The First Mesozoic Ants

Abstract. *Two worker ants preserved in amber of Upper Cretaceous age have been found in New Jersey. They are the first undisputed remains of social insects of Mesozoic age, extending the existence of social life in insects back to approximately 100 million years. They are also the earliest known fossils that can be assigned with certainty to aculeate Hymenoptera. The species,* Sphecomyrma freyi, *is considered to represent a new subfamily (Sphecomyrminae), more primitive than any previously known ant group. It forms a near-perfect link between certain nonsocial tiphiid wasps and the most primitive myrmecioid ants.*

Until now the earliest known fossils of ants, and of social insects generally, have been Eocene in age (*1*). Large assemblages of ant species, most belonging to living tribes and even genera, occur in the Baltic Amber (Oligocene), the Sicilian and Chiapan ambers (Miocene), and the Florissant and Ruby Basin shales (Miocene) (*2*). The diversity of these faunas and the advanced phylogenetic position of many of their elements have long prompted entomologists to look to the Cretaceous for fossils that might link the ants to some ancestral nonsocial wasp group, but until now, with one doubtful exception, no relevant fossils have turned up.

The exception is the hymenopterous forewing described by Sharov (*3*) as *Cretavus sibiricus*, from the Upper Cretaceous of Siberia. This wing is rather similar to that of the wasp family Plumariidae, and also approaches a reasonable possible precursor pattern for the venations of known primitive ants. However, we have no guarantee that venational characters evolved concordantly with other, more truly diagnostic body characters, so we cannot even regard it as certain that *Cretavus* is an aculeate.

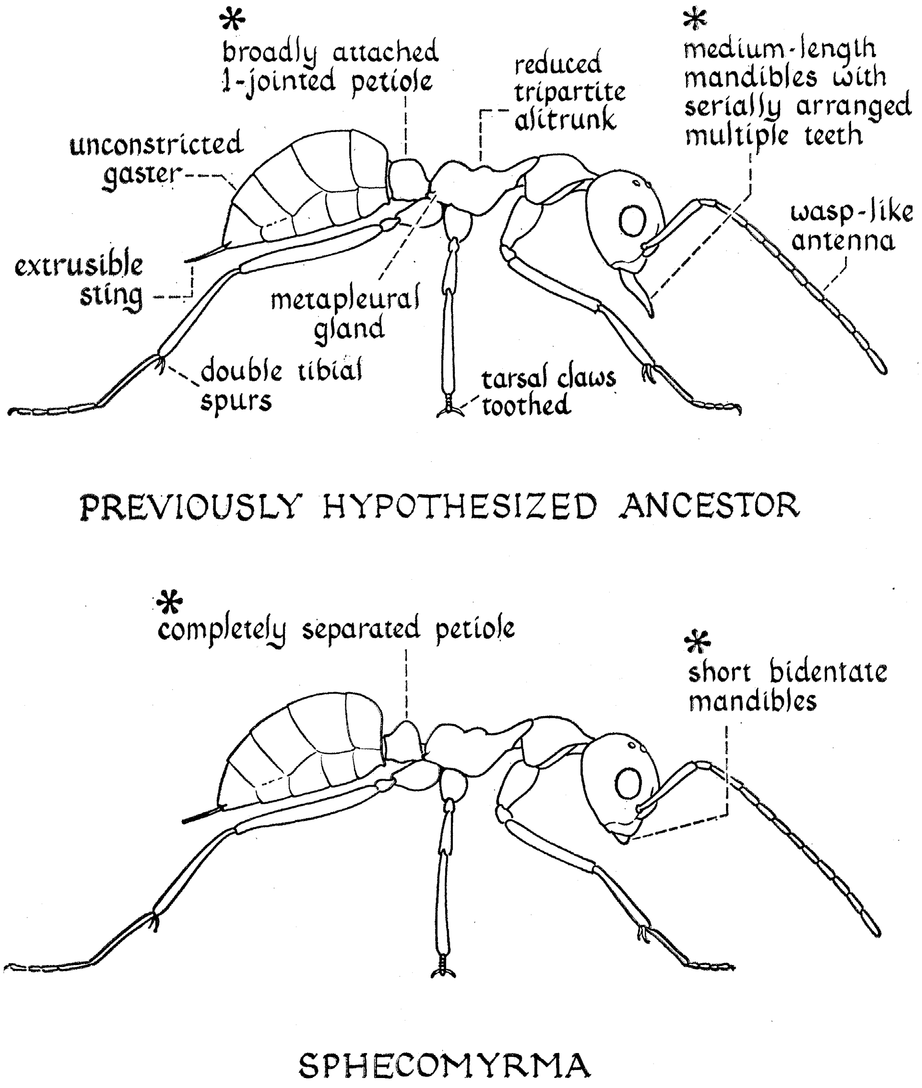

Fig. 1. A comparison of the main features previously hypothesized by the authors to characterize the external morphology of the ancestral ant, and *Sphecomyrma* itself. The minor details of body form are arbitrarily made the same. In the drawing of *Sphecomyrma*, the starred character states indicate where our phylogenetic hypothesis proved in error.

Cretaceous amber from Canada and Alaska contains a moderate number of insects (*4*), but no ants or aculeate Hymenoptera of any kind are present among them (a fact now suggesting that the Canadian amber, which has never been precisely dated within the Cretaceous, may have been formed in an earlier part of the period). Amber securely dated to the lower part of the Upper Cretaceous is fairly common from Maryland to New Jersey in deposits of the Magothy Formation, but until recently almost no insect inclusions had been reported. In 1965, Mr. and Mrs. Edmund Frey (*5*), mineral collectors of Mountainside, New Jersey, found a lump of amber in clay of the same formation at the base of seaside bluffs at Cliffwood, New Jersey. The fragile lump broke into pieces, and two of these bear insects, including two well-preserved worker ants.

The two specimens appear to belong to the same species; one is shown in the cover photograph. We judge this species, *Sphecomyrma freyi*, to be by far the most primitive member of the Formicidae (ants) yet discovered. It is sufficiently removed from all other ants to be received into a distinct subfamily, the Sphecomyrminae. The most distinctive morphological features, and our assessment of their phylogenetic significance, can be summarized as follows.

1) The head capsule resembles that of a generalized aculeate wasp or ant. The clypeus and frontal carinae are antlike, but are of such simple conformation as not to depart significantly from these structures in some aculeate wasp groups. We regard the large, convex form of the compound eyes and their placement near the center of the sides of the head as primitive characters for aculeates generally. The presence of three large ocelli is certainly primitive.

2) The mandibles are short, curvilinear, and bidentate, and closely resemble those of certain species of several existing aculeate wasp families.

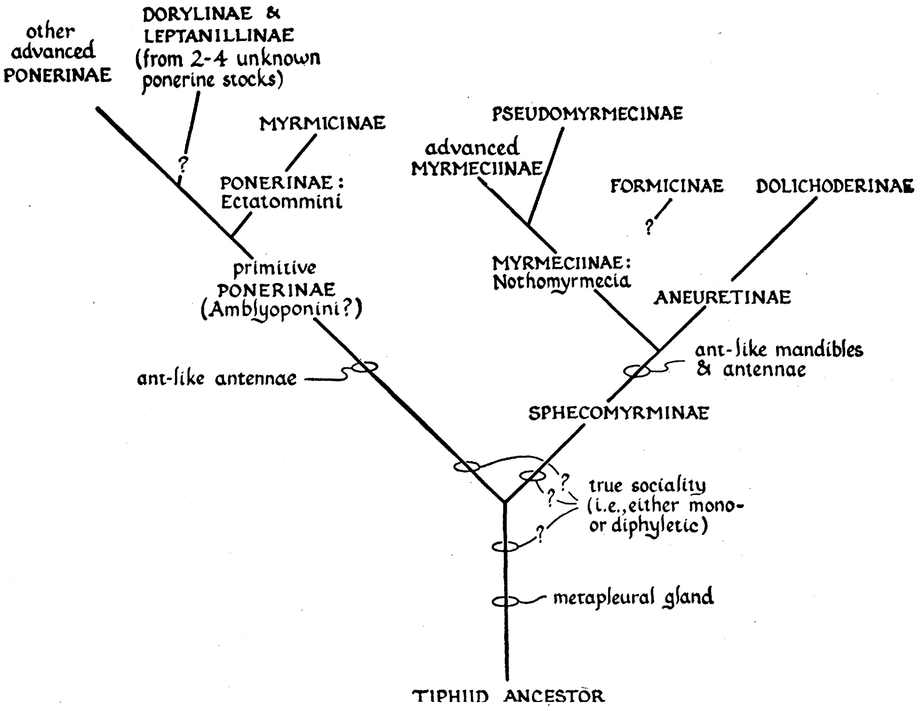

Fig. 2. A new hypothetical cladogram of the ant subfamilies taking into account the morphology of *Sphecomyrma*.

3) The antennal funiculi are long and filiform, a trait more wasplike than antlike. The antennal scapes (basal segments) are elongate, a characteristic of ants generally but exceptional among other aculeates; still, the scapes are shorter than is usual for worker ants.

4) The alitrunk (thorax + propodeum) is more completely sutured, and therefore more primitive, than that of any other worker ant, and is almost identical with that of the wingless females of the tiphiid genus *Methocha*. Prothorax, mesothorax, and metanotopropodeum are separated each from the next by two complete and possibly flexible sutures; and the mesonotum is composed of well-defined, convex scutum and scutellum, separated by a narrow sunken area. In fact, the only major alitruncal difference from *Methocha* is the presence in *Sphecomyrma* of apparently well-developed metapleural glands, which are peculiar to the Formicidae.

5) The single-segmented petiole, narrowly constricted behind, is an ant character state; the absence of a constriction in the gaster and the presence of a well-developed, extrusible sting are states shared by most wasps and primitive myrmecioid ants.

6) The legs show two character states that we have long regarded as primitive for ants: two spurs on each tibial apex of the middle and posterior legs, and toothed tarsal claws.

In summary, *Sphecomyrma* presents a mosaic of wasplike and antlike character states. There are nevertheless enough truly antlike traits to place *Sphecomyrma* within the Formicidae, where the most similar (but still quite different) forms are the living myrmeciine *Nothomyrmecia macrops* of Australia and the primitive aneuretine Dolichoderinae, such as *Paraneuretus* and *Protaneuretus*, of Oligocene age, described by Wheeler (*2*). These are primitive forms in the myrmecioid complex (*6*).

It is interesting to compare our earlier conception of the archetypal ant with the actuality presented by *Sphecomyrma*. This is done in pictorial form in Fig. 1. It can be seen that our vision of what was yet to be revealed differs from *Sphecomyrma* in only one essential respect: we guessed that antlike mandibles evolved before the antlike "waist" (petiole), but the reverse actually proved to be the case.

Compared with living wasp genera, *Sphecomyrma* appears to come closest to the tiphiid genera *Methocha* (Methochinae) and *Rhagigaster* (Thynninae) (*7*). One interesting aspect of the morphology of *Sphecomyrma* is that in "ant characters" it does fall so close to the myrmecioid complex of genera, yet bears so little resemblance to *Amblyopone* and other genera of the Ponerinae previously regarded as nearly as primitive as the myrmecioids. The possibility is thus raised that divergence between myrmecioid and poneroid lines may already have taken place by the time *Sphecomyrma* lived. However, the presence of the complex metapleural gland in *Sphecomyrma* and all other primitive ants speaks for a monophyletic origin of the Formicidae from tiphiid ancestors. The function of the metapleural gland is still unknown, but if it turns out to mediate some phase of social behavior, then monophyletic origin of social life would be strongly implied for the ants as we know them. These new considerations are incorporated into a cladogram of the ant subfamilies (Fig. 2).

Finally, the origin of social life in the insects has now been put back from the Eocene, about 60 million years ago, to the middle or lower part of the Upper Cretaceous, about 100 million years ago. It may be true that social life in insects is not much older that that. *Sphecomyrma* is evidently only a little changed from tiphiid wasps, and it is possible that this relatively slight transformation indicates a correspondingly short period of social evolution. Perhaps as more hymenopteran fossils become available from the New Jersey and similar ambers, new light will be shed on the origin of the ants.

A fuller account of *Sphecomyrma* and its phylogenetic implications, together with a formal taxonomic description, is published elsewhere (*8*).

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References and Notes

1. The oldest Eocene ant fossil is *Eoponera berryi*, based on a forewing from the Wilcox Clay of Tennessee; F. M. Carpenter, *J. Wash. Acad. Sci.* **19**, 300 (1929).
2. The Baltic Amber ants were monographed by W. M. Wheeler [*Schrift. Phys.-ökon. Ges. Königsberg* **55**, 1 (1914)]; and the Florissant ants by F. M. Carpenter [*Bull. Mus. Comp. Zool. Harvard* **70**, 1 (1930)]. W. L. Brown, Jr. (unpublished) has examined the few available ant fossils from the Ruby Basin (Montana) shales and found them to match the dominant Florissant species; he has also cursorily examined the ants of the Chiapas Amber and found them related to those of the Florissant and the existing tropical Mexican faunas.
3. A. G. Sharov, *Dokl. Akad. Nauk* **112**, 943

(1957). For a comparison with wings of ants and Plumariidae, see W. L. Brown, Jr., and W. L. Nutting, *Trans. Amer. Entomol. Soc.* **75**, 113 (1950).

4. F. M. Carpenter, J. W. Folsom, E. O. Essig, A. C. Kinsey, C. T. Brues, M. W. Boesel, H. E. Ewing, *Univ. Toronto Stud. Geol. Ser.* **40**, 7 (1934).
5. We gratefully acknowledge the splendid cooperation of Mr. and Mrs. Frey, as well as the intermediary aid of Dr. Donald Baird of Princeton University and Mr. David Stager of the Newark Museum.
6. W. L. Brown, Jr., *Insectes Sociaux* **1**, 21 (1954).
7. We acknowledge the aid of H. E. Evans, who gave us the benefit of extensive comparisons of *Sphecomyrma* characters with those of various wasp genera. In classifying tiphiids, we have arbitrarily followed the system of V. S. L. Pate, *J. N.Y. Entomol. Soc.* **55**, 115 (1947).
8. E. O. Wilson, F. M. Carpenter, W. L. Brown, Jr., *Psyche*, in press.

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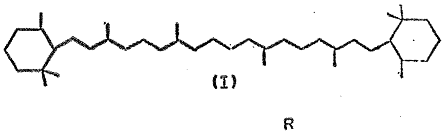
Perhydro-β-Carotene in the Green River Shale

Abstract. *Several triterpenes and the tetraterpene perhydro-β-carotene have been identified in the branched-cyclic hydrocarbon fraction of this Eocene shale. The analytical procedure included thiourea adduction followed by combined gas chromatography and mass spectrometry.*

The identification of an optically active triterpene, gammacerane, in the Green River Oil Shale bitumen (*1*) and the isolation of three pentacyclic—but as yet unidentified—triterpenes from an optically active petroleum distillate from a Nigerian crude oil (*2*) have provided further evidence for the biogenesis of some of the organic matter indigenous to these geological situations. Similar chemical markers are the acyclic isoprenoid hydrocarbons, phytane and pristane, along with their corresponding acids, reported for the Green River shale (*3, 4*) and a California petroleum (*5*). The presence of these compounds is significant because they appear to be stable geologically, and because the developed analytical methods are now available for other specimens such as Precambrian sediments, meteorites, and returned lunar samples.



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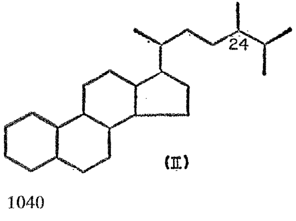

(II)

The Green River Formation is known to have suffered little from geological stresses such as temperature, pressure, and fracture (*6*). From this richly organic deposit resulting from fresh water lakes of Eocene age (50 to 60 million years old), we have now identified perhydro-β-carotene, $C_{40}H_{78}$ (I). This is the first time that a tetraterpene has been isolated from a geological sample, though sesqui-, di-, and triterpenes have been identified in this and other sediments (*7*). Thus the presence of a tetraterpene completes the typical isoprenoid pattern found in plants today. In fact, almost all of the peaks observed in the gas chromatograms of the Green River shale alkanes are accountable as hydrocarbons of obvious biological origin. The precise history and the apparent stability of these hydrocarbons under geological conditions require further study.

A sample of Green River shale (600 g) from Rifle, Colorado, (*8*) was crushed to 1-cm (about) chunks and cleaned with a mixture of benzene and methanol (1 : 1). After being dried in air, the rock was pulverized to pass 100 mesh and then extracted in 50-g amounts with *n*-hexane (200 ml). Three extractions with fresh solvent were completed for each batch of rock. The suspensions were subjected to ultrasonic vibration for 20 minutes, each time, before the mixture was centrifuged to permit decanting of the solvent. After the hexane was evaporated the extracted organic matter (5.3 g) was chromatographed on an alumina column (85 by 5 cm), and the hydrocarbon fraction was eluted with *n*-hexane (1 liter). The first 600 ml contained the desired hydrocarbons, as monitored by thin-layer chromatography (silica gel G, hexane developed). This fraction was dissolved in isooctane and passed through a 5-Å molecular sieve (Linde, activated at 320°C under a stream of dry N_2 for 24 hours) to remove the normal alkanes. The branched-cyclic alkanes (1.4 g) remaining in the isooctane were further separated by formation of adduct with thiourea (*9*). For formation of adducts, alkanes (10 mg) were dissolved in chloroform (1 ml) in a Craigee tube. A saturated solution of thiourea in methanol (1 ml) was added, the mixture was heated until the solution was homogeneous, cooled, and held at room temperature for 24 hours; during this time adduct crystals formed. In appearance, the hexagonal adduct needles were distinct from the usual tetragonal thiourea crystals (*10*). The needles were collected, washed twice with cold chloroform, and then dissolved in hot water to release the trapped (adduct) hydrocarbons. The ratio of adduct to nonadduct hydrocarbons in the branched-chain cyclic fraction was 1:7.

The gas chromatograms of the adduct and nonadduct fractions are presented in Fig. 1. The acyclic isoprenoid hydrocarbons reported previously (*3*) are adducted almost completely, but rather unexpectedly some cyclic isoprenoids are also included by thiourea. Both fractions were then separated further by preparative gas-liquid chromatography (3 percent SE-30, 6-m by 6-mm column). Repeated collection of single chromatographic peaks in capillary tubes provided sufficient sample for infrared spectroscopy (micro) and combined gas chromatography–mass spectrometry (GCMS). Several significant peaks in the triterpene region were analyzed in the LKB-9000 gas chromatograph–mass spectrometer (1 percent SE-30, 3-m by 3-mm column). Cholestane (II, R=H), ergostane (II, $R=CH_3$), and sitostane (II, $R=C_2H_5$) were identified in the adduct fraction. Ergostane is present in the largest amount. However, most of the sitostane remains in the nonadduct, and accounts for the component present in the largest amount in the triterpenes isolated from the shale. Further identification of these components awaits extended purification and comparison with standard samples, many of which are not available at the present time.

Before this investigation, substituted naphthalenes and anthracenes were the largest molecules known to be included by the thiourea channel (*11*). The adduction of cholestane under the same experimental conditions as the adduction of acyclic isoprenoids has been confirmed by x-ray analysis (*12*). The adduct crystal of cholestane shows predominantly the same reflections as does that of the pristane adduct, differing thereby from the thiourea crystal. The weak intensities of the reflections from the organic guest molecules compared with those from the thiourea presently preclude the determination of the way in which the cholestane molecule is included in the thiourea chan-