THE FIRST FOSSIL DORYLINAE WITH NOTES ON FOSSIL ECITONINAE (HYMENOPTERA: FORMICIDAE)[1]

Mark B. DuBois [2, 3, 4]

ABSTRACT: Two army ant species, *Dorylus molestus* and *Neivamyrmex iridescens*, are reported from copal of undetermined age (possibly Upper Pliocene and Pleistocene respectively). The presence of such fossils is remarkable given the disposition of many such species to foraging underground. Until more precise dates for this material are available, historical and biogeographic implications of these fossils remain uncertain.

Ants are represented in the fossil record from Cretaceous through Pleistocene (Carpenter 1992; Bolton 1994). The currently recognized classification includes 16 extant subfamilies and four extinct subfamilies (Bolton 1994). A number of species are known from impressions in Tertiary shale (Carpenter 1930) and are mostly represented by reproductives. Many ants have been preserved in amber (Wheeler 1914; Mayr 1868; Wilson 1985) and are mostly represented by workers. Foraging workers were trapped in resins which became amber, while reproductives flying over bodies of water were drowned and buried in silt (which later became shale). Some species, such as *Stenamma berendti* (Mayr), are known only from reproductives preserved in amber (Mayr 1868). Most publications have concentrated on pre-Pleistocene fossils; a few have dealt with sub-fossils (Francoeur and Elias 1985; DuBois 1993). Limited work has been done on specimens preserved in copal, which is usually Pleistocene or Pliocene in age (Poinar 1992, Larsson 1978).

Most fossil worker ants belong to the extant subfamilies Formicinae, Dolichoderinae, Myrmicinae, and Ponerinae. Though some wing fragments have been tentatively identified as belonging to army ants, until recently, no fossil worker army ants were known. Wilson (1985) described *Neivamyrmex ectopus* from workers preserved in amber in the Dominican Republic. These fossils are thought to be late Oligocene or early Miocene in age. The rarity of fossil worker army ants is probably due to their behavior because many species principally forage underground.

Recently, I had the opportunity to study fossil ants of both Ecitoninae and Dorylinae preserved in copal. Although copal is considered much younger in

---

[1] Received Dec. 27 1996. Accepted January 31 1997.

[2] 116 Burton St., Washington, Illinois 61571-2509, U.S.A.

[3] Research Affiliate, Center for Biodiversity, Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, U. S. A.

[4] Send reprint requests to Washington, Illinois address.

age (Recent, Pleistocene or Pliocene), these specimens provide a link (geologically and biogeographically) with older material. Both species are briefly discussed below.

There appears to be a vast number of ant specimens preserved in copal from various deposits. The species discussed above represent a minuscule portion of available material. I hope this paper will stimulate further study of such fossils and subfossils. The precise age of the material discussed below is unknown (this is true for much copal). Although ages ranging from Recent through Pliocene have been proposed for various copal deposits, the stratigraphy of sites containing this material (and associations with micro-fossils) must be established to determine proper age.

Dorylus molestus (Gerstäcker)

This species can be distinguished from related *Dorylus* species through the following combination of characters: head with convex sides; posterior angles of head pointed; ventral lobe of petiole well developed (Raignier and Van Boven 1955). Specimens appear identical to modern forms (as described in Raignier and Van Boven 1955). Bill Gotwald examined selected specimens and concluded they were this species ("... the common driver ant of East Africa, especially Kenya and Tanzania.") (Gotwald, pers. comm.). Wheeler (1922: 740) gave the distribution of this species in Eastern Africa (including Mombassa, Mt. Kenia (2400 - 2800 m), Bura Mountains, Freretown, and Naivasha, Rift Valley).

Two hundred and seventy one specimens contained in 12 pieces of copal were examined. This material was collected along the Tanzania - Kenya border (Tanzania side, approximately 100 km south-west of Mombassa, Kenya). Individual pieces of copal were covered in caliche and found in a layer 11 m below the soil surface (Alan Graffham, pers. comm.). Specimen disposition is as follows. Lloyd Davis, Jr. provided two pieces of copal containing *Dorylus*. These have been returned to him. All remaining pieces discussed are from my personal collection and were obtained from Allen Graffham and other sources. Of these, one piece containing *Dorylus* has been donated to the British Museum of Natural History and another piece containing *Dorylus* has been donated to the Museum of Comparative Zoology.

Schluter and von Gnielinski (1987) indicated this copal was derived almost entirely from resin of *Hymenaea verrucosa* (Leguminosae: Caesalpinaceae). Deposition sites were listed as in the forest soil (primary), in the mangrove fringed estuary (secondary), and along the beach (tertiary).

These deposits are part of the Mikindani beds (Stockley 1928). Stockley (1928) assigned an age of Upper Pliocene. Poinar (1992) indicated this Tanzanian copal may be Pliocene in age (1.6 - 5 Ma). Schluter and von Gnielinski

(1987: 11) presented an age of Pleistocene, but cautioned that ". . . stratigraphically well defined associations of copal with index- or guide-fossils do not exist." von Gnielinski (pers. comm.) reiterated the uncertainty with the dating of copal from that region (Pleistocene or Pliocene could be argued). Additionally, Ken Anderson who is currently studying amber and copal deposits from around the world (pers. comm.) indicated these were "resins of undetermined geological age, but probably not of great antiquity."

Schluter and von Gnielinski (1987: 18) further stated: "Generally, it can be assumed that the fauna of the East African copal does not show significant differences from the fauna living today, i.e., all the trapped specimens represent recent species..." Although a number of insects have been reported from these deposits (including nine species of Hymenoptera), no ants have previously been reported (Schluter and von Gnielinski 1987).

Figures 4 through 8 illustrate typical features of these specimens. Figures 11 and 12 show the general appearance of these specimens within the copal. Other arthropods were preserved with the ants. Their state of preservation, coupled with problems in identification of many East African insects, did not permit precise identifications. Specimens include other ants (several male Ponerinae, two male Myrmicinae, three worker Dolichoderinae, one minor worker *Pheidole* sp., one worker *Crematogaster* sp.), four Chalcidoidea, one alate termite, and a number of flies, beetles, leafhoppers, and spiders. After examining the fossils in cross section, it appears a foraging column of driver ants became trapped on the sticky resin and were then covered with another resin flow.

Neivamyrmex iridescens Borgmeier

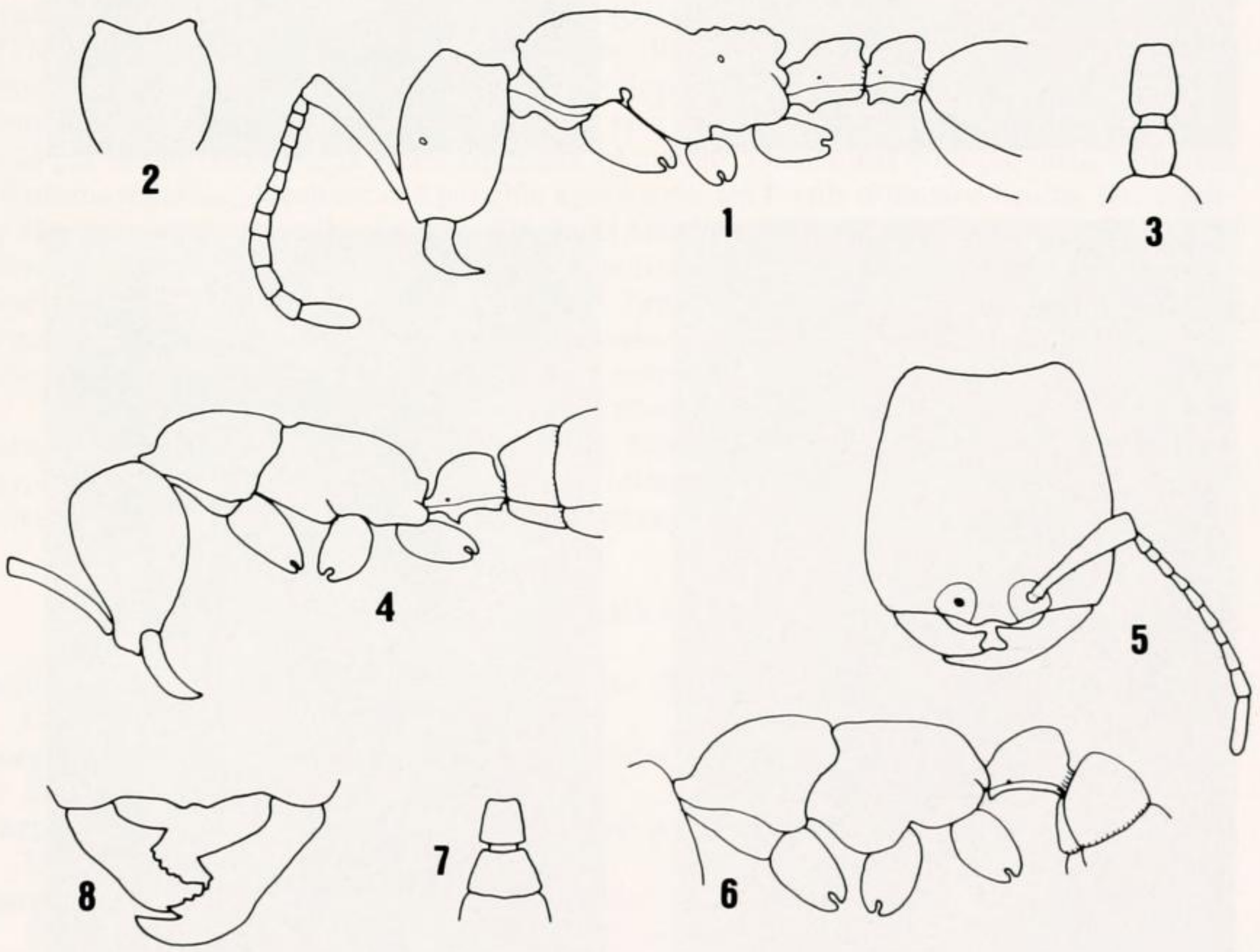
This species can be distinguished from related *Neivamyrmex* species (Borgmeier 1955 - Group VII) through the following combination of characters: postpetiole about five-sixths as long as high; head with violet reflections (difficult to see in fossil material); postpetiole about as long as wide, higher than long with posterior surface of node more steeply sloping than anterior surface; head smooth and distinctly shining; apex of scape closer to upper margin of head than eye level (Watkins 1976). Julian Watkins II identified the *Neivamyrmex* in one of these samples. He indicated the fossil is most similar to specimens of *Neivamyrmex iridescens* from Cundinamarca, Colombia in his collection. The only significant difference is a slightly longer than usual petiole. (Julian Watkins II, pers. comm.). Specimens key to *N. iridescens* using Watkins (1976) and fit the description provided by Borgmeier (1955: 540 - 542). This species is presently known from scattered localities: Panama, Guianas, Surinam, Bolivia, Colombia (Borgmeier 1955; Watkins 1976).

Four specimens contained in two pieces of copal were examined from Colombia. Disposition of specimens: these *Neivamyrmex* remain in my collec-

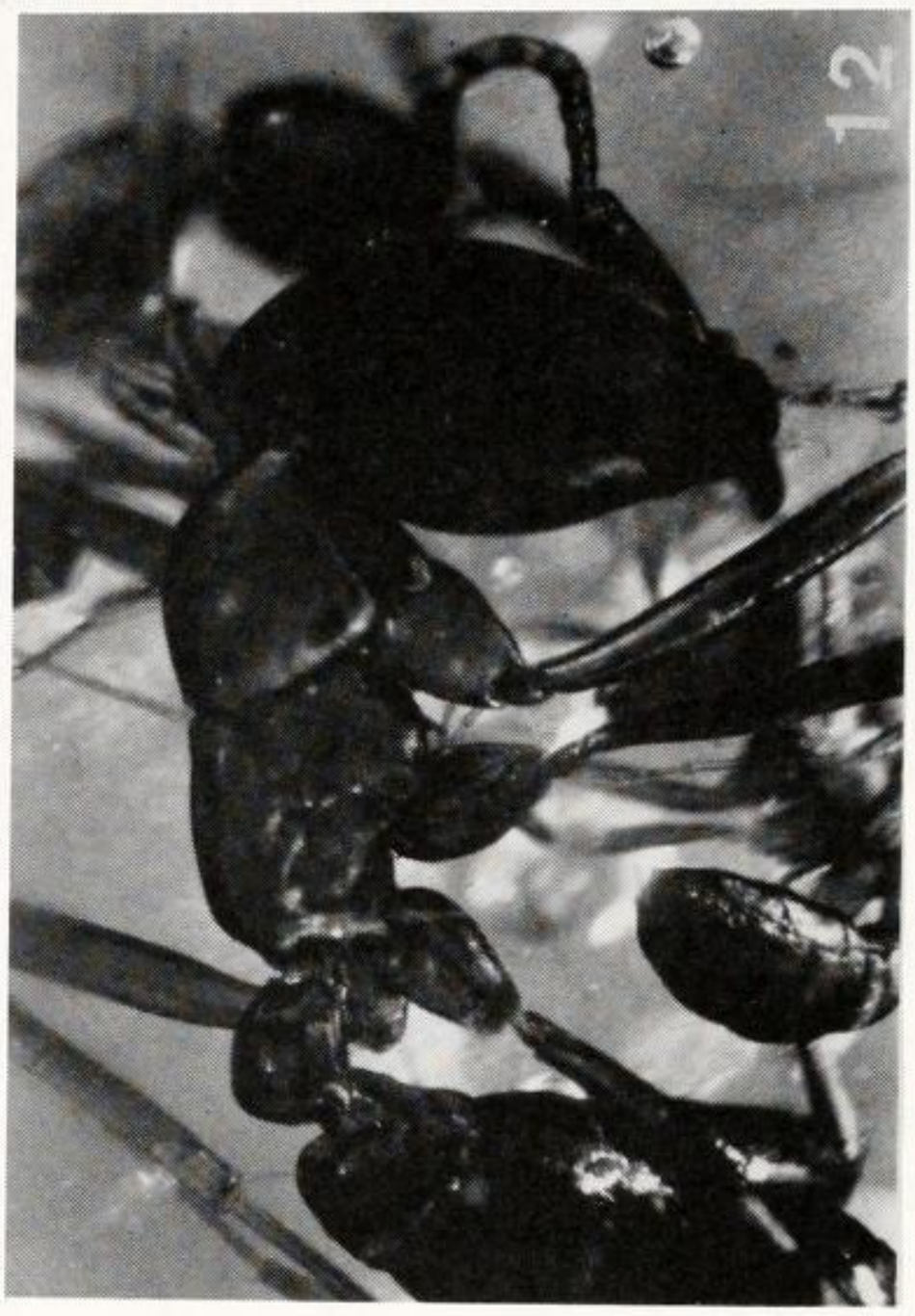
tion. They originally came from Colombia via Mr. Allen Graffham.

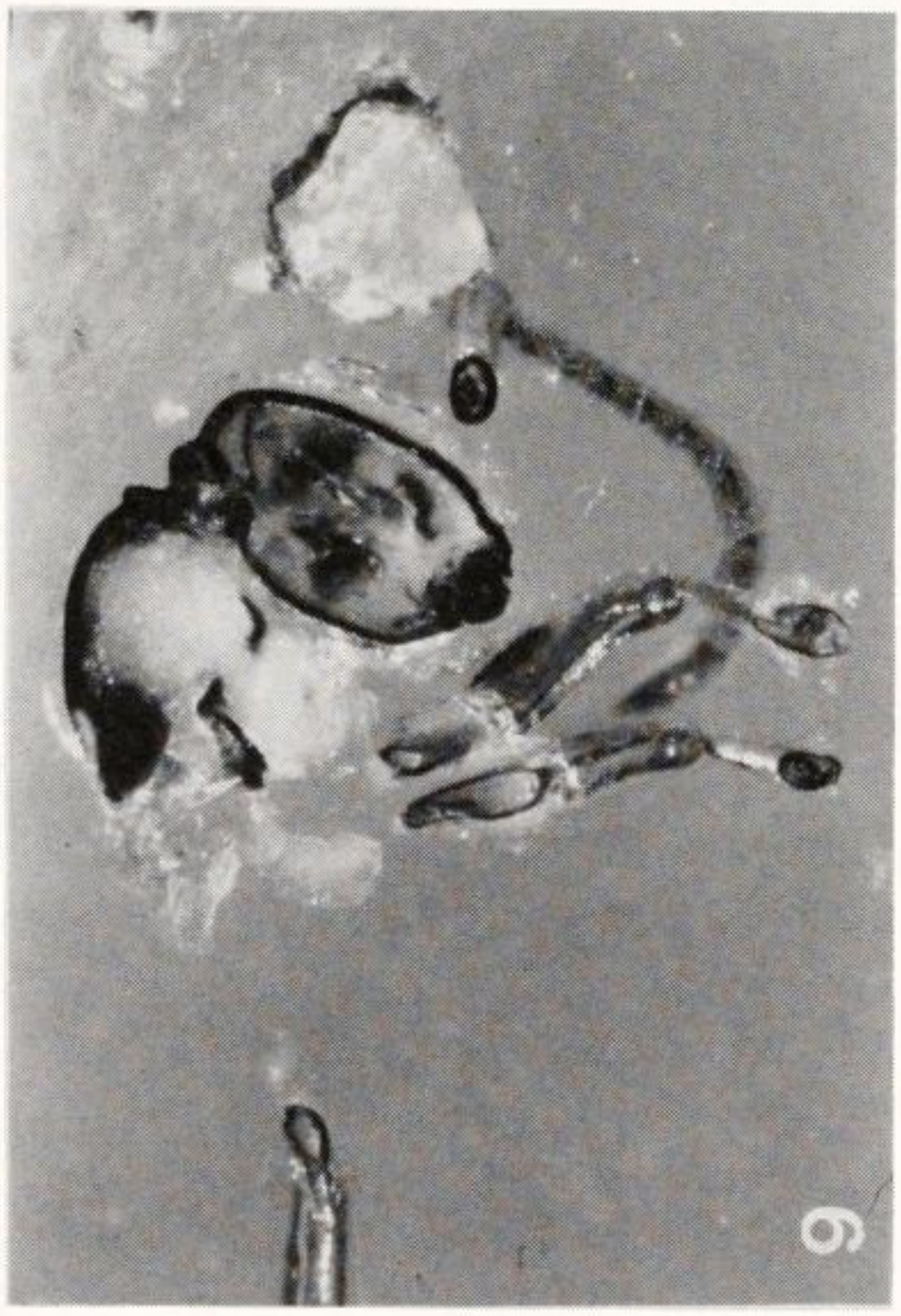
The specific locality for this material is unknown, but Schlee (1984) indicated this may be from "Peña Blanca." This material bears locality information of Santander Department, Colombia. Allen Graffham (pers. comm.) indicated it came from a roadcut and provided several photographs. He indicated that he doubts any deposition has occurred in this area for a very long time as it is quite mountainous with very steep slopes. I have examined fossil ants in copal from both Santandar and Boyaca departments. Most material was collected at a depth of 2 - 3 meters in Santandar and up to 10 meters in Boyaca. Poinar (1992) indicated all known Colombian material is of Pleistocene age. Ken Anderson (pers. comm.) also considered these were "resins of undetermined geological age, but probably not of great antiquity."

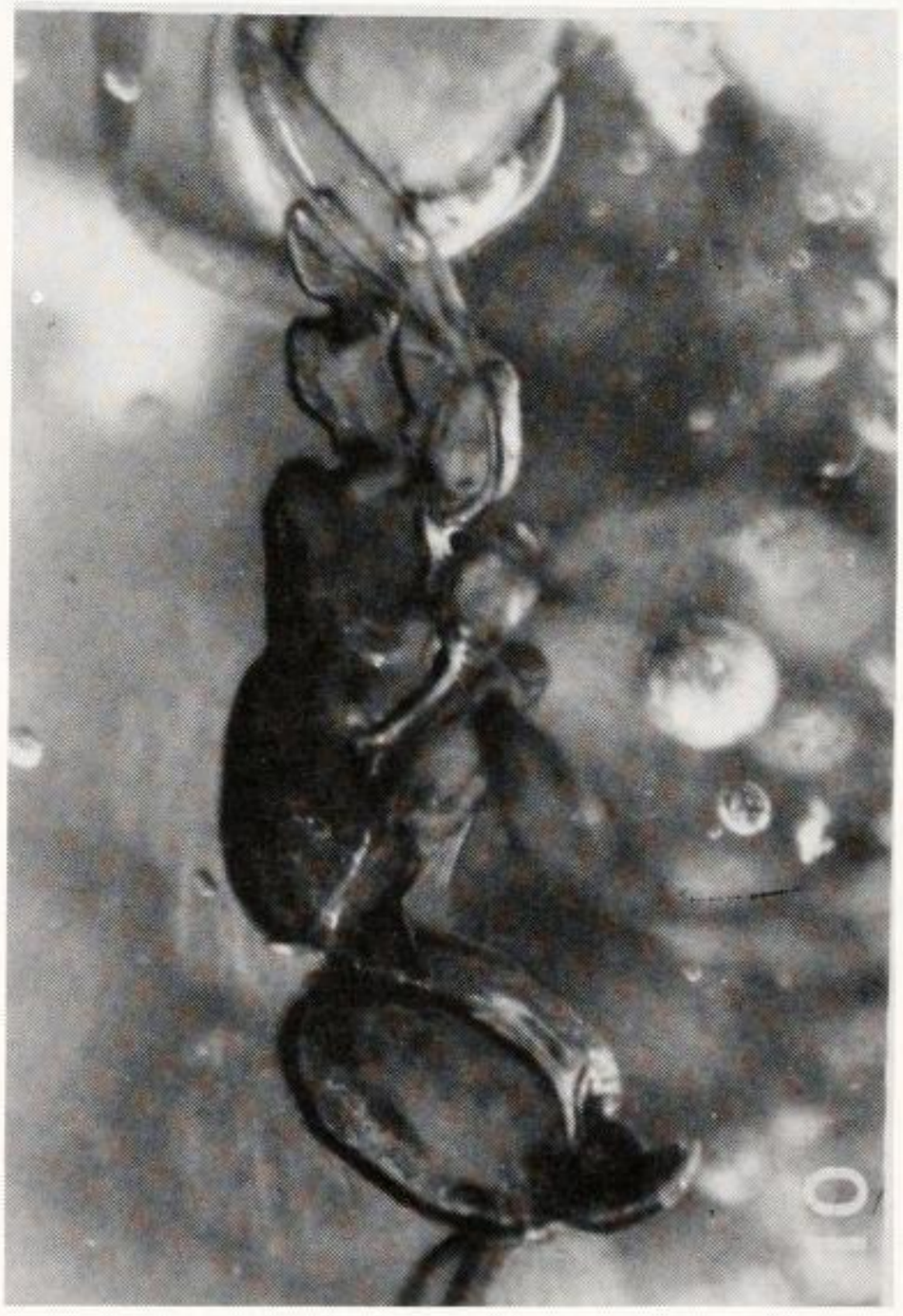
This copal is presumed to be derived from a species of *Hymenaea*, but details regarding this locality, deposition, and origin of this material are sketchy at best. It is not known to this author whether any species of *Hymenaea* live in



Figures 1 - 8. Scale varying. Legs, pilosity, and sculpture omitted. Figures 1 - 3. *Neivamyrmex iridescens*. Figure 1. Worker, lateral view. Figure 2. Head, profile of occipital vertex. Remainder of head obscured by position within copal. Figure 3. Petiole and postpetiole, dorsal view. Figures 4 - 8. *Dorylus molestus*. Figure 4. Minor worker, lateral view. Figure 5. Major worker, head, full face view. Figure 6. Major worker, lateral view. Figure 7. Worker, petiole and postpetiole, dorsal view. Figure 8. Major worker, mandibles and anterior clypeal margin.







Figures 9 - 12. Photographs of fossilized army ants and driver ants. Scale varying. Figures 9 - 10. *Neivamyrmex iridescens*. Figure 9. Damaged specimen (damaged previously by polishing). Figure 10. Worker, lateral view. Figures 11 - 12. *Dorylus molestus*. Figure 11. Numerous workers in copal. Figure 12. Major worker, lateral view.

the area today.

Figures 1 - 3 show typical features of these specimens. Figures 9 and 10 depict the general appearance of these specimens within the copal. Other arthropods were preserved with the ants. Their state of preservation coupled with problems in identification of South American insects did not permit precise identifications. Specimens include two other ants (one minor worker *Pheidole* sp., one worker *Anochetus* sp.), one Chalcidoidea, one fly, one worker termite, one set of termite wings, and one spider. Since only four ants were trapped, it is possible that they were on the periphery of a foraging column which encountered the resin.

ACKNOWLEDGMENTS

This paper is dedicated to the memory of the late Frank M. Carpenter (Museum of Comparative Zoology, Harvard Univ. advisor and friend for the past 2 decades). His encouragement was appreciated.

My continuing thanks is extended to Jeri and Benjamin DuBois for their support and understanding. They make it all possible. Lloyd Davis (Gainesville, Florida) provided some specimens of *Dorylus*. Julian Watkins II (Baylor University, Waco, Texas) identified some specimens of *Neivamyrmex iridescens*. Bill Gotwald (Utica College of Syracuse University, Utica, New York) identified some specimens of *Dorylus molestus*. Merrill Foster (Bradley University, Peoria, Illinois) put me in contact with Allen Graffham (Ardmore, Oklahoma) who provided numerous comments regarding localities and possible ages for the ant fossils discussed herein. The majority of fossil ants discussed herein also came from Allen Graffham. F. von Gnielinski (Geological Survey of Queensland, Brisbane, Queensland) provided insights into the age and conditions of deposition of the African copal. Thanks also to Ken Anderson (Argonne National Laboratory, Argonne, Illinois) who reviewed his current analyses of assigning ages to copal and amber worldwide and discussed his view of the age of these resins with me.

This paper has been reviewed by Wallace LaBerge and Don Webb (Illinois Natural History Survey, Champaign, Illinois), Julian Watkins II, Stefan Cover (Museum of Comparative Zoology, Harvard University), and three anonymous reviewers. Where possible, I have tried to incorporate their comments. I accept responsibility for any remaining errors or omissions.

LITERATURE CITED

Bolton, B. 1994. Identification Guide to the Ant Genera of the World. Harvard Univ. Press, Cambridge, MA. 222 pp.

Borgmeier, T. 1955. Die Wanderameisen der Neotropischen Region (Hym. Formicidae). Studia Entomol. 3: 1 - 716.

Carpenter, F. M. 1930. The fossil ants of North America. Bull. Mus. Comp. Zool., Harvard Univ. 70: 1 - 66.

Carpenter, F. M. 1992. Part R, Arthropoda 4, Volumes 3 and 4, Superclass Hexapoda. In Kaesler, R. J., E. Brosius, J. Keim, J. Priesner (eds.), Treatise on Invertebrate Paleontology, xxii + 655 p. 1489 figs. Univ. Kansas Press, Lawrence, KS. [Formicidae, pp. 490 - 495].

DuBois, M. B. 1993. What's in a name? A clarification of *Stenamma westwoodi*, *S. debile*, and *S. lippulum* (Hymenoptera: Formicidae: Myrmicinae). Sociobiology 21(3): 299 - 334.

Francoeur, A. and S. A. Elias. 1985. *Dolichoderus taschenbergi* Mayr (Hymenoptera: Formicidae) from an early Holocene fossil insect assemblage in the Colorado Front Range. Psyche 92 (2-3): 303 - 307.

Larsson, S. G. 1978. Baltic amber – a palaeobiological study. Entomonograph Vol. 1. Klampenborg, Denmark. 192 pp.

Mayr, G. 1868. Die Ameisen des baltischen Bernsteins. Beitr. Naturk. Preussens 1: 1 - 102.

Poinar, G. O., Jr. 1992. Life in Amber. Stanford Univ. Press, Stanford, Calif. xiii + 350 pp., 8 pl.

Raignier, A. and J. Van Boven. 1955. Étude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera Formicidae). Ann. Musée Royal Congo Belge n.s. 4 (Sci. Zool.) 2: 1 - 359.

Schlee, D. 1984. Notizen uber einige Bernsteine und Kopule aus aller Weit. Stuttg. Beitr. Natkde. 18: 29 - 38.

Schluter, T. and F. von Gnielinski. 1987. The East African Copal Its geologic, stratigraphic, palaeontologic significance and comparison with fossil resins of similar age. Nat. Mus. Tanzania Occ. Pap. 8: 1 - 34.

Stockley, G. M. 1928. Report on the geology of the Zanzibar Protectorate. 126 pp. Zanzibar.

Watkins, J. F., II. 1976. The identification and distribution of New World army ants (Dorylinae: Formicidae). Markham Press Fund Baylor Univ. Press, Waco, TX, x + 102 pp.

Wheeler, W. M. 1914 (1915). The ants of the Baltic amber. Schriften der Physikalisch Ökonomischen Gesellschaft zu Königsberg 55: 1 - 142.

Wheeler, W. M. 1922. Ants of the American Museum Congo Expedition, a contribution to the myrmecology of Africa, I: On the distribution of the ants of the Ethiopian and Malagasy regions; II: The ants collected by the American Museum Congo Expedition; VII: Keys to the genera and subgenera of ants; VIII: A synonymic list of the ants of the Ethiopian region; IX: A synonymic list of the ants of the Malagasy region. Bull. Amer. Mus. Nat. Hist. 45(1): 13 - 27, 39 - 269, 631 - 710, 711 - 1004 1005 - 1055.

Wilson, E. O. 1985. Ants of the Dominican amber (Hymenoptera: Formicidae). 2. The first fossil army ants. Psyche 92 (1): 11 - 16.