

3366

W L Brown

1927a

only copy

OBSERVATIONS ON GIGANTIOPS DESTRUCTOR
FABRICIUS AND OTHER LEAPING ANTS.

Please return

WILLIAM MORTON WHEELER.

[Reprinted from BIOLOGICAL BULLETIN, Vol. XLII., No. 4, April, 1922.]

Please return to
W. L. Brown, Jr.

[Reprinted from BIOLOGICAL BULLETIN, Vol. XLII., No. 4, April, 1922.]

OBSERVATIONS ON GIGANTIOPS DESTRUCTOR
FABRICIUS AND OTHER LEAPING ANTS.¹

WILLIAM MORTON WHEELER.

In any study of the very exuberant ant-fauna of the Neotropical Region one can not fail to be impressed by the striking contrast between certain genera like *Eciton*, *Pseudomyrma*, *Solenopsis*, *Crematogaster*, *Cryptocercus*, *Azteca*, and *Camponotus*, each represented by a large number of variable species, and genera like *Paraponera*, *Acanthognathus*, *Daceton*, *Blepharidatta*, *Stegomyrmex*, and *Gigantiops*, each represented by a single, very stable species. Of course, such monotypic groups may be regarded either as very ancient, embracing during some former age many species of which only one has survived, or as single species which, after acquiring generic status in the remote past, have since undergone little or no modification. The individuals of a species representing a monotypic genus may be either very rare or local, mere relicts of a bygone age, or prominent and ubiquitous over larger geographical areas. This is true of such ants as *Paraponera clavata* Fabr. and *Gigantiops destructor*, which I have recently had abundant opportunity to study in the jungle about the Tropical Laboratory of the New York Zoölogical Society at Kartabo, British Guiana. As the latter species is the more imperfectly known, I have singled it out for special consideration.

The name *Gigantiops destructor* conjures up visions of a huge-eyed, insatiable monster, a kind of Cyclopean insect-jaguar. Fabricius, when he first described the insect in 1804 as *Formica destructor*, certainly knew nothing of its behavior and probably gave it what seemed to him an appropriate specific name for any ant measuring a centimeter in length. More than half a century later ('58) Frederick Smith received specimens taken by Bates at Ega, Brazil, and believed them to represent a new species which he described as *Formica solitaria*. The following note was appended

¹ Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University. No. 177.

to the description: "This is a very remarkable insect; for independent of the enormously developed eyes and produced clypeus, the palpi are elongated to half the length of the thorax, the maxillary are six-, and the labial four-jointed. Mr. Bates says: "This curious solitary ant is never seen by more than one at a time, prowling about fallen leaves, etc., in the forest; I have never seen its formicarium and, from its solitary habits, have no clue to guide me in looking for it." Perhaps Smith was confirmed in his choice of the specific name by the monastic or ascetic appearance of the insect, its somber black livery, relieved only by the golden-yellow tips of its antennæ, its long, emaciated limbs and its huge eyes, perpetually dilated as if in astonishment and chagrin at the indecent behavior of other insects.

Two short notes, however, by later observers indicate that *Gigantiops* may be neither an insatiable assassin nor a humble anchorite, but a harmless and perhaps rather frivolous creature, that may have become permanently goggle-eyed through an age-long endeavor to enjoy to the full the riotous beauties of its environment. Emery ('93) was informed by Albert Schulz that the "Brazilian ant, *Gigantiops destructor* Fabr., which is distinguished by its enormous eyes, leaps from twig to twig, like the *Odontomachus hæmatodes* living in the same places," and Mann (1916) says: "In life this is one of the most attractive ants encountered. It lives always in the forest, where it forages either among the branches of trees or on the ground. The movements of the foraging worker are rapid, comparable to some of our species of *Cicindela*, and the bicolored antennæ are kept constantly in motion."

Roger ('63) was the first to throw Smith's *Formica solitaria* into the synonymy and to establish the peculiar genus *Gigantiops*. In more recent myrmecological literature mention of the insect recurs sporadically and at long intervals, showing that it was rarely seen in the many collections of South American ants examined by Mayr, Forel, Emery, Santschi, and others. Its known range, as indicated by the literature and by specimens in my collection, is as follows:

Brazil: Ega (Bates); Pará (E. Goeldi, ex coll. Forel); Maranhão (Ducke); Pará, Abuná, Porto Velho, and Madeira-Mamoré R. R. (W. M. Mann).

French Guiana (Jelski).

British Guiana: Kaieteur Falls, Tukheit, and Tumatumari (F. E. Lutz); Penal Settlement, Bartica District (W. Beebe); Kartabo and Kalacoon (Wheeler).

Peru: Callanga (Staudinger).

Bolivia: Rio Beni (L. Balzan).

These localities show that *Gigantiops* has a very limited range compared with many Neotropical ants, since it is confined to a strip of South America east of the Andes and extending from about 10° north to 10° south of the equator.¹

Gigantiops (Fig. 1) is a common ant in the forested portions of British Guiana, preferring shady places rather free from undergrowth and spending most of its time on the ground, running over the dead leaves. It occurs singly, as stated by previous observers, and really belongs to a forest-floor ant-fauna comprising also *Neoponera apicalis* Latr., *obscuricornis* Emery and *commutata* Roger, *Mesoponera constricta* Mayr, *Pachycondyla crassinoda* Latreille and *harpax* Fabr., *Paraponera clavata* Fabr., and *Ectatomma quadridens* Fabr. Those who are interested in mimicry will observe that in its form, the dull black color of its body and yellow antennal tips, *Gigantiops* bears such a striking resemblance to *N. apicalis* and *obscuricornis* that the latter might be regarded as

¹ I find a note by von Motschulsky in a letter published in his "Études Entomologiques" (1855) and referred to in the "Stettiner Entomologische Zeitung" (1859), which seems to apply to *Gigantiops*. Speaking of the insects which he observed at Obispo, Panama, he says: "I observed a lot of ants of diverse and bizarre form, among others one bearing the closest resemblance to a spider, especially to a *Salticus*, and as it also has the ability to leap, I have named it *Salticomorpha nigra*." There are two objections to accepting the name *Salticomorpha* as antedating *Gigantiops*: first, there is no record of this insect's having been taken in Central America or even in Colombia, and second, von Motschulsky may have seen a *Pseudomyrma gracilis* Fabr., which resembles a black Attid spider in form and color, and have mistaken its erratic movements for leaps. The well-known arachnologist, E. Simon (in Emery, "Voyage de M. E. Simon" (Dec., 1887-Avril, 1888). Formicides, Ann. Soc. Ent. France 1890, p. 65 *nota*) noticed that "all the species of the genus *Pseudomyrma* reproduce exactly the forms and colors of the spiders of the genus *Simonella* Peckh. (Attidæ) and the resemblance is equally striking in their gait." For the present it seems advisable, therefore, either to treat *Salticomorpha nigra* Motsch., as a *nomen nudum* or to include it with a query in the synonymy of *Gigantiops destructor* Fabr.

its models. Furthermore, these Ponerines sting very severely, whereas *Gigantiops* can be picked up with impunity. In Kartabo, nevertheless, the models are much less frequently seen than the mimic. This is interesting in connection with the observations of Mr. Tee Van, who finds that in the same region many of the

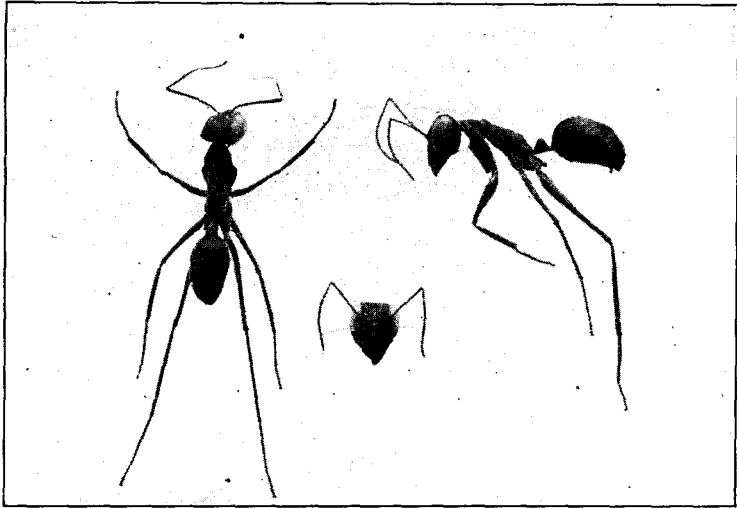


FIG. 1. *Gigantiops destructor* Fabr. Worker, about twice natural size; dorsal and lateral views and head from above.

mimetic butterflies are much more abundant than their putative Heliconid models. It would be a mistake to suppose that *Gigantiops* acts as if it derived any benefit from its striking resemblance to the stinging Ponerines. It greatly surpasses them in agility and when pursued will even leap several inches in a very graceful, cat-like manner. On the rather infrequent occasions when it climbs onto bushes and is running over their foliage it will, if disturbed, leap, without the slightest hesitation, to another leaf or even to the ground and make off with great alacrity. When two *Gigantiops* happen to meet face to face, they exhibit a peculiar play. After stroking each other's heads for a moment with the yellow tips of their antennæ, they move from side to side, precisely like two persons who meet on the sidewalk and try to prevent each other from passing.

On rare occasions *Gigantiops* may be seen carrying a termite worker or other small insect in its jaws, but even such individuals are not easily followed to their nests. Forel's placing of this ant in his tribe *Ecophyllini*, *i.e.*, with *Ecophylla smaragdina* Fabr., the well-known tree-ant of the Old World tropics, naturally led me to suppose that the nest must be in the trees, but this supposition, which has probably been shared by other myrmecologists, proves to be erroneous. On July 14, after much careful search and persistent following of single workers, my son Ralph succeeded in finding a nest in a partly decayed log only three or four inches in diameter lying on the ground at the edge of the Puruni trail and brought the portion inhabited by the ants into the laboratory. As soon as I began to dig into their nest the workers leaped out and made off, holding their larvæ in their mandibles. The colony comprised only fifty or sixty workers, which had been living in some large cavities made by *Passalus* or other wood-inhabiting beetles. In one of the chambers there were empty cocoons, showing that the pupæ of *Gigantiops* are not nude as in *Ecophylla*, its supposed nearest ally among the Formicinæ. I failed to secure the queen and believe she must have escaped unobserved among the workers. From these she differs merely in her somewhat larger size and slightly more voluminous thorax.

Notwithstanding careful search by my son and myself, ten days elapsed before I could again observe a *Gigantiops* nest. I found the second nest in a similar situation, in a partly decayed piece of a *Cecropia* trunk about a foot and a half long and three inches in diameter, lying loosely on the dead leaves in the shade of a bush. I noticed one of the workers timidly guarding a small hole and hastily retreating into it on my approach. The hole was plugged with cotton and the log carried back to the laboratory. In order that the ants might not elude me as on the previous occasion, I opened the log over a pail of water, but notwithstanding these precautions a few of the workers managed to escape. The entire colony, which was inhabiting one of the large internodal cavities so peculiar to *Cecropia*, was scarcely larger than the former colony, but contained more larvæ and several freshly spun worker cocoons.

No males were present and future attempts to find them and other colonies were unsuccessful.¹

Two matters call for further discussion in connection with the foregoing observations, the taxonomic affinities of *Gigantiops destructor* and its *modus saltandi*. The generally accepted view of its taxonomic position can be traced to the various papers which Forel has published from time to time on the classification of the subfamily Formicinæ (= Camponotinæ Forel). In 1878 he placed the genus *Gigantiops* between *Opisthopsis* and *Æcophylla* in his first tribe of the subfamily. In his classification of 1893 he omitted all mention of *Gigantiops*, though he enumerated the various other genera of the subfamily. In 1912 he remodeled the classification and considerably augmented the number of tribes, to one of which, the *Æcophyllini*, he assigned the three genera *Gigantiops*, *Myrmecorhynchus*, and *Æcophylla*. The same arrangement is preserved in his paper of 1917. I endeavored to show in the same year that *Myrmecorhynchus* could not be retained among the *Æcophyllini*, but should probably constitute an independent tribe, the *Myrmecorhynchini*. The characters of the *Æcophyllini*, according to Forel, are the following: gizzard long and narrow, with straight calyx; clypeal fossa more or less distinct from the antennary fossa; antennæ inserted a little behind the frontal area, but near the anterior ends of the frontal carinæ. The gizzard characters are not peculiar to this tribe, but recur also in the *Camponotini*, and the remaining characters are decidedly weak, since they depend on slight differences in the proportions of the anterior portions of the head. When we compare *Gigantiops* with *Æcophylla* we are struck by the great differences in the structure of the larva, pupa and adult and in habits. That the habits of the two ants are totally different will be seen from a comparison of the observations above recorded with what we know of *Æcophylla*, and its various subspecies and varieties, which are arboreal ants inhabiting peculiar nests made of leaves and silk spun by their larvæ. Still it may be objected that such ethological peculiarities have little significance, since we have species of *Camponotus* that

¹ Dr. W. M. Mann, who has just returned with the Mulford Expedition from Bolivia, informs me that he found *Gigantiops* nesting under stones in the forests of the Rio Beni.

live in similar nests (*C. senex* Smith and *formiciformis* Forel) and others that live in the ground or in rotten logs (*C. maculatus* Fabr. and *herculeanus* DeGeer). Turning to morphological characters, which the taxonomist regards as much more reliable, we find that the only resemblances between *Gigantiops* and *Æcophylla* (apart from the shape of the gizzard which both share with *Camponotus*) are the shape of the clypeus, with its great, projecting lobe, the shape of the mandibles, and the feeble characters cited by Forel. There are great differences in the size of the eyes and claws, in the shape of the thorax and petiole of the worker, and in the size and shape of the thorax of the female, though the venation of the wings is similar. The larva of *Gigantiops* is like that of *Camponotus*, but very different from that of *Æcophylla*, and the pupa is inclosed in a cocoon. Probably the male *Gigantiops* will be found to exhibit some peculiar differences. Emery (*in litt.*) calls my attention to the singular fact that the tarsal claws of the male *Æcophylla* are almost completely atrophied. It would therefore be very interesting to know the condition of these organs in the corresponding sex of *Gigantiops*. The foregoing considerations seem to me to render it advisable to remove *Gigantiops* from Forel's tribe *Æcophyllini* and to provide an independent tribe for its accommodation. I find that Ashmead in 1905 had created such a tribe "Gigantiopini," though he included it in a subfamily *Gesomyrmicinae*, with *Gesomyrmex* and *Myrmoteras*, genera which, in my opinion, are only remotely related to *Gigantiops*.

It is practically certain that *Gigantiops* is one of a number of ancient, large-eyed, active Formicinae, once of very wide distribution, but now narrowly confined to the tropics. This group, which embraces also the genera *Æcophylla*, *Dimorphomyrmex*, *Gesomyrmex*, *Opisthopsis*, *Santschiella*, and *Myrmoteras*, represents merely the surviving specialized tips of diverging branches of a primitive stock. In regard to *Æcophylla*, *Gesomyrmex*, and *Dimorphomyrmex*, we are actually in possession of considerable paleontological information. Mayr ('68), Emery ('05), and I ('14) have recorded the occurrence of two species of each of these three genera in the Baltic amber, of Lower Oligocene age; Emery ('91) has recorded an *Æcophylla* and a species allied to *Gesomyrmex* (*Sicelomyrmex* Wheeler) from the Sicilian amber, which is

referred to the Middle Miocene; Förster ('91) a species of *Æcophylla* from the Middle Oligocene of Alsace, and Heer ('49) and Mayr ('67) two species from the Lower Miocene of Croatia.¹ More recently Cockerell ('20) described a species of this genus from the Eocene of England, and he ('15) and Donisthorpe ('20) three species from the Middle Oligocene of the same country. The one, or possibly two, extant species of *Æcophylla* are now confined to the hottest portions of the Ethiopian, Indo-malayan, and Papuan Regions. Similarly the few extant species of *Gesomyrmex* and *Dimorphomyrmex* are known to occur only in Borneo and the Philippines.² In the same regions and in Burma we find the four species of *Myrmoteras*. *Santschiella* is known only from a single specimen taken in the Belgian Congo, the species of the genus *Opisthopsis* are confined to the Australian and Papuan Regions, and the Neotropical Region possesses only one of these ancient large-eyed Formicines, *Gigantiops*. This, as we have seen, has a rather limited range and is in all probability a true tropical relict, originally developed in and since mainly confined to that portion of the ancient South American continent known as Archiguiana. All of the genera above mentioned are forest ants and most of them are arboreal, but, as we have seen, *Gigantiops* spends most of its time on the forest floor and nests in small, partly decayed logs. *Opisthopsis* nests under bark, in the ground or in earthen termitaria, and I may add that Dr. F. X. Williams, who took the types of *Myrmoteras williamsi* Wheeler in the Philippines, informs me that this ant nests in the soil. From what we know, therefore, of the living and extinct forms, we are justified in concluding that the large-eyed Formicinæ originated during the early Tertiary, or more probably during the Cretaceous, and that the extant forms have since undergone little or no modification, owing to the very stable ecological conditions in which they were able to survive. *Gigantiops*, in particular, may

¹ Since the completion of this paper Professor Cockerell ('21) has described a peculiar large-eyed ant from the Green River Eocene of Wyoming as *Eoformica eocenica*. It seems to belong to the subfamily Formicinæ and resembles the Australian *Opisthopsis* in the shape of the head and the position of the prominent eyes.

² Since this paper was written I have published the description of a *Gesomyrmex* (*G. howardi*) from China.

be said to have an even more remote origin than the archaic though highly specialized Neotropical vertebrates, such as the opossums, manatees, sloths, armadillos, ant-eaters and tapirs among mammals, or the ostriches and hoatzins among birds.

The jumping or leaping habits of *Gigantiops* are so unusual that a more general account of this behavior as it occurs in various Formicidæ may not be out of place. There are two very different kinds of leaping ants, one which I shall call "retrosalient," which always leaps backward, and one that may be called "prosalient," because it always leaps forward. Some authors regard the former as not "leaping," in the proper sense of the term, probably because of the direction and because it is not performed by means of the legs. But such very abrupt displacements of the body are effected in so many different ways in different insects, as, *e.g.*, in Elaterid beetles, Lepismids, Collembolans, cheese-maggots, fruit fly and *Vermileo* larvæ, the extraordinary Coleopteran (?) cocoons described by Berlese ('20, p. 631), etc., that such words as "leaping" can hardly be avoided without pedantry. We even speak of fish or of a cataract "leaping."

Retrosalience has been repeatedly observed in two quite unrelated groups of ants, one embracing the Ponerine genera *Odontomachus* and *Anochetus*, the other the Myrmicine genus *Strumigenys*. By convergence both of these groups have developed very similar long, straight, and linear mandibles, inserted close together on the front of the head and furnished with large, abruptly incurved teeth at their tips. When excited these ants open their mandibles so widely that they stand out at right angles to the long axis of the head or are even directed slightly backwards. And if one of the insects comes in contact with a solid object in its path, it closes them so suddenly and with such force that they make an audible "click" and the insect is thrown backwards through the air to a distance of several inches. I have described this behavior in detail in *O. clarus* of Texas ('00). It has also been observed in *O. chelifera* of Brazil by Schupp (Wasmann, '92) and in the common tropicopolitan *O. hæmatoda* by Nietner ('58), Ferguson (Wroughton, '92), Forel, myself, and others.¹ The method of

¹ Borgmeier ('20) has recently described the similar habits of *O. affinis* in Brazil. "They strike their mandibles against the solid substratum and at the same moment leap 30 to 35 cm. vertically into the air."

leaping in *Anochetus* is precisely similar, as shown by the observations of Wroughton ('92) on *A. sedilloti* var. *indicus* of India, and of Biró (Emery, '97) on a Papuan species. Among the Dacetoniini it has been observed by Hetschko in the Brazilian *Strumigenys saliens* (Mayr, '93) and by Biró ('97) in *S. chyzeri* Emery ('97) of New Guinea. The worker of the latter species is able to leap backward to a distance of 20–25 cm., or about 100 to 150 times the length of its body, but this behavior is not exhibited by the female. Forel ('93) believed that the Neotropical *Acanthognathus ocellatus* Mayr and *Daceton armigerum* Latr. might be able to leap in the same manner. I have failed to observe the habit in the allied Australian ants of the genus *Orectognathus*. All the retrosalient ants, however, leap rather reluctantly and only under certain conditions, and the length of their leaps varies directly as the degree of solidity of the objects against which they happen to close their mandibles.

Prosalience is exhibited by at least three very different groups of ants: certain bull-dog ants of the Australian genus *Myrmecia*, *Gigantiops*, and the extraordinary genus *Harpegnathos*, or *Drepanognathus*, as it was formerly designated, of the Indomalayan Region.

The leaping Myrmecias, popularly known as "jumpers" in Australia, comprise the members of Emery's subgenus *Pristomyrmecia* (*fulvipes* Rog., *mandibularis* Sm., and *piliventris* Sm.) and the smaller species of *Myrmecia* sens. str. allied to *nigrocincta* Sm. and *pilosula* Sm. I have frequently seen these ants jump distances varying from one to a few inches. When disturbed *M. nigrocincta* and *pilosula*, especially, present a ludicrous appearance as they bound out of their small mound nests in a series of short hops like Lilliputian cavalry galloping to battle. Examination of these ants reveals a structural peculiarity which has been overlooked by previous observers, namely, a distinct elongation and basal incrassation of their hind femora, as compared with the hind femora of the other nonsalient species of the genus. In Fig. 2 the hind femur of a worker *M. nigrocincta* (*c*) and that of a small worker of *M. sanguinea* of the same size (*d*) are drawn to the same scale. The greater length and volume of the femur of the former species shows a distinct approach to the conditions in the

saltatory Orthoptera and is evidently to be interpreted as an arrangement for the accommodation of a more voluminous and therefore more efficient extensor, or abductor muscle in the hind leg. This morphological peculiarity, together with the leaping habit, seem to me to be sufficient to justify a separation of these jumping species from the remaining *Myrmecias* as a distinct subgenus, for

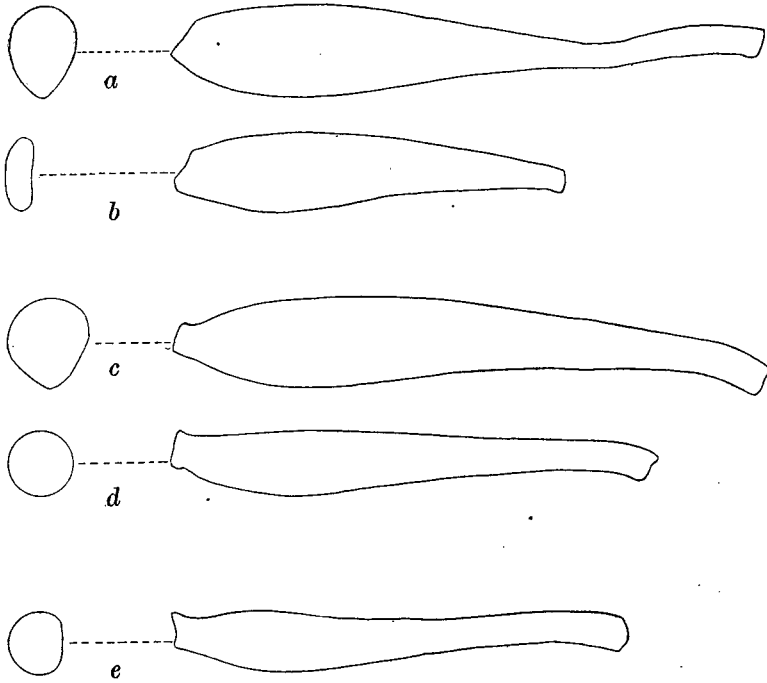


FIG. 2. Femora in profile and cross section of five species of ants drawn to the same scale. *a*, *Gigantiops destructor*; *b*, *Componotus castaneus americanus* Mayr; *c*, *Myrmecia nigrocincta* Smith; *d*, small *Myrmecia sanguinea* Smith; *e*, *Harpegnathos saltator* Jerdon.

which the name *Halmamyrmecia* subgen. nov. (with *pilosula* F. Smith as subgenotype) may be proposed.

In *Gigantiops* I find an even more pronounced elongation and basal incrassation of the hind femur than in *Pristomyrmecia* or *Halmamyrmecia*. As there is only one species of *Gigantiops*, I have compared its hind femur (Fig. 2*a*) with that of a non-leaping *Componotus* worker of the same size (*b*). It will be seen that the difference in the length of the two femora is very pronounced,

but that the difference in the basal incrassation is not so striking when the parts are seen from the side. The shapes of the cross-sections of the bases of the two femora, nevertheless, show that the *Gigantiops* femur is much more voluminous and therefore capable of furnishing attachment for a much larger and more powerful extensor muscle, as in the crickets and grasshoppers.

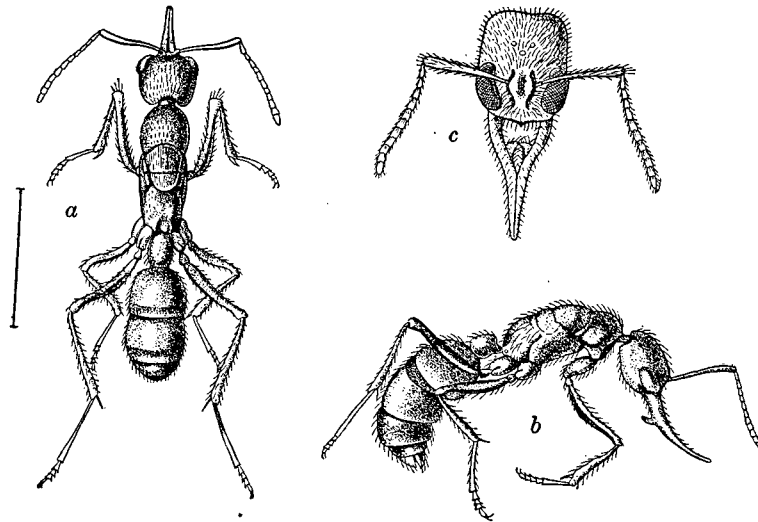


FIG. 3. Female of *Harpegnathos saltator* Jerdon (after Mayr.). *a*, dorsal view; *b*, lateral view; *c*, head of same from above.

Extraordinary feats of leaping are performed by the species of *Harpegnathos*, a genus confined to Indochina and the Philippines. In these ants (Fig. 3) the structure of the head is very singular, the eyes being very large, larger, in fact, than in any other Ponerine, and placed very far forward, and the mandibles are quite unlike those of any other known species. They are very long, separated at the base but approximated, arcuately curved upward, and gradually tapering toward their tips and finely serrate along their inner borders. Each is provided at the base with a large, flat, triangular tooth, projecting inward and somewhat downward and backward. In cabinet specimens the blades of the mandibles are applied to one another and the basal teeth overlap. The leaping habits of this insect have been observed by Lefèvre,

Lewis ('82), Wroughton ('92), and Bingham ('03). Lefèvre states that it can make leaps of 20 to 25 cm., and Lewis saw it rise into the air to a height of 5 or 6 inches till exhausted, when its leap did not exceed an inch. Wroughton says: "The single specimen of the genus, which I have had the luck to find, made leaps of a foot or 18 inches with perfect ease, exactly like a grasshopper. I had much trouble in securing this specimen, and, when I succeeded, I found she could sting better than she could leap." Unfortunately we have no observations on the *modus saltandi* of this curious insect. Its hind legs are really very short and even thinner than those of many nonsalient ants as indicated in the figure of the hind femur of a worker *H. saltator* Jerdon (Fig. 2e). As this ant is nearly of the same size as the specimens selected for the other femora (a-d), and as the outline is drawn to the same scale, it will be evident that no such feats of leaping as described by Wroughton can be performed with such appendages. We must conclude, therefore, that the mandibles are employed for this purpose, but how they function is a matter of pure conjecture till the living insect can be carefully studied. It is conceivable that when about to leap the *Harpegnathos* opens her mandibles slightly till the two basal teeth just barely touch, and that she presses the tips of the mandibles against the ground so that their long, slender, and probably very elastic blades are more arcuately bent. We may suppose, moreover, that if the two teeth are suddenly permitted to slide over each other, with a concomitant sudden unbending of the mandibles, the insect would be precipitated forward much like a very elastic strip of metal or whalebone bent in an arc and suddenly released. It is less probable that the insect leaps by inserting the tips of the mandibles in the ground and bending them in the opposite direction, *i.e.*, by more nearly straightening them and then suddenly allowing them to return to their original curvature.¹

¹ Since this paragraph was written I find that Professor Forel (1921, p. 47) gives some notes on the method of leaping employed by *Harpegnathos*. He states, apparently on the authority of some correspondent in India or China, that this ant "fait des bonds formidables de plus d'un mètre à l'aide de ses longues mandibules un peu recourbées en haut. La tête entière se recourbe sous le corps, se rejettant ensuite en avant, un peu à la manière du thorax de nos insectes d'Europe nommés taupins."

In conclusion, two interesting matters of a more speculative nature may be briefly discussed:

1. The various macrophthalmic, or large-eyed, tropical ants mentioned in this paper, namely, the Formicine genera *Gigantiops*, *Opisthopsis*, *Æcophylla*, *Gesomyrmex*, *Dimorphomyrmex*, *Santschiella* and *Myrmoteras*, the Ponerine genera *Myrmecia* and *Harpegnathos*, and I may add also the whole subfamily Pseudomyrminæ, constitute only a small percentage of the more than 10,000 extant species, subspecies, and varieties of Formicidæ. In the great majority of forms the eyes and ocelli of the female, and especially of the workers, have undergone considerable reduction in size or have entirely disappeared. In the male, however, which is the more conservative sex in ants, the eyes and ocelli are always large. These facts, together with what is now known of the ants of the Baltic amber, suggest that not later than Cretaceous time the females and workers were also all large-eyed, like the Scoliidoid wasps from which the Formicidæ are derived, and that they preserved this condition till after the social habit and a wingless worker caste had been evolved. During the Eocene and owing to the further development of the peculiar nesting and foraging habits, the females and workers became increasingly microphthalmic and anophthalmic till the small-eyed or blind condition became established in the majority of existing forms.

2. It will have been noticed that all the known prosocial ants have very large, convex, and minutely faceted eyes, and that all belong to archaic genera. I have already discussed the antiquity of *Gigantiops*. The *Myrmecias* are, I believe, justly regarded as the most primitive of existing ants, survivors, without more than specific diversification, from the early Eocene or the late Cretaceous. *Harpegnathos* includes only a few rare species of very restricted geographical range, evidently relicts on the verge of extinction. It would seem, therefore, that the leaping habit may have been much more general among the most ancient macrophthalmic Formicidæ, but had been abandoned as incompatible with a more highly developed social organization. This seems to be shown even within the genus *Myrmecia*, the larger and more dominant species of which no longer leap. That this habit should still persist, probably in a degenerate stage, in a few large-eyed forms,

may be due to the fact that ants endowed with unusual visual powers can retain such a habit with some impunity. Santschi ('11) and Brun ('14) have shown that vision is an essential factor in the homing behavior of ants that do not adhere very strictly to the topochemical trail made by themselves or their fellows from and to the nest. The leaping habit, if preserved and assiduously practiced in small-eyed ants, would, of course, often render it difficult or impossible to find the nest by means of the antennal sense alone.¹

LITERATURE.

Ashmead, W. H.

- '05 A Skeleton of a New Arrangement of the Families, Subfamilies, Tribes and Genera of the Ants, or the Subfamily Formicoidea. *Canad. Ent.*, 1905, pp. 381-384.

Berlese, A.

- '20 *Gli Insetti*, Vol. 2. Milan, Soc. Edit. Libreria. 1920.

Bingham, C. F.

- '03 Ants and Cuckoo Wasps. Hymenoptera, Vol. 2. In *Blanford's Fauna of British India, including Ceylon and Burma*. London, Taylor and Francis, 1903.

Biró, L.

- '97a *Pattago hangyak* (Jumping Ants). *Rovart. Lapok.*, 4, 1897, pp. 73, 74.
'97b *Biologische Mittheilungen aus New Guinea*. III Springende Ameisen. *Berliner Ent. Zeitschr.*, 42, 1897, pp. 136, 137.

Borgmeier, T.

- '20 *Zur Lebensweise von Odontomachus affinis Guérin*. *Ihering-Festschrift*. *Zeitschr. Ver. Wiss. Kunst.*, 1920, pp. 31-38.

Brun, R.

- '14 *Die Raumorientierung der Ameisen und das Orientierungsproblem im allgemeinen*. Jena, Gustav Fischer, 1914, viii + 284 pp., 51 figs.

Cockerell, T. D. A.

- '15 *British Fossil Insects*. *Proc. U. S. Nat. Mus.*, 49, 1915, pp. 469-499, 6 pls.
'20 *Fossil Arthropods in the British Museum*, I. *Ann. Mag. Nat. Hist.* (9), 5, 1920, pp. 273-279, 3 figs.
'21 *Some Eocene Insects from Colorado and Wyoming*. *Proc. U. S. Nat. Mus.*, 59, 1921, pp. 29-39, 1 pl., 9 text-figs.

Donisthorpe, H. S. J. K.

- '20 *British Oligocene Ants*. *Ann. Mag. Nat. Hist.* (9), 6, 1920, pp. 81-94, 1 pl.

¹ The mollusks of the genus *Pecten* are interesting in this connection, since, as is well known, they are able to leap considerable distances through the water by rapidly opening and closing the valves of the shell and have their mantle margins beset with large, highly specialized eyes.

Emery, C.

- '91 Le Formiche dell 'ambra siciliana nel museo mineralogico dell Università di Bologna. Mem. R. Accad. Sc. Ist. Bologna (5), 1, 1891, pp. 141-165, 3 pls.
- '93 Zirpende und springende Ameisen. Biol. Centralbl., 13, 1893, pp. 189, 190.
- '97 Formicidarum Species Novæ vel minus Cognitæ in Collectione Musæi nationalis Hungarici, quas in Nova Guinea, Colonia Germanica, collegit L. Biró. Termeszetr. Füzetek 20, 1897, pp. 571-599, 2 pls.
- '05 Deux Fourmis de l'Ambre de la Baltique. Bull. Soc. Ent. France, 1905, pp. 187-189, 2 figs.

Förster.

- '91 Abh. Geol. Spezialk. Els. 3, 1891.

Forel, A.

- '78 Études Myrmécologiques en 1878. Bull. Soc. Vaud Sc. Nat., 15, 1878, pp. 337-392, 1 pl.
- '93 Observations Nouvelles sur la Biologie de Quelques Fourmis. Bull. Soc. Vaud Sc. Nat. (3), 29, 1893, pp. 51-53.
- '93b Sur la Classification de la Famille des Formicides avec Remarques Synonymiques. Ann. Soc. Ent. Belg. 37, 1893, pp. 161-167.
- '12 Formicides Néotropiques. Part VI. Mém. Soc. Ent. Belg. 20, 1912, pp. 59-62.
- '17 Cadre Synoptique Actuel de la faune universelle des Fourmis. Bull. Soc. Vaud Sc. Nat., 51, 1917, pp. 229-253.
- '21 Le Monde Social les Fourmis. Tome. I. Genève, Kundig, 1921.

Heer, O.

- '49 Die Insektenfauna der Teriärgelände von Oeningen und von Radoboj in Croatien. II Neue Denkschr. Schweiz. Ges. Naturw., 11, 1849, pp. 1-264, 17 pls.

Lefèvre.

- (Letter on *Drepanognathus*.) Ann. Soc. Ent. France (6), 3, p. LXXXIII.

Lewis, G.

- '82 (Letter on Histeridæ, etc.). In Nouvelles et Faits Divers. L'Abeille (4), 2, 1882, p. 155, 156.

Mann, W. M.

- '16 The Ants of Brazil. Bull. Mus. Comp. Zoöl., 60, 1916, pp. 339-490 7 pls.

Mayr, G.

- '67 Vorläufige Studien über die Radoboj-Formiciden. Jahrb. K. K. Geol. Reichsan., 17, 1867, pp. 47-62, 1 pl.
- '68 Die Ameisen des baltischen Bernsteins. Beitr. zur Naturkunde Preussens. I. K. Phys. Oekon. Ges. Königsb., 102 pp., 5 pls., 1868.
- '86 Notizen über die Formiciden-Sammlung des British Museum in London. Verh. zool. bot. Ges. Wien, 1886, pp. 353-365.
- '87 Südamerikanische Formiciden. Verh. zool. bot. Ges. Wien., 37, 1887, pp. 511-532.
- '93 Ergänzende Bemerkungen zu E. Wasmann's Artikel über springende Ameisen. Wien. Ent. Zeitg., 12, 1893, p. 23.

von Motschulsky, V.

- '55 Lettre à M. Menetries in Motschulsky's "Etudes Entomologiques,"
1855, pp. 8-28.
- '59 Briefliche Notiz über springende Ameisen. Stettin. Ent. Zeitg., 20,
1859, p. 201.

Nietner, J.

- '58 Über eine springende Ameise in Ceylon. Brief an Chr. Drewsen. Stet-
tin. Ent. Zeitg., 19, 1858, pp. 445, 446.

Roger, J.

- '63 Verzeichniss der Formiciden-Gattungen und Arten. Berlin, A. W.
Schade, 1863.

Santschi, F.

- '11 Observations et remarques critiques sur le mécanisme de l'orientation
chez les fourmis. Rev. Suisse, 19, 1911, pp. 303-338, 6 figs.

Smith, F.

- '58 Catalogue of Hymenopterous Insects in the Collection of the British
Museum. VI. Formicidæ, 1858, 216 pp., 14 pls.

Wasmann, E.

- '92 Einiges über springende Ameisen. Wien. Ent. Zeitg., 11, 1892, pp.
316-317.

Wheeler, W. M.

- '00 A Study of Some Texan Ponerinæ. BIOL. BULL., 2, 1900, pp. 1-31,
10 figs.
- '14 The Ants of the Baltic Amber, Schr. Physik. Ökon. Ges. Königsb.,
55, 1914, pp. 1-144, 66 figs.
- '17 The Australian Ant-Genus *Myrmecorhynchus* (Ern. André) and its
Position in the Subfamily Camponotinæ. Trans. Roy. Soc. Austral.,
41, 1917, pp. 14-19, 1 pl.
- '18 The Ants of the Genus *Opisthopsis*. Bull. Mus. Comp. Zoöl., 62, 1918,
pp. 343-362, 3 pls.

Wroughton, R. C.

- '92 Our Ants. Part I. Journ. Bombay Nat. Hist. Soc., 1892, pp. 13-60,
2 pls.