Taxonomy and Biology of a New West African Ant Belonging to the Genus *Amblyopone* (Hymenoptera: Formicidae)[1]

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ABSTRACT

Amblyopone pluto, n. sp., has been discovered in unburned savannas of central Ivory Coast. It represents the 3rd *Amblyopone* species to be found in sub-Saharan Africa, although the conspicuous absence of the genus from the central Ethiopian region now appears less an indication of abundance than of collecting procedures. This new, moderately sized species is hypogaeic, its cryptobiotic lifeways preventing its discovery until only recently. A taxonomic description of the species is given. This species is narrowly specialized, particularly regarding prey specificity, feeding only on geophilomorph chilopods. The workers forage alone and paralyze the prey with their sting. The prey is then dragged into the nest and is deposited in the vicinity of the brood. The workers penetrate the chilopod integument and feed, but they do not subdivide the prey. Eventually the larvae are carried by the workers to the prey and begin feeding, characteristically thrusting their heads into the soft interior of the chilopod. Several of the behavior patterns of this species, particularly with respect to the level of larval autonomy, reflect a primitive social organization, which supports the placement of the genus *Amblyopone* near the base of the formicid line represented by the Ponerinae, Myrmicinae, and Dorylinae.

The genus *Amblyopone* has up to now been known in Africa from samples of only 5 species: *denticulata* (Roger), *emeryi* Saunders, *mutica* (Santschi), *normandi* (Santschi), and *santschii* (Menozzi). Of these, only *mutica* and *santschii* are sub-Saharan. The distribution of these 5 species is peripheral, being limited to the northern and western fringes of the continent. The absence of the genus from the central Ethiopian region now is being proven more apparent than real. First, excavations by one of us (J.L.) in the inland wet savanna region of the Ivory Coast have revealed a subterranean faunule of Amblyoponini, including the genus *Apomyrma* (Brown et al. 1971) and at least 4 species of *Amblyopone* (*A. mutica, A. pluto*, n. sp., described hereinafter, and 2 or 3 other species related to *A. normandi* and *A. santschii*). Workers of another undescribed species of the *normandi-santschii* group from the Congo have recently been shown us by A. Francoeur. Thus our ideas about the African *Amblyopone* fauna are undergoing radical changes, and doubtless will be further transformed as systematic investigation of soil-inhabiting arthropods is extended in Africa.

One of the most interesting of the soil-inhabiting *Amblyopone* is *A. pluto* and it is the purpose of this paper to describe this new species and to offer a series of preliminary observations on its biology.

METHODS

Measurements were made of a series of 15 workers, 5 queens, and 2 ♂. Several abbreviations are used in the presentation of these data: TL = total length, HL = head length, HW = head width, CI = cephalic index, AL = alitrunk length, PL = petiole length, GL = gaster length.

The mouthparts of several specimens were prepared and examined according to the methods outlined by Gotwald (1969). The genital capsule was removed from 1 ♂, and its components were mounted on microscope slides.

The drawings were done with the aid of microprojector and a Wild M-5 dissecting microscope equipped with a drawing tube. All of the drawings were made by the 1st author. The photographs are by the 2nd author.

TAXONOMY OF THE SPECIES

Amblyopone pluto, n. sp.

WORKER, COMPOSITE DESCRIPTION.—TL 5.66–6.38 mm, HL 1.08–1.17 mm, HW 0.94–1.08 mm, CI 87–96, AL 1.53–1.75 mm, PL 0.67–0.85 mm, GL 2.11–2.43 mm, scape length 0.67–0.72 mm, length of petiolar node 0.67–0.81 mm, width of node 0.81–0.90 mm, hind femur length 0.76–0.85 mm.

Habitus as shown in Fig. 2. Head and alitrunk black to dark reddish-orange (fully pigmented?); genae, clypeus, and frontal carinae of head, and ventrolateral margins of alitrunk often lighter, approaching a yellowish-orange; gaster dark brown to reddish-orange; petiole (abdominal segment II) sometimes black dorsally; legs rufous to yellow; antennae dark rufous to yellowish-red and always lighter in color than head.

Head as shown in Fig. 4. Genal angle rounded, not prolonged into a genal tooth; frons and genae coarsely punctate, although frons is less so and glossy; eyes greatly reduced, usually with 10 or fewer facets, greatest diameter less than 0.09 mm. Frontal carinae widely separated, strongly diverging from midsagittal line caudad; carinae not prominent but enlarge to form widely separated, expansive frontal lobes which conceal the antennal sockets in dorsal view. Areas surrounding antennal sockets deeply depressed and sculptured with striae which sweep out from the sockets. Clypeus concave medially, descending sharply from area between frontal lobes and bearing a row of elongate tubercles, usually 9–11, the longest (as long as 0.10 mm) placed medially while those placed laterally decrease in length sequentially; clypeal tubercles appear flattened dorso-ventrally and are rounded or truncated apically. Antennae 12-segmented; scape almost straight in dorsal view (Fig. 18).

Internal margin of mandible broadly convex (Fig. 8); masticatory margin smoothly continuous with basal margin; internal margin with a conspicuous, elongated apical tooth followed closely by a conical 1st subapical, 2nd subapical often truncated, 3rd subapical followed by as many as 7 or 8 additional teeth which become progressively more rounded and shorter proximad, teeth single ranked. Labrum cleft medially along distal margin (Fig. 7); lateral margin slightly concave along distal two-thirds, deeply notched along proximal third; numerous setae inserted along distal margin and on extensor surface. Maxillary palpus 4-segmented (Fig. 10). Stipes with a conspicuous transverse stipital groove which curves distad, running longitudinally along external face and ending at the level of palpal insertion; lateral shoulder well developed (Fig. 10). Galea with a typically well-developed maxillary comb (Fig. 9); galeal crown with numerous long setae, incuding a series of closely arranged setae (usually 7) forming a distinct comb; galeal comb present and composed of 6 or 7 peglike setae. Lacinia triangular with a distinct lacinial comb along ⅔ of free margin (Fig. 9).

Labial palpus 2-segmented (Fig. 11); subglossal brushes well developed; paraglossae absent.

Alitrunk finely punctate, punctures far less numerous per unit of area than on head; surface of integument otherwise smooth and glossy, particularly on dorsum; areas immediately above insertions of 2nd and 3rd coxae and covering bullae of metapleural glands impressed with a series of longitudinal striae. Declivity of propodeum steep and slightly concave. Petiolar node with vertical, flat anterior face, rounding off into the dorsal face at a slightly larger than 90° angle.

Gastral tergites finely punctate, punctures widely scattered; surface of tergum otherwise smooth and glossy except for opaque acrotergites. Sternites of gaster more coarsely punctate, not as smooth or glossy.

Head moderately pubescent, with numerous short, erect and suberect setae, primarily on frons. Ali-
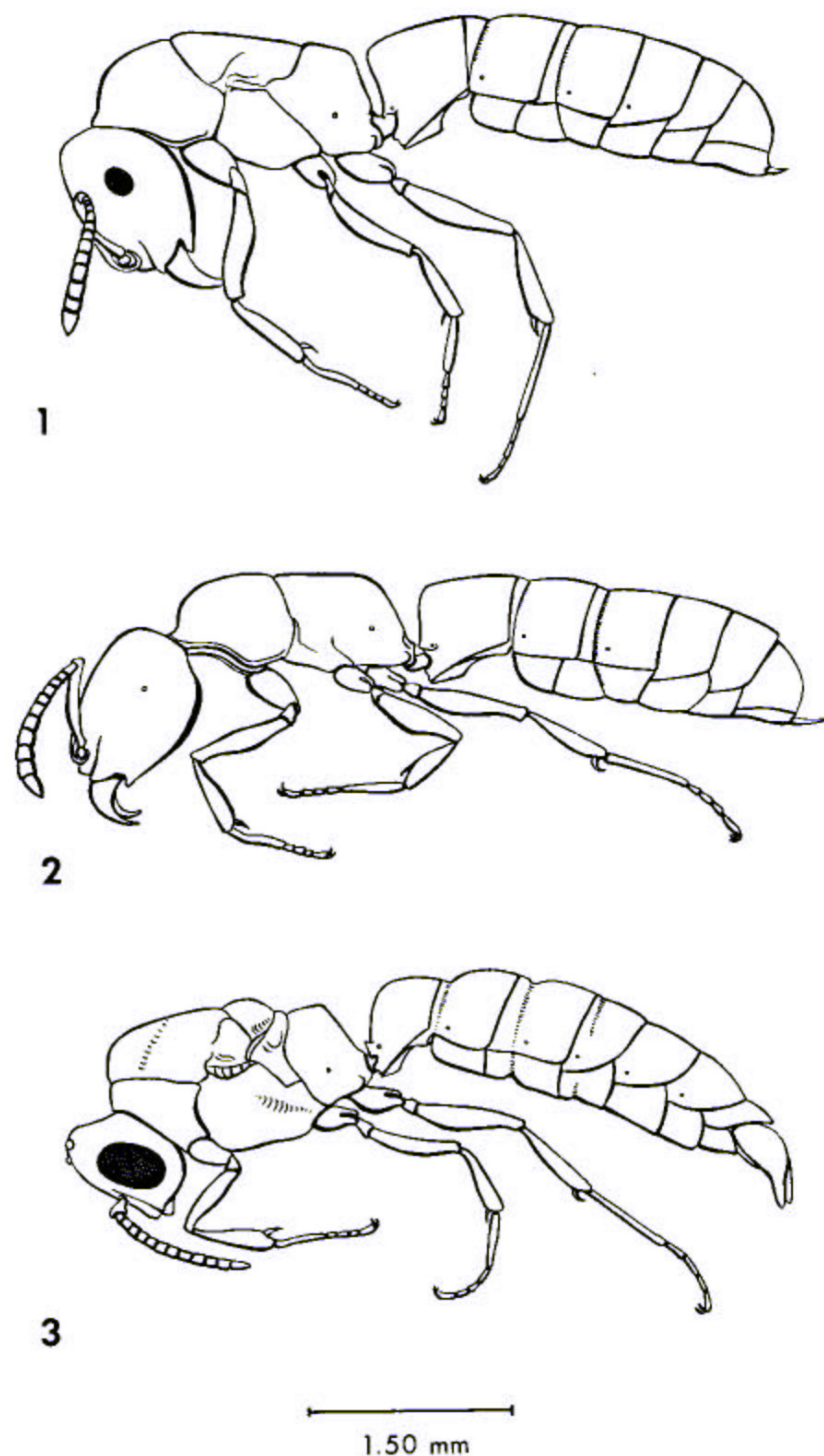

FIG. 1–3.—*A. pluto,* habitus drawings, pilosity omitted. 1, Queen, lateral view, wings omitted. 2, Worker, lateral view. 3, Male, lateral view, wings omitted.
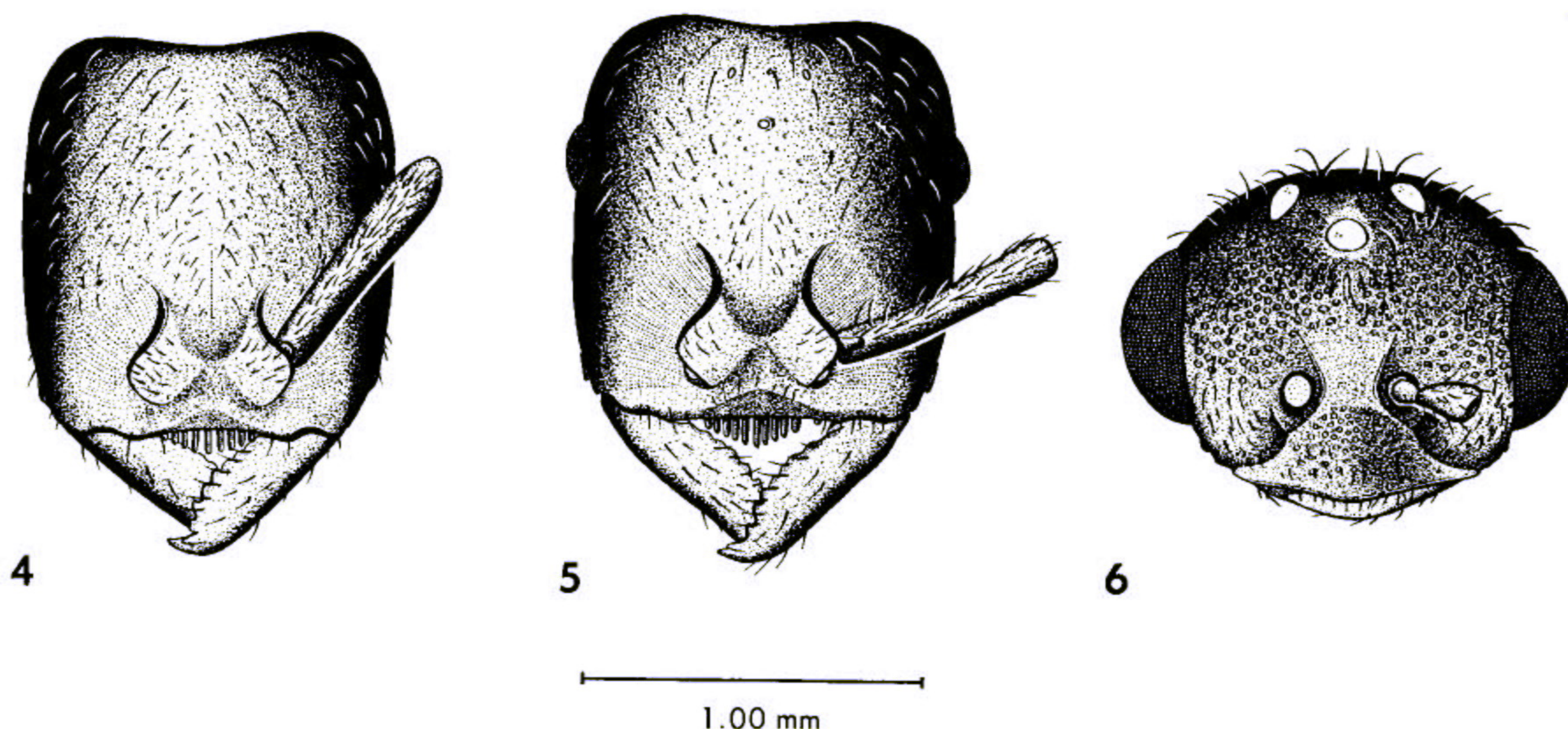
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FIG. 4–6.—*A. pluto,* heads in dorsal view, right antenna and funiculus of left antenna omitted in each drawing. 4, Worker. 5, Queen. 6, Male.
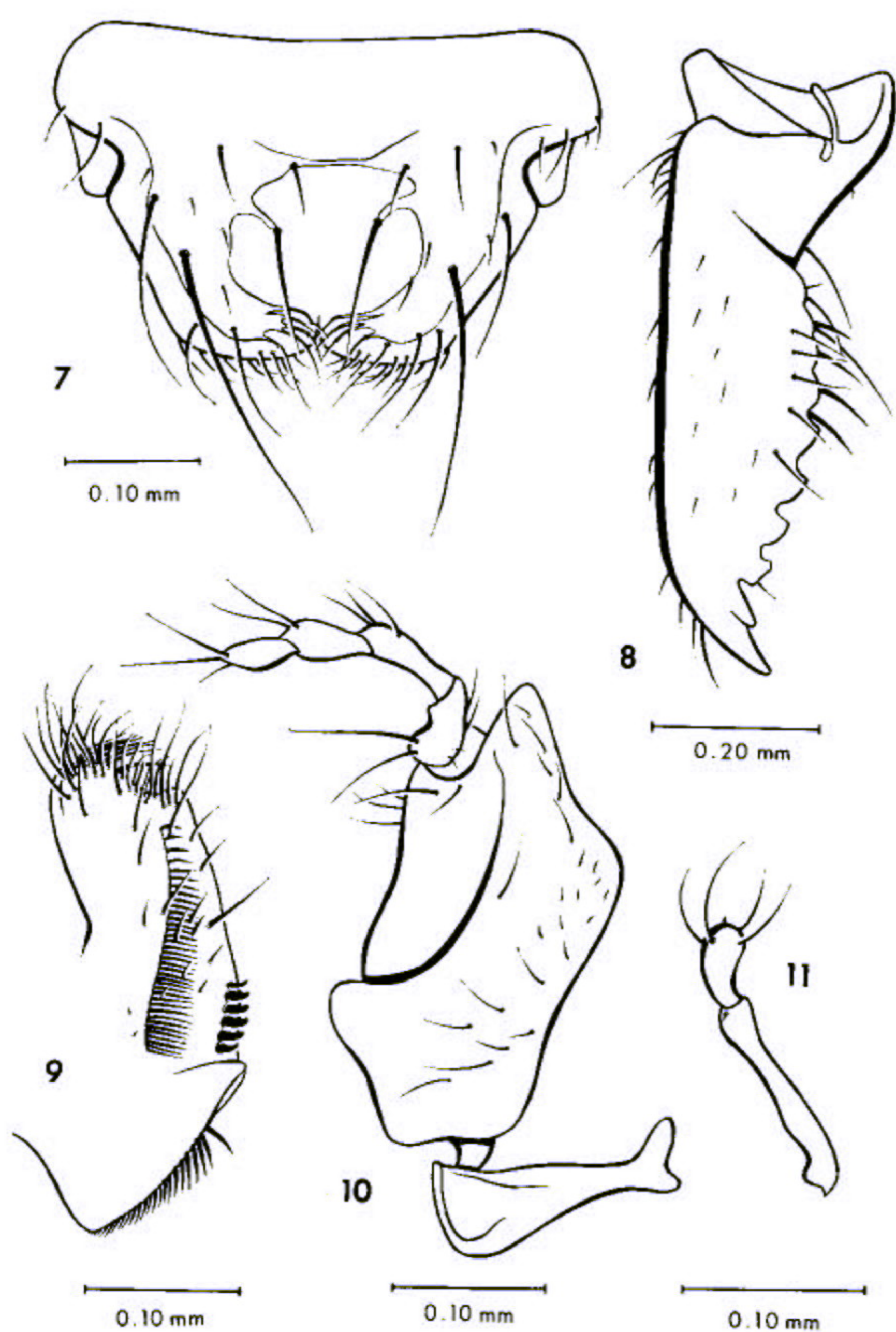

FIG. 7–11.—*A. pluto,* mouthparts of worker. 7, Labrum, external view. 8, Right mandible, dorsal aspect. 9, Left galea and lacinia, external view, the maxillary comb drawn as seen through the transparent galea. 10, Left maxillary palpus, stipes, and cardo, external view. 11, Left labial palpus, lateral view.

trunk sparsely pubescent with short setae scattered over dorsal and pleural regions; dorsum with several long, erect setae. Gaster sparsely pubescent except for visible terminal segment, which bears many erect and suberect setae; each segment bears a row of erect setae, in addition to scattered setae, near and parallel to posterior margins of tergites and sternites.

Tarsal claws simple. Tibial spurs 1, 2, 2; meso- and metathoracic tibiae each with a large, broadly pectinate spur and a smaller nonpectinate spur.

QUEEN, COMPOSITE DESCRIPTION.—TL 6.43–6.78 mm, HL 1.12–1.21 mm, HW 1.03–1.12 mm, CI 92, AL 1.89–2.07 mm, PL 0.72–0.81 mm, GL 2.16–2.43 mm, scape length 0.72–0.76 mm, length of petiolar node 0.67–0.81 mm, width of node 0.81–0.94 mm, hindfemur length 0.85–0.94 mm, greatest diameter of compound eye 0.18–0.22 mm, forewing length (1 specimen) 3.70 mm.

Habitus as shown in Fig. 1. Generally darker and more homogenous in color than worker. Gaster lighter than head and alitrunk; legs not yellow as sometimes seen in workers.

Head as shown in Fig. 5. General configuration of head, including absence of genal teeth, similar to worker. Punctation and structure of frontal carinae as in worker. Head with conspicuous multifaceted compound eyes and with 3 ocelli. Areas surrounding antennal sockets deeply depressed and striated as in worker. Clypeus concave medially and bearing a row of conspicuous tubercles (10 in each specimen examined); clypeal tubercles up to 0.11 mm long; when an even number of tubercles occurs, the middle two are of equal length and one is situated on each side of the midsagittal line. Antennae 12-segmented; scape almost straight in dorsal view.

Mouthparts almost identical to those of worker. Second subapical tooth of mandible may be con-
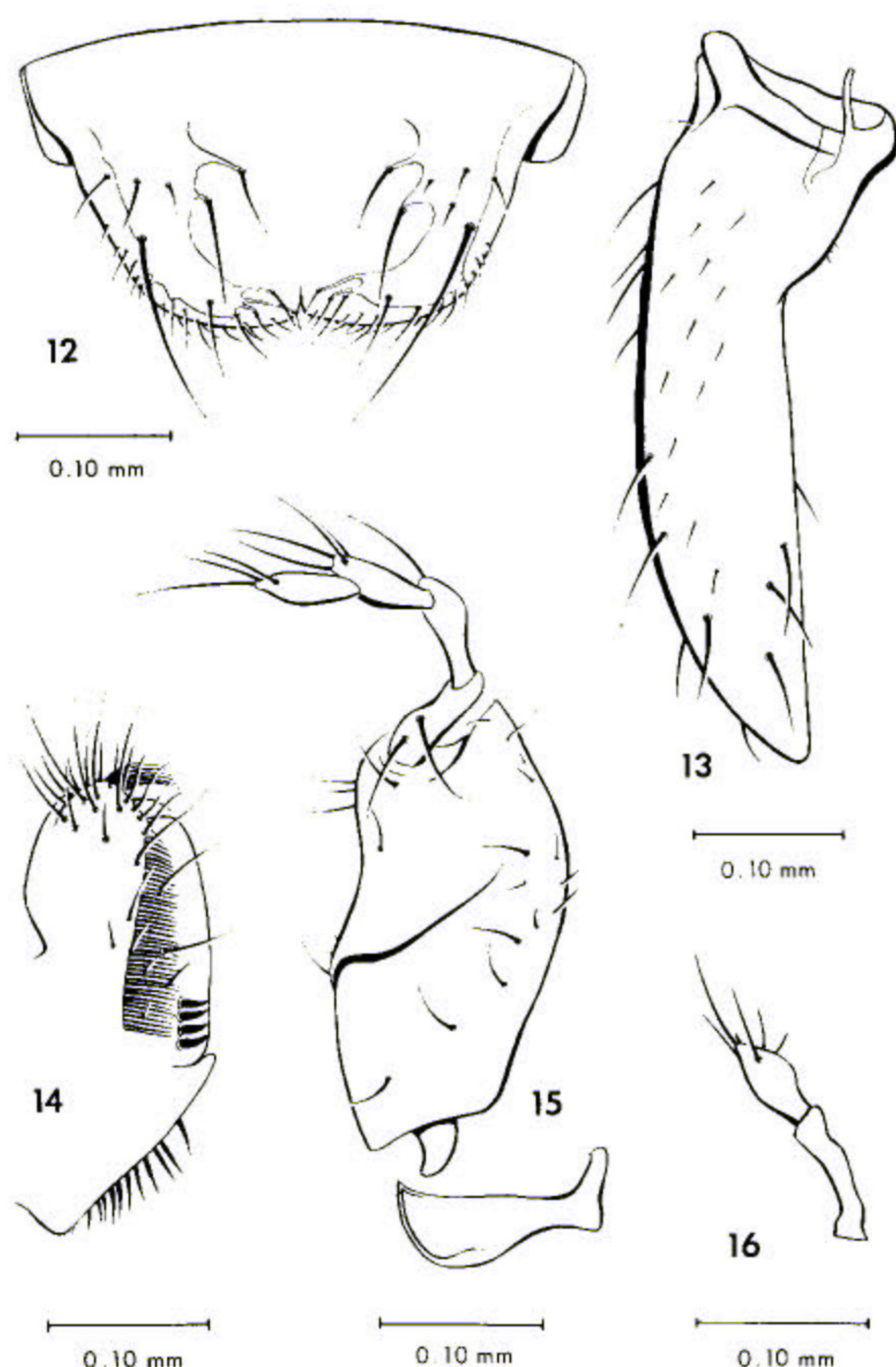
FIG. 12–16.—*A. pluto,* mouthparts of male. 12, Labrum, external view. 13, Right mandible, dorsal aspect. 14, Left galea and lacinia, external view, the maxillary comb drawn as seen through the transparent galea. 15, Left maxillary palpus, stipes, and cardo, external view. 16, Left labial palpus, lateral view.

spicuously truncated; galeal comb with as many as 9 setae.

Alitrunk finely but more sparsely punctate than in worker; dorsal surface otherwise smooth and glossy. Longitudinal pleural striae present above insertion of meso- and metathoracic coxae. Declivity of propodeum steep and slightly concave as in worker. Petiolar node as in worker.

Sclerites of gaster finely punctate; abdominal segments II through IV more sparsely punctate than remaining segments.

Pubescence as in worker.

Tarsal claws simple. Tibial spurs 1, 2, 2.

Wing venation (Fig. 17) as in *A. pallipes* (Haldeman).

MALE, COMPOSITE DESCRIPTION.—TL 5.39–6.07 mm, HL 0.90–0.94 mm, HW 0.99–1.03 mm, CI 109–110, AL 1.84–1.89 mm, PL 0.54 mm, GL 2.02–2.61 mm, scape length 0.13–0.18 mm, length of petiolar node 0.40–0.45 mm, width of node 0.67–0.72 mm, hindfemur length 0.81–0.85 mm, greatest diameter of compound eye 0.49–0.54 mm, forewing length 2.96–3.33 mm.

Habitus as shown in Fig. 3. Head and alitrunk black; scape of antennae black to dark brown; funiculus light brown; coxae black to dark brown, trochanter and proximal end of femur yellowish-brown, remainder of femur dark brown, tibia yellowish-brown, tarsus light yellowish-tan; petiole and gaster black to dark brown with pleurae and intersegmental regions yellowish-tan.

Head as shown in Fig. 6. Genae, frons, vertex, and clypeus coarsely reticulate-punctate; fine punctulae superimposed over coarse punctures; small area between antennal insertions with fine punctulae only. Head glossy. Compound eyes large; 3 prominent ocelli present. Frontal carinae low and inconspicuous, continuous with rims of antennal sockets; carinae not forming frontal lobes. Antennae 13-segmented (Fig. 20); funicular segments with 2 types of setae, one type similar to that of queen and worker, the other type, restricted to the male, larger and seated in a small pit.

Mandible linear with a straight internal margin not differentiated into basal and masticatory aspects, external margin broadly convex, only apical tooth present (Fig. 13). Labrum broad, cleft medially along the distal margin (Fig. 12); general configuration as in worker but without conspicuous proxi-
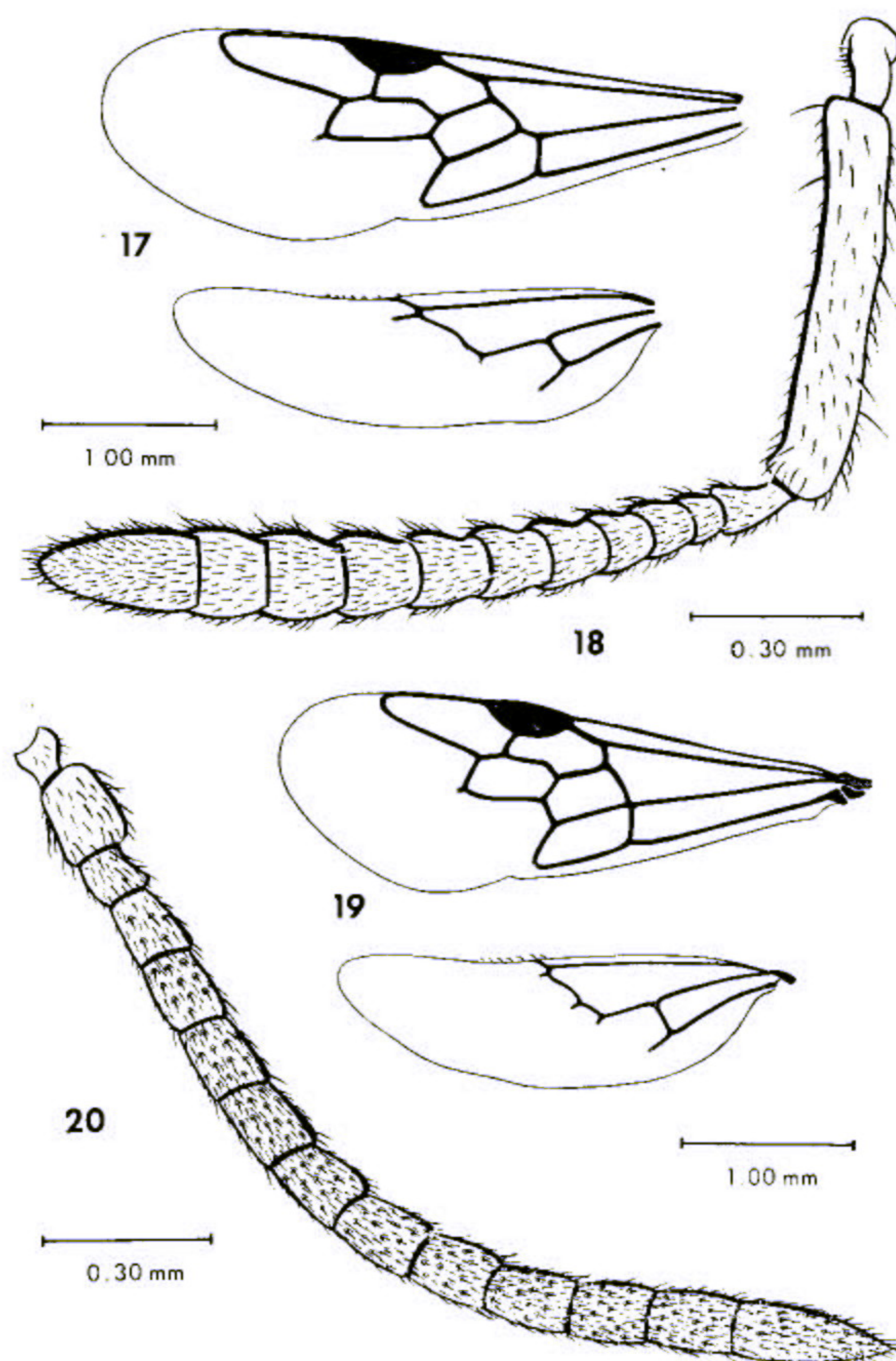

FIG. 17–20.—*A. pluto,* wings and antennae. 17, Wings of queen. 18, Left antenna of worker. 19, Wings of male. 20, Right antenna of male.

mal notch along lateral margin; setal pattern on extensor surface similar to worker pattern. Maxillary palpus 4-segmented (Fig. 15). Stipes with diagonal transverse stipital groove; lateral shoulder broadly and smoothly rounded (Fig. 15). Galea and lacinia as in worker except galeal comb with fewer setae and lacinial comb irregular (Fig. 14). Labial palpus 2-segmented (Fig. 16); subglossal brushes well developed, paraglossae absent.

Alitrunk coarsely reticulate-punctate; fine punctulae superimposed over coarse punctures. Alitrunk glossy. Declivity of propodeum gently concave. Anterior face of petiolar node flat but broadly rounded in transition to dorsal surface.

Anterior tergites of gaster with punctures reduced to shallow depressions but still with superimposed fine punctulae of head and alitrunk, tergal sculpturing progressively reduced caudally. Sculpturing of sternites similar to but less pronounced than on tergites. Gaster semiopaque.

Head moderately pubescent with numerous conspicuous suberect and subdecumbent setae. Alitrunk with numerous erect and suberect setae, the longest inserted on the dorsum. Petiolar node and gaster moderately pubescent, with suberect setae most numerous near the posterior margin of each sternite and tergite; number of setae per gastral sclerite increasing caudally.

Tarsal claws simple. Tibial spurs 1, 1, 2.

Wing venation (Fig. 19) as in female.

Genitalia as in Fig. 21–26.

The type-nest and 4 additional samples, upon which the descriptions are based, came from the Lamto Field Station of the University of Abidjan in south-central Ivory Coast. Lamto is off the main highway, ca. 50 km south of Toumodi at 6°13′N, 5°41′W. The holotype worker, from the type-nest AA 104 collected Aug. 16, 1965, and some paratypes are deposited in the Musée Nationale d'Histoire Naturelle, Paris. Other paratypes are deposited in the Museum of Comparative Zoology at Harvard University and in the British Museum (Natural History).

Taxonomic Discussion.—A. pluto represents the 3rd species of *Amblyopone* to be described from Africa south of the Sahara Desert. The other 2 species are *A. santschii,* described by Menozzi (1922) from Dakar, Senegal, and *A. mutica,* described by Santschi (1914) from Ibadan, Nigeria. Menozzi described the workers of *santschii* as reddish-brown and measuring 4 mm long, or much smaller than *pluto,* and he said that the head of *santschii* was "molto più lungo che largo, subparallelo, appena un poco più allargato anteriormente che alla base." In *A. pluto,* the head is only slightly longer than wide, and is not at all broadened anteriorly. The mandibles of *A. santschii* are "strette . . . leggermente striato," while in the new species, the mandibles are shorter and broader than is usual in the genus, and their dorsal surfaces are smooth and shiny, with scattered punctures. Evidently also, the mandibular and clypeal dentition of *A. santschii* are more "as usual" for the genus. *A. mutica* (3.5 mm long or smaller), on the other hand, is easily separated from both *santschii* and *pluto*: its clypeus is devoid of teeth or tubercles, and its petiole is narrowed anteriorly to form a short peduncle. On the basis of these latter characteristics, Santschi erected the subgenus *Xymmer* (to include *mutica*), which was subsequently synonymized with *Stigmatomma* Roger by Brown (1949).

The worker and queen of *A. pluto* exhibit most of the definitive *Amblyopone* characteristics. The petiole is broadly attached to the postpetiole (abdominal segment III), the eyes are situated behind the middle of the head, the mandibles bear more than 3 teeth, the frontal carinae form expansive lobes, the antennae are 12-segmented, the promesonotal suture is distinct and complete, the sting is functional and conspicuous, and the clypeus bears a row of tubercles. *A. pluto* departs slightly from the *Amblyopone* pattern in its lack of genal teeth and in the shape of the mandibles, which are not as "linear" as in many *Amblyopone* species.

The clypeal tubercles of *A. pluto* are particularly

left paramere

cuspis of volsella

digitus of volsella

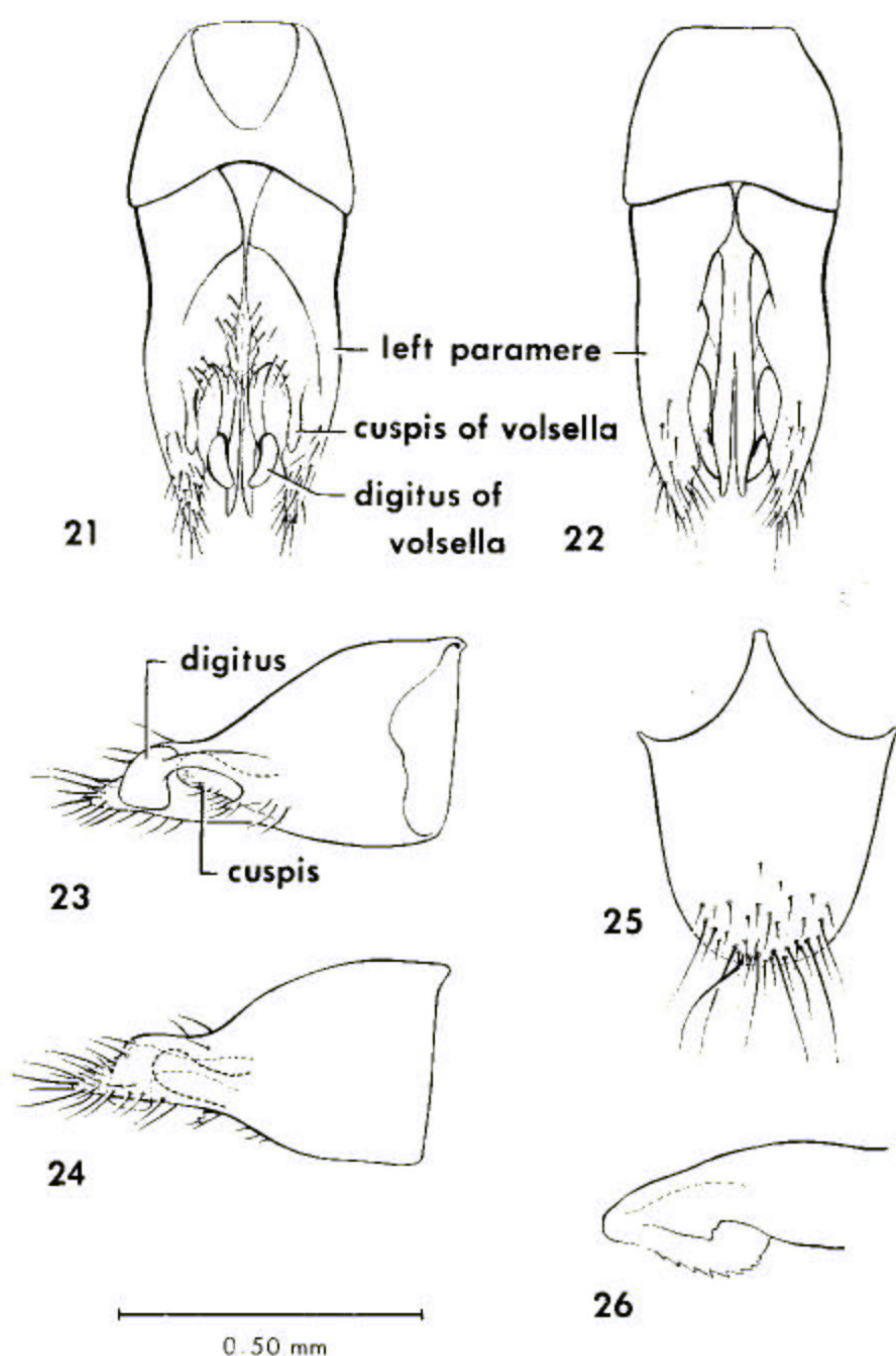21   22

digitus

cuspis

23

25

24

26

0.50 mm

FIG. 21–26.—*A. pluto,* male genitalia. 21, Genital capsule, ventral view. 22, Genital capsule, dorsal view. 23, Left paramere and volsella, mesal aspect. 24, Right paramere and volsella, lateral aspect. 25, Subgenital plate (9th sternite), ventral view. 26, Aedeagal valve, lateral view.

conspicuous and appear to be much longer than those found in many other species. Although their function has not been determined, they may aid in grasping prey or brood. In the case of brood, this idea is an attractive one, because the workers commonly carry their larvae to the freshly captured prey, once the prey has been dragged into the nest. Analogous tubercles or teeth are present in other species of ants and are not restricted to the clypeus. They appear, for instance, on the labrum of the amblyoponine, *Apomyrma stygia* Brown, Gotwald, & Lévieux.

The stipites of *A. pluto* have strongly developed transverse stipital grooves. When the mouthparts are withdrawn, the labrum closes, and its distal margin fits snugly into these grooves. Together, then, the labrum and stipites securely close the oral cavity and protect the softer mouthpart components. The transverse stipital groove is well developed in the Dorylinae, Cerapachyinae, and Pseudomyrmecinae. However, it is not present in *A. pallipes,* which unlike *A. pluto,* possesses paraglossae. However, in most respects the mouthparts of *A. pluto* and *pallipes* are quite similar.

The workers of 1 colony sample of *A. pluto* (AA104), consisting of 2 workers and 1 queen, are smaller than other specimens examined. The 2 workers have total lengths of 5.66 and 5.79 mm, while the range for all other workers is 5.98–6.52 mm. The queen of this sample is 6.61 mm long and falls within the range for the other queens (6.43 and 6.78 mm). The lengths of the heads, alitrunks, and petioles of these 2 workers represent the lowest measurements in the ranges for the species, while the gaster lengths fall within the species range, although at the lower end. The eyes of these 2 workers are reduced and are represented by only a change in the pigmentation of the integument. They may well consist of a single facet. This reduction in eye size appears to be allometric. In all other respects, this colony sample conforms to those characteristics which distinguish this species. Evidence suggests that polymorphism is not well developed within the colonies examined, and this condition is true as well for other species in the genus (Brown 1960). There is little doubt that the colony of smaller individuals is the same species, but we have yet to explain why they are smaller.

Perhaps *A. pluto* is most interesting in its apparent conspicuousness. It is a moderately sized ant and is clearly a new species, but its cryptobiotic existence has seemingly hindered its discovery. It may be that other "conspicuous" species of *Amblyopone* remain to be discovered in the Ethiopian Region, and that their apparent absence from this Region may be a reflection more of collecting technique than of actual abundance.

BIOLOGY OF THE SPECIES

This species was discovered in the humid savannas of central Ivory Coast. Indeed, the distribution of this species is limited, so far as is known, to savannas that have not been burned for several years (Fig. 27). Neither foraging workers nor nests have been observed in those parts of the savanna burned annually.

Unlike other *Amblyopone* found in the same habitat (*A. muticum, A.* near *normandi,* also *Apomyrma stygia*), this species has not been found in the forest. However, like other species of the same genus, it is possible that it extends into the savanna from the neighboring forest, but its density, while modest (several nests per hectare), is at least higher in savanna.

The collected nests were situated at a mean depth of 20 cm in black clay soil with a thick cover of litter derived from several years' accumulation of grass. Microclimatic recordings showed that in this environment conditions (light, temperature, relative humidity, etc.) at soil level are like those found in the humus of gallery forests.

Adult males and females as well as sexual brood have been collected from nests during March and April. It is therefore probable that, as with *A. mutica,* the time of mating for the species is correlated with the beginning of the rainy season. No sexual forms of the species were collected at UV light, despite persistent UV collecting within its area of distribution.

It is impossible to determine times of foraging activity or the full extent of the foraging range for *A. pluto* or for the other species of Amblyoponini observed. The ants belonging to the genus *Amblyopone* never forage, from what we have been able to observe, on the surface of the ground, even on the humus of areas as well covered by vegetation as the unburned savanna. Australian *Amblyopone* sometimes come to the surface of the soil, but do not normally forage there (R. W. Taylor, personal communication; Brown 1960). There are no stones on the savanna that might serve to cover near-surface nests or nest fragments.

Isolated workers are encountered foraging at a depth of 15 cm or more in the ground. The radius of activity from the nest is significant; the workers have been observed foraging up to 6 m in a straight line from the nest. That these workers belonged to the colony under consideration was verified by observing the absence of reciprocal hostility when they were placed in the presence of workers from the nest.

Isolated wingless queens were found moving about in the soil several meters from the colony. It would not be astonishing to find that queens forage in this species, because ponerine foundress queens often do. Haskins and Haskins (1951) observed, in *A. australis* Erichson, that during rearing the queens continue, for a long time after nest foundation, to participate in provisioning the nest concurrently with the workers. Because the observations on *A. pluto* were carried out in March, i.e., during the species' reproductive period, it could be that the females collected were foundresses in search of a nesting site or practicing progressive provisioning (Wheeler 1932; Haskins and Enzmann 1938; Haskins and Haskins 1950, 1955; Le Masne and Bonavita 1969).

Prey were gathered in 2 of the 3 nests opened in

FIG. 27.—Savanna habitat of *A. pluto* at Lamto, Ivory Coast, during the dry season. Note the palm, *Borassus ethiopum.*
FIG. 28.—*A. pluto* in laboratory nest, queen indicated by arrow.
FIG. 29.—*A. pluto* in laboratory nest, a larva feeding on a geophilomorphic chilopod indicated by the arrow.

1968; all were geophilomorph chilopods. In the nest already described, 2 chilopods were found in a cavity next to the brood. One was already dead and decayed; the second was still living, although paralyzed. The brood was in a pile beside the chilopod, but no larvae were feeding. It should be noted that in all the nests observed, the presence of visible prey remains belonging to animal groups other than Chilopoda was never noticed.

Since then, 7 nests of *A. mutica*, the most abundant amblyoponine in this region, have been opened. The only food debris that has been observed inside these nests were the remains of chilopods. Brown (1960) indicated an analogous diet for *A. pallipes* in the United States and *A. hackeri* Wheeler in Australia. On the other hand, the large Australian species *A. australis* gathers various arthropods (e.g. Coleoptera).

The specialized diet of some *Amblyopone* can be compared with that of other neighboring hymenopterous families. It is interesting to note that aculeate families ancestrally close to the ants (according to Brown 1954, Wilson et al. 1967), like *Amblyopone*, have specialized alimentary needs. Thus Scoliidae and most Tiphiidae attack the larvae of lamellicorn Coleoptera, while methochine tiphiids live at the expense of cicindelid larvae (Clausen 1940). Although there are many notable exceptions, the higher ants tend to utilize a wider variety of prey.

Because the observations on these archaic ants are generally so sketchy and hard to come by, some detailed observations on *A. pluto* are offered below. Taking into consideration the limited spatial distribution of this species in the area studied and the small number of colonies discovered, certain observations could only be made once, so more data are needed for confirmation or revision of some details.

The Nest of A. pluto.—Three nests were excavated in March 1968, all at ca. 10 AM. The general plan of the nest was much the same in all cases. The total population of one of them was closely estimated. This nest, ranging from 10 to 30 cm deep in the soil, showed the following plan. An ellipsoidal passage (5×3 mm) ca. 15 cm long had in some places pockets spacious enough to contain brood. This passage could have been created by the ants, or, more simply it could be that they had reutilized a portion of a burrow elaborated by another soil organism or a part of the site of a missing root. This channel led to a 1st chamber measuring 0.5 cm diam by 1.2 cm high. This chamber contained at the time of opening only cocoons. Another opening could be distinguished in the floor which led to a larger cavity, ca. 3 cm high. This chamber contained the greater part of the larvae and workers. Another channel left this latter chamber laterally, but its destination could not be determined.

The colony contained in this nest at the time of opening consisted of 18 workers, 2 winged females, and 7 wingless females. It was not necessarily a polygynous colony, and such a composition can be interpreted in several ways. Taking the date of collec-

tion into consideration, it may have been a colony with its foundress queen and its new queens ready to leave the nest to found other colonies. Possibly new queens lose their wings before leaving the nest. It should be noted that there were queen larvae amongst the brood. Supposing that a certain number of individuals was foraging at the time of opening of the nest, it is possible to estimate its total population at ca. 40 individuals. This colony was less populous than another collected in August 1965 at the same hour. It reached 35 individuals, and this count was during the nonreproductive period of the species. Although no precise census was made for the 2 other nests excavated, they were estimated to contain ca. 30 adult individuals each. One of them contained males.

Observations on Feeding Behavior in Laboratory Nests.—After several fruitless tests with nests made in plastic or clay boxes stuffed with blotting paper, rearing was accomplished in plaster nests of the Janet type (1893). These nests consist of 4 connected chambers. The internal temperature, measured with a thermocouple, varied with the time of day between 25 and 30°C. Relative humidity, measured with a probe, remained permanently at the saturation point. The observations described below were carried out with 6 colonies collected between February and May.

Feeding Behavior of Adults.—Different types of food were tried, but only chilopods were accepted. Chilopods belonging to the same genus as those collected in the nests were introduced to the laboratory nests. They measured from 3 to 4 cm long as against 6 mm for the ants. Although quite superior in size, the chilopod usually moved about rapidly without aggressive manifestations from the ants. Generally, after moving about the chambers making up the nest and exploring all the cavities and cracks encountered, the chilopod took refuge in a corner where it would remain for up to several hours without moving. When the chilopod remained in the cell adjoining the chamber containing the brood, or even at the other end of this chamber, apparently the ants did not detect its presence. Aggressive reactions appeared when the prey passed near the ants, or, eventually, when an ant, during its wanderings, came near the chilopod.

The nature of the process by which the excitement in the ants is provoked must be examined. These ants, like all others, are very sensitive to the slightest movement of air, as for instance in moving the lid of the nest. Detection takes place at a short distance, and certainly it could involve vibration or olfaction linked to a movement of the air generated by the motion of the chilopod. Observation seems to suggest that the ants cannot locate their prey at very great distances: 2 cm would be the maximum, and perhaps it is a matter of only several millimeters. At any rate, the discovery is probably not visual, as this species normally hunts in the dark, and like the majority of *Amblyopone* has small, poorly developed eyes.

If the prey flees to the other end of the nest, the

workers will not follow it. The attack will occur when a foraging worker in the nest passes near the prey. The ant immediately becomes much more active (rapid movements in all directions, antennal movements, etc.). It attempts to catch a leg or cercus in its mandibles. The chilopod flees. There is a very distinct lack of persistence in the attack of the workers. The majority do not attack more than once or twice. At the end of a few minutes, they seem to lose track of the prey in its flight. The workers no longer bother with it, and return to the brood piled in another corner of the chamber. After a while, a foraging worker seemingly by chance, discovers the chilopod in another corner of the nest. In its flight the latter may pass through that portion of the chamber containing the brood, thus causing general excitement. There follows a number of attacks which increase when the chilopod is in the region of the brood. Generally, the attack is concentrated on the posterior features of the chilopod, since they are more easily accessible to the ants during pursuit.

In general, several hours pass before a systematic attack on the chilopod begins. But in 1 case an immediate attack on the prey was recorded. It involved a colony collected in the preceding hours and immediately put into the laboratory chamber. From the moment the prey was introduced to the chamber, the workers dashed to the attack, and the chilopod was quickly immobilized at the end of a brief period (several minutes). Generally in these cases of collective aggressiveness, the attack on the chilopod becomes continuous and finally efficacious. The degree of aggressiveness revealed in this case was stronger than usual. No prey was present in the nest when it was collected, so that it may have been a hungry colony. The other 2 colonies collected contained prey at the time of opening. (Also, there is undoubtedly some significant structural difference between the soil channels where prey is naturally found, and the artificial chambers in which these observations were made.)

During the skirmishes between predator and prey, the chilopod defends itself with its ventral glands, which secrete a liquid that flows onto the cuticle. This liquid contains, among other things, HCN. It has the affect of causing the assailant worker to stop abruptly, to arch itself, and to remain immobile. Most often the 1st pair of legs is immobilized, sometimes the head and all of the anterior part of the body. This paralysis generally lasts only a few minutes, but the worker can be killed (1 observation).

The chilopods found in the nest belong to the genus *Schendylurus* (*S. paucidens* Silvestri). The prey accepted by the laboratory colonies belonged to *Schendylurus* and *Pleuroschendyla,* and to the species *Paratringonocryptos planquettei* Demange, all geophilomorphs.

The chilopod system of defense varies enough to help hold the *Amblyopone* to considerable alimentary specificity. For example, the scolopendromorphs have no repugnatory glands, but their very powerful, venom-containing claws, added to their size and mobility, make them formidable adversaries. In fact, they are never attacked by the African *Amblyopone*. The introduction into the nest of a 6-cm *Rhysida nuda togoensis* Kraepelin created great excitement in the workers, which fled in all directions. It was the same for *Cryptos* (sensu lato), which possesses, in addition to powerful claws and large quantities of venom, hind legs that can serve as tearing claws. This fleeing behavior did not occur in the presence of geophilomorphs which, in 'spite of their ventral glands, are systematically attacked. In this group, the poison claws are not very powerful. There is no mechanism for spraying the venom which, although toxic because of the HCN it contains, does not seem to be secreted in an efficient enough manner to make it a good defense mechanism against these ants.

Cyanogens as principal components of defensive allomones are found in polydesmid diplopods (Eisner and Meinwald 1966) and geophilomorph chilopods (Schildknecht et al. 1968; Eisner, personal communication). For a review of chemical defenses against predation, see Eisner 1970.

Apparently, only living prey is attacked and eaten. An attempt was made (1 trial) to feed a colony a chilopod killed an hour earlier by slightly crushing its head. Several workers approached and touched it with their antennae. The chilopod was abandoned without being eaten, even though the workers and their larvae had had nothing to eat for 2 days.

Because of the prey's rapid movement, the workers try to grip the hind legs and the cerci, although the more accessible cerci break easily. Usually at most 2 workers effectively participate in the attack, but sometimes only 1 is involved, even when the alarm is transmitted to the majority of the ants while the chilopod is in the region of the colony. Thus there is no real coordination among the workers in locating or attacking the prey. The worker that has "discovered" the chilopod returns excited (agitated behavior, rapid movements in all directions). The worker's excitement appears to be transmitted to 1 or 2 others, rarely more, but never to the entire colony, which is numerically small and occupies only a few square centimeters.

When a worker has succeeded in hanging on to an appendage of its prey, it tries to sting by curving its abdomen between its legs. Many of these attempts fail as the sting appears to glide across the prey's cuticle. It is impossible at the moment to relate the number of abdominal flexions with the number of effective sting contacts.

Several effective stings are necessary to paralyze a prey (perhaps up to 4). Although it is not dead, the chilopod's motor system becomes progressively paralyzed. The paralysis can be seen to spread slowly from the stung area, but it appears to move more rapidly caudad. Although the legs can no longer move, the body can still be contracted. Uncoordinated movements of the chilopod body occur,

movements which are not typical of normal walking movements and which are characterized by repeated dorsal arching of the body. This observation is similar to a series of analogous observations made by Brown (1960) which concerned a colony of the little amblyoponine *Prionopelta modesta* Forel from Veracruz: "The centipede showed impairment of locomotor activity of the segments behind the point where the ant had been attached . . . but after a few minutes showed partial recovery." A case was observed in the present study where a chilopod was able to move again several minutes after the sting. However, in this case, because the act of stinging was very rapid, it could not be ascertained for sure as to whether there was an effective sting.

Once immobilized, the prey is dragged by 1 or more workers into the region where the brood is kept. Still there is a lack of any obvious coordination among the various ants doing the work at any given time. However, on the whole, there is a coordination of sorts in that the prey finally arrives at its destination. The chilopod is then dragged to a point varying in distance (several millimeters to 4 cm) from the brood. This action is the most frequent, but occasionally the chilopod can be found even on the brood, or buried among it (1 observation, which apparently was exceptional). The prey remains alive, as shown by some movement of its body.

These observations confirm and supplement the work of other investigators on other species. The partial paralysis of prey has already been observed by Brown (1960) for *A. pallipes* and by Wilson (in Brown 1960) for *Myopopone castanea* (Fr. Smith) of New Guinea. This *Amblyopone* prey paralysis contrasts with other ants, where the prey is killed (Le Masne 1953). In time the prey is carried to the area containing the brood. This observation agrees with Brown (1960) who wrote of *Prionopelta*, "the following day, the ants were found to have removed the centipede . . . to the brood chamber . . ." Consequently the brood are moved and placed on the prey. However, the 2nd movement is less important than the first in terms of the distance covered. Wilson (1958) and Brown (1960), nevertheless, found evidence in nature that the workers of some species of *Amblyopone* transport their brood to the prey when it is impossible to move the latter from the place where it is killed.

In nature, females can be found 2 or 3 m from the nest (foraging?), but in the laboratory nests the female is less active than the workers. She stirs less and spends less time with the brood, but will on occasion glossate the larvae just as the workers do. The queen is likewise involved in mutual lickings with the workers. The queen was never seen to assist in a direct attack on a chilopod, and although such behavior is probable in nature, at least on the part of foundresses, it is clearly much rarer than for workers when the latter are present.

As with the prey of *Aphaenogaster* (Le Masne, personal communication) and most dacetine species

the chilopod is never immediately dismembered by the workers. In fact, the *Amblyopone* contrast sharply with other ants that cut up the food reserved for the larvae.

The *A. pluto* workers open their prey by biting at the intersegmental membranes. They also touch or pull violently on the appendages. Though it is relatively difficult to detach a piece of the leg, the cerci yield more readily. However, workers are most successful at destroying the membrane. Independent of these contacts, several workers touch and bite the extremity of the prey, which is often damaged more than the middle of the body. This fact is a direct consequence of the pursuit. They place their mouthparts on the openings thus made, probably attracted to the fluids flowing from the wounds.

When 1 or more openings are made in the area of the intersegmental membranes, the workers feed on them first. They put their mandibles into the body; sometimes even a part of the head is inserted, and thrust into the soft parts of the organism. When the head of the worker is withdrawn a remnant of food in the form of a long whitish filament can be seen stretching between the labium of the ant and the prey. Though it is indispensable for feeding that the prey be alive at the beginning, the feeding of the different castes can continue after death, although eventually they will have nothing to do with a cadaver. It should be noted that the workers feed or try to feed first, accompanied by wingless queens, regardless of the length of time from the last meal and without regard for their brood. The winged females are much less active than the workers; they do not show up until the prey is immobilized in the region of the brood. However, they try to feed at the same time as the workers.

The males do not participate in the preliminary phases of discovering and capturing the centipedes. The male's position in the feeding succession follows the workers and females in accordance with the ineffectiveness of their mandibles. Although they appear to try their mouthparts on the prey cadaver, every attempt to penetrate the integument on their part is unfruitful. Thus they are obliged to utilize previously cut openings.

To determine the degree of feeding specificity for *A. pluto*, a colony was starved 3 days and then presented with members of various arthropod groups (experimental allophagy). A 1st series of trials was carried out by simultaneously introducing samples of termite workers and soldiers, the first belonging to the genus *Nasutitermes*, the second to the genus *Bellicositermes*. Each introduction unleashed a violent battle in which the termite soldiers momentarily proved superior, causing the death of larvae and sometimes workers. However, the termites were finally killed, and their bodies, treated like other debris, were taken to the zone containing refuse without the ants ever attempting to feed on them.

A 2nd trial, repeated 4 times, with bee's honey

deposited on various holders (paper, cardboard, glass, wood) showed that the workers are totally indifferent to honey. After sensing the material with their antennae, they finally turned away, confirming Haskins and Haskins' (1951) conclusion that *Amblyopone* will not accept honey. We note, though, that the male of *A. pallipes* can eat honey and fruit juice.

A test conducted with the successive introduction of a campodeid and a japygid was more interesting. Their size was 5–7 mm. They were immediately attacked by the workers, as are all living arthropods passing close to the brood. The japygid was killed with a single sting; the campodeid required three. However, as in the case of the termites, there was no attempt to feed on them. Therefore, at the moment, it is concluded that living geophilomorph chilopods make up the entire diet of this primitive ant.

It was impossible to quantify the amount of nutrients taken in nature. However, a laboratory nest could consume 2 chilopods every 3 days. It is possible, taking into account the number of prey observed in the opened nests, that this number is superior to that actually ingested in nature. However, if the laboratory values are used, a colony of ca. 50 individuals could consume 200–250 chilopods a year. If one estimates that the density of *A. pluto* colonies can reach from 10 to 20/ha in their preferred biotope and that, at a given time, one can find at least 1 chilopod/m³ (value arrived at in counts without particular sampling of this group), colonies within this hectare would consume 2000–5000 chilopods/year. Keeping in mind the chilopod replacement rate and the fact that their real density is probably higher than the estimates indicate, it is possible that this genus of ants is, within its zone of maximal density, an important factor in the limitation of the number of chilopods.

Trophallactic transmissions of food in *Amblyopone* are very rare; in 1 hr of continuous observation of *A. pluto,* 1 sure exchange was recorded and 1 probable exchange. The duration of the first was ca. 30 sec. The 2 partners approached each other face to face. After a few contacts with the antennae, the head of one pivoted ca. 90°, while the other raised its head to the head of the other, thus permitting the mouthparts to come into contact. Liquid could not be seen between the labia.

It is impossible at the moment to conclude whether a division of labor (polyethism) exists among the various workers making up the colony. This division of labor can be seen in other primitive ants like *Myrmecia gulosa* (F.) (Haskins and Haskins 1950, Freeland 1958) or *Mesoponera caffraria* (Fr. Smith) (Bonavita and Poveda 1970), and it is well known for more highly evolved ants (e.g. *Camponotus* and *Myrmica*). It could not be ascertained for *A. pluto* whether certain workers were more particularly concerned with the brood, while others were involved in foraging.

The following conclusions on *A. pluto* hunting can be made, based on field and laboratory observations. a, The workers forage alone in their search for prey. b, They attack their prey with their mandibles and paralyze it with their sting. c, The prey is then dragged into the nest to a position near the brood. d, The workers penetrate the integument of the paralyzed prey without cutting it up, and feed on the soft parts. e, The prey probably consists exclusively of geophilomorph chilopods.

Note that the range of observed behavior patterns (prey discovery, contact, attack, stinging, transport, etc.) never takes place in a continuous fashion. There is a more or less marked interruption after each pattern, the longest interruptions taking place at the beginning (the discovery and attack phases), at least in the artificial nest.

Larval Feeding.—Before examining the manner in which the larvae are fed, an examination of larval transport is appropriate. This transport occurs in 2 stages. In the first, the worker moves the larva to be fed to the side of or eventually onto the chilopod (Fig. 28, 29). In the second, the larva, through independent movements of its thorax, next attempts to stick its head into the chilopod.

The worker can therefore move a larva and place it beside the chilopod. The larva lies on its side or back. The worker usually seizes the larva dorsally, either behind the head or at the junction of the thorax and abdomen. Seizure occurs in this latter region from 60 to 70% of the time. The worker may also grasp the larva in the abdominal region (2 observations). The larva is carried with its abdomen dragging because late-stage larvae are almost as long as the workers. Two cases of larval transport occurred in which the larva involved was left isolated in the middle of the nest without any prey contact. Even in well-fed colonies, the workers drag their prey to the brood area, and as a result of this prey transport, the larvae can sometimes find their own way to the prey. The winged queens behave like the workers and try to place the larvae, although awkwardly, on or beside the chilopod. However, they make this attempt less frequently than the workers.

Once beside the chilopod, the hungry larva elongates its thoracic segments, turns its head by prolonging the thorax and bends it to the side. It may also slightly bend the thorax toward the posterior. Its flexibility is such that this part of the body can assume an S-shape (Fig. 28). If the head moves over to the side, the larva can rock itself from this dorsal position to a lateral position. It then attempts to hook onto the prey, moving its mouthparts over the surface of the cuticle of the chilopod. If it is situated at the middle of a segment, it is evidently unable to pierce the cuticle. If, on the other hand, it is opposite an intersegmental membrane, it searches for a tear in the membrane. If it is next to a place not previously cut by the workers, it will try to pierce the cuticle, but it can do so only where the integument is thinnest. The larval mandibles can be seen through the transparent larval integument

biting at and trying to cut the prey cuticle. Once it has breached the cuticle, the larva attaches itself to the prey by means of its mandibles and forces its head into the interior, where it can reach the internal soft parts or fluids (Fig. 29). The attachment serves to anchor the larva, and because of the prey-larva weight differential, the larva is able to draw itself to the prey, and extend itself within, without moving the prey, by contracting its thoracic segments. While this movement is thus not completely autonomous, it is evident that the flexibility of the thorax permits movements not seen in larvae belonging to other genera examined. The larvae of *Amblyopone* are distinguished, by their mobility and by their relative autonomy, from the larvae of more advanced ants. It was also noted that the larva, apparently seeking food, may try to attach itself either to other larvae or to the workers.

It should be noted that there is no preparation of the food by the workers beyond its paralysis and transport; not even their simple piercing of the integument seems to be needed by the larvae. When it has finished eating, the larva withdraws its head from the chilopod body and remains completely immobile. It may attempt to reenter the chilopod, but only after a considerable period of time. The workers may at times move the prey while one or more larvae are trying to feed, causing the larvae to suddenly detach themselves. Workers can withdraw a larva and place it back with the other brood. This observation agrees with that of Le Masne (1952) on *Hypoponera eduardi* (Forel) where the prey may be taken away from the larva before it is entirely eaten. In certain cases, the larva is so well attached to the prey when it is eating, that a worker, in attempting to take the larva away, does not succeed and moves the chilopod at the same time. Workers were never observed to bring food to a larva that remained with the rest of the brood. Dietary differences between the youngest and oldest larvae were not detected.

The different castes once fed, the chilopod is abandoned although it is often far from being completely consumed. Before the 1st signs of decomposition are manifested externally by a blueing of the cuticle (yellowish in life), it is removed from the brood and placed at a distance of from 1 to 4 cm. This observation appears to be different from that of Haskins and Haskins (1951), who noted that in *A. australis*, pieces of insect chitin are left in the brood chamber for a relatively long time and are frequently licked by the brood.

The duration of feeding time on a given chilopod is evidently quite variable. However, in most cases it is only intense for a few hours. The prey, although far from being entirely consumed, can be used for 24 hr and then is removed without being cut up.

We do not know if there is any regurgitation of stomodeal food from the workers to the larvae, a phenomenon seen in those Ponerinae that are more advanced than *Amblyopone*, such as *Hypoponera* (Le Masne 1953) and also in the possibly less advanced genus *Myrmecia* (Haskins and Whelden 1954). In the instance of *A. pluto*, trophallaxis with the larvae was never observed, nor was there any evidence of such exchange. Here again, a fundamental act of important social behavior in advanced ants seems to be lacking in *Amblyopone*.

The workers can also stimulate the larvae with their antennae (and anterior tarsi?) between the 8th and 12th abdominal segments. From the extremity of the larval abdomen, as a result, there comes a liquid which congeals quickly on contact with the air. The drop can also ooze out without solicitation. The worker extends its mouthparts and ingests the droplet. Deposits of this liquid were never found on the plaster substrate of the laboratory nests. Le Masne (1953) has similarly described workers of *Ponera* ingesting larval excretions.

Neither liquids nor solid pieces of food were seen to have been passed from adults to larvae. Neither were the workers ever seen to lick or chew cocoons, meconium, or fluids from the cocoons. It should be noted that the cocoon debris are not put in a particular corner of the nest (another primitive characteristic?). Everything is cast away at eclosion and is simply put at a distance from the brood. The workers can breach the skins of larvae that have been dead for a short while. They pierce the body with their mandibles, causing the hemolymph to ooze out, and then ingest this fluid. Toward the end of this activity, the exudate becomes more viscous and forms filaments between the worker mouthparts and the larval body. This feeding behavior can last several minutes.

Several cases of cannibalism have been observed for *A. pluto*, confirming the observations of Haskins and Haskins (1951) for *A. australis*. In 1 colony subjected to fasting for 4 days, the workers consumed half of the larvae present among the brood. Cannibalism can also occur between sibling larvae. The contents of certain cocoons are dismembered and eaten by the larvae which thrust their head and 1st thoracic segments into the interior of the pupating larva. The mandibles can be observed through the larval integument to shear the tissue contents and to draw the alimentary debris toward the labium. It was not possible to predict which larvae would be eaten by their congeners (perhaps diseased or otherwise unhealthy larvae?). In any case, this cannibalism, which takes place on all stages (eggs, larvae, pupae), cannot be confused observationally with such care as is furnished the larvae by the workers. One curious larval behavior pattern was observed: the larvae often rub their heads and thoracic segments against their sister larvae as though they were seeking to devour them.

One last trait reflects finally the primitive behavior of this species, considering the term "primitive" as indicating the marked independence of the individual with respect to its society. Although cocoon spinning

was not observed, we did see the eclosion of a worker from the cocoon. This completely pigmented worker cut with its mandibles a lateral, semicircular trap door a little before the apex of the cocoon. The cocoon is otherwise left intact. The worker leaves the cocoon unassisted, as Wheeler (1900) and Haskins and Haskins (1951) have already indicated for the genus. This behavior pattern distinguishes them from *Myrmecia,* where the workers assist incompletely pigmented workers to emerge from the cocoon.

The following observational events present a nutritional sequence for the larvae. a, The larvae are carried by the workers to the prey and are placed on or beside it within the brood chamber. b, The larva, as a result of its thoracic flexibility, thrusts its head into the interior of the prey in the area of the intersegmental membrane and feeds within. c, When the feeding of the different castes is completed, the prey is discarded regardless of its degree of depletion. d, The workers never deposit prey on the bodies of the larvae.

DISCUSSION AND CONCLUSION

The observations we now have in hand strengthen our conception of the genus *Amblyopone* as an extremely primitive stock among living ants. In *A. pluto* we are dealing with a narrowly specialized subterranean form whose behavior and prey specificity place it bionomically closer to the nearctic *A. pallipes* than to the Australo-Pacific *A. australis.* Apparently its diet remains the same the year round, and is the same for larvae and adults.

Numerous features of *Amblyopone* colony life are held in common with other formicid genera. However, several behavior patterns reflect primitive social organization. For instance, some interindividual relationships widespread among ants occur only rarely in an *Amblyopone* society, and others are manifested in only a very simple form. Thus, although the prey are captured and brought paralyzed to the nest by the adults (a social act), the larvae are virtually autonomous in feeding activities once the prey is placed near them. Such a pattern contrasts with the behavior of other ant larvae, even including those of most ponerines, which are more totally dependent on the adults around them. These larvae show evidence of cannibalism, a behavior not so common among higher ants. The adult worker ecloses from the cocoon unassisted. Coordination among workers during foraging is nonexistent, and trophallactic exchange is rare. The workers, at least of *A. pluto,* do not cut up the prey as do those of most other genera. There seems to be an overall weaker dependence of the brood on the workers than in other genera studied, save perhaps in *Myrmecia.* The characteristics listed apparently link *Amblyopone* to the solitary aculeate wasps, and they seem to justify the placement of *Amblyopone* near the base of the major branch of Formicidae represented at present by the Ponerinae, Myrmicinae, and Dorylinae.

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