The oldest fossil bee: Apoid history, evolutionary stasis, and antiquity of social behavior

(Meliponinae/stingless bees/Apidae/Cretaceous pollinators/amber)

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ABSTRACT   *Trigona prisca*, a stingless honey bee (Apidae; Meliponinae), is reported from Cretaceous New Jersey amber (96–74 million years before present). This is about twice the age of the oldest previously known fossil bee, although *Trigona* is one of the most derived bee genera. *T. prisca* is closely similar to modern neotropical species. Most of bee evolution probably occurred during the ≈50 million years between the beginning of the Cretaceous when flowering plants (on which bees depend) appeared and the time of *T. prisca*. Since then, in this phyletic line of Meliponinae, there has been almost no morphological evolution. Since the fossil is a worker, social organization had arisen by its time.

The oldest previously known fossil bees are various species (six families) from the Late Eocene Baltic amber (1), about 40 million years old (Myr B.P.) (ages in years B.P. are those tabulated in ref. 2). We report here on a meliponine bee fossil from New Jersey amber about twice that old. The finding of a Cretaceous bee of modern aspect is of special interest for paleobotanists interested in the evolution of pollination systems and entomologists interested in bee evolution. The relevant Eocene Baltic fossil is also of the apid subfamily Meliponinae, genus *Trigona* sensu lato (3, 4), now an abundant tropical genus of stingless honey bees. This fossil has, however, been removed to a separate genus or subgenus, *Kelnermelia*, no longer extant (5). Mid-Tertiary (Oligocene?) *Trigona* fossils known from the Western Hemisphere have a tropical distribution, from the Dominican Republic (where no meliponines now exist) and the state of Chiapas (Mexico) (4).

The New Jersey specimen is from the late Cretaceous, of the Cenomanian to Campanian series, 96–74 Myr B.P., about the same age as the amber containing the first known Cretaceous ant, *Sphecomyrma* (6, 7), also from New Jersey. For convenience in the discussion below, we use the figure 80 Myr for the age of the fossil bee. Though representing a distinct species, *Trigona (Trigona) prisca* (8), the bee is remarkably similar to extant South American forest bees of the genus and subgenus *Trigona*. It does not show distinctive features likely to be important at the genus or higher levels, as do some of the Eocene Baltic fossil bees.

Source and Dating of the Fossil

In view of its modern aspect, the dating of the New Jersey specimen is crucial. It is in a piece of transparent yellow amber collected by the late Alfred C. Hawkins at Kinkora, Burlington County, NJ (40° 07′15″ N, 74° 45′30″ W), and was deposited in the mineral collection of Columbia University where it was unstudied for many years. This collection was recently transferred to the American Museum of Natural History. Before polishing there was lignite on one side of the

piece of amber; lignite gives its dark color to the clays of the Merchantville, Magothy, and Raritan formations that are exposed at Kinkora and elsewhere in New Jersey (9). It therefore seems likely that the amber came from one of these clays. Further discussion of the stratigraphy involved is presented in ref. 8.

We have further verified the age and source of the fossil by comparison with amber more recently obtained from known sites. New Jersey ambers of known origins and stratigraphy were available as follows: (*i*) clear yellow, two pieces, from the Sayre-Fisher Pits, Sayreville [Woodbridge Clay Member of Raritan Formation, palynological zone IV of R. A. Christopher (10), Cenomanian to early Turonian, *ca*. 92 Myr B.P.]; (*ii*) clear yellow, one piece, from Ellisdale (Marshalltown Formation, late Campanian, *ca*. 75 Myr B.P., D. Parris, personal communication); and (*iii*) opaque orange, one piece, from Kinkora. Samples from these pieces, together with two samples from the piece containing the *T. prisca*, were analyzed by Curt W. Beck of the Amber Research Laboratory, Vassar College, using a Fourier transform infrared (IR) diffractometer. He reports (personal communication) that the bee piece and the other clear yellow pieces gave similar IR spectra, characterized by a carbonyl absorption band between 1695 and 1704 cm^{-1} (mean at 1698 cm^{-1}) and by a band at 888 cm^{-1} that results from a terminal double bond (RRC=CH$_2$). These traits indicate that this amber is an acid resin (not an ester) with an exocyclic methylene group, such as is seen in some Southeast Asian copal produced by *Dammara* and *Agathis* (Araucariaceae), which contains agathic acid. The IR spectra corroborate palynological and megafossil evidence (11) that the amber was of araucariaceous origin (12). Beck considers it extremely probable that the clear yellow pieces, including the piece containing the bee, were derived from plants of the same species or genus. Spectra of these and other New Jersey ambers, including those of two samples of the piece containing the bee, are on file in the Entomology Department, American Museum of Natural History, New York City.

These chemical results show that the dating indicated above is reasonable. Other than Maastrichtian amber (just below the Cretaceous–Tertiary boundary), more recent ambers are not known from New Jersey. Since amber can be carried in streams and rivers, it should be noted that reworked material from upstream in the Delaware River drainage would have to come from Triassic or older sediments (13).

Biogeographical Problems

Modern species of *Trigona* sensu stricto occur principally in moist Neotropical forests, north to the states of Veracruz and Jalisco, Mexico. The Late Cretaceous flora of New Jersey was probably tropical or subtropical with abundant angio-

Abbreviation: Myr, million years.

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sperms; for the Cenomanian and Turonian stages (96–89 Myr B.P.) Dorf reported 169 plant taxa, of which 131 were angiosperms (14, 15). The gymnosperms in the flora do not indicate a temperate climate since Araucariaceae today occur in tropical and temperate areas.

The presence of *Trigona* sensu stricto in the Late Cretaceous of New Jersey throws doubt on speculations as to the origin and intercontinental spread of the subgenus (16, 17). Its present abundance in South America may not indicate an origin there. *Trigona* is very unlikely to cross even narrow water barriers because of the gradual progressive nest and colony establishment; it does not now reach the Antilles (except Trinidad) in spite of numerous species in nearby mainland areas. Tectonic events, however, could have had an effect on the present distribution of meliponines. Probably during the Tertiary *Trigona* disappeared, with the climatic deterioration, from most of North America. Thus the *Trigona* species now in Mesoamerica may not represent a northward extension from South America; instead they could be remnants of a formerly wide tropical Nearctic distribution.

Absence of *Trigona* sensu stricto from Africa would be explained if it was absent in South America until after that continent was well separated from Africa. Although separation of these continents began by early Cretaceous, the major gap began in the Campanian (*ca.* 75 Myr B.P.).

Inferred Social Organization and Behavior

The fossil verifies that social organization existed among bees in the Late Cretaceous. *T. prisca* is closely related to modern highly social bees and therefore likely to have been social. Moreover, it is a female with a remarkably small abdomen (Fig. 1). Egg-laying bees, whether queens of social species or females of solitary species, have relatively large abdomens. Abdomens as small as that of *T. prisca* are found only in workers of certain highly social species, such as *Trigona cilipes*, and are clearly diagnostic of a worker caste. Bees probably had a long prior history of social evolution toward the elaborate meliponine type prior to the time of *T. prisca*.
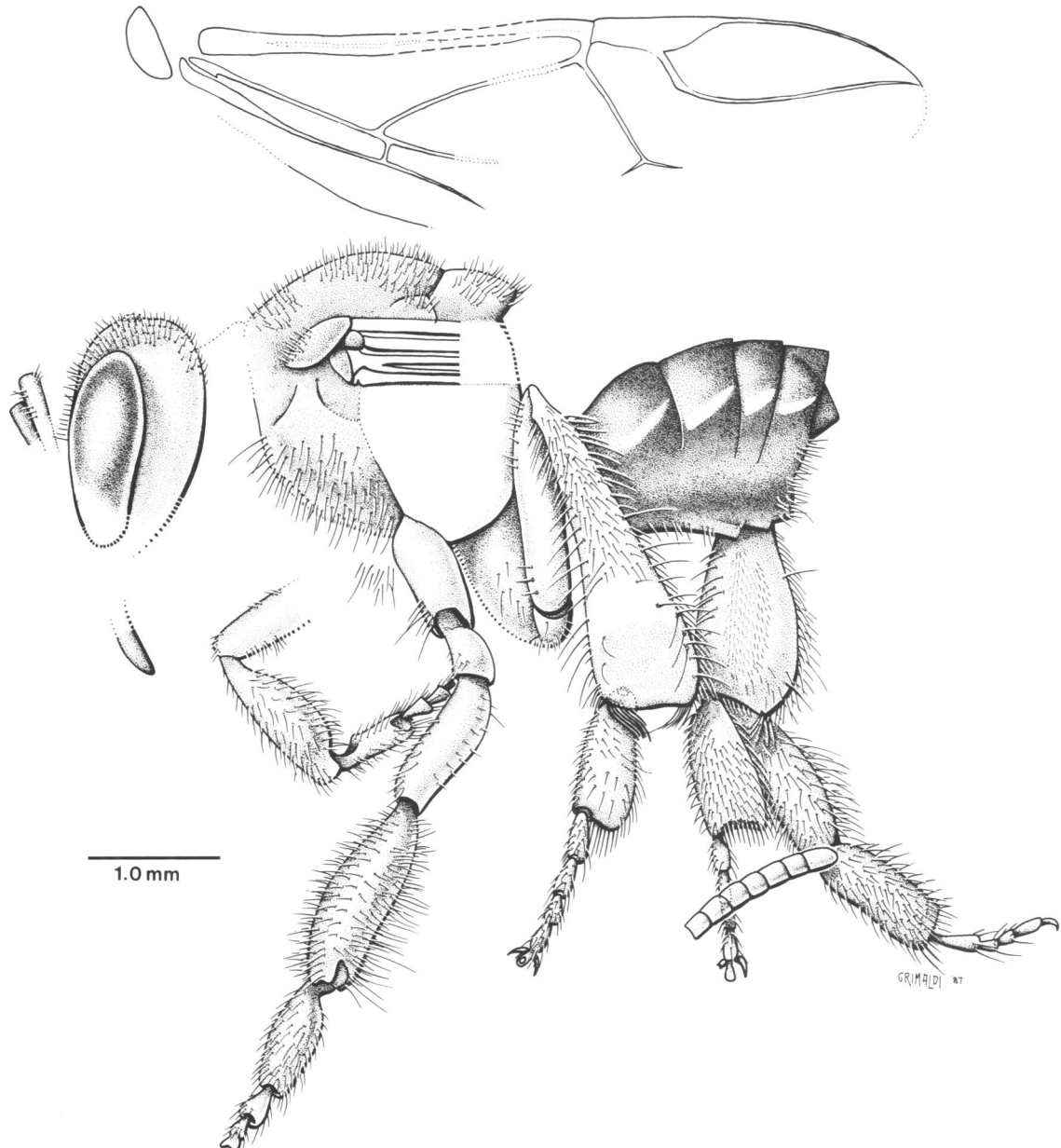

FIG. 1.   Side view of worker of *T. (T.) prisca*, based on *camera lucida* sketch, with reconstruction of much of a forewing based on contorted wings of fossil. The leg extending farthest back is the right middle leg.

Thus apoid social behavior may be as old as or even older than that of ants (6, 7).

It is clear from its structure that the details of the pollen-manipulating and carrying behavior of *T. prisca* were like those of modern *Trigona*. The strongly hairy anterior ventral part of the thorax and probably front coxae and the presence of the corbicula, rastellum, and penicillum on the hind tibia and of posteriorly directed hairs on the base of the hind basitarsus (Fig. 1), together with the structure of the front and middle legs, are all evidence that the complicated foraging behavior (18) of modern species existed also in the Cretaceous. No pollen is evident in the amber on or near the fossil. This is not surprising since bees collecting resin for nest construction (the ones most likely to be trapped and fossilized) are not simultaneously pollen collectors.

Trigona and Apoid Evolution

Considering its age, *T. prisca* is unexpectedly similar to the modern *T. (T.) cilipes* and its close relatives, which are abundant in the Amazon Basin and the Guianas, rarely in Panama, with a single Costa Rican record. The specific characters of *T. prisca* are presented in detail elsewhere (8). The differences between *T. prisca* and *T. cilipes* are small compared to differences among most meliponine subgenera or genera or to differences between *Trigona* sensu stricto and the meliponine bees known from the Baltic Amber and more recent Tertiary ambers (4). It has to be admitted, however, that noteworthy convergence occurs in external characters of workers of some meliponine bees. For example, two African groups (*Liotrigona* and *Hypotrigona*), formerly thought to be in the same subgenus by one of us (C.D.M.), turn out to be only distantly related, each closest to other subgenera or genera, after examination of mostly internal male characteristics (19) and the sting rudiments of workers. But even if *T. prisca* could be shown not to be a member of the subgenus *Trigona*, its similarity to some modern species is remarkable. It easily falls in the genus *Trigona* sensu lato, as shown by its body form, wing venation, hind tibial structure, etc.

Bees are dependent on floral materials (nectar, oil, pollen) for food and therefore are assumed to have evolved with or after the angiosperms (17, 20–22). Angiosperms appeared at least by the earliest Cretaceous (about 130 Myr B.P.) (23, 24). Since *Trigona* is a specialized genus (25) in a derived family (Apidae) of a supposedly derived group of families (long-tongued bees) (26), it seems that much of bee evolution must have occurred during the period from about 130 Myr B.P. to about 80 Myr B.P. when *T. prisca* lived. During part or all of this 50-Myr period, evolutionary changes such as the following occurred: change from prey to pollen as the protein source for larval feeding; from solitary to highly social with a caste system; from short-tongued to long-tongued; from having simple labial palpi to sheath-like palpi that form part of the complex proboscidial sucking apparatus; from complete to much reduced wing venation; from grooming behavior patterns that serve only for cleaning to modified grooming behavior that manipulates pollen, perhaps related to the origin and maintenance of plumose hairs; perhaps from transporting pollen internally in the crop to carrying it dry in a bushy scopa, and certainly thence to carrying it moistened in a smooth corbicula surrounded by long hairs; and many more. That such extensive reorganization in physiology, behavior, and morphology could occur between the origin of angiosperms and the time of the diverse bee fauna of the Baltic Amber has seemed surprising (17). The finding of *T. prisca* emphasizes the problem as well as the long period of evolutionary stasis in its phyletic line during the last 80 Myr or more.

Of course if angiosperms arose earlier than we now believe—for example, in the Jurassic—bees could have had a longer evolutionary history. The same could be true if early bees depended on something other than angiosperm flowers. For example, the Mesozoic gymnosperm order Bennettitales had showy bracts around its reproductive structures (27) and was probably insect pollinated, possibly visited by bees before the Cretaceous. No matter when it began, however, the meliponine characteristics of structure, physiology, and behavior, as listed above, involved impressive changes from the ancestral characteristics of sphecoid wasps.

The antiquity of *Trigona*, and the numerous records of certain palms (a family established by late Cretaceous) visited by and presumably pollinated by *Trigona* (28), suggest that *Trigona* and its relatives may have foraged from palms and perhaps other relictual angiosperms, such as Winteraceae, Magnoliaceae, Nymphaeaceae, Lauraceae, and Piperaceae. At a general level a coevolutionary relationship may have existed, although so far as known no *Trigona* species are specific to any particular plant families.

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