CONCERNING THE ANTIQUITY OF SOCIAL INSECTS

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In the March 1941 number of this journal J. C. Bequaert and F. M. Carpenter¹ published a six-page discussion of the antiquity of social insects. Two thirds of this space was given to a formulation of criticisms purporting to cast doubt on my identification of an object from Upper Cretaceous strata in southwestern Utah as the comb of a wasp nest called *Celliforma favosites*.² As most of these criticisms do not appear to be well founded a rejoinder is necessary to clarify the issue.

A small matter of terminology first needs attention. In footnote 2 Bequaert and Carpenter object to my use of the term *mold* for the fossil and say that they consider *cast* more appropriate. The popular conception of a *cast* is that of a *casting*, which is anything that has been poured into and, after hardening, has been removed from a *mold*. *Casting* in this sense is a general term. Paleontologists, sculptors, and others, however, use the term *cast* in a specific sense, namely, as a duplicate or positive of the original object; and *mold* as the reverse or negative of that object. Consequently, as the fossil I have described is merely the filling of the cells, it is not a duplicate of the original paper nest itself and is therefore not a *cast* but a *mold*.

It should be noted particularly, before considering their arguments in detail, that Bequaert and Carpenter do not deny that the object in question is a fossil, although I myself had qualms on this point and withheld publication for four years, because I sought evidence from mineralogy to account for the origin of the specimen by inorganic means alone. Re-

¹Bequaert, J. C., and Carpenter, F. M. *The antiquity of social insects*. *Psyche*, vol. 48, pp. 50-55, 1941.

²Brown, Roland W. *The comb of a wasp nest from the Upper Cretaceous of Utah*. *Am. Jour. Sci.*, vol. 239, pp. 54-56, 1941.

ceiving no encouragement in this direction from mineralogists I conceived and published a solution based on the hypothesis of an organic origin. That this hypothesis has the weight of evidence in its favor is apparent from two considerations. The object is enclosed in an ironstone concretion. Organic matter as a nucleus is frequently responsible for initiating the chemical and physical changes that produce concretions, as witness the well-known fossil-bearing nodules from Pennsylvanian strata on Mazon Creek, Illinois. Secondly, the structure of the fossil is apparently not correlatable with any produced by inorganic processes.

Inasmuch as *Celliforma favosites* is definitely from Upper Cretaceous strata, and as no social Hymenoptera themselves have yet been reported from strata older than Eocene, Bequaert and Carpenter (p. 50) intimate that such evidence suggesting the existence of the social habit among insects in Cretaceous time should be received with great reservations. Do these writers support the idea that the social habit appeared suddenly by accident, or special creation, and was not the result of a long, gradual evolution? Moreover, relatively little is known of Cretaceous insect life as compared with that of the Eocene, so that the discovery of a Cretaceous social insect is by no means precluded.

"The counterpart of the fossil is lined by shallow cavities which fit over the ends of the projections. One portion of this counterpart also has projections like those on the other half, so that when the parts of the concretion are placed together, the dome-shaped projections extend inwards from both sides. This extraordinary condition, which is not mentioned by Dr. Brown, seems to require an explanation, if the specimen is regarded as a nest" (p. 51). The portion of the counterpart referred to is at one end of the specimen, near the margin, and it is only in this portion that the condition described occurs. Have Bequaert and Carpenter never seen disintegrating nests in which portions around the margin of the comb are loose and turned back in inverted position on the main portion of the comb? Instead therefore of discrediting the fossil as a wasp nest, the recognition of this condition, it seems to me, is distinctly a positive contribution toward certainty of the original identification.

My critics chide me gently for leaving "to the reader the

pleasure of speculating as to the circumstances and method by which the original comb became this fossil" (p. 51). Nevertheless, despite the fact that "the method by which a wasp nest might be preserved so as to resemble the fossil in question is very difficult to imagine" (p. 51), they accept my invitation and supply a probable version of the process. Their chief difficulty, although they admit they have not experimented with nests, is to see how it would be possible for a paper nest to retain its shape long enough to permit the mud and sand contents of the cells to become so hard as to retain its form after the disintegration of the paper walls. "The thin, soft walls between the cells would, in our opinion, inevitably disappear within a short time long before the foreign material could harden" (p. 51).

Obviously I do not know whether the postulated original nest hung from a tree, rock, or other support, or was a subterranean structure. Neither have I any information as to its topographic location; its proximity to a stream or other body of water; nor the conditions at the site of entombment whether on land or in water. These are the "circumstances" I had in mind when inviting the reader of my paper to speculate. As to the difficulties alleged by Bequaert and Carpenter in imagining a method of fossilization, it may be pointed out that if the cells of a papery nest were quickly buried in fine mud and sand so that pressure would be equal in all directions there would be little likelihood under normal conditions for much distortion of the cells, and the paper walls could conceivably serve as partitions for a long time, particularly if the paper were first partly carbonized or lignitized, as would very likely be the case in a comparatively short time. Something of this nature probably occurs during the fossilization of wood. Contrary to most statements in textbooks about "replacement atom by atom of carbon by silica," silicification of wood is essentially a process of infiltration and deposition of silica in the cells, and only secondarily one of replacement. The delicate cell walls generally remain carbonized as is shown by the fact that peels displaying the cellular structure as a deposit of carbon can be pulled from sections of the wood appropriately treated with hydrofluoric acid. Those who have seen fossil wood in which the minute details of anatomy are exquisitely pre-

served without distortion, or many other fragile structures of plants and animals equally well-preserved, need no further persuasion that fragility of the original object is necessarily a bar to perfect preservation provided other conditions are right.

Bequaert and Carpenter remark about the regularity and perfection of preservation of all the cells in the fossil, and suggest that, in view of the fragility of paper nests such regularity would seem impossible to be attained; and that if only a few cells were so preserved the identification of the fossil as a wasp nest would seem more plausible. The answer to this contention is that the fossil is apparently only a small portion of what was very probably a large nest and that it represents a protected portion which escaped injury and disintegration during the process of getting entombed in the sediments. I have had part of a nest of *Polistes* in water for some days now and, although waterlogged, it still retains its shape and can with care be handled without much distortion, especially of the cells several rows inward from the margin.

Comparing the fossil with nests of living wasps Bequaert and Carpenter allege a number of discrepancies. Some of these criticisms are in part well-taken, but all seem to rest on the assumption that primitive social wasps had nest-building habits that must have been exactly like those of living wasps. Such a rigid interpretation of the law of uniformity, although perhaps applicable to inorganic processes, does not seem appropriate for organisms. Without variation there can be no evolution of organisms or their habits.

In the fossil the dome-shaped projections representing the bottoms of the cells are arranged in parallel rows in three different directions. In the nests of living wasps, however, according to Bequaert and Carpenter, although the open ends of the cells may show such regular arrangement, the bottoms or closed ends are irregularly arranged, particularly as may be seen when the paper cover is removed. In all nests I have examined the paper surface covering the bottoms of the cells displays parallel rows of cells in three different directions with the same degree of regularity as the open ends of the cells. This is well-illustrated by figures

246, 248, and 249 in Duncan's³ recent publication on vespine wasps. Irregularities such as tapering and curving of the bottom portions of the cells is common around the margin of the comb, and probably varies considerably with different species. Sections cut carefully along a row of cells through the central part of a comb usually show as much regularity of cell bottom arrangement as that in the fossil. See Duncan's figure 212.

The dome-shaped cell bottoms shown in Duncan's figure 212 will also serve to refute the statement that "the bottoms of the cells of vespine nests are not dome-shaped, as in the fossil, but are flattened or angular." It is true that around the margins of the combs of most nests the cell bottoms are flat or angular; but this is not true for all parts of the comb or for all conditions. The bottoms of most cells in long-abandoned nests are filled with irregular fecal pellets or other debris. In combs where remnants of the silk cocoons spun by the larvæ still line the cell walls and cover the fecal pellets deposited by previous inhabitants the bottoms of the cells are perfectly dome-shaped as may be seen in a nest of the common hornet, *Vespa* (= *Dolichovespula*) *maculata*, now in my possession.

The statement that the heights of the dome-shaped projections on the fossil are "remarkably uniform" is an unwarranted exaggeration. The degree of irregularity in height is as great as any observed in the nests of living wasps. To the criticism that the cells of vespine nests taper, being wider at their openings than at their bases, whereas in the fossil the cells have a constant width, the reply is that the degree of tapering varies from nothing to very considerable proportions in different nests and different species.

"In the fossil the substance between the cells is nearly as thick as half the diameter of the cells" (p. 53). This measurement was evidently estimated by looking down upon the dome-shaped projections of the fossil and noting the yellowish clay lying between the bases of adjacent domes. This extraneous material, however, is no indication whatever of the thickness of the original vertical cell walls, but may be

³Duncan, Carl D. *A contribution to the biology of North American vespine wasps*. Stanford Univ. Pub., Biological Sciences, vol. 8, no. 1, 1939.

a replacement of thickened portions of the paper over and between the bottoms of the cells. The true thickness becomes apparent at once in a vertical section where it can be seen as a paper-thin, yellowish deposit between adjacent cells.

Although Bequaert and Carpenter reject my specimen as the comb of a wasp nest, they do not, as stated, deny that it is a fossil. However, they offer no suggestion as to its probable identity except to point out a resemblance to nests called *Uruguay auroranormai* described by Roselli.⁴ It appears from Roselli's description that these nests were taken from Cretaceous strata in Uruguay, but the evidence is not clear that they were made in Cretaceous time. However this may be, the resemblance between *Celliforma favosites* and *Uruguay auroranormai* is only superficially suggestive. The cells of both nests are arranged in parallel rows in three different directions. Those of *U. auroranormai* are larger, and it is quite evident from Roselli's figures 19, 20, and 31, that the cells are separated from one another by matrix approximating in thickness one-third the diameter of the cells. In *C. favosites* the cells, as stated before, are separated from one another by a thin deposit of paper thickness only. Roselli's figure 20 shows one cell that displays a spiral seal,⁵ a circumstance which indicates strongly that the constructor of the cell was a mining bee rather than a wasp.

For the reasons given I am not convinced that the Bequaert and Carpenter arguments rule out the possibility of a vespine, or in broader terms, a social hymenopterous origin of the fossil. I would, however, make it clear that I am open-minded on the issue and am ready to accept satisfactory evidence, no matter what the result may be.

⁴Roselli, F. Lucas. *Sobre insectos del Cretaceo del Uruguay o descubrimientos de admirables instintos constructivos de esa epoca.* Boletin de la Sociedad Amigos de las Ciencias Naturales "Kraglievich-Fontana", tomo 1, num. 2, pp. 72-102, 1938.

⁵Brown, Roland W. *Celliforma spirifer, the fossil larval chambers of mining bees.* Jour. Wash. Acad. Sci., vol. 24, pp. 532-539, 1934.