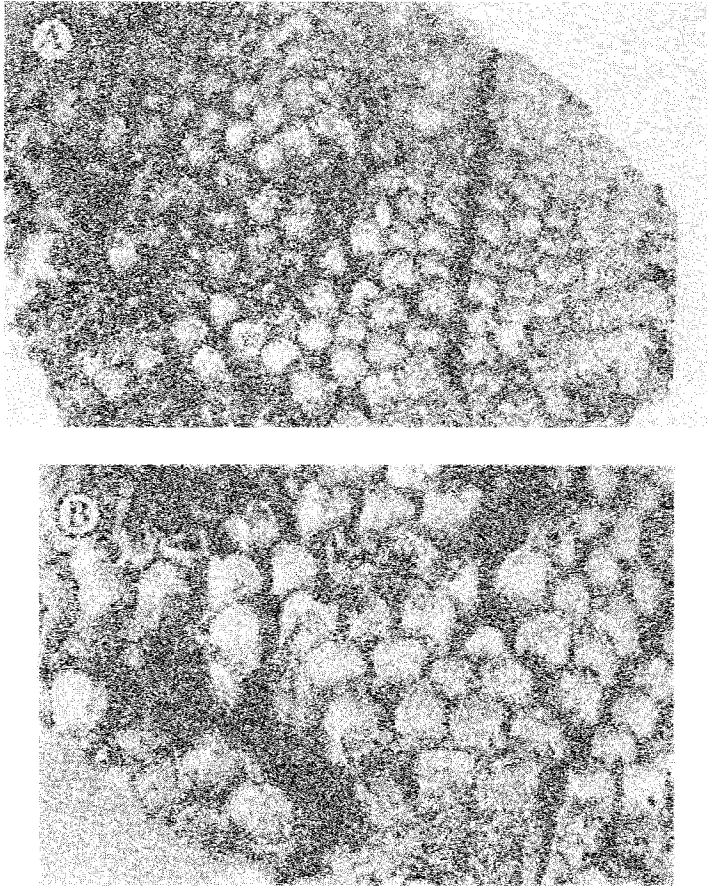


Figure 2. *Polistes annularis*. A. Back of decaying comb viewed obliquely from above, note domed ends of cocoons. B. Cocoons at margin, note wide separation between adjacent cocoons.

BIOGEOGRAPHIC SIGNIFICANCE

Large combs and strong silk cocoons are produced by vespids of either of two subfamilies: the hornets and yellowjackets (Vespinae), and the paperwasps (Polistinae). Excluding the possibility that *Celliforma favosites* is from an extinct lineage unrelated to surviving taxa, the fossil appears to compromise the dominant theories of the origin of one or both of these groups.

Vespinae is now represented by two basal genera, *Vespa* and *Provespa*, which are most speciose in Southeast Asia, and the more apical *Vespula* and *Dolichovespula*, which have holarctic distributions (Akre et al. 1981, Carpenter 1987). None are native to sub-Saharan Africa, nor to Australia, and only one widespread American species reaches as far south as Guatemala. Polistinae, on the other hand, has a rather typical gondwanian austral distribution. Other than *Polistes*, few of the nearly 800 polistine species occur north of latitude 30 degrees N. The phylogenetic affinities within this group are less well understood than in Vespinae, but the cosmopolitan *Polistes* appears to be basal to a cluster of three taxa (Carpenter 1990): neotropical *Mischocyttarus*, a monophyletic group of 23 other South American genera, and a monophyletic group of four genera that populates the paleotropical realm, including Madagascar and Australia.

Prevailing opinion to date is that both these subfamilies originated in Southeast Asia (Vecht 1957, 1967, Richards 1978), and thus each colonized the New World at least twice after West Africa and Brazil separated in the late Cretaceous, (Vecht 1965, Richards 1978). A simpler explanation for the distribution of Polistinae invokes one event of vicariance: the tropical taxa radiated from a common Gondwanian ancestor after South America and Africa separated (Carpenter 1981). *Celliforma favosites* appears to spell doom for these hypotheses since it is both older than seems to be allowed and found on the wrong side of the globe.

If *Celliforma favosites* represents an ancient vespine in Utah, USA, then clearly this fossil lends support to the less popular opinion that the Vespinae have a common northern origin (Bequaert 1932, Carpenter 1981). Some early Tertiary lineages of plants and mammals once found in arctic North America during periods of warmer global climate are now restricted to Southeast Asia, such as

broadleaf evergreen *Cocculus*, *Glyptostrobos*, *Hypserpa*, or the woody euphorb *Macaranga* (Wolfe 1972), or flying lemurs similar to today's *Cynocephalus* (Dawson 1986). Perhaps the older lineages of Vespinae have likewise found refuge there despite northern origins.

If *C. favosites* is a *Polistes*, then it is possible that the ancestor to modern tropical genera could have been drifting apart in the southern hemisphere while *Polistes* nests were falling into streams in Utah, leaving the vicariance hypothesis intact. However, if *C. favosites* represents any form higher in the polistine phylogeny, it is again on the wrong continent to support a theory of vicariance corresponding to the formation of the South Atlantic ocean. Again we are left with the *ad hoc* hypothesis that a group historically associated with the northern hemisphere has been pushed south by the contraction of the tropics.

SUMMARY

While *Celliforma favosites* seems to be a good fossil of a social wasp nest, it upsets the prevailing theories about Southeast Asian or gondwanian origins of Vespinae or Polistinae.

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LITERATURE CITED

- AKRE, R. D., A. GREENE, J. F. MACDONALD, P. J. LANDOLT, AND H. G. DAVIS
1981. The yellowjackets of America north of Mexico. U. S. Dept. Agr. Handbook 552.
- BEQUAERT, J.
1932. A tentative synopsis of the hornets and yellow-jackets (Vespinae; Hymenoptera) of America. *Entomologica Americana* (n.s.) 2: 71-138.
- BEQUAERT, J. C., AND F. M. CARPENTER
1941. The antiquity of social insects. *Psyche* 48: 50-55.

- BROWN, R. W.
1941a. The comb of a wasp nest from the Upper Cretaceous of Utah. *Am. Jour. Sci.* **239**: 54–56.
1941b. Concerning the antiquity of social insects. *Psyche* **48**: 105–110.
- BURNHAM, L.
1978. Survey of social insects in the fossil record. *Psyche* **85**: 85–134.
- CARPENTER, J. M.
1981. The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). *Syst. Ent.* **7**: 11–38 (1982).
1987. Phylogenetic relationships and classification of the Vespinae (Hymenoptera, Vespidae). *Syst. Ent.* **12**: 413–431.
1990. Phylogenetic relationships and the origin of social behavior in the Vespidae. *In* Ross, K. G., and R. W. Matthews, eds., *The Biology of Social Wasps*. Cornell Univ. Press (in press).
- CARPENTER, J. M., AND A. RASNITSYN
1990. Mesozoic Vespidae (in prep).
- DAWSON, M. R.
1986. Discovery of a Dermopteran skull of the Paleogene of arctic Canada. *National Geographic Research* **2**: 112–115.
- EICKWORT, G. C., AND S. F. SAKAGAMI
1979. A classification of nest architecture of bees in the tribe Augochlorini (Hymenoptera: Halictidae; Halictinae), with description of a Brazilian nest of *Rhinocorynura inflaticeps*. *Biotropica* **11**: 28–37.
- MICHENER, C. D., AND D. A. GRIMALDI
1988. The oldest fossil bee: Apoid history, evolutionary stasis, and antiquity of social behavior. *Proc. Nat. Acad. Sci. USA* **85**: 6424–6426.
- RASNITSYN, A.
1975. Hymenoptera Apocrita of Mesozoic. *Trans. Paleont. Inst.* **147**: 1–132 (Russian).
- RICHARDS, O. W.
1978. *The Social Wasps of The Americas Excluding The Vespinae*. British Museum (Natural History).
- ROSELLI, F. L.
1939. Sobre insectos del Cretaceo del Uruguay o descumbrimientos de admirables instintos constructivos de esa epoca. *Bol. Soc. Amigos Ciencias Nat. "Kragleivich-Fontana" Nueva Palmira* **1**(2): 29–102.
- VECHT, J. VAN DER
1957. The Vespinae of the Indo-Malayan and Papuan areas (Hymenoptera, Vespidae). *Zool. Verhand.* **34**: 1–83.
1965. The geographical distribution of the social wasps (Hymenoptera; Vespidae). *Proc. XII Int. Congr. Ent. London, 1964*, 440–441.
1967. Bouwproblem van sociale Wespen. *Proc. K. ned. Akad. Wet.* **76**: 59–68.
- WENZEL, J.
1989. Endogenous factors, external cues, and eccentric construction in *Polistes annularis* (Hymenoptera: Vespidae). *J. Insect Behav.* **2**: 679–699.
1990. Evolution of nest architecture in the social vespids. *In* Ross, K. G., and R. W. Matthews, eds., *The Biology of Social Wasps*. Cornell Univ. Press (in press).

WILSON, E. O., AND R. W. TAYLOR

1964. A fossil ant colony: new evidence of social antiquity. *Psyche* **71**: 93–103.

WILSON, E. O., F. M. CARPENTER, AND W. L. BROWN

1967. The first Mesozoic ants, with the description of a new subfamily. *Psyche* **74**: 1–19.

WOLFE, J. A.

1972. An interpretation of Alaskan Tertiary floras *In* Graham, A., ed., *Floristics and Paleofloristics of Asia and Eastern North America*, 201–233.

ZEUNER, F. E., AND F. J. MANNING

1976. A monograph on fossil bees (Hymenoptera: Apoidea). *Bull. Brit. Mus. (Nat. Hist.) Geology* **27**: 151–268.



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