

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 2917, pp. 1–10, figs. 1–12
May 4, 1988

A *Trigona* from Late Cretaceous Amber of New Jersey (Hymenoptera: Apidae: Meliponinae)

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ABSTRACT

Trigona prisca new species is based on a fossil worker in Late Cretaceous amber from Kinkora, New Jersey. *T. prisca* is placed in the subgenus *Trigona* s. str. and is remarkably similar to *T. (T.)*

cilipes of tropical America. Infrared spectrometry shows the amber to be of araucariaceous (Coniferae) origin.

INTRODUCTION

The oldest known fossil bee is the *Trigona* (subgenus *Trigona*) described below from a specimen in Late Cretaceous New Jersey amber. Considering the rarity of New Jersey amber, it is surprising that the first Cretaceous fossil ant to be found (*Sphecomyrma*) came from amber in a nearby deposit of approximately the same age (Wilson et al., 1967). A diverse fauna of bees comes from the late Eocene Baltic amber (Zeuner and Manning, 1976), about 40 mybp, but no older fossil bees have been known until now. Baltic amber bees have been placed in the families Andrenidae, Melittidae(?), Ctenoplectridae, Megachilidae, Anthophoridae(?), and Apidae. Among the most interesting are two extinct genera thought to belong to the rare paletropical family Ctenoplectridae. Other

extinct genera are also present among the Baltic amber bees, as would be anticipated for an ancient fauna. The most relevant for the present study are the Apidae that resemble *Trigona*. They are (a) *Trigona*, an extant tropical genus of stingless honey bees (Keller-Pillault, 1970), (b) *Sophrobombus*, an extinct genus possibly ancestral to the Meliponinae (Zeuner and Manning, 1976), and (c) *Electraxis*, an extinct genus now thought to be related to the true honey bees (*Apis*) (Wille, 1977). The *Trigona* has been removed to a separate genus or subgenus, *Kelnermelia* (Moure and Camargo, 1978), not present in the modern fauna.

The Cretaceous bee, although about twice as old as those from the Eocene, appears to be a member of a modern neotropical sub-

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genus. This is particularly surprising considering the distinctiveness of the Eocene Baltic bee fauna, and considering that the fossil ant *Sphecomyrma*, also from the Late Cretaceous, is placed by itself in an archaic subfamily, the Sphecomyrminae. One might suspect that the bee is mislabeled or that its stratigraphic position has been misinterpreted. The history of the specimen since its discovery, as well as its stratigraphic position and amber chemistry, are explained here in detail in order to dispel doubt as to the age of the specimen.

THE AMBER

The piece of amber was found by the late Alfred C. Hawkins in Kinkora, Burlington County, New Jersey (40°07'15"N, 74°45'30"W), a locality on the eastern shore of the Delaware River and at the edge of the Atlantic Coastal Plain. It was probably found in the 1920s or 1930s, possibly as a result of mining the sugary, ferruginous sand in that area. More likely it was found in situ at one of several points along the Delaware River in Kinkora where three formations of black clay lie exposed. These are the Merchantville (Santonian to Campanian Stages, 88–74 mybp) (Petters, 1976), Magothy, and Raritan Formations (the last one Cenomanian to Turonian, 96–89 mybp) (Berry, 1906; Owens and Minard, 1964). Since there was lignite on one side of the piece before grinding and polishing, and this is the material that causes the clay's dark gray stain, it is likely that the amber was found in one of the three clay formations. The locus typicus of the Kinkora Late Cretaceous is described by Ries et al. (1904: 381, 383) as "Loc. 113, Murrell Dobbins' brickyard, Kinkora," and as belonging to the upper portion of the Raritan Formation. This deposit apparently corresponds to the Magothy Formation on the map by Owens and Minard (1964).

The piece was originally deposited at Columbia University, but the Columbia University mineral collection has recently been moved to the American Museum of Natural History and the piece is now in the amber insect collection of the Entomology Department of that museum (AMNH C88720). Its dimensions are 1.2 × 1.7 × 1.2 cm and it

contains 12 other arthropods (some only fragments) in the following taxa: Phoridae, Milichiidae, Curculionidae, Scelionidae, Reduviidae (Emesinae), Cecidomyiidae, Isoptera, and Acarina. These taxa will be treated elsewhere. Of these fossils, the bee is by far the largest. The amber is transparent yellow.

Amber from the Atlantic Coastal Plain varies in age from about 95 to 70 mybp, and is reported from Maryland to Cape Cod in strata of sand, fine clay, and lignite, along with variable quantities of pyrite and glauconite. A list of New Jersey amber localities based on museum specimens and published records is available from D. Grimaldi. Amber from this region is probably mostly gymnospermous in origin. There are two chemically distinct forms of New Jersey amber among eight sample sites tested by Langenheim (1969): one of araucariaceous (Coniferae) origin, with Kinkora listed as one of the sites, the other [from Harrisonville and Pemberton (Burlington Co.)] similar to the resin of *Liquidambar* (Hamamelidaceae: Angiospermae).

To our knowledge, only four New Jersey amber sites have some sort of stratigraphic (in each case, palynological) correlation (in order from oldest to youngest): (1) Sayre-Fisher Pits, Sayreville [Woodbridge Clay Member of Raritan Formation (palynological zone IV of Christopher, 1982), which is late Cenomanian–early Turonian (ca. 92 mybp) and extends into Long Island (Sirkin, 1986)]; (2) Cliffwood Beds, Cliffwood Beach [Magothy Formation (pollen zone CA-1), late Santonian (ca. 85 mybp; Sirkin, 1986)]; (3) Ellisdale [Marshalltown Formation, late Campanian (ca. 75 mybp; D. Parris, personal commun.)]; (4) Sewell [Hornerstown Formation, Cretaceous–Tertiary Boundary (ca. 66 mybp; D. Parris, personal commun.)]. We have followed Haq et al. (1987) as to approximate ages in years.

Chemical comparisons of the bee-containing amber were made with two of the ambers of known stratigraphy listed above. Five samples from four pieces of clear yellow New Jersey amber were analyzed by Dr. Curt W. Beck of the Amber Research Laboratory, Vassar College, using a Fourier Transform Infrared Diffractometer. The samples were as

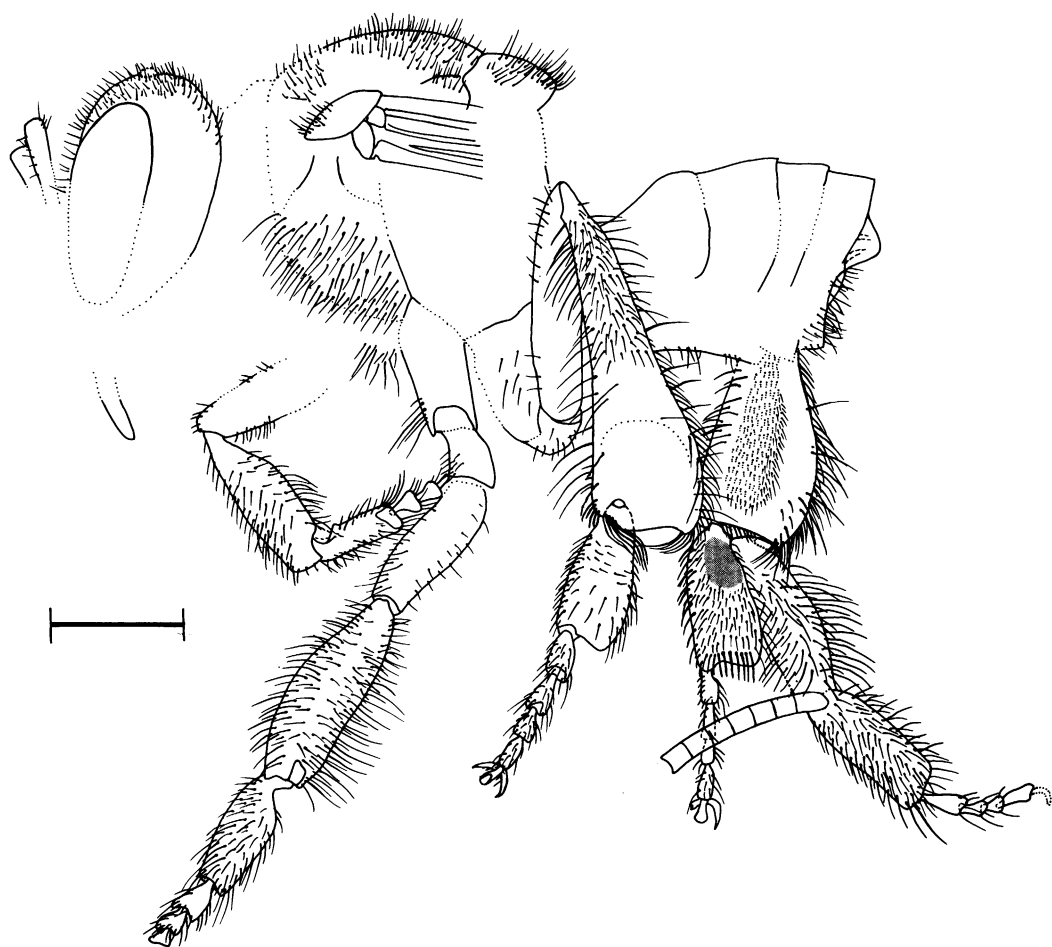


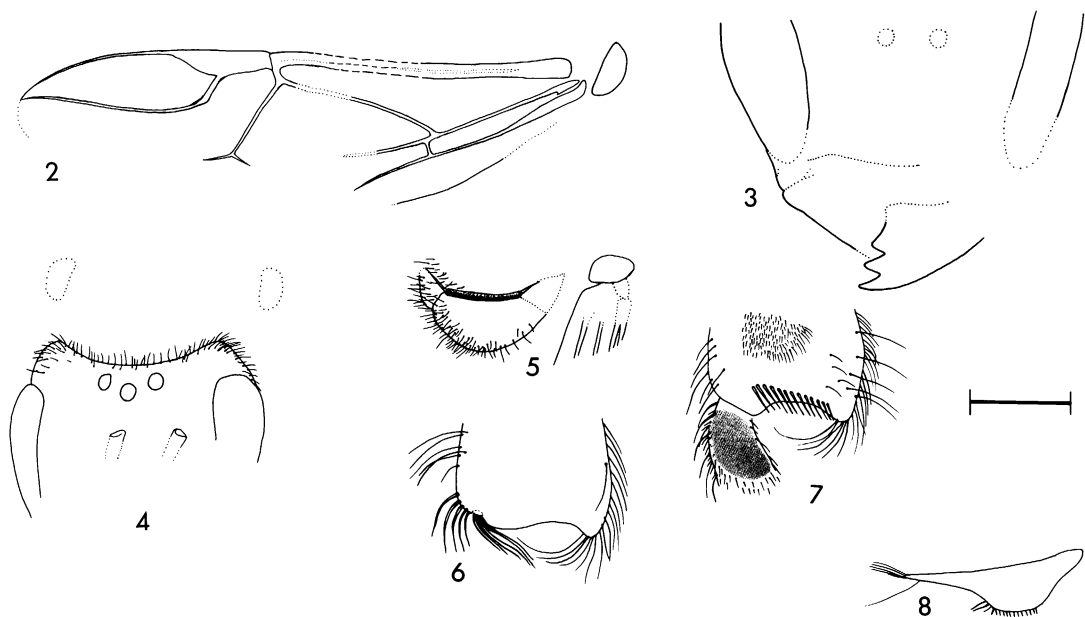
Fig. 1. Side view of worker of *Trigona (Trigona) prisca* new species. Dotted lines represent structures that can only be seen vaguely or in the case of the minute hairs on the inner side of the right hind tibia, can only be inferred. Broken lines represent structures that are hidden in the view illustrated. Scale line = 1 mm. The leg reaching farthest to the rear is the right middle leg.

follows: two samples of AMNH C88720 (bee piece), two pieces from the Sayre-Fisher Pits, and one piece from Ellisdale. In addition, an opaque, orange piece, also from Kinkora, was analyzed. To check on reproducibility, each sample was run twice.

Dr. Beck reports that the bee piece and the three other clear yellow pieces are so similar in infrared (ir) spectra that they are either of the same botanical origin, with variations introduced by the vicissitudes of their depositional histories, or else they are of closely related botanical origin, i.e., of different species within the same genus. This group of samples is characterized by a carbonyl absorption between 1695 and 1704 cm^{-1} (mean

at 1698 cm^{-1}), which indicates a free carboxylic acid function that is probably, but not certainly, conjugated with a carbon-carbon double bond. The double bond, i.e., the unsaturation, is plainly evident in all ir spectra of all four pieces as consistent absorption at 888 cm^{-1} ; this is due to a terminal double bond, i.e., the structural feature $\text{RRC}=\text{CH}_2$.

Much less consistent are other absorption bands indicative of unsaturation, e.g., the out-of-plane carbon-hydrogen bending absorptions near 980 cm^{-1} , 946 cm^{-1} , 924 cm^{-1} , 820 cm^{-1} , and 795 cm^{-1} . Also, the confirming carbon-hydrogen stretching absorptions at 2080 and/or 3040 cm^{-1} are visible in only four out of the eight spectra of this group.



Figs. 2–8. *Trigona (Trigona) prisca* new species, worker. 2. Reconstruction of much of forewing, also showing a tegula. 3. Anterolateral view of lower part of face and mandibles. 4. Anterior-dorsal, slightly lateral, view of head with positions of vaguely seen tegulae shown by dotted lines. 5. Dorsolateral view of scutellum, one wing base, and tegula. 6, 7. Outer and inner views of apex of hind tibia, and base of basitarsus in fig. 7. 8. Imaginary cross section of hind tibia at distal fourth, showing thin posterior expansion (to left) and median, minutely hairy, elevated area (below). Scale line = 1 mm except = about 0.5 mm for figs. 3, 6, and 7. Dotted and broken lines as explained for fig. 1.

But the 888 cm^{-1} band is enough to say that all four samples are of an acid (not an ester) resin with an exocyclic methylene group, and that means a labdane skeleton like that of agathic acid. That molecular type occurs in fossil resins like the copal of southeast Asia, derived from the genera *Dammara* and *Agathis* (Araucariaceae). (The opaque orange piece proved to be a completely saturated acid resin, very different from the clear yellow pieces, and is probably highly oxidized.) The ir spectra corroborate palynological and megafossil evidence (Hollick and Jeffrey, 1909) that the amber source was araucariaceous. The spectra are filed in the Department of Entomology, American Museum of Natural History.

Dr. Jaap Boon, Fom-Instituut voor Antoom-en Molecuulfysica, Amsterdam, tested four samples of New Jersey amber, including a small fragment of the bee piece, using pyrolysis gas chromatography (see Poinar and Haverkamp, 1985, for application of a related technique to amber). The chromato-

graphic results, like the ir spectra, confirm the similarity of the piece to other New Jersey ambers. A detailed characterization of the New Jersey ambers is in preparation by D. Grimaldi and C. Beck and will be presented elsewhere.

The ir data are not useful for extrapolating the age of the bee piece, but do confirm a common botanical origin for it and certain New Jersey ambers of known age (92–75 mybp). Similar ambers are not known in the New Jersey Tertiary. Thus the age based on the exposures at Kinkora (96–74 mybp) seems entirely reasonable; for brevity one can say about 80 mybp.

THE BEE

The parts that can be seen are shown in the illustrations. Much of the lower part of the head and the neck region and the posterior lateral part of the thorax are enveloped in "schimmel," a whitish moldlike covering. The bee must have been damaged early in

the preservation process. Both antennal flagella are broken off although the apical part of one of them is near the tarsi. One front leg is some distance away in the amber. The wings are badly folded, broken, torn, and the tips bent. The hind wing and posterior apical part of the forewing cannot be seen; figure 2 is a reconstruction of structures visible in different views. Because of the difficulty of seeing black hairs against black surfaces of the body, lack of hair in some body areas in the figures does not necessarily mean that hair is absent there. The genal area, except for its upper part, does seem hairless in the fossil, however.

***Trigona (Trigona) prisca*, new species**

Figures 1–8

DIAGNOSIS: This is a Cretaceous amber fossil of a worker *Trigona* of the subgenus *Trigona*, as indicated by the toothed distal margin of mandible and other features. Only the probable absence of branches on the hairs of the posterior margin of the hind tibia suggests a different subgeneric placement. The form and structure, including the small, compressed metasoma, closely resemble those of *T. (T.) cilipes* (Fabricius), formerly called *T. compressa* Latreille. This fossil differs from *T. cilipes* in the slightly acute posterior apical angle of the hind tibia and the weak rastellum (only about 12 bristles).

DESCRIPTION: Comparisons below are frequently with *Trigona cilipes*, because it is common and is similar to the fossil. There are, however, related species that are almost as similar as *T. cilipes* is to the fossil. The particularly distinctive features of the fossil are set in capital letters.

WORKER: Length slightly over 5 mm; hind tibial length 2.5 mm. Black with no evident pale markings. Wings nearly uniformly transparent, weakly brownish. Surface of head and thorax not smooth and shining, rather close small punctures visible at least on certain parts of scutellum (as in *T. cilipes*); surface of metasoma apparently not punctate. Vestiture dark, rather dense, erect on head and thorax (as in *T. cilipes*); genal area probably without erect hair except above, as in *T. cilipes*. (In *T. cilipes* the genal area lacks erect hairs but is covered with minute, appressed white hairs.

When placed in immersion oil, these hairs disappear and the genal area of *T. cilipes* then looks like that of the fossil.) First four metasomal terga bare; remaining terga and sterna with hairs (as far as visible) as in *T. cilipes*.

Head about as wide as thorax; metasoma unusually small, much narrower than thorax. (An occasional dried specimen of *T. cilipes* has an almost equally small metasoma.) First tergum wider than long; fifth and sixth terga largely hidden beneath fourth, possibly damaged; posterior part of metasoma with longitudinal middorsal fold, so that metasoma is laterally compressed (as often in *T. cilipes*). Mandible with three teeth on lower part of apical margin; above these teeth a long, gently concave margin probably followed by an upper tooth as in figure 3, but this only weakly visible and possibly wrong interpreted. (If correctly interpreted, mandible almost exactly as in *T. cilipes*; see Schwarz, 1948, for illustration.) Vertex not elevated behind ocelli; positions of ocelli as in *T. cilipes*.

Scutellum short, rounded posteriorly, slightly overhanging metanotum (figs. 1, 5); PROPODEUM SEEN (not clearly) IN PROFILE DECLIVOUS, without slanting basal zone. Anterior wing slightly shorter than body, visible parts of venation (fig. 2) as in *T. cilipes*. Wing covered with minute hairs, not much enlarged along veins. Midtibia with long, fine hair (as in *T. cilipes*). Hind tibia longer than femur and trochanter together (tilting the specimen shows that it is not as much longer as appears in the possibly slightly dorsolateral view of fig. 1). [Left hind tibia probably somewhat deformed by pressure (constricted medially) and appearing narrower, with posterior margin not as convex as it should be (fig. 1).] Basal half of hind tibia densely hairy on outer surface (more densely than in *T. cilipes*); POSTERIOR APICAL ANGLE STRONGER THAN IN *T. CILIPES* OR OTHER *Trigona* s. str., SLIGHTLY ACUTE. Inner surface of hind tibia with long, raised area, presumably covered with minute hairs (at least distally; they are not resolvable elsewhere on right hand tibia but dark color of area suggests their presence; on left hand tibia abundant hairs along posterior margin of elevated area visible through tibia from outer surface and shown on right hand tibia in fig. 1); raised area seemingly not as abruptly descending to posterior marginal

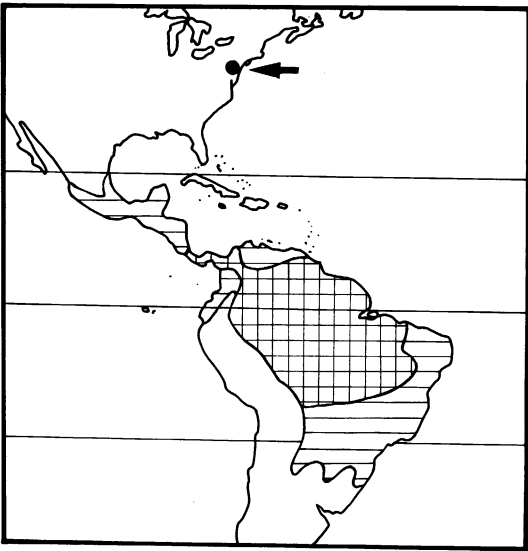


Fig. 9. Map showing the locality for *Trigona* (*Trigona*) *prisca* (arrow), the present distribution of the subgenus *Trigona* (horizontal lines), and the range of *T. (T.) cilipes* (vertical and horizontal lines).

area as in *T. cilipes* (fig. 8). Posterior margin of hind tibia with PROBABLY SIMPLE HAIRS (branches mostly not resolvable) ARISING FROM MARGIN PROPER, directed apicad, seemingly mixed with some clearly simple hairs of similar length, THESE HAIRS, EXCEEDED BY A FEW LONG HAIRS, several of which arise on inner surface of tibia near margin, at least two on outer surface at margin (figs. 1, 6, 7).

Corbicular area weakly (or not?) concave, WITHOUT HAIRS. Penicillus well developed; anterior parapenicillus present, of rather robust hairs; posterior parapenicillus represented only by slender curled hairs arising from posterior apical tibial angle (fig. 6). Rastellum present but apparently consisting of about a dozen bristles, shorter, less robust, and less closely placed than in *T. cilipes* (fig. 7). Hind basitarsus little over twice as long as wide, basal half narrowed basally, INNER SURFACE WITH BASAL SERICEOUS AREA not sharply defined, posteriorly directed setae on outer surface near base few and short.

HOLOTYPE: The unique specimen is in the amber collection of the Department of Entomology, American Museum of Natural History (no. C88720). It is from the Late Cre-

taceous deposits at Kinkora, New Jersey, as discussed in detail above.

ETYMOLOGY: The specific name is the feminine form of the Latin adjective *priscus*, meaning ancient.

GEOGRAPHIC POSITION: Figure 9 shows the present distribution of *Trigona* s. str. and of *T. (T.) cilipes*. *Trigona* has evidently retreated from a formerly broad Laurasian distribution, presumably as a result of Tertiary climatic cooling.

TAXONOMIC POSITION

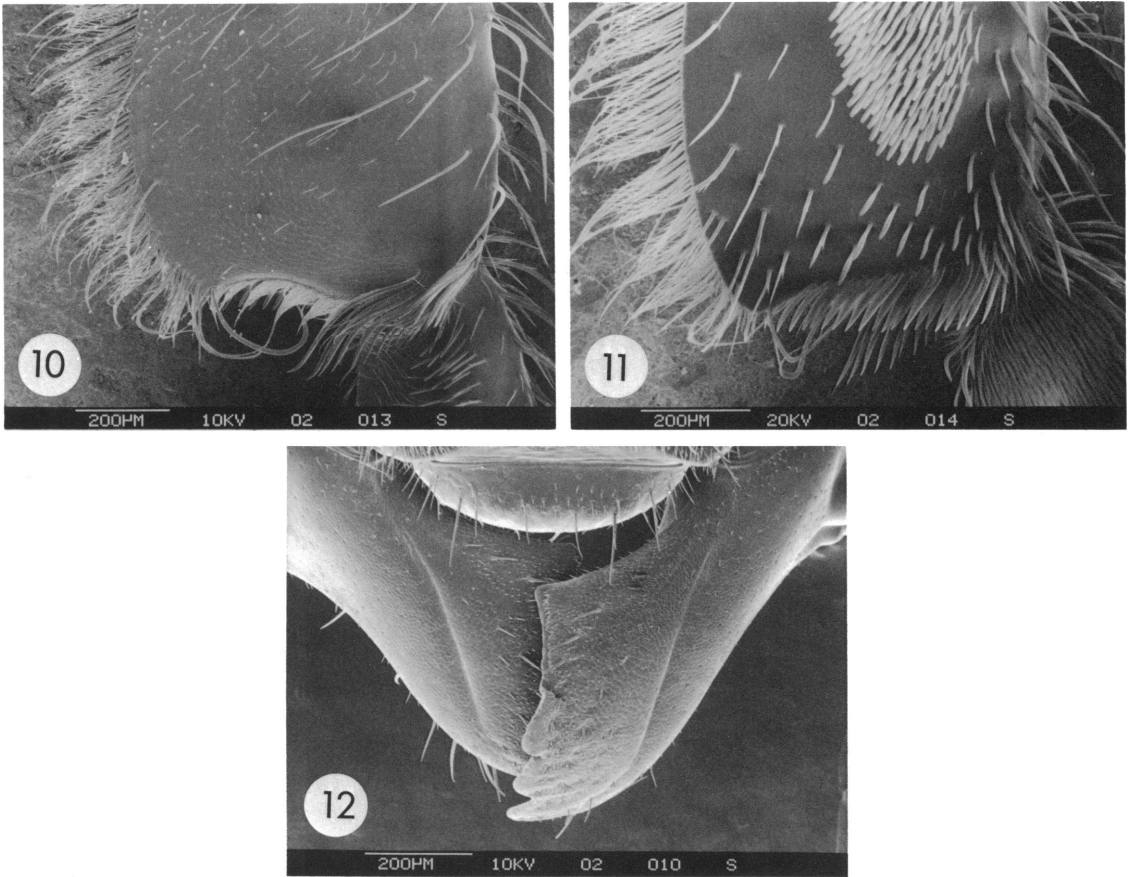
The presence of a sericeous area on the inner surface of the hind basitarsus indicates that this species belongs either to the subgenus *Trigona* s. str. or the subgenus *Tetragona* (not all species of which have such an area). This placement is supported by the two types of hair on or near the posterior margin of the hind tibia—a few long coarse simple hairs and abundant soft hairs, plumose in living species of *Trigona* s. str. and *Tetragona*. Some of these hairs were possibly plumose in the fossil; it is impossible to resolve branches clearly but a few apparent branches can be seen.

No species of *Tetragona* are particularly similar to the fossil. Nearly all the New World species lack the sericeous hind basitarsal area found in the fossil. Nearly all species have the propodeum in profile arched posteriorly, with a slanting surface below the metanotum, instead of being wholly declivous as is probably true of the fossil. Nearly all have the marginal cell distinctly open at the apex, unlike the fossil.

Among the living species of *Trigona* s. str., however, *T. cilipes* and its allies are similar to the fossil. The strongly toothed apical mandibular margin clearly supports the placement of this species in *Trigona* s. str. (compare figs. 3 and 12). Visible features of the fossil that differ or may differ from *T. cilipes* are as follows:

1. Base of hind tibia a little more densely punctate and hairy (fig. 1).

2. Raised area of inner surface of hind tibia less abruptly differentiated from posterior marginal area. (This seems to be true but one cannot get the various views of the right hind tibia needed to verify it. See fig. 8.)



Figs. 10–12. *Trigona (Trigona) cilipes* (Fabricius). **10.** Apex of hind tibia of worker, inner view. **11.** Same, outer view. **12.** Mandible (SEM photos by D. Grimaldi).

3. Hind tibia distinctly longer than femur and trochanter together (fig. 1). (Only slightly so in *T. cilipes*; position and direction of view influence one's perception of this character in the fossil.)

4. Posterior apical angle of hind tibia slightly acute, sharper, and more prominent than in *T. cilipes* (figs. 1, 6, 7) or other modern *Trigona* s. str. (In *T. cilipes* the angle is obtuse, rarely approaching right angular; see Schwarz, 1948, and figs. 10, 11.)

5. Weak hairs of posterior marginal fringe of hind tibia directed apicad and shorter than simple hairs arising on inner surface of tibial margin (figs. 1, 8). (This appears to be partly an artifact due to flow of the matrix, bending these soft hairs apicad. On the distal part of the right tibia, these hairs are more erect and appear about as long as the simple hairs.)

6. Hairs of posterior marginal fringe of hind tibia probably simple. The number of branches is clearly less than in *T. cilipes*; in most places the hairs of the fringe appear simple and nowhere are branches unequivocally present.

7. Corbicular surface hairless (fig. 1). (Other meliponines including *T. cilipes* have a few long, simple hairs arising from the corbicular surface. We cannot see why they would not be visible, if present, in the fossil.)

8. Rastellum consisting of fewer (about 12), shorter, and less closely placed bristles than in *T. cilipes* (fig. 7), not fully visible in direct lateral view. (This feature is hard to see in the fossil but appears to differ from the long, well-formed rastellum of about 20 bristles in *T. cilipes*.)

9. Propodeum in profile entirely declivous

(fig. 1). (It is a little arched posteriorly in *T. cilipes* but unfortunately is not clearly visible in fossil.)

10. Wings seemingly unicolorous. (In *T. cilipes* the forewings are bicolored, milky distally, and slightly brownish basally. The pallid distal coloration largely disappears in immersion oil; thus this character may be meaningless.)

As can be seen from the above comparisons, the fossil is incredibly similar to *T. cilipes* considering its age, although a different species. The most convincingly different characters are 4 (which is easy to see accurately but the difference is not great), 6, 7, and 8 which are difficult to be really sure of in spite of the apparently clear view provided by the fossil. However, they appear to be valid differences between the fossil and *T. cilipes*, and differentiate the fossil also from the other species of *Trigona* s. str. as well as from the species of *Tetragona*. If the marginal hairs of the hind tibia (character 5 above) are indeed simple or nearly so in *T. prisca*, as they appear, this is strikingly different from all living *Trigona* s. str. and *Tetragona*.

João M. F. Camargo examined our drawings and description of *T. prisca*, and sent careful drawings of hind tibiae and basitarsi of various species of *Trigona* s. str., some of them undescribed, for comparison. (See also Schwarz, 1948, for comparative illustrations.) His conclusions were similar to ours. He called attention to the less convex posterior hind tibial margin in *T. prisca* compared to other species. This is true for the left tibia (fig. 1) which, as indicated above, is somewhat deformed, perhaps by flowing of the amber. The visible part of the margin of the right tibia, however, is more convex, as in the related species.

A serious problem as to relationships within the genus *Trigona* and its relatives is convergence in external characters of workers. For example, Brooks and Michener (in press) showed that the African groups called *Liotrigona* and *Hypotrigona* differ greatly in the ground plan of the male genitalia and hidden sterna; it is difficult even to homologize some parts in detail. The genitalic characters show that each is related to other groups. But externally the workers of *Liotrigona* and *Hypotrigona* are extremely similar and the char-

acters that are supposed to separate them intergrade. The similarity of *T. prisca* and modern *Trigona* could also result from convergence. Unfortunately it is not possible to dissect out the sting rudiments and the like; placement in *Trigona* s. str. is indicated by the characters that one can see, except for number 6 in the above list. The toothed distal mandibular margin is an especially strong indication of the placement in *Trigona* s. str.

DISCUSSION

Since the Apidae have a long tongue, sheath like labial palpi, a corbicula for pollen carrying, diverse structures for gathering the pollen and transferring it to the corbicula (Michener et al., 1978), etc., it is regarded as a recently derived family of bees (specifically, as derived from the paraphyletic Anthophoridae; see Sakagami and Michener, 1987). The Meliponinae may be an early branch of the Apidae (Winston and Michener, 1977; Kimsey, 1984), but *Trigona* (*Trigona*) is one of the most derived groups of Meliponinae according to Wille (1979). We see no evidence in the characters used that indicate Wille was incorrect in this assessment; *Trigona* (*Trigona*) appears to have many apomorphies. (See Michener and Grimaldi, in prep., for further discussion of such matters.)

Since the fossil, like other apids, possesses many apomorphies relative to other families of bees, the origin of Apoidea must be considerably older than 80 mybp, probably Early Cretaceous (ca. 130 mybp). This extrapolated date may appear surprising, for the Apoidea are often considered to have appeared with the "flowering" of the angiosperms in the middle Cretaceous (Michener, 1979). There is, however, considerable fossil and biogeographic evidence that angiosperms arose by at least the earliest Cretaceous (Crane et al., 1986; Doyle et al., 1982). Thus an Early Cretaceous origin for the bees seems not only possible but probably necessary. In fact, the Mesozoic gymnosperm order Bennettitales had flowers with showy bracts (Doyle, 1978) and was probably insect pollinated, possibly visited by bees, before the Cretaceous.

By the time of *Trigona prisca*, New Jersey had a rich angiosperm flora. According to Dorf's (1952) compilation, of the 169 plant

taxa known from the Raritan Formation of New Jersey (Cenomanian to Turonian, 96–89 mybp) as macrofossils, 131 are angiosperms, many belonging to extant genera. Kimyai's (1966) work on the Raritan Formation plants was entirely palynological, and he found that 6–7 pteridophyte families were most heavily represented and the only angiosperms found were Palmae, Proteaceae, Ulmaceae, and Dicotyledones incertae sedis. (He also provided reasons for the discrepancy between studies of palynological and macrofossil evidence.) All indications are that at 80 mybp New Jersey was tropical or subtropical in climate and that angiosperms comprised a substantial portion of the flora. At least by middle Eocene there appear to have been intricate relationships between flowers and pollinators, probably bees, such as exist today, for middle Eocene malpighiaceae flowers appear to have had oil-producing glands like those of modern Malpighiaceae (Taylor and Crepet, 1987); the oil is collected by anthophorid bees to feed their larvae.

It is interesting that no bees or other aculeate Hymenoptera have been found in the Canadian amber (McAlpine and Martin, 1969), which is slightly more recent (ca. 72 mybp) than the New Jersey material. The amber from Manitoba, like some of the New Jersey material, also has an araucarian ir spectrum (Langenheim, 1969) and it matches the New Jersey amber in color, hardness, and fractal characteristics. It has been collected in great quantities and has been well surveyed for fossils.

ACKNOWLEDGMENTS

It is a pleasure to thank David Parris of the New Jersey State Museum, Trenton, for discussion of excavations of Cretaceous deposits in New Jersey; Donald Baird of Princeton University for discussion of relevant stratigraphy; and Joseph Peters, Mineralogy Department, American Museum of Natural History, who helped search the Columbia University collection for New Jersey amber and provided information on Alfred Hawkins. We are especially indebted to Curt W. Beck of the Amber Research Laboratory, Vassar College, Poughkeepsie, New York, for analyses of amber and permission to use his

conclusions. João M. F. Camargo of the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Estado de São Paulo, Brazil, provided useful comparative data and drawings of various species of *Trigona* s. str. Alvaro Wille of the Universidad de Costa Rica examined our drawings and the specimen and agreed with our interpretations. The following persons kindly read this or related manuscripts and contributed useful ideas or information: Peter Bernhardt of St. Louis University, William L. Crepet of the University of Connecticut, David L. Dilcher of Indiana University, James A. Doyle of the University of California at Davis, Jean H. Langenheim of the University of California at Santa Cruz, and Jerome G. Rozen, Jr., of the American Museum of Natural History. Joetta Weaver helped with editorial matters. C. Michener's participation was supported by National Science Foundation grant DEB82-12223.

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