A Study of the Weaver Ant, Oecophylla smaragdina (Fab.)[1]

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Recent attention to certain ants of the Asiatic fauna has directed particular interest toward the genus *Oecophylla;*[2] specifically, to *Oecophylla smaragdina* (Fabricius). In reviewing available papers on the species, and in our investigations of collected material, certain features have seemed noteworthy. Also, we were made aware of the scarcity and remoteness of literature concerned with this most interesting genus. For these reasons, in presenting recent observations, a general report on the genus is included, although particular reference is devoted to *Oecophylla smaragdina.*

Taxonomy.—The following description of the genus is taken from Wheeler's report on the *Ants of the Belgian Congo* (1922).

"Worker medium-sized, slender, slightly polymorphic. Head rather large, broader behind than in front, with rounded sides and posterior corners and semicircularly excised occipital border, very convex above. Eyes large, convex, broadly elliptical, situated in front of the middle of the head. Ocelli absent. Palpi very short, maxillary pair 5-jointed, labial pair 4-jointed. Mandibles long and large, triangular, with nearly straight lateral borders, a very long curved apical tooth and numerous short denticles along the straight apical border. Clypeus very large and convex, but not distinctly carinate, its anterior border entire or very feebly sinuate in the middle, depressed and projecting over the bases of the mandibles. Frontal area rather large, subtriangular; frontal carinae moderately long, subparallel. Antennae very long, 12-jointed, the scapes inserted some distance from the posterior corners of the clypeus, rather abruptly incrassated at their tips; the first funicular joint very long and slender, longer than the second and third together, joints 2 to 5 much shorter, subequal, slender, the remaining joints except the last, shorter and distinctly thicker. Thorax long and narrow; pronotum longer than broad, evenly convex above, narrowed and colliform anteriorly; mesonotum anteriorly long and constricted, subcylindrical, suddenly broadened behind where it joins the small, short, unarmed epinotum, which is rounded and convex above and without distinct base and declivity. Petiole long and slender, much longer than broad, subcylindrical, with a very low rounded node near its posterior end, its ventral surface near the middle more or less convex, its posterior border on each side with a small rounded, projecting lamella, appearing like an acute tooth when the segment is viewed from above. Gaster short, broadly elliptical, its first segment suddenly contracted to the petiole, the tip rather pointed. Legs very long and slender; claws, pulvilli, and last tarsal joint enlarged. Gizzard with long slender sepals, which are not reflected at their anterior ends."

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2 Described by F. Smith, Journ. Proc. Linn. Soc. Lond., Zool., Vol. 5, p. 102, 1861.

Taxonomically, the genus consists of two distinct species with their subspecies and varieties. One of these is *Oecophylla smaragdina* (Fab.) with two subspecies, *subnitida* Emery and *virescens* (Fab.) and with its three varieties, *selebensis* Emery, *gracilior* Forel and *gracillima* Emery. The other species is *Oecophylla longinoda* (Latreille) with four varieties: *textor* (Santschi), *rubriceps* (Forel), *annectans* Whlr. and *fusca* (Emery). These members of the genus are easily separated by Wheeler's key (1922) as follows:

1. Petiole very slender, its stigmata seen from above very prominent, its ventral surface nearly straight or very feebly convex in profile (*smaragdina*) 2
   Petiole stouter and higher, its stigmata seen from above not prominent, its ventral surface strongly convex in profile (*longinoda*) 7
2. Body ferruginous or testaceous 3
   Gaster and sometimes the head pea-green, head more rounded and less truncated behind; size smaller, petiole somewhat shorter (Queensland, New Guinea, the Islands Aru and Key) .....subspecies *virescens* (Fab.)
3. Integument opaque or subopaque 4
   Integument more or less distinctly shining 5
4. Color ferruginous (India, Ceylon, Cochin China, Indonesia) ....*smaragdina* (typical)
   Smaller and more testaceous, mesonotum and petiole a little narrower (Java) ....var. *gracilior* Forel
5. Large forms, integument slightly shining (Papua, Philippines, Melanesia) ....subspecies *subnitida* Emery
   Smaller forms, integument more shining 6
6. Body very shining and slender, color testaceous, head rather elongate ....var. *gracillima* Emery
   Less shining and less slender, head shorter (Celebes) .....var. *selebensis* Emery
7. Ferruginous or testaceous throughout 8
   Brown or black 9
8. Color ferruginous (West Africa) .....*longinoda* (typical)
   Color paler, more testaceous, petiole shorter, head slightly broader, apical tooth of mandibles shorter (Zanzibar) .....var. *textor* (Santschi)
9. At least the thorax and mandibles black 10
   Body rather uniformly brown (Belgian Congo) ....var. *annectens* Wheeler
10. Head dull red, gaster often brownish (Belgian Congo) .....var. *rubriceps* (Forel)
    Head and gaster black or dark brown (Belgian Congo, Nigeria, Liberia, Cameroon, Spanish Guinea) .....var. *fusca* (Emery)

Distribution.—A tabulation of records shows that the genus is confined to the Old World Tropics, ranging over the Indo-Malayan, Papuan and Ethiopian regions but does not occur in Madagascar. *O. smaragdina,* with its subspecies and varieties, ocurs in the Ethiopian region. At one point in his discussion Wheeler remarks, "Several authors have cited the true *smaragdina* from east Africa. Unfortunately I have little material from that region and what I have is certainly *longinoda,* presumably belonging to *textor,* though this variety seems to me to be poorly characterized and possibly not distinct from the typical form of the species. I am unable to say, therefore, whether *Oecophylla smaragdina* actually occurs on the African Continent."

Dr. M. R. Smith[3] has stated that he believes the form most commonly recorded from Australia to be *Oecophylla smaragdina* in the broad sense and has kindly furnished us with a specimen of the subspecies *virescens* in the collection of Pergande and bearing the locality label "Central Australia."

Dodd (1902) has collected the species in Australia and has reported on *Notes on the Queensland Green Tree Ant,* doubtless in reference to *Oecophylla smaragdina* subsp. *virescens.*

Döflein (1905) gives interesting acocunts of the species from Ceylon and mentions records from western India at Bombay.

Mr. Fredric Smith (1864), past assistant in zoology at the British Museum, listed *Oecophylla smaragdina* from the islands of the Eastern Archipelago; specifically, the islands of Mysol, Timor, Waigion; Gilolo; Bachian; Dory; Aru; Borneo; the Philippines; and from Java, these records constituting a part of the report on the Hymenoptera collected by Mr. A. R. Wallace in the Eastern Archipelago. In a following report (1864) Smith adds Malacca, China, Celebes and Sumatra. He further states: "I have considerable doubts of its (*O. smaragdina*) being really specifically distinct from the African species *Oecophylla virescens,* which insect also occurs in Australia."

Other writers have referred to the "red tree ant" of the old world tropics and have listed the genus from Australia, India and Africa.

Although Forel (1894) states, ". . . *Oecophylla smaragdina,* one of the most common ants of tropical Africa . . .," it can now be shown that this species is not known from the Ethiopian region, *longinoda* being restricted to the continent of Africa and, in all probability, the species to which Forel has reference.

Other records of distribution of the genus include Weber's (1946) specimens of *O. longinoda* from the Belgian Congo, Mafia Island, Tanganyika, the Sudan, West Africa and Akkra. In addition, Keuchenius (1914) reports *O. smaragdina* from Java.

Colonel Bingham (1903) records the species from the whole of India, Burma and Ceylon except in the desert and treeless tracts, also listing the ant from Australia and New Guinea.

It is interesting to note that fossil forms representing four species of *Oecophylla* are to be found in European Tertiary deposits. *O. brischkei* is known from Baltic amber and *O. sicula* from the Sicilian amber deposits, both of the early Oligocene age and both species closely related to *smaragdina.* These constitute the only known fossil records of the genus, indicating that present day distributions are relicts, probably due to former land connections.

Biology.—The genus *Oecophylla,* together with two other genera (*Camponotus* and *Polyrhachis*) of the same subfamily are unique among ants in that some of the species construct nests largely made up of silk produced by the larvae, in which case the larvae themselves are used as tools. In the case of both *Oecophylla longinoda* and *smaragdina* the larvae are utilized as "shuttles" held by the mandibles of the minima worker caste in fastening leaves together into a nest. Here then, is a case in which the larvae are actually

3 By personal correspondence.

known to produce silk, but the pupae of these larvae are always nude. In each instance it has been observed that only immature larvae are utilized in producing the silk used in nest construction and that the well developed larvae are not utilized in producing this material.

The nests of *O. smaragdina* are generally confined to the scrubs and not commonly found in the forest proper. The species is polydomous and nests of varying sizes form "patches" in trees of which the foliage may be sparse (See Fig. 2). Frequently the old nests may be abandoned when the leaves become withered. No queens or winged forms were present in any of the nests examined nor was a winged individual found among the hundreds of specimens collected in India, although larvae were present in relative abundance. Dodd (1902) has written: "It is astonishing what myriads of inmates these nests contain; many of the chambers appear to be almost filled with the ants and their pupae and larvae. A new nest may be torn open, and though many larvae are present, no queen can be discovered; perhaps the queen may live in a central nest. . . ." Later Dodd (1902) asks the question, "Do queens live any length of time, or do they die at the approach of winter, leaving enough eggs to supply larvae to the several colonies for some weeks or even months?" In another paper (1902), this same author states: "During the wet season, queens

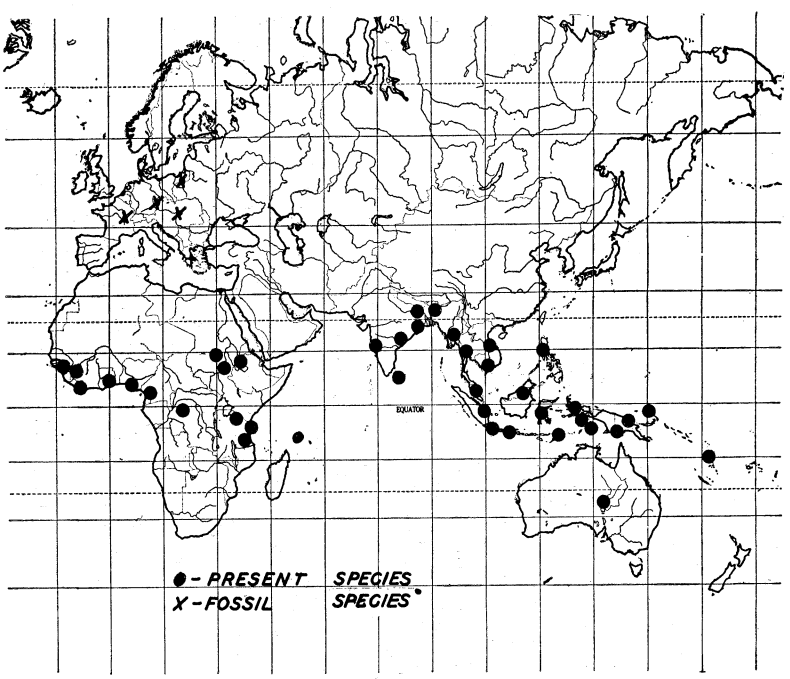

Fig. 1.— A map of the east showing range of the genus *Oecophylla* and its fossil species.

may be found singly throughout the scrubs in little retreats formed by few leaves."

The nests examined by the senior author represented myriads of all sizes and positions, including the succursals and shelters some distance from the nest, yet the grass-green females and the black males were not found.

Fig. 2.—Nests of *Oecophylla smaragdina* in trees, Upper Assam, India. Photo by A. C. Cole, Jr.

Fig. 3.—Typical nest of *Oecophylla smaragdina*. Photo by A. C. Cole, Jr.

It is interesting to note that food is not stored within the nest of the species but that the ants do tend aphids, feeding upon the exudates of the scales, and also commonly attend Lycaenid larvae. Frequently the larvae and aphids may be found within shelters constructed in the same fashion as the primary nests and approximate to these nests. Indeed, Keuchenius (1914) holds the view that *Oecophylla smaragdina* is very noxious to coffee plantations through its habit of keeping and protecting in its nests the green coffee scale, *Lecanium viride,* a most serious pest of the coffee tree.

The workers do not possess a sting but are nevertheless very effective in defending themselves and the nests from invasion by the instinctive pattern of biting rather severely and then ejecting a "spray" of formic acid from the tip of the abdomen, the gaster having been turned forward beneath the head and directed to the area of the bite.

Dimorphism.—The observations published by Weber (1946) concerning dimorphism and possible caste division among workers of the African species *longinoda,* were concurrent with similar observations of the impressive size variation in workers of the Asiatic species collected by the senior author in the interior province of Assam in northeastern India during 1943 and 1944. Moreover, it had been noted that Wheeler (1910) referred to the workers of the genus as "monomorphic," yet postulated a possible division of labor: "A remarkable example of division of labor, without corresponding structural differentiation, is seen also in the *Oecophylla,* an ant which inhabits nests of leaves sewn together with fine silk. According to the observations of Dodd (1902) and Döflein (1905), when the nests are torn apart the monomorphic workers separate into two companies, one of which stations itself on the outside of the nest, draws the separated leaves together and holds them in place with the claws and mandibles, while the other moves the spinning larvae back and forth within the nest till the rent is repaired with silken tissue." Still more interesting is the direct speculation of Döflein (1905), which the authors have translated as follows: "We saw that an interesting division of labor between the different individuals of the *Oecophylla* enables them to carry on a surprisingly artful building activity. Is it not possible that all individuals take over in the different roles, or do we find a differentiation of the instincts in special individuals? Do we find that they are actually morphologically differentiated? That is, are there worker castes which we can distinguish by their morphology, each of which is associated with a special task? I was made aware of this possibility by questions during a lecture because the material which was put on exhibition during the lecture showed small workers as bearers of the larvae and also, side by side, the large workers. Actually it can be shown from the material which comes from one nest that a noticeable size difference between the various worker individuals does exist. Also, it was very noticeable that all individuals which still held larvae between the mandibles in death, were small individuals. I also remember that during my observations I noticed particularly that there was a difference of size of the individuals which held the leaves together and of those which acted to defend the nests. It might,

therefore, be possible that such differences are actualities, and I should like to beg future investigators to observe if special individuals have the task (1) of holding the leaves, (2) of weaving with larvae, (3) defense, (4) of collecting honey from aphids. It would be very easily possible that the size differences observed by myself are accidental."

With these accounts brought to light in searching through the scant literature on the subject, it has been thought worthwhile to follow up speculation with actual facts in so far as the preserved material might be utilized. First of

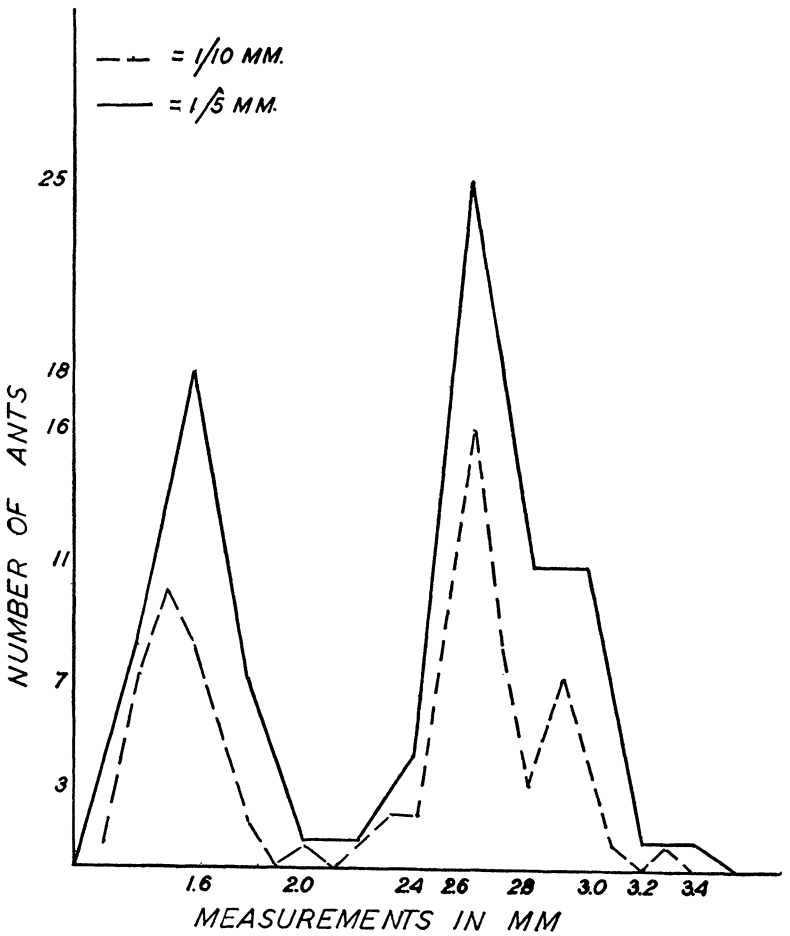

Fig. 4.—Graph showing the bimodal curve obtained from thoracic measurements of 88 ants from NEST 1. The broken line gives a plot when measurements were adjusted to 1/10 mm frequency and the continuous line indicates a plot of the same series adjusted to 1/5 mm. frequency. Actual measurements were made to 1/100 mm.

all, was there actually a dimorphic condition in the workers of *O. smaragdina* and if so were there actual morphological differentiations?

With this view in mind, and following the approach set by Weber (1946) it was decided to measure the random samples of two colonies (one large, the other small) and to see if the apparent size difference was a gradual intergradation representing extremes from a mean average, or to observe if two size groups were involved and, if so, how sharply divided the two "castes" might be. It was apparent that an overall measurement of each ant would not yield an accurate algebraic curve because of variable extensions of the gaster

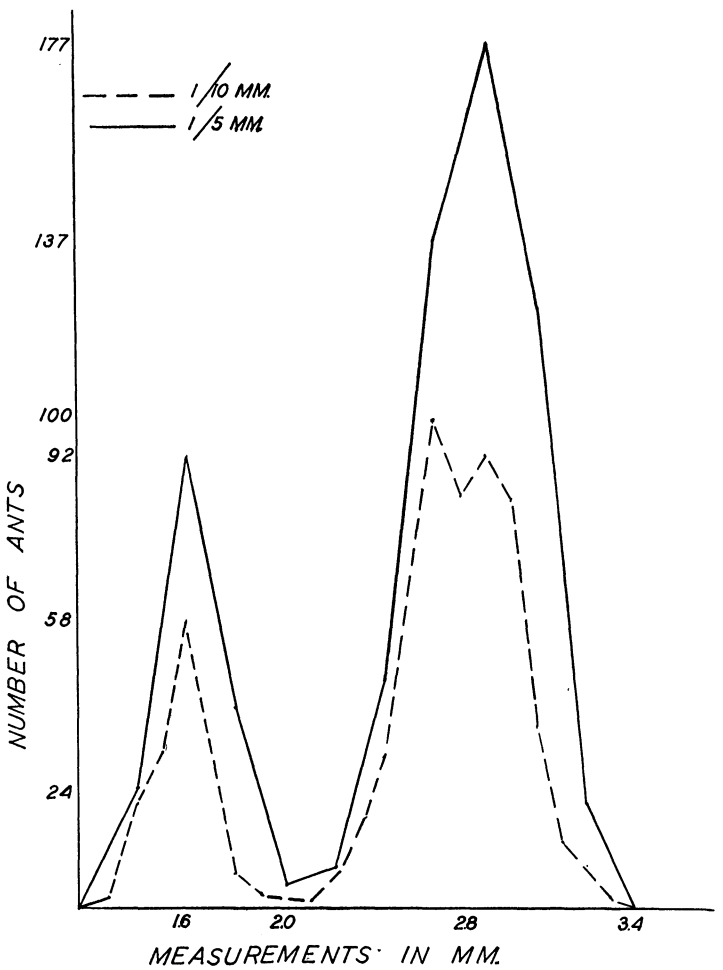

Fig. 5.—Graph showing the bimodal curve obtained from thoracic measurements of 674 ants from Nest 2. These plots are constructed on the same basis as in Fig. 4.

due to preservation. On this basis, a measurement of the overall thorax length was used, since the relative shape and extension of this body region were constant, and an accurate correlation of this length to body length was established.

All specimens were soaked overnight in warm 50% alcohol, becoming somewhat flaccid so that appendages lay in a natural position. Measurements were made by a reticle mounted in a binocular microscope. All measurements were to 1/100 mm. for close accuracy, and translated to the graphs figured. Only workers were used and the results are summarized as follows:

NEST ONE: Of a total of 88 ants from this small nest, measurements gave a very decided bimodal curve which shows two distinct size groups with no overlap. From this nest, 34 ants are represented as minima and 54 as maxima. Extremes for the minima ants are from 1.26 mm. to 1.98 mm. with the greatest frequency lying at 1.50 mm. Maxima extremes are from 2.21 to 3.30 mm. with the greatest frequency at 2.60 mm. The overall extremes for the nest, then, are from 1.26 mm. to 3.30 mm. as far as the thoracic measurements are concerned.

NEST TWO: Of a total of 674 ants taken from this nest, two size groups are shown by a clear bimodal curve. From this nest, 163 ants are represented as minima and 511 as maxima. Extremes for the minima of this nest are from 1.29 mm. to 2.01 mm. with the mode lying at 1.60 mm. Maxima extremes are from 2.16 mm. to 3.30 mm. with the

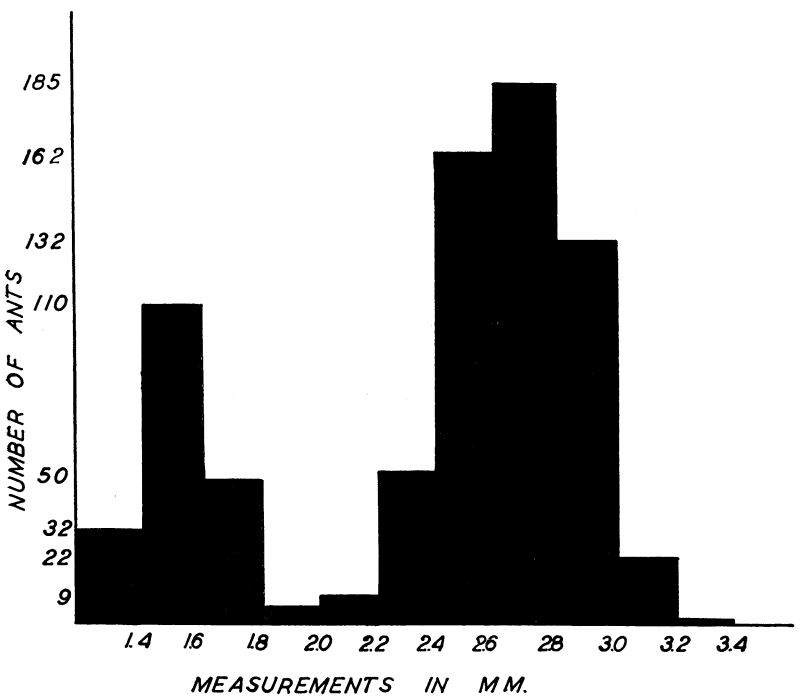

Fig. 6.—A graphic total of all ants measured to show the general trend of the workers of the species.

greatest frequency at 2.65 mm. The overall extremes for individuals of this nest, then, are from 1.29 mm. to 3.30 mm., an essential duplication of size range in nest 1.

Conclusions regarding size range are *indicative*. If, as mentioned, the workers of the species were not dimorphic, one would expect to find, on measurement, a normal frequency curve, the single mode of which would represent the *typical* size and the extremes indicated by the sides of the curve. However, the bimodal curve found in measurements of *O. smaragdina* shows two distinct size groups. An ant of this species selected at random, then, would be either of the maxima series or of the minima series. The variation from the minima mode might be expected to overlap the variation of the maxima mode, but such did not occur in the series to any appreciable extent. Only a single individual fell between the adjacent extremes of the castes and, morphologically, this specimen compared with the minima series. It should also be mentioned, in view of Döflein's observations, that three ants of the minima caste held larvae in their mandibles.

Morphologically, there were found to be certain consistent characteristics which will differentiate one worker caste from the other. Neglecting the very evident size factor, one can correctly state that members of the minima caste are more obviously compact and thickened, whereas the larger caste may be characterized by its long and slender form. The following table lists comparative features of six structures based on actual inspection of twenty-five specimens from each caste:

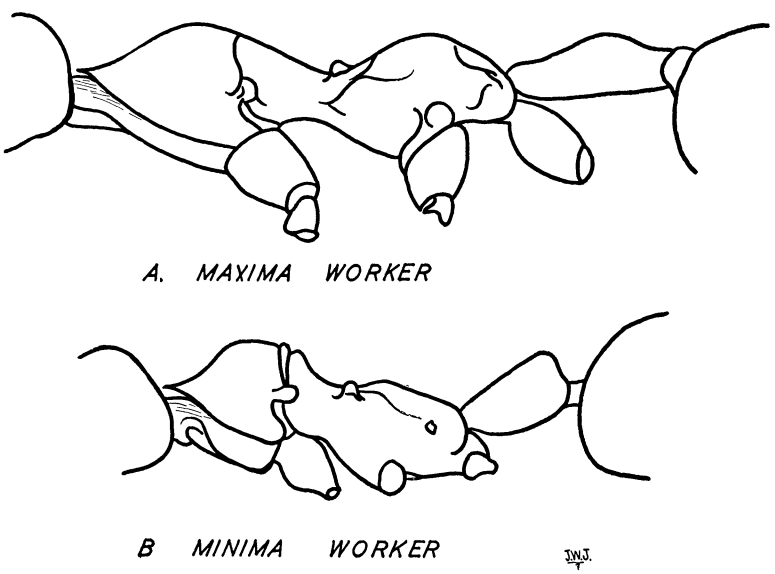

Fig. 7.—Contrasting features of the maxima worker (A) and the minima worker (B) as seen in profile. (Camera lucida drawings from typical specimens.)

	Minima	*Maxima*
Antennal Scape	Never as long as the head, not including the mandibles.	Always as long as or longer than the head including the mandibles.
Clypeus	More convex than in maxima.	Less convex but still not flattened.
Mandibles	Terminal tooth not markedly prominent.	Terminal tooth very prominent.
Pronotum	Spherical: much more convex when viewed in profile.	Longer: not as markedly convex when viewed in profile.
Mesonotum	Not elongated: not cylindrical: tapering uniformly to the posterior margin.	Slender: cylindrical: on the average, three times as long as the constricted width.
Petiole	Never as much as three times as long as thick in profile.	Always at least four times as long as thick as profile.

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