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CONTRIBUTIONS TOWARD A RECLASSIFICATION OF THE FORMICIDAE. III. TRIBE AMBLYOPONINI (HYMENOPTERA)

By William L. Brown, Jr.

CAMBRIDGE, MASS., U.S.A.
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No. 4 — *Contributions toward a Reclassification of the Formicidae. III. Tribe Amblyoponini (Hymenoptera)*

By William L. Brown, Jr.

CONTENTS

Page

Introduction 145
Tribal characters 146
Ecology and behavior 149
Relationships, distribution and evolution of the genera 151
Treatment of species-level taxonomy 153
Key to the genera of Amblyoponini (workers and females) 154
The genera 155
  Amblyopone Erichson 155
  Mystrium Roger 169
  Myopopone Roger 170
  Prionopelta Mayr 173
  Onychomyrmex Emery 178
Incertae sedis 181
  Paraprionopelta Kusnezov 181
  Dorylozelus Forel 181
Appendix 182
  Key to the New World species of Amblyopone 191
  Key to the neotropical species of Prionopelta 218
  Key to the Indo-Australian species of Prionopelta 221
  List of references cited 224

INTRODUCTION

The tribe Amblyoponini Forel as dealt with in this section has as its core the old tribe Amblyoponini of the Emery-Wheeler classification, with *Amblyopone*, (including *Stigmatomma* and other synonyms), *Myopopone* and *Mystrium*. From tribe Ectatommini is transferred the genus *Prionopelta*, as already indicated in Part II of this series (see Brown, 1958a: 177, and below, under genus *Prionopelta*). *Onychomyrmex*, placed by Emery in tribe Ponerini, and by Wheeler in a separate tribe Onychomyrmicini, is here recognized as a specialized group of amblyoponines, following Clark, 1928.

In addition to these clearcut members of the tribe, there are two insufficiently known ants that may or may not belong to the Amblyoponini. One of these is *Dorylozelus mjoebergi* Forel (see below, p. 181), and the other is *Paraprionopelta minima* Kusnezov (see p. 181). These last two genera will be treated here as *''incertae sedis''* members of subfamily Ponerinae, not definitely assigned to Amblyoponini or any other tribe. However, I feel that both genera, when better known, will probably fit into existing tribes.

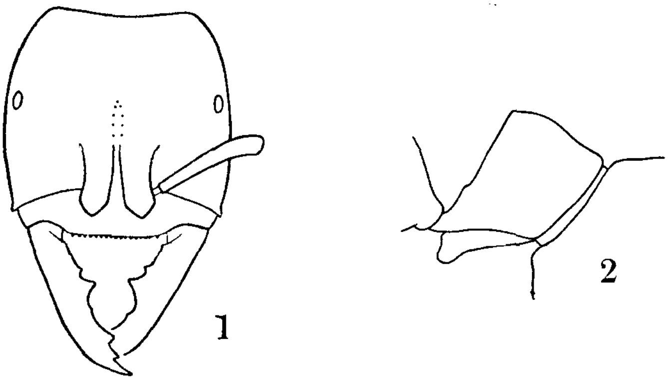
TRIBAL CHARACTERS

The Amblyoponini are rather homogeneous as compared to many other ant tribes. Size varies from minute (*ca.* 2 mm. total length) to medium (*ca.* 1 cm.) for workers and females, and males are within this range. The workers and females are similar in most respects, though the latter are usually larger and more heavily pigmented, with large eyes, three ocelli, and, when virgin, well-developed wings and flight sclerites in the thoracic part of the alitrunk. Females of *Onychomyrmex* form a conspicuous exception in that they are minute-eyed, wingless and otherwise ''dichthadiiform.'' In additon, ergatoid females occur in some *Amblyopone* species, but no species is yet known to have ergatoids completely replacing normal females. The workers are essentially monomorphic, but may show wide variation in size in a single colony.

Workers and females. Amblyoponine workers have the ocelli absent (sometimes represented by one or more pits), and the compound eyes are never as well developed as in most epigaeically-foraging ant groups; typically, they are reduced to very small remnants, and they may even be absent or so shrunken as to escape ordinary microscopic observation of the integument. When they are present, the eyes are characteristically placed behind the middle of the sides of the head.

The worker-female cranium is slightly depressed (elliptical or broadly ovoid in cross section), with straight or gently convex, parallel or posteriorly converging sides. The occiput has a transverse posterior border (straight, weakly concave, or weakly convex) and broadly rounded occipital angles merging smoothly into the sides, not forming conspicuous lobes. The anterior genal angles may or may not be toothed. Clypeus well developed, the median portion often forming a median lobe or apron and frequently with a series of teeth, tubercles or denticles along the free margin. Mandibles varying widely with genus and species, always strongly developed and inserted remotely, at the corners of the head (Figs. 1, 3, 4, 10, 15, 18, 19, 29, 30, 33-40, 48).

The labrum is broad and shield-shaped, folding back up over the smaller mouthparts when retracted, and often bearing denticles near its base, presumably to help in holding prey. The palpi are short, with segmentation ranging from 5, 3 downward, normally the same in both worker and female (with some exceptions).



Amblyopone australis, worker from near Auckland, New Zealand. Figure 1. Head and mandibles, with left antennal scape, full-face view. Figure 2. Petiolar node and adjacent parts, viewed from the side.

Frontal carinae short, situated more or less near the midline, widely separated from each other or, in smaller forms, contiguous. The antennae are simple, often with a rather short, heavy scape; funiculus slender throughout to distinctly clavate at apex; the whole antenna usually has 12 segments; more rarely there are 11 segments, and in one species only 7.

Alitrunk, petiole and gaster conservative in form throughout all genera. Alitrunk long and narrow, usually more or less parallel-sided (pronotum often slightly wider) and the dorsum more or less horizontal from front to rear; promesonotal suture normally complete and possibly often mobile; metanotal groove well-marked to obsolete. Propodeum with distinct dorsal and declivitous surfaces, rounding into each other, no propodeal teeth or angles. Metapleural glands with well-developed bulla and orifice. Petiole with little or no extended peduncle; node with steep anterior face and extensive dorsal face, but usually firmly attached to postpetiole over all or nearly all of its posterior extent, so that the dorsal face of the node is generally more or less continuous in level with the postpetiolar dorsum (Figs. 2, 31, 32, 46). This type of node is very characteristic for the tribe, and only a few scattered convergences to it exist in other ant tribes; it may well represent a structural holdover from the tiphioid wasps that gave rise to the ants. The postpetiole (abdominal III) and first gastric (IV) segments are usually subequal and ringlike, separated by a modest constriction; the succeeding segments are also ringlike, but shorter. The petiole, postpetiole and gaster together form a rather regular cylinder, usually rather long and straight (shorter in *Mystrium*). Sting present and functional.

Sculpture varying from foveolate or rugulose through reticulate-punctulate to smooth and shining. Pilosity simple, fine, varying from fairly sparse to dense, short, and pubescence-like; *Mystrium* is an exception, with many body hairs spatulate, clavate, or squamose. Color varying from blackish to pale yellow; depigmentation is common in this predominantly cryptobiotic group. Tarsal claws simple.

The known males of all genera agree in general with the description of that sex given for *Amblyopone* on page 161. The wing venation for both male and female is also covered by the variation found in *Amblyopone* (Figs. 5-7, 17, 47).

The internal anatomy of the *Amblyopone pallipes* worker and female has been studied in some detail by Whelden (1958), and the cytology by Whelden and Haskins (1954). Whelden thinks there are 9-10 Malpighian tubules in *A. pallipes,* and he covers the glandular system in some detail; the glands are apparently generally similar in kind and position to those of higher ants like *Myrmica.*

Larvae of species of *Amblyopone, Mystrium, Prionopelta* and *Onychomyrmex* have been described and figured by G. C. and J. Wheeler (1952: 113-117, 120, 637-639, 653-660), though these authors group them according to the Emery-Wheeler classification. The larvae belong to the more primitive group among the Ponerinae, lacking tubercles over the body. Their hairs are moderately to fairly abundant and simple (denticulate or branched in most Ectatommini), though hairs are sparse or virtually lacking on the cranium in *Amblyopone.* Thoracic segments forming a slender neck in *Amblyopone;* only the first segment much narrowed in *Prionopelta;* thoracic segments broader than the first abdominal segment in *Onychomyrmex mjoebergi. Amblyopone* larvae are rather similar to those of *Myrmecia,* and probably approach the primitive type of larvae among ants, while *Prionopelta* is slightly and *Onychomyrmex* is more strongly specialized in the direction of the Cerapachyinae or even the Dorylinae, in agreement with their presumed nomadic existence.

Amblyoponine pupae are generally enclosed in cocoons, from which the workers can frequently emerge unaided (unlike higher ants). *A. celata* Mann apparently lacks cocoons, and the pupae are unknown for most species.

ECOLOGY AND BEHAVIOR

The members of this tribe are all, so far as known, obligatory predators of other arthropods. All or nearly all species are predominantly cryptic foragers in the soil, leaf litter or rotting logs. The nests, beyond the first stages of foundation, often tend to be diffusely spread through the substrate, and their limits may be very ill-defined and constantly shifting. One gets the impression that there is little permanent centralization of brood chambers, and that the larvae are moved about a great deal. Perhaps it is common in this tribe for the larvae to be moved to large dead prey wherever the latter is killed, rather than the reverse. I have several times found *Amblyopone pallipes* workers and larvae clustered about large lithobiid chilopods under stones in such a position as to suggest that the larvae had been transferred to the prey; Wilson (1958a) reports that *Myopopone castanea* apparently does the same thing with the large beetle larvae it preys upon in rotten logs in New Guinea. Wilson (1958b) has already proposed that behavior like that of some Amblyoponini could have led to the true army-ant foraging and nomadism, and of course we can point to *Onychomyrmex* as an *Amblyopone*-derived stock that has already travelled a long way along this road.

Observations, some of which are reported in more detail elsewhere in this section, indicate that amblyoponine workers and nest-founding females generally attack living prey (in the form of chilopods, beetle larvae, or other arthropods), seize it in the formidable mandibles, and sting it to death with the long sting while holding on with the jaws. The prey may be much larger than the ant, and high potency is indicated for the ants' poison. The jaws, clypeus and labrum are usually toothed and well-suited to gripping active victims. The larvae feed directly on the prey when they are placed on it, or when it is given to them, and they may insert their heads into the prey's body to feed. Despite repeated trials, no one has yet succeeded in inducing *Amblyopone* workers or females to take honey, but Haskins (1928) says that *A. pallipes* will sample fruit, and that the males of this species feed avidly on honey, an interesting point in view of the importance of nectar or honeydew to tiphioids and other lower Hymenoptera, as well as to all the castes of *Myrmecia.*

Amblyopone and its relatives are moisture-loving species, most abundant in forested, temperate or tropical areas. *A. pallipes* is, for instance, often the commonest ant in wet *Rhododendron* stands in the Appalachians, and *A. australis* and several other smaller species of *Amblyopone* are common in wet, dark, fern gullies in Tasmania and southeastern Australia where most other ants are scarce. In drier areas, such as the Kansas plains or North Africa, the ants stay deep in the soil during the dry season, and are usually only found in flood times or by chance in deep man-made excavations.

Nuptial flight has been observed, at least in part, by Haskins (1928) for *A. pallipes* and by Haskins and Haskins (1951) for *A. australis.* The sum of evidence indicates that in these species, the female emerges from the nest, either flies or walks to an exposed position on rocks or foliage, and is found and mated by the male, which arrives in active flight. *A. australis* was observed "extending and arching the gaster and rubbing it with the hind legs," which suggests that it may have been releasing an attractant to draw the males. After mating, the females may return to the parent nest (*A. pallipes* always or usually; *A.*

australis sometimes) or may enter the soil or rotten wood after a time and construct a cell (*A. australis*), from which it forages actively for the prey it catches and stings to death. The cell may or may not be closed by the young female when she leaves to hunt, and prey is brought back to the cell regardless of whether brood is yet present or not. Sometimes two or more dealate females of *A. australis* apparently combine to produce a primarily polygynous nest. The most complete accounts of behavior and nest-founding are those of Haskins and Haskins (1951), and they give all the relevant earlier references. We need more information on the behavior, food and nest-founding of these and other species of Amblyoponini, because they are obviously so primitive in many ways that we may hope to learn a great deal from them about the evolution of ants in general.

RELATIONSHIPS, DISTRIBUTION AND EVOLUTION OF THE GENERA OF AMBLYOPONINI

The present record indicates that 70-75 valid species are known for the Amblyoponini of the world, of which about two thirds belong to genus *Amblyopone*. Although it is likely that more species remain to be discovered in this cryptobiotic tribe, the chances are that the proportion of *Amblyopone* species to those of other genera will increase rather than decrease. *Amblyopone* includes both generalized and specialized forms within the tribe, and it seems reasonably clear to me that all four of the remaining genera can be derived separately and directly from this large genus.

Mystrium, with 6 species in the Malagasy area, one in West Africa, and one in the Indo-Australian area, looks as though it probably arose from an African *Amblyopone* stock, although *Amblyopone* is now represented in Africa only by a very few rare species found along the western and northern fringe of the continent. *Prionopelta* is very rare in southeastern Africa and Madagascar, but is better represented in tropical America, New Guinea and the southwest Pacific islands, with outliers in New Caledonia and tropical Queensland.

Prionopelta tends to be best represented in numbers and in species where the smaller species of *Amblyopone* are rare or absent, which may indicate that *Prionopelta* has been competing with small *Amblyopone* and winning out in some tropical areas. In similar fashion, *Myopopone castanea* may be replacing *Amblyopone australis* in a specialized rotting-log niche in Melanesia (see page 173).

Two fifths of all the *Amblyopone* species, and by far the most massive populations maintained by any members of the tribe, occur in the Australian region. Here several species, most typically *A. australis,* appear to have broken out of a small-predator adaptive zone and have secondarily enlarged in body size and become general arthropod predators. Their reduced wing venation and palpi indicate much smaller (and probably more oligophagous) ancestors, presumably much like the intergradient series of species, still existing in the Australian region, that connects them with the small "*Fulakora*" group forms. If this reasoning is correct, *A. australis* represents a case, parallel to that of *Strumigenys nidifex* Mann of Fiji, of "countercurrent evolution" (for an explanation see Brown and Wilson, 1960). The whole picture of the considerable *Amblyopone* radiation in Australia speaks of the arrival of an early stock of the genus in a practically unexploited series of niches in this isolated land mass. As we see it there today, the genus still occupies a prominent place in the cryptobiotic-predator zone in the forests of southern Australia.

One other niche left empty on the Australian continent was the army-ant niche, but this was eventually entered by an *Amblyopone* stock that developed into *Onychomyrmex* and stayed within the northern forests. *Onychomyrmex* is now probably in competition with two or three species of the army-ant genus *Aenictus* Shuckard that appear to have extended their ranges into tropical Australia from the north in recent times.

Other relatively weak relictual representations of *Amblyopone* occur in the Americas, especially in temperate North America and southern South America, in New Zealand, in the Mediterranean area, in southern and eastern Asia, and in the East Indies. A single small species in Hawaii may have been introduced by man. But the presence of undoubted endemic members of the tribe in extralimital regions like Chile, New Zealand, New Caledonia, southwestern Australia, Tasmania, Cuba, Japan, Madagascar and the Solomons, speaks for an old, worldwide distribution. Tribe Amblyoponini apparently is the surviving remnant of a much larger and more varied group of ants, probably dating back to the Cretaceous. Today, the tribe is reduced to the few stocks that survived contact with more progressive ant groups only because they became specialized for relatively constant, predominantly cryptobiotic niches. Even though they thus managed to avoid the heaviest competition, the general scarcity of amblyoponines outside a few limited and usually more or less peripheral areas points to their decline as a world group.

Unfortunately, we have no fossil record of the tribe, although the morphology, habits and distribution indicate a greater age than for the Ectatommini, which were present and widespread in the Oligocene. The petiolar-gastric structure may indicate direct lineage from the proto-formicid stem, but in other characters (including loss of anal lobe in hind wing, reduction of palpi and eyes, elaboration of mandibles, simple tarsal claws, and 6-partite proventriculus) the tribe is specialized.

TREATMENT OF SPECIES-LEVEL TAXONOMY

As already stated in Part II of this series, the primary aim of the work is a revision of classification at the generic level. But in the course of such work there is always uncovered a mass of information concerning new synonymy, undescribed forms, geographical variation, biology, etc., at the species level, which logically should go with a survey of this kind. As in Part II, such information has been placed in the Appendix, where the items are listed consecutively against boldface numbers in brackets corresponding to the bracketed numbers in the text.

Former varieties and subspecies have been eliminated as such in the species lists, and are either synonymized or treated as species. Revisionary studies at species level were carried to completion only in the cases where a clearcut decision seemed possible on the basis of the available material. In a few other cases, the taxonomic problems involved have been discussed, but not settled. It is obvious that more work needs to be done at the species level, particularly in *Prionopelta,* in the Madagascan *Mystrium,* and among the Far Eastern *Amblyopone.* In the case of the few names arbitrarily raised from infraspecific to specific rank, this action does not necessarily carry any implication of support for their distinctness as species.

The capital letters placed in parentheses before each specific name indicate the kind of evidence upon which the present generic placement is directly based.

(T) indicates that type material, nidotypes, reliably type-compared material, or similarly authentic specimens have been examined, in most cases by myself; rarely, examination has been made by other myrmecologists.

(P) means that material identified from reasonably good descriptions, or from other satisfactory evidence, has been examined and is thought to be correctly determined.

In cases where the species is not seriously questioned, but no specimens referable to it have been seen, or if specimens seen cannot be satisfactorily verified as to identity, no entry has been made before the species name.

(?) signifies that, in my opinion, the species is inadequately described for purposes of distinction and that its taxonomic status is doubtful.

The species lists have been based on various myrmecological compendia and basic papers, and were checked against Emery's Genera Insectorum list and the Zoological Record, 1908 through 1955. References through 1958 are included so far as I am aware of them. I shall consider it a great favor if readers will send me notice of the inevitable omissions for inclusion in a corrective supplement.

Key to the Genera of Amblyoponini, based on the workers and females

1. Mandibles short, narrow, closing tightly against the clypeus, their apical borders distinct and completely occupied by 3 large teeth, of which the middle tooth is shortest; basal border of mandible unarmed (Fig. 15; widespread in tropics) .... *Prionopelta* Mayr[1]
   Mandibles of another form, usually strongly projecting beyond clypeus when closed, and with more than 3 teeth (Figs. 19, 29, 48) .... 2.

2. Antennal funiculi markedly compressed; when head is viewed in perfect full-face view, lobes of frontal carinae are approximately even with, or slightly surpass, the anterior clypeal border beneath them (Fig. 10; Indo-Melanesian area, widespread) .... *Myopopone* Roger

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[1] *Dorylozelus* Forel, of Queensland, may be an amblyoponine, in which case it would key out to *Prionopelta*.

Antennal funiculi not compressed, approximately round in cross section; in full-face view of head, lobes of frontal carinae distinctly behind the anterior median clypeal border (Figs. 19, 29, 40) .... 3.

3. Apex of mandible bluntly rounded or subtruncate as seen from above, although the inner apical margin may bear two or more small teeth, triangular in shape and often retrorse; many body hairs clavate or spatulate (Fig. 4; Madagascar, w. Africa, Indo-Australian area) *Mystrium* Roger

Apex of mandible in the form of an acute tooth (Figs. 19, 29, 30, 33, 40, 48); body hairs simple, fine and tapered .... 4.

4. Tibia of posterior leg without an apical spur, or at most with a very small, straight, non-pectinate vestigial spur; small, slender, predominantly smooth and shining species with greatly enlarged tarsal claws on middle and posterior legs; queens wingless, small-eyed ("dichthadiiform"); probably with legionary habits (Figs. 46-48; Queensland) *Onychomyrmex* Emery

Tibia of posterior leg with a well-developed apical spur having a curved, broadly pectinate inner margin; species of diverse size and form, with tarsal claws rarely enlarged; in cases where they are enlarged, the head and alitrunk tend to be coarsely sculptured and often opaque; virgin queens normally winged and with large compound eyes (Figs. 29, 33, 40; widespread in temperate and tropical areas, but often local; not known from c. and s. Africa or Madagascar) .... *Amblyopone* Erichson

THE GENERA

AMBLYOPONE ERICHSON

> *Amblyopone* Erichson, 1842, Arch. Naturg., 8(1): 260. Type: *Amblyopone australis* Erichson, 1842, monobasic.

> *Stigmatomma* Roger, 1859: 250. Type: *Stigmatomma denticulatum* Roger, 1859, by designation of Bingham, 1903. N. syn.

> *Arotropus* Provancher, 1881, Naturaliste Canad., 12: 205. Type: *Arotropus binodosus* Provancher, 1881, monobasic.

> *Stigmatomma* subgenus *Xymmer* Santschi, 1914: 311. Type: *Stigmatomma (Xymmer) muticum* Santschi, 1914, monobasic.

> *Stigmatomma* subgenus *Fulakora* Mann, 1919: 279. Type: *Stigmatomma (Fulakora) celata* Mann, 1919, by original designation.

> ***Amblyopone*** subgenus *Neoamblyopone* Clark, in Wheeler, 1927: 1. Type: *Amblyopone (Neoamblyopone) clarki* Wheeler, 1927, by original designation, monobasic.

> ***Amblyopone*** subgenus ***Protamblyopone*** Clark, in Wheeler, 1927: 1. Type: ***Amblyopone (Protamblyopone) aberrans*** Wheeler, 1927, by original designation, monobasic.

Lithomyrmex Clark, 1928: 30. Type: *Lithomyrmex glauerti* Clark, 1928, by original designation, monobasic. N. syn.

Ericapelta Kusnezov, 1955: 273. Type: *Ericapelta egregia* Kusnezov, 1955, monobasic. N. syn.

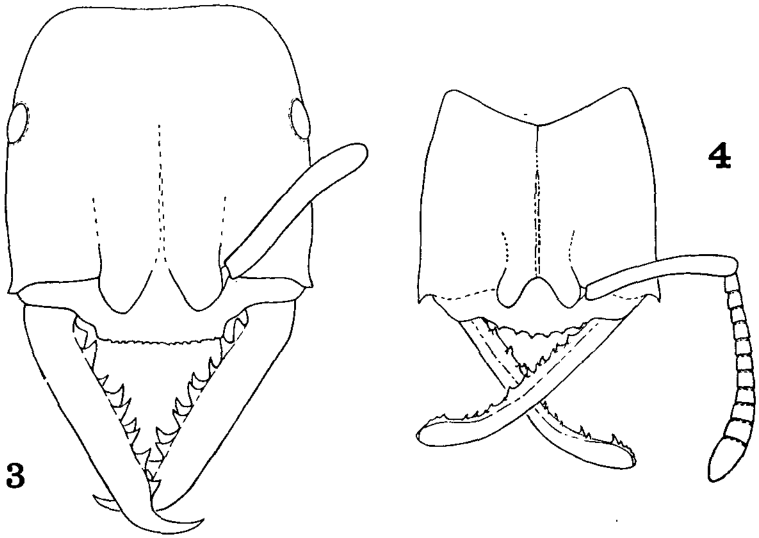
(For previous writings on synonymy and relationships of *Amblyopone* at generic and subgeneric level, see Wheeler, 1927; Clark, 1928; Brown, 1949).

Amblyopone is a curious genus containing a large and heterogeneous array of species, which represents the residue left after dividing a few specialized amblyoponines among the few other genera recognized here. *Amblyopone* is not only residual as a genus; it is ''central,'' which is to say that it is probably to be regarded as the stock from which the other genera have risen. While its species differ widely in size, color, sculpture and in the structure of the cranium, clypeus and mandibles, the general form of the remainder of the body is remarkably uniform in nearly all of them. In fact, departures such as the pedunculate petiole of *A. mutica* are slight when compared to the variation among species of other genera of ants, and stand out in *Amblyopone* only because the great majority of species in the genus are so monotonously similar in postcephalic body form.

The most characteristic trait of *Amblyopone* (and most other Amblyoponini), aside from general habitus, is the structure of the petiole and its mode of attachment to the postpetiole (Figs. 2, 31, 32). The petiole is nodiform and robust, with an abruptly descending anterior face to the node and an approximately horizontal dorsal face. No true posterior face is differentiated, the node attaching directly, with little or no posterior constriction, to the postpetiole. There is usually an anteroventral process adorning the petiolar keel. The postpetiole is functionally a part of the gaster, and is large, with only a moderate constriction between it and the structurally similar succeeding segment (IV abdominal). In both the postpetiole and the IV abdominal segment, the tergites are immovably fused to the sternites.

These characters of the petiole and gaster are shared by all castes, including the males, and they are also more or less faithfully copied by all of the other genera of the tribe. The conformation of this region appears to be of a very primitive kind among the ants, and is similar to that seen among scolioid (tiphioid) wasps. This group of wasps is primitive among the aculeate Hymenoptera, and probably included, sometime during the Cretaceous, the ancestral stem of the Formicidae. The sting in worker and female *Amblyopone* is long, sharp, heavily sclerotized and obviously functional.

In the female and worker *Amblyopone* there is a fundamental uniformity in the structure of the head and mandibles despite the great interspecific differences one finds in detail. The mandibles always end in an acute (usually dentiform or spiniform) apex, and the eyes, when present, are situated behind the middle of the sides of the head. The clypeus forms a band across the anterior part of the head, and its median portion is usually more or less projecting to form a low, broad lobe or apron, which in most but not all species bears a row of denticles or small tubercles.



Heads of amblyoponine workers, full-face view. Figure 3. *Amblyopone* sp. of *reclinata* group from Macao. Figure 4. *Mystrium camillae* from near Darwin, northern Australia.

The mandibles are linear (rarely triangular) and inserted far apart at the corners of the clypeus; when at rest, their apical portions cross over one another. In most species, the basal border is absent or very poorly developed, and the masticatory margin may either include it or be formed entirely of the apical border. The dentition consists of few (more than 3) to many teeth, varying in size and form, and ranked in one or two rows along the masticatory border (Figs. 1, 18, 19, 29, 30, 33-40). The dentition, of course, varies widely according to species, and some species show considerable intraspecific variation also. Fundamental generic characters are the presence of more than three teeth and the more or less acute nature of the apex.

Most, but not all, species of *Amblyopone* bear on each anterolateral angle of the head a more or less distinct and usually acute, dentiform extension of the gena (Figs. 3, 33, 40) which I have previously called the ''amblyoponine tooth.'' However, the term ''genal tooth'' used by Wilson (1958a) is more specific and objective, and I feel should be preferred.

The frontal carinae form narrow lobes in front; the carinae and lobes may be widely separated (Fig. 29), close together or even fused (Fig. 40), fusion or close proximity usually being correlated with extreme reduction of size, depigmentation and other traits of specialized subterranean life forms. The lobes reach or overlap the clypeus in front, but do not surpass the anterior border of the median lobe or apron (Figs. 29, 40).

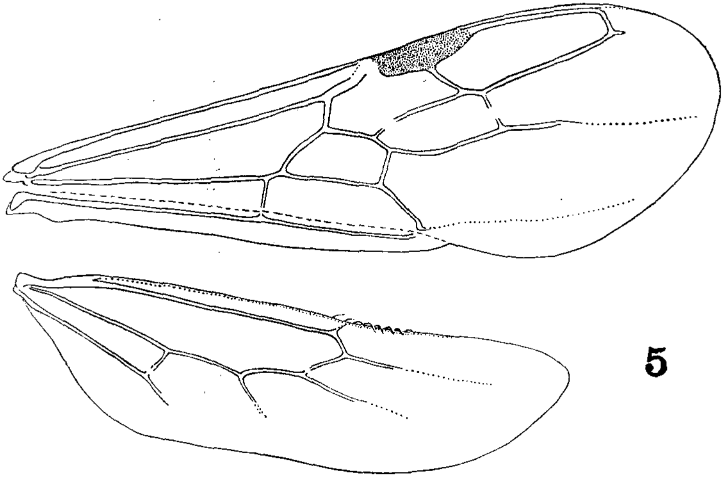
The antennae are usually 12-segmented in the female castes, but in one species. *A. degenerata* Borgmeier, fusion has reduced the number to only 7 distinct segments. The flagellum varies from slightly incrassate toward the tip to distinctly clavate, according to species.

The labium is a broad, tongue-shaped flap or shield, apically more or less deeply emarginate, hinged at the base so as to be able to cover the smaller mouth-parts when in repose, or to swing forward under and between the mandibles to assist in holding prey or perhaps other objects as well. The maxillary and labial palpi are always more or less reduced, as usual in ants with hypogaeic tendencies; there is wide variation in the number of segments among the different species, and some variation has also been noticed within certain species. The highest counts noted are those of *A. impressifrons* (5 maxillary, 3 labial) and the *reclinata* group (5, 3 or 4, 3), and several species are known to have counts of 4, 3, or 3, 2, or 2, 2; a female of *A. saundersi* from

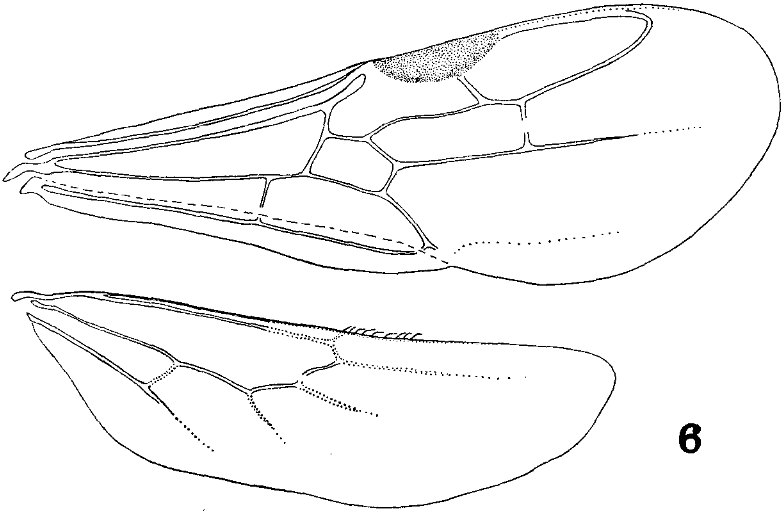
New Zealand had maxillary 1, labial 2, although a worker assigned to the same species had 2 and 2.

The alitrunk is elongate, more or less parallel-sided, with a distinct and complete promesonotal suture, in most species apparently representing a flexible joint separating the two main parts of the alitrunk. Metanotal groove present and distinct in most larger forms, but lost or obsolescent in most smaller species. Mesonotum (when fully distinguishable) short and transverse. Propodeum unarmed, bluntly rounded into declivity. Sting long and stiff, fully functional.

Female like worker, and usually only slightly larger in size, with large compound eyes, ocelli well developed, and flight sclerites differentiated; however, the alitrunk is low and has a relatively straight profile. Wings present; venation varying widely with the species, and often within species, but relatively complete even in the smaller species. Some of the larger or medium-sized species have all of the ''primitive'' ant venation in both wings, except for the first radial crossvein, which is present only as an occasional atavism (Brown and Nutting, 1950:125). In many of the smaller species, as well as in the large *A. australis* and some of its large and medium-sized relatives, the forewing has lost Rsf2·3 partly or entirely (compare Figures 5 and 6 with Figure 7). Venation is particularly variable in *A. australis* (of both sexes), and this appears to be the normal situation, not just due to ''abnormality'' as suggested by Kusnezov (1955:268). In this species, Rsf2·3 may be completely absent, present as a spur of varying length in its apical portion, or, more rarely, present only as a variable free section attached to an atavistic first radial crossvein; Mr. John Clark long ago sent me many sketches of forewings of this last type. The anal vein varies in development with the species, and may extend to or very nearly to CuA (thus closing a ''second discoidal'' cell), or may fall short by a greater or lesser distance. The ''open'' or ''closed'' condition of ''cubital'' or ''discoidal'' cells, upon which Kusnezov so largely based his 1955 classification, is in my opinion a virtually useless character-system because of the wide variation and subtlety of the occurrence of the veins themselves, among species as well as within certain single species. I should like to reemphasize the position taken in 1950 by Brown and Nutting: the



5



6

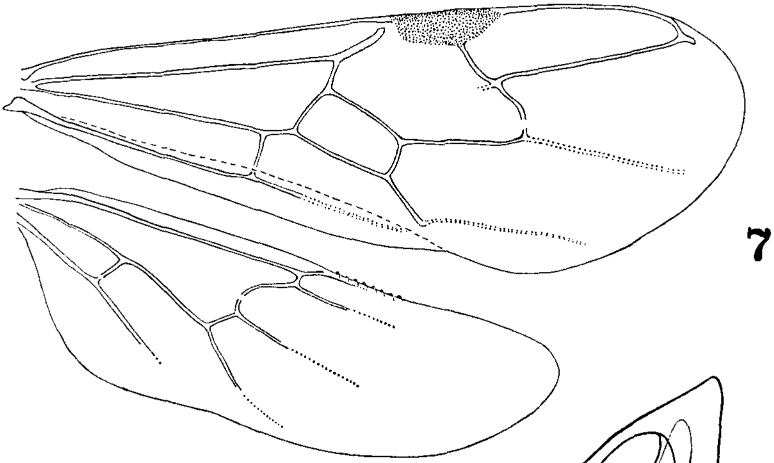
Wings of males of the *reclinata* group, species indeterminate. Figure 5. Specimen from Los Baños, Luzon, (terminalia shown in Figs. 22, 24, 27). Figure 6. Specimen from Chipon, Formosa (terminalia shown in Figs. 23, 25, 28).

most attention should be paid to the veins themselves; descriptions of ''cells'' in ant wings convey much less information, and convey it less precisely. In the *Amblyopone* species so far checked, the hind wing always lacks an anal lobe.

The sculpture of worker and female is much alike in general, but varies according to species and species-groups. The head, and to a lesser extent the alitrunk, is usually much more distinctly sculptured than the gaster; frequently the gaster is predominantly smooth and shining, with scattered fine punctulae. The sculpture of the head varies from smooth and shining, with or without some foveolae or costulae, through coarse or fine striation (in most cases predominantly longitudinal), subvermiculate rugulation, to fine, dense, reticulopunctation or reticulo-striolation. The mandibles may be striate, punctate or smooth. The posterior sides of the alitrunk, especially near the metapleural glands, are frequently superficially striate, a feature that may be connected with distribution of material from the glands. Pilosity is simple and fine, and ranges from short, dense, pubescence-like pile to longer and sparser hairs of irregular length.

The male of *Amblyopone* is normally smaller and more slender than the corresponding female, and has an entirely different head, usually or always broader than long, including the large, convex compound eyes. The mandibles are slender, curved, strap-like, the apex simple and acute or with two coarse teeth; when closed, their tips meet or overlap, and the entire blades are usually tucked away (rarely not) under the clypeus in such a way that only their external margins show externally along the anterior clypeal border. Clypeus usually convex and most often with a rounded anterior border or apron that frequently carries serially-arranged denticles or tubercles homologous to those of worker and female, where they are present in these castes. Anterior border more rarely transverse and approximately straight.

The male antennae are slender, but often slightly to moderately incrassate toward their apices; the scape is short, but usually more or less slender-cylindrical; funiculus 12-segmented in all of the species for which the male is known, but could conceivably be of a smaller count in unknown males of species like *A. degenerata* (see under *Paraprionopelta,* below). The funicular segments increase in length toward the tip, the apical segment being the longest one.



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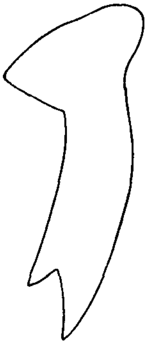
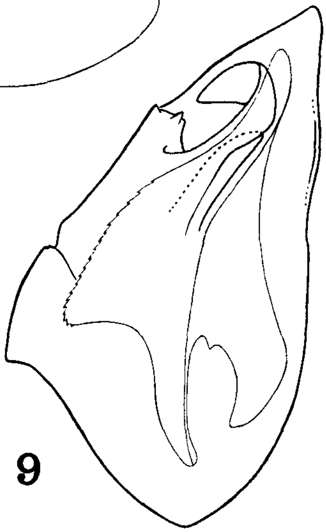




9

Amblyopone australis, male taken with workers at Dorrigo, New South Wales. Figure 7. Wings. Figure 8. Mandible dissected out of head. Figure 9. Left half of genitalia as viewed from midline; valve of aedeagus drawn as a very light line.

The under-mouthparts are in many ways similar to those of the corresponding workers and females, and frequently the palpi have the same segmental counts as the workers (2, 2 to 5, 3, of course varying with the species). In *Amblyopone australis*, however, the male has a formula of 4, 3, while the worker has only 2 and 2. A similar situation probably holds in some of the other species, particularly those related most closely to *A. australis*. The formula of the male may therefore be said to be either like that of the corresponding worker, or else more conservative.

Alitrunk with well (but not excessively) developed flight sclerites; notauli present and distinct, usually forming a complete Y. Propodeum unarmed. Petiolar node in general shape as in worker-female, but may be more slender or differ otherwise in proportions; a ventral lobe or process is usually present anteriorly. Petiolar attachment and general form of anterior gaster much as in worker; posterior portion modified, of course, to receive genitalia. The VIII, and often the VII, sternites are broadly emarginate posteriorly. The subgenital plate (or hypopygium, sternite IX) varies greatly with the species; sometimes it is rather simply tongue-shaped, but it is highly modified in some species, and may even (some species of *reclinata* group) possess a more or less well developed slender median caudal process (Fig. 23). The pygostyles are usually present, but occasionally are absent, or at least so reduced that they were not noticed in the dissections. The phallus is constructed on the usual formicid plan, but there is a great deal of modification of the particular components in many of the species, so that the genitalia in this group furnish much better species characters than is usual in ants. A few of the variations are illustrated in Figures 9, 24, 25, 27, 28 and discussed in **[8]**. The genitalia are, however, not very useful in distinguishing *Amblyopone* from other genera of the tribe, because the intrageneric variation is much greater than the intergeneric.

Males tend to be blackish in general color, or at least darker than the corresponding workers, but some of the forms from Old World desert areas are lighter, more brownish or even yellowish in color. Probably many of the males are nocturnal, so that more species will be found to be light in color. Male sculpture often follows in a rough way that of the workers of the same species, but tends to be much better developed and coarser over the head and alitrunk, though often less regular and more rugose or vermiculate.

In general size, the species of *Amblyopone* vary considerably, the smallest workers (*A. degenerata*) being in the neighborhood of 2 mm. outstretched length, while large workers and females of *A. australis* are robust insects, reaching a centimeter and more in length. Some of the species are very variable in size in the worker caste, but polymorphism is not well developed even in these. Allometric differences affect mostly things like proportions (width) of head and petiole, and size of eyes.

The synonymy of *Amblyopone* and *Stigmatomma* was discussed in detail, and previous references to the subject mentioned, in Brown, 1949: 86; see also Brown and Nutting, 1950: 124. In the 1949 paper, *Stigmatomma* was reduced once again to subgeneric status under *Amblyopone*. *Xymmer* and *Fulakora* were synonymized with *Stigmatomma*. *Stigmatomma* had previously been separated on the basis of its ''double-ranked'' (vs. ''single-ranked'' in *Amblyopone*) mandibular dentition; its finer, more opaque cephalic sculpture; and the supposed absence of teeth on the anterior clypeal border of *Amblyopone*. But, as is now fairly widely appreciated by myrmecologists, the double-ranked condition grades through, especially in some Australian species of the *ferruginea* group. Most of the ''true'' *Amblyopone* as formerly separated have denticulate anterior clypeal borders, although this denticulation is often very fine, and may occasionally be absent, as explained below. The sculptural distinction is worthless, since some species with *Stigmatomma* characters otherwise, e.g. *A. normandi, A. elongata,* have the dorsal surface of the head predominantly smooth and shining. On the other hand, some *Amblyopone s. str.* have densely sculptured heads (e.g., *ferruginea* group). There remains the question of the presence or absence of Rsf2·3 (which determines whether there are one or two cubital cells). In 1949, I maintained this as a provisional separatory character at the subgeneric level, stating at the same time my doubts as to its usefulness when more material became available. Now that we have more material of the winged castes of various species, it is clear that Rsf2·3 has been lost independently at least twice, and possibly more than three times, that is, in the Australian ''true'' *Amblyopone* (where variable remnants of Rsf2·3 are common), in a South American species (the ''*Ericapelta egregia*'' of Kusnezov), and in certain of the smaller species (e.g., *A. saundersi* of New Zealand). A generic split along these lines would certainly be discordant with divisions that might possibly be drawn on the basis of other characters, and as a matter of fact, it turns out that some species that would be placed in *Amblyopone* on the basis of venational characters have workers that would go into *Stigmatomma.* The *Amblyopone-Stigmatomma* dichotomy certainly loses its former supposed sharpness, and I see no reason to maintain a separate formal subgenus for *Stigmatomma* any longer.

The subgenus *Xymmer,* based on the sole West African species *Stigmatomma* (*Xymmer*) *muticum* Santschi, has a median clypeal apron absolutely devoid of teeth along its anterior margin, but in 1949 I synonymized this subgenus with *Stigmatomma* because of the similar condition reported by Forel for *S. bellii* of southeastern Asia. However, the types of *S. bellii* have been examined again, and they have been found to possess denticulation of the clypeal apron, although the denticles are small and rather indistinct. Since *muticum* also has the petiole conspicuously narrowed into a slender, short peduncle at its base, a case might be made for the resurrection of *Xymmer* as a generic or subgeneric name for this aberrant species. However, we now know at least one more species, *A. gingivalis* sp. nov., that definitely lacks teeth or denticles on the clypeal margin; *gingivalis* is aberrant in the form of its mandibles, but the petiole is normal for the genus. Several species, especially *A. bruni,* have clypeal denticulation reduced very nearly to the vanishing point. I have examined types of *S.* (*X.*) *muticum,* and in the light of what we now know about variation among *Amblyopone* species, I believe that this species should be included in the genus without subgeneric distinction. (In practice, I have found formal subgenera to be awkward and confusing, and I much prefer to use informal species-groups that do not clutter the nomenclature.) Actually, *A. mercovichi* and *A. gingivalis* are more aberrant in some respects than is *A. mutica,* to say nothing of *A. degenerata,* which Borgmeier wisely placed in *Amblyopone* when he first described it.

Clark has suggested (*in litt.,* 1948) that *A. reclinata, A. rothneyi* and allies with more or less large compound eyes should be segregated in a separate genus, but here again there seems to be much variation leading toward more "normal" kinds of *Amblyopone,* of which perhaps *A. pallipes* or *A. silvestrii* would represent an average species. Probably further investigation will only strengthen the links between this group and the rest of the *Amblyopone* species.

Lithomyrmex is another generic name proposed for a single species, *glauerti* Clark from Western Australia. This species, as Clark suggests, may indeed represent an intermediate form leading from *Amblyopone* to *Onychomyrmex,* but the females are normal (winged as virgins), and the three castes cannot be separated from the corresponding ones of *Amblyopone* by any really important character. As an *Amblyopone, glauerti* cannot even be considered as more than a moderately aberrant species.

The species of *Amblyopone* are found in many countries widely scattered over the earth, ranging from tropical to cool temperate in climate, and from wet to rather arid. The Australian Region, with about two-fifths of the known species, is the headquarters of the genus. Another fifth of the species is found in tropical Asia, and still another fifth is distributed through the Americas, from Canada to Chile. The remainder of the species are scattered; several are in the Mediterranean area, two are on the western fringe of Africa in Nigeria and Senegal, one is in Japan, and one, possibly introduced from Melanesia, is in Hawaii. The concentration of species in extralimital regions such as Chile, Argentina, Cuba, Japan, Australia, the Solomons and New Zealand speaks for the age of the genus. Its absence or great rarity in the central Ethiopian Region is parallel to that of other ancient groups, such as tribe Ectatommini and the "*Notomyrmex*" group of *Monomorium,* that are well developed in the peripheral areas listed above with *Amblyopone.* Unlike the more open-foraging ectatommines, however, the amblyoponines are not represented in Tertiary fossil faunas, indicating that even during those periods, *Amblyopone* did not include prominently arboreal foragers, at least in the Northern Hemisphere.

This leads us again to the obvious observation that *Amblyopone* species are mostly small and hypogaeic specialists, although it should be noted that some of the members of the tropical Oriental *reclinata* group are fairly large in size, are heavily pigmented, and have fairly large eyes in the worker caste, like workers of some known epigaeic foragers in other tribes of ants. However, we have no direct information on the habits of any member of the *reclinata* group, and it seems unlikely that species of this group are strongly epigaeic in foraging habits.

Most species of *Amblyopone* so far known have been found in moist, forested areas, where they may nest in rotten wood, in the leaf litter, or in the soil under stones or logs. Nevertheless, several species are known to be tolerant of rather arid conditions in treeless regions in Australia, North America, Argentina, North Africa and the Middle East, where the subterranean habits are strongly developed, and some species are known only from males taken at light [**1**, **12**].

So far as my reading and experience go, the *Amblyopone* species feed nearly or quite exclusively on arthropods, dead or alive at time of interception. *A. pallipes,* and probably other species, specialize on chilopods [**2**, **16**]. *A. australis,* judging from remains in the nests, collects various arthropods, including beetles.

AMBLYOPONE Species

(T) *aberrans* Wheeler, 1927:26. W. Australia [**16**, Fig. 35]
amblyops Karawajew, 1935:57. N. comb. Indo-China [**11**]
(P) *armigera* Mayr, 1887:547. se. Brazil, n. Arg. [**1**]
(P) *australis* Erichson, 1842, Arch. Naturg., 8(1):261 [**13**, Figs. 1, 2, 7-9]
(P) = *obscura* Fr. Smith, 1858, Cat. Hym. Brit. Mus., 6:109.
(P) = *cephalotes* Fr. Smith, 1876, Trans. Ent. Soc. Lond., p. 490.
(T) = *laevidens* Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, 25:447.
(T) = *fortis* Forel, 1910:1.
(P) = *maculata* Stitz, 1911, Sitzb. Ges. Naturf. Freunde, Berlin, p. 351.
(P) = *nana* Emery, 1914, Nova Caledonia, Zool., 1:394.
(T) = *minor* Forel, 1915:1.
(T) = *foveolata* Wheeler, 1927:9.
(T) = *pallens* Wheeler, 1927:11.
(T) = *queenslandica* Wheeler, 1927:12.
(T) = *norfolkensis* Wheeler, 1927:15.
(T) = *howensis* Wheeler, 1927:15.
(T) *bellii* Forel, 1900:55. India [**8**]
bierigi (Santschi), 1930, Bull. Soc. R. Ent. Egypte, (n. s.) 14:17. Cuba [**7**]
(P) *bruni* (Forel), 1912, Ent. Mitt., 1:45. Formosa [**9**, Fig. 21]

(T) = *juergi* (Forel), 1922, Rev. Suisse Zool., 30:87. N. syn.
(T) *celata* (Mann), 1919:279. Solomon Is. [**18**]
(P) *chilensis* Mayr, 1887:547. Chile [**1**]
(T) *clarki* Wheeler, 1927:24. sw. Australia [**16**, Figs. 33, 37, 38]
(T) *degenerata* Borgmeier, 1957:111. se. Brazil [**7**]
(P) *denticulata* (Roger), 1859:251. N. comb. s. Europe [**12**]
= *gheorghieffi* Forel, 1892, Verh. zool.-bot. Ges. Wien, 42:309. Syn. by Emery, 1916:100.
(P) =*gracilicornis* (Menozzi), 1936, Boll. Lab. Zool. Portici, 29:268. N. syn.
(P) *elongata* (Santschi), 1912:519. se. Brazil to n. Arg. [**1**]
= *barretoi* (Bruch), 1921, Rev. Mus. La Plata, 26:184. Syn. Borgmeier, 1957.
= *minor* (Santschi), 1922, An. Soc. Cient. Arg., 94:241, *nec* Forel, 1915. Syn. Borgmeier, 1957.
(P) = *paranensis* (Santschi), 1924, Ann. Soc. Ent. Belg., 64:6. Syn. Borgmeier, 1957.
(T) *egregia* (Kusnezov), 1955:274. N. comb. n. Argentina [**1**]
(T) *emeryi* (Saunders), 1890, Ent. Mon. Mag., 26:203. N. comb. n. Africa [**12**]
(P) *exigua* Clark, 1928:35. Australia: Victoria [**17**, Fig. 44]
feai (Emery), 1894, Ann. Mus. Civ. Stor. Nat. Genova, 34:454. Burma [**8**]
(T) *ferruginea* Fr. Smith, 1858, Cat. Hym. Brit. Mus., 6:110. Australia: vic. Melbourne [**16**, Fig. 36]
(T) = *mandibularis* Clark, 1928:33. Syn. Brown, 1952.
(T) *gingivalis* Brown, sp. nov. e. N. S. Wales [**15**, Figs. 30, 31]
(T) *glauerti* (Clark), 1928:31. N. comb. W. Australia
(T) *gracilis* Clark, 1934b:52. Australia: Victoria [**16**, Fig. 41]
(T) *hackeri* Wheeler, 1927:22. se. Queensland [**16**, Fig. 39]
(P) *impressifrons* (Emery), 1869, Ann. Accad. Aspir. Natural., Napoli, (2)2:13. Italy [**12**]
(T) *leai* Wheeler, 1927:16. Lord Howe I. [**13**]
(T) *longidens* Forel, 1910:1. se. Australia [**16**, Fig. 34]
(T) *lucida* Clark, 1934a:27. Australia: Capital Terr. [**17**, Fig. 45]
(T) *luzonica* (Wheeler & Chapman), 1925:56. N. comb. Philippines [**11**]
(T) = *williamsi* (Wheeler & Chapman), 1925:56. N. syn.
(T) *mercovichi* Brown, sp. nov. se. Australia [**14**, Figs. 29, 32]
(P) *michaelseni* Forel, 1907, Fauna SW Australia, 1:264. sw., se. Australia [**13**]
(T) *minuta* (Forel), 1913, Zool. Jahrb. Syst., 36:4. E. Indies [**10**]
(T) *monrosi* Brown, sp. nov. Chile [**5**]
(T) *mutica* (Santschi), 1914:311. N. comb. Nigeria

(T) *mystriops* Brown, sp. nov. Guatemala [**4**, Fig. 19]
(T) *normandi* (Santschi), 1915:54. N. comb. Tunisia [**12**]
(T) *oregonensis* (Wheeler), 1915:389. n. California to Brit. Columbia. N. status [**2**]
(T) *orizabana* Brown, sp. nov. Mexico: Mt. Orizaba [**6**]
(P) *pallipes* (Haldeman), 1844, Proc. Acad. Nat. Sci. Philadelphia, 2:54. s. Quebec and Iowa to Florida and Arizona [**2**]
[= *serrata* (Roger), *Arotropus binodosus* Provancher, *arizonensis* (Wheeler), *wheeleri* (Santschi), *montigena* (Creighton). Synonymy in Creighton, 1940; Brown, 1949:84.]
(T) = *subterranea* (Creighton), 1940:8. N. syn.
(P) *punctulata* Clark, 1934a:28. Tasmania [**17**]
(?) *quadrata* (Karawajew), 1935:57. N. comb. Gulf of Siam [**8**]
(P) *reclinata* Mayr, 1878, Verh. zool.-bot. Ges. Wien, 28:667. Java [**8**]
(T) *rothneyi* Forel, 1900:56. India: Bengal [**8**]
santschii (Menozzi), 1922, Ann. Mus. Civ. Stor. Nat. Genova, 49:347. N. comb. Senegal [**12**]
(T) *saundersi* Forel, 1892, Mitt. schweiz. ent. Ges., 8:336. N. Zealand [**17**]
(T) *silvestrii* (Wheeler), 1928, Boll. Lab. Zool. Portici, 21:97. Japan [**11**]
(T) *smithi* Brown, sp. nov. S. Australia: Lofty Range [**17**, Fig. 40]
(T) *trigonignatha* Brown, 1949:81. N. Carolina [**3**, Fig. 18]
wilsoni Clark, 1928:34. se. Australia [**17**]
zwaluwenburgi (Williams), 1946, Proc. Hawaii. Ent. Soc., 12:639. N. comb. Hawaii: Oahu [**19**]

MYSTRIUM Roger

= *Mystrium* Roger, 1862:245. Type: *Mystrium mysticum* Roger, 1862, monobasic (+7 spp.).
= *Mystrium,* Wheeler, 1922:758, 1006, synonymic catalog of African and Malagasy spp.
= *Mystrium,* Menozzi, 1929:518-536, revision of the genus.

This most aberrant genus is close to *Amblyopone.* The workers and females differ from those of *Amblyopone* in their shorter, thicker bodies and broader heads, as well as their odd, blunt-tipped mandibles (Fig. 4). The sculpture is rather coarse and consists of bold reticulation or costulation over head and much of alitrunk. Within the reticular basins and elsewhere are situated the peculiar body hairs, which are generally squamose-pointed, clavate, or otherwise broadened or bizarre. Menozzi notes that the worker-female palpal formula is 4, 3, a count that I have confirmed for an *M. rogeri* worker in the Museum of Comparative Zoology.

Male like that of *Amblyopone,* coarsely sculptured and with notauli distinct. Wing venation of both sexes of the ''complete'' type (Fig. 5).

Genitalia not studied. Pygostyles apparently lacking.

So far as known, *Mystrium* is limited in distribution to Madagascar and adjacent islands (six nominal species), Cameroons (one species), and the Indo-Australian area, where one species *M. camillae,* has been found in Burma, the East Indies, Luzon, New Guinea and the Darwin district of northern Australia. It is assumed that *Mystrium* is predaceous, but there is no direct evidence known to me on its feeding habits. Almost equally scanty is information on colony size, nest site and structure, and most aspects of ecology and behavior.

Menozzi's revision (1929) includes a key to the species, plus illustrations and descriptions. It is difficult to judge the status of the species from Madagascar, since most of these are known from inadequate material. Since Menozzi gives full references to all species, only the dates of description are given in the list below.

MYSTRIUM Species

(P) *camillae* Emery, 1889. Burma to n. Australia. [Fig. 4]
(P) = *javana* Karawajew, 1925. N. syn.
fallax Forel, 1897. Madagascar: Nossi Be.
(P) *mysticum* Roger, 1862. Madagascar, Comoro Is.
(T) *oberthueri* Forel, 1897. Madagascar.
(T) *rogeri* Forel, 1899. Madagascar.
silvestrii Santschi, 1914. Cameroons.
stadelmanni Forel, 1895. Madagascar.
(T) *voeltzkowi* Forel, 1897. Madagascar: Nossi Be.

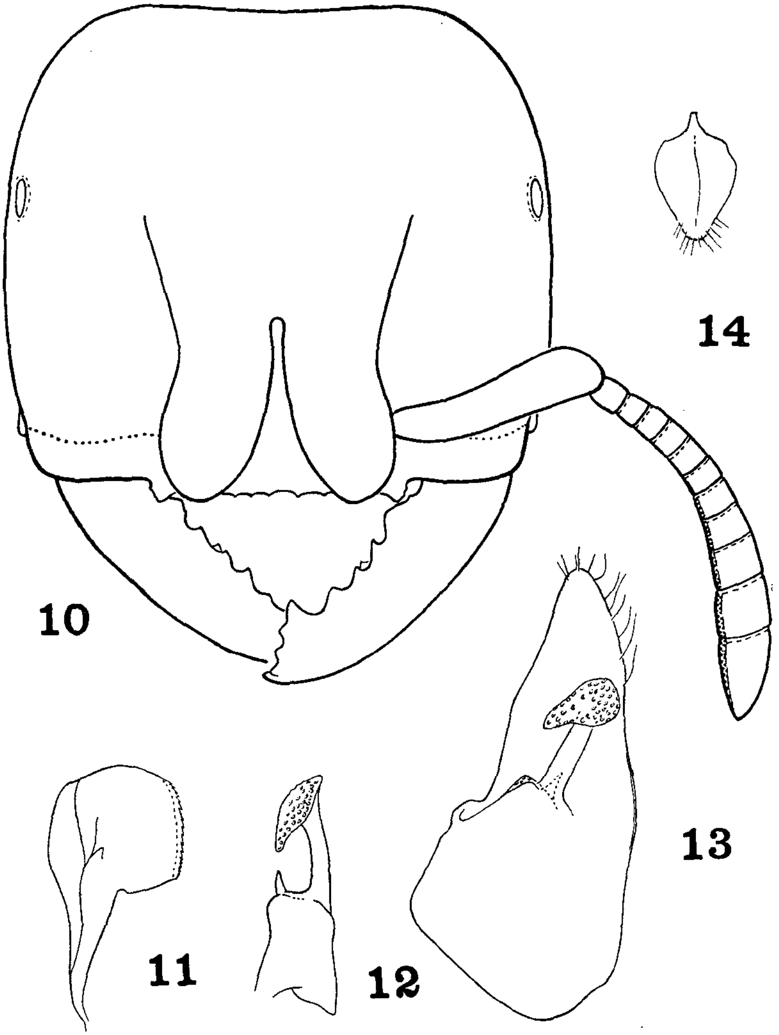
MYOPOPONE Roger

= *Myopopone* Roger, 1861:49. Type: *Myopopone castanea* var. *maculata* = *Myopopone maculata* Roger = *Amblyopone castaneus* Fr. Smith, 1860, by designation of Bingham, 1903.

In general habitus, to the naked eye, *Myopopone* workers look very much like those of *Amblyopone australis,* and they show variation of similar scope. In fact, *Myopopone* is probably monotypic **[20]**, and may be regarded as a more than usually aberrant species of *Amblyopone.* The characters are, however, sufficiently marked and numerous in the worker-female castes to justify the retention of *Myopopone* as a genus apart from *Amblyopone.* The head shape (Fig. 10) is like that of *Amblyopone,* without the "amblyoponine teeth" at the corners anteriorly, but the lobes of the frontal carinae are large and placed well forward, so as to overreach slightly the concave median lobe or apron of the clypeus (in *Amblyopone* the lobes never reach the anterior border of the median clypeal lobe). The antennal funiculi are strikingly broadened and flattened, differing in this from *Amblyopone.* The legs are short and with spiniform processes or spine-like setae developed at several points; in particular, the extensor surface of the middle tibia is provided with a number of sharp peg-like spines, also the metatarsus of the posterior leg. The mandibles, as can be seen from Figure 10, are different from those of any given species of *Amblyopone,* but are not strikingly outside the range of variation seen among *Amblyopone* species.

The female is winged and is markedly larger and darker than the worker; there are also differences in sculptural detail. The differences between these two castes have been responsible for much of the synonymy at species level. The male is decidedly smaller and more slender than the female, and is typically amblyoponine in its habitus and general characters, with rugulose head and alitrunk and piceous to blackish in color. Notauli present.

Pygidium and subgenital plate both subtriangular, with broadly rounded apices. Parameres rather long, tapered and incurved so that their apices meet or even slightly overlap at the half-retracted position. Volsellae (Fig. 12) much like those of *Amblyopone australis* (Fig. 9); digitus with a flat, plate-like apical portion, which is convex and tuberculate over its lateral surface; cusp reduced to a vestigial swelling at the base of the digitus, but the heel well developed and bearing a sharp erect tooth. Aedeagus of a peculiar shape, as shown in Figure 11. In all castes, the middle and posterior tibiae have two pairs of spurs, one of the posterior pair being larger than its mate, slender, curved, narrowly barbulate and with a peculiar obliquely truncate tip. Antennae stout, but not flattened as in the worker.



Myopopone castanea. Figure 10. Head of worker, full-face view (from type series of synonymous *M. rossi* Donisthorpe, Finschafen, New Guinea). Figure 11, aedeagal valve of male from Pematang Siantar, Sumatra. Figure 12. Volsella of same specimen, ventral view. Figure 13. Volsella in place in left paramere, viewed from midline, aedeagal valve omitted; same specimen. Figure 14, sub-genital plate of same specimen.

Workers and females with 4 maxillary and 3 labial palpal segments. Wings in both sexes similar to those of ''complete-veined'' *Amblyopone* species, narrow, glassy, with dark veins; Mf2 usually completely or nearly completely contracted in forewing.

I consider that the present evidence [20] indicates the probability that all of the *Myopopone* specimens so far collected belong to one species, *M. castanea* (Fr. Smith), which ranges from Sikkim, Ceylon, and the Nicobars in the west to the Philippines, New Guinea through the Solomons, and central Cape York Peninsula of northern Australia in the east. In Melanesia, *M. castanea* is predominantly a lowland species, occurring mostly at or below 500 m.; apparently it replaces *Amblyopone australis* in this zone. *A. australis* in Melanesia is predominantly a mid-mountain rain forest species, living chiefly at altitudes of 1000 m. or more. In southeastern Asia and the Philippines, where no similar *Amblyopone* species is known to exist, *M. castanea* exists at altitudes up to more than 2000 m.

M. castanea, like rain forest populations of *A. australis* found in the tropics, inhabit rotting logs, where they feed on large beetle larvae and probably on other comparatively helpless arthropods. Wilson's observations indicate that, as in the case of at least some *Amblyopone,* the colonies are very loosely organized, and that the workers may bring their brood to the site where the prey has been found, stung and killed, rather than attempt removal of the largest kinds of prey to a central nest or brood area. As has been suggested, such behavior may grade into primitive nomadism (Wilson, 1958 a, b).

PRIONOPELTA Mayr

= *Prionopelta* Mayr, 1866:503. Type: *Prionopelta punctulata* Mayr, 1866, monobasic (+9 spp.).

> *Renea* Donisthorpe [23], see under *P. majuscula.*

> *Examblyopone* Donisthorpe [23], see under *P. majuscula.*

When Mayr originally described *Prionopelta,* he demonstrated clearly the amblyoponine affinities of the sole species then included (*P. punctulata*), rendering inexplicable Emery's later placement of the genus in tribe Ectatommini. Wheeler (1922) followed Emery in this placement, making it ''generally accepted.'' But when the relationships of the known *Prionopelta* species are seriously studied now, there is simply no question about Mayr's opinion that *Prionopelta* is close to *Amblyopone*. In fact, the characteristic narrow, short, 3-toothed mandible is the only thing really consistently marking *Prionopelta* (Fig. 15) off from *Amblyopone* of the *Fulakora* group of species, as represented by *A. smithi* (Fig. 40). Except in *P. brocha,* which is very *Amblyopone*-like in everything but mandibular structure (Fig. 15), the *Prionopelta* species run to more nearly parallel-sided heads, usually broadest near the middle; that is, not broadest anteriorly near the anterior corners. The genal tooth at the corner on each side is, again with the exception of *P. brocha,* absent or present only as a minute vestige.

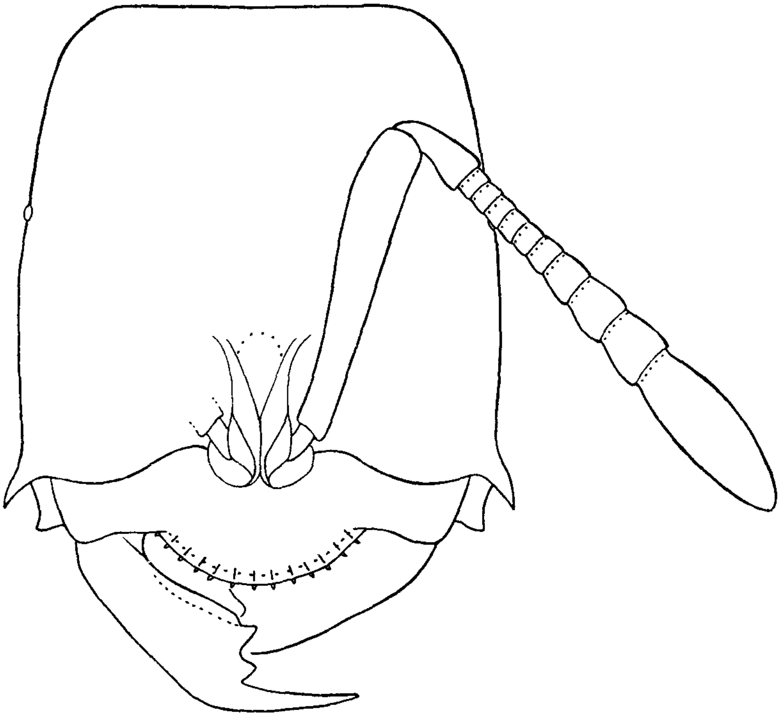
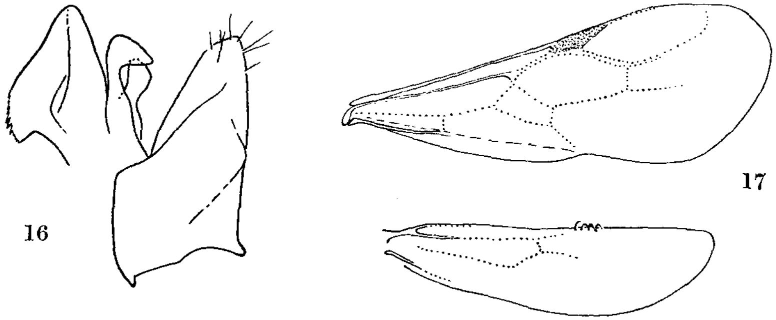


Figure 15. *Prionopelta brocha,* full-face view of holotype worker.

The anterior clypeal border is normally convex or moderately projecting and armed with a row of inconspicuous denticles corresponding to the clypeal armament of *Amblyopone*. The eyes are small to minute in the worker, moderate-sized in the female, and are normally placed behind the middle of the sides of the head in both worker and female. The antennae are 12-segmented in worker and female, or more rarely 11-segmented; apical 3-4 segments incrassate, forming a more or less distinct club. Male antennae 13-segmented, filiform, with feebly thickened apex; scape very short. Maxillary and labial palpi both 2-segmented in all castes. Male mandibles like those of *Amblyopone*, 2-toothed. Notauli present in male. Genitalia of male not unusual in shape (Fig. 16); volsella without second cusp. Wings as shown in Figure 17, though the veins are more distinct in some species. The female usually has slightly heavier and more complete venation than in the male of a given species. Variation extends to Mf4, which may be completely lacking (e.g., *P. kraepelini* female), and to CuA in the hindwing, present in the females of some species as a distinct spur (e.g. *P. majuscula* female).



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Prionopelta punctulata male from Tucumán, Argentina. Figure 16. Left aedeagal valve, volsella and paramere, partly detached as flattened on slide. Figure 17. Wings.

The *Prionopelta* species are all small to minute in size, and mostly have depigmented (testaceous to reddish-brown) workers, though in some species (e.g., *P. majuscula*), the female is piceous. Males are black or piceous; the three castes are usually similar in size (length), but in *majuscula,* the female is distinctly larger. The sculpture consists of close punctulation, varying in coarseness with the species, but most distinct on the dorsum of the head, and weakening posteriorly toward the gaster, the last usually being wholly or in part smooth and shining. Pilosity simple, short, reclinate to erect, usually rather abundant.

The characteristics of the worker *Prionopelta* are mostly adaptations indicating a cryptobiotic mode of life, and the direct information available on the ecology of several species all goes to show that these are inhabitants of the soil and soil cover. Most of the species are at home in moist tropical forest, but some of them can survive in semiarid areas such as northwestern Argentina (Kusnezov, 1955: 276) by keeping to a strictly hypogaeic mode of existence in the moister microhabitats. Kusnezov (*loc. cit.*) has questioned the inclusion of the Old World *Prionopelta* species in one genus with those from the New World, but I see no reason to question the judgment of older authorities in this matter. Leaving the somewhat primitive *P. brocha* to one side, the present species of *Prionopelta* form an exceptionally homogeneous group so far as we can tell from the known examples of all castes and from the known biology. *P. brocha,* while sharing a number of characters with *Amblyopone,* is nevertheless clearly a *Prionopelta* in the form of the mandibles. Since the mandibular differences are complex ones that have probably accompanied an adaptive shift (in feeding habits?) of some significance, I see no need to exclude *P. brocha* from *Prionopelta.*

The characters of *Prionopelta* include many that are reductions from average or primitive characters of *Amblyopone,* so that it seems likely that the latter is the parent genus. In the tropics of both hemispheres, *Prionopelta* appears to be distributed geographically and ecologically roughly so as to replace the smaller *Amblyopone* of the *"Fulakora"* group. As examples of this may be cited New Guinea (with two widespread *Prionopelta* species) and the Solomons (with *Amblyopone celata*) plus southeastern Australia (with several of the small *"Fulakora"* species). A somewhat similar situation apparently holds in the American tropics, where in some areas *Prionopelta* is very common **[21]**, but the smaller, depigmented *Amblyopone* species are either unknown or tend to be restricted to geographically or ecologically peripheral ranges.

Prionopelta, on the other hand, does not extend significantly into the temperate or cool montane regions (except perhaps in Australia), and is represented on the Asian-African mainlands only by a single collection from Zululand. So far as is known, of course, amblyoponines are in general very poorly represented in Africa below the Sahara, and no species have yet been found in the Congo rain forests. *Prionopelta* ranges in the New World from southern Mexico south into northwestern Argentina, in the West Indies extending only into the Lesser Antilles, where *P. antillana* may be introduced. In Cuba, a small species of *Amblyopone* that has been collected only once may take the place of the absent *Prionopelta* **[7]**. Two species of *Prionopelta* are widespread and fairly abundant in New Guinea, but these tend to have different ranges within the area, or at least different modes of abundance. One of the species, *P. opaca,* has a close counterpart in the East Indies (Java) and the Philippines (*P. kraepelini*), and these two species may intergrade in the Micronesian islands, where they have probably been introduced by man **[23]**. The curious species *P. brocha* is known only from the type collection on New Caledonia. Since New Caledonia appears to have received by far the greatest bulk of its ant fauna by way of eastern Australia, the recent discovery of a species in Queensland **[23]** is not surprising. In this connection, the little-known *Dorylozelus* must be re-examined (see below).

PRIONOPELTA Species

aethiopica Arnold, 1949, Occ. Pap. Nat. Mus. S. Rhodesia, 2(15):263, fig. 4, 4a, worker. N. status. Zululand. **[23]**

(T) *amabilis* Borgmeier, 1949, Rev. Brasil. Biol., 9:203, figs. 3-5, worker. Costa Rica. **[21]**

(T) *antillana* Forel, 1909:239. N. status. Lesser Antilles, n. S. America, etc. **[21]**

(T) *brocha* Wilson, 1958a:147. New Caledonia. **[23**, Fig. 15]

descarpentriesi Santschi, 1924, Rev. Zool. Afr., 12:195, worker. Madagascar. **[23]**

(P) *kraepelini* Forel, 1905, Mitt. Naturh. Mus., Hamburg, 22:3, female, worker. E. Indies, Philippines, Micronesia. **[23]**

(P) *majuscula* Emery, 1897:595. N. Guinea & nearby islands. (=*Ponera simillima* Fr. Smith, *Prionopelta poultoni* Donisthorpe, *Renea testacea* Donisthorpe, *Examblyopone churchilli* Donisthorpe, synonymized by Brown, 1953b:12; see also Wilson, 1958a:148.) **[23]**

(P) *modesta* Forel, 1909:241. C. America, s. Mexico. [21, 22]
(T) *opaca* Emery, 1897:596. N. Guinea, Micronesia, Australia. [21, 23]
(T) = *mocsaryi* Forel, 1907, Ann. Mus. Nat. Hungar., 5:1, worker. Synonymized by Brown in Wilson, 1958a:149.
(P) *punctulata* Mayr, 1866:505. s. Brasil, n. Argentina. [21]
(P) = *mayri* Forel, 1909:239. N. syn.
(P) = *bruchi* Santschi, 1923, Rev. Suisse Zool., 30:245, "female" (*recte* worker?). N. syn.

ONYCHOMYRMEX Emery

Onychomyrmex Emery, 1895:349. Type: *Onychomyrmex hedleyi* Emery, 1895, monobasic.
Onychomyrmex, Forel, 1915:2, characters.
Onychomyrmex, Wheeler, 1916; revision of genus, ecology, ethology, larva.

This genus evidently represents a development of the army-ant or legionary life-form that has arisen independently from an Australian *Amblyopone* stock. The worker of *Onychomyrmex* (Figs. 46, 48) is accordingly more slender and has longer appendages than is usual for *Amblyopone*, and the integument is smooth and shining, the mandibles more down-curved and hook-like, and the tarsal claws much enlarged, particularly those of the last two pairs of legs. The spurs of the posterior pair of tibiae are reduced to minute, straight, almost setiform vestiges, or else are lacking altogether. In *O. hedleyi*, the spur vestiges may be present or absent in different workers from the same nest. To complete the resemblance to certain true army ant genera (subfamily Dorylinae) the *Onychomyrmex* female (known for two of the three species) is dichthadiiform, that is, it has the head peculiarly broadened, very small eyes, workerlike alitrunk without wings or corresponding sclerites, and elongate, bulky gaster.

Despite these characters, which misled Emery and most other authors to consider the genus as an aberrant and independent tribal group within subfamily Ponerinae, the amblyoponine affinities are so clear that one wonders why it was so long before they were properly interpreted. The mandibles, clypeus, position of the eyes on the posterior half of the sides of the head, the long sting, and the basic form and structural relationships of alitrunk, petiole, postpetiole and remainder of gaster in the worker are all unmistakably amblyoponine. The larva also shows no features that seem to contradict an amblyoponine affinity (Wheeler, 1916; G. C. and J. Wheeler, 1952: 637), although the Wheelers consider it to show specialization in the direction of the Cerapachyinae larva.

Males from southeastern Queensland are believed to belong to *O. mjoebergi;* these are similar in size to the worker, and have the general characters of some of the slender small *Amblyopone* species. The wing venation is shown in Figure 47; the genitalia are peculiar in having short, broad parameres, which are bent sharply inward, then caudad, the apical portion forming a curved vertical plate on each side with a cultrate transparent margin. The subgenital plate is narrowly tongue-shaped and projecting at its apex. The sculpture is predominantly smooth and shining. Mandibles with 2 apical teeth; palpi segmented 2,2.

John Clark (1928) was the first to relate *Onychomyrmex* to *Amblyopone* unequivocally when his relict *Lithomyrmex* (now *Amblyopone*) *glauerti,* from Western Australia, turned up and was recognized as intermediate between *Amblyopone* and *Onychomyrmex* in many worker characters. *A. glauerti,* however, has a normal winged female, and in other ways follows *Amblyopone* so closely that I was unable to separate it from that genus. On the other hand, the intermediacy of *A. glauerti* confirms beyond reasonable doubt the amblyoponine affinities of *Onychomyrmex.* Emery's position in isolating *Onychomyrmex* can be explained, I think, by his belief in the taxonomic significance of the tibial spurs. At present, we know that these spurs are not always reliable classificatory guides, particularly among the Ponerinae. Clark's paper appears to have been seen by few myrmecologists, and *A. glauerti* by still fewer, so Emery's and Wheeler's classifications have in the main been followed until very recent years.

As now known, *Onychomyrmex* has three species, all occurring in eastern Queensland in rain forest, chiefly in rotten logs. Probably the genus extends into northeastern New South Wales. It is much rarer in the southern than in the northern part of its range.

Wheeler (1916) relates his finding workers of *O. mjoebergi* "biting and stinging to death a huge lamellicorn beetle larva more than two inches in length, which they had just found in a cavity'' in a rotten log. It is not clear from Wheeler's account whether the beetle larva was attacked after he broke the log open, or before. Furthermore, it would seem that a two-inch lamellicorn (probably of family Passalidae, common in rotten logs in North Queensland rain forests) would be an impossible burden for even several hundred of the very small *Onychomyrmex* to move through the narrow passages of the usual rotten log. Until the habits of *Onychomyrmex* can be checked in detail, it is interesting to speculate that the colonies of this genus may migrate from one large victim to the next, after subduing the prey by mass stinging attacks.

Wheeler found small companies of workers moving through logs in the manner of army ants mass-foraging, and I myself have found aggregations answering this description well in the species *O. hedleyi* and *O. doddi.* One party of *O. hedleyi* found in a log at Malanda on the Atherton Tableland numbered several hundred workers, without queen or brood.

The behavior of these workers reminded me very much of the actions of foraging groups of *Leptogenys* and *Aenictus* that I have seen in Australia, Western China and Assam. A colony of *O. mjoebergi* found by Wheeler at Kuranda ''comprised at least 400 workers, a single queen, with the abdomen greatly distended with eggs, and a large number of nearly mature larvae but no pupae.'' These circumstances suggest that *Onychomyrmex* may resemble the New World army ants studied by Schneirla in having brood-rearing and nomadism synchronized.

Key to the Species of Onychomyrmex — workers

1. Mandibles predominantly smooth and shining, with a few coarse punctures; robust species, with broad head (CI usually > 78); color yellowish-red to reddish-brown .... *mjoebergi*
Mandibles densely striate above; more slender species, with narrower head (CI usually < 78) .... 2.

2. Larger species; length of alitrunk (WL) > 1.2 mm.; full adult color black or dark piceous .... *hedleyi*
Smaller species; length of alitrunk (WL) < 1.2 mm.; full adult color deep reddish-brown .... *doddi*

ONYCHOMYRMEX Species

(T) *doddi* Wheeler, 1916:53. n. Queensland [**24**]
(T) *hedleyi* Emery, 1895:350. e. Queensland [**24**, Figs. 46, 48]
(T) *mjoebergi* Forel, 1915:2. e. Queensland [**24**, Fig. 47]

INCERTAE SEDIS

PARAPRIONOPELTA Kusnezov

= *Paraprionopelta* Kusnezov, 1955:270. Type: *Paraprionopelta minima* Kusnezov, 1955:271, figs. 1, 2, 5a, male; monobasic.

This monotypic genus was based on males taken separately, presumably at light, at Tucumán, Argentina. These males are minute (under 2 mm. TL), dark in color, and have a somewhat *Amblyopone*-like petiole. They differ from the known males of Amblyoponini in the oblong shape of the head, in the shape of the mandibles, and especially in having 10-segmented antennae. There are no distinct teeth on the anterior clypeal margin, but the hind tibiae do bear broadly pectinate spurs. Possibly this genus really is an amblyoponine, but since a similar type of petiole occasionally appears convergently in other groups of ants, I do not consider this a certainty. If it is in the Amblyoponini, then one is tempted to match it with the worker of *Amblyopone degenerata* from southern Brazil; the two are similar in size, and both have reduced antennal segmentation.

DORYLOZELUS Forel

= *Dorylozelus* Forel, 1915:24. Type: *Dorylozelus mjoebergi* Forel, 1915:25, fig. 4, worker; monobasic.

This genus is known only from the type (or types?) of *D. mjoebergi*, taken by Mjöberg in the Blackall Range in southern Queensland. Despite all efforts to locate the type material in the Forel Collection at Geneva, in the Naturhistoriska Riksmuseet in Stockholm, and in various Australian collections, it could not be found.

Failing in the effort to find the type, I spent a week searching the rain forests in and around the Blackall Range for more specimens, but found none. T. Greaves and the Darlingtons have also looked for *Dorylozelus* in the Blackalls without success. It is important that this ant be rediscovered, and the sexes and larvae examined, because its systematic position at the moment is anything but clear. Wheeler placed it in a separate tribe Dorylozelini, but probably he never saw a specimen of *D. mjoebergi.*

As characterized by Forel, this species is a mixture of characters like those of *Dorylus* and *Ponera.* The petiole and gaster are supposed to be like those of tribe Ponerini. The frontal lobes are contiguous, as in Ponerini, but also as in some amblyoponines. The mandibles, as drawn by Inez Forel, are like those of *Prionopelta* in general pattern, narrow and straplike, with three apical teeth, of which the middle tooth is smallest. The antennal funiculi are incrassate, with only 10 segments. Inez Forel's drawing is highly diagrammatic and difficult to interpret. One even wonders whether there is any possibility that the specimen is a compound one, so disharmonious is the image created by the original characterization. *Dorylozelus* remains one of the most puzzling anomalies among the ants. Only with more material will we be able to place it more satisfactorily.

APPENDIX

The pages of this appendix are reserved for notes and descriptions dealing chiefly with species-level taxonomy and biology. In the descriptions, the abbreviations for measurements and indices are as follows: TL, total outstretched length of body, including mandibles (sum of all tagmata) ; HL, maximum measurable length of head, including clypeus, but not mandibles; HW, maximum measurable width of head, ignoring eyes if present (head measurements are made from dorsal full-face view) ; CI, or cephalic index, is HW/HL × 100. WL, or Weber's length, is the diagonal length of the alitrunk as measured from side view. L, of course, generally stands for length, and W for width (in mm.).

Places where types or other specimens are deposited are indicated within brackets where convenient, especially the abbreviation MCZ, which stands for the Museum of Comparative Zoology at Harvard College, Cambridge, Massachusetts.

[1] Borgmeier (1957: 108-112) has discussed *A. armigera* and *A. elongata* and brought their descriptions up to date. His synonymy for *elongata* is followed here. He found the worker of *elongata* to have the palpi segmented 3, 2.

Kusnezov's *Ericapelta egregia,* described from isolated males, is about the right size to be the male of *A. armigera,* and I expect that association of the sexes will eventually prove this synonymy.

A. chilensis has been collected by Ross and Michelbacher in southern Chile on the northern shore of Lake Lllanquihue and in valley forest 18 km. west of Purranque, both localities to the south of the type locality, Valdivia.

[2] *Amblyopone pallipes* is a rather common ant in forested areas of the eastern United States and in the St. Lawrence Valley near Montreal. Brown (1949:84) has shown that the subspecies *montigena* Creighton is based on individual nest variants occurring sporadically in the eastern United States. In the 1949 paper, *subterranea* Creighton, based on samples from deep subterranean collections made in the plains states, was raised to species rank on the basis of what were thought to be diagnostic sculptural characters. Now, however, after the examination of many more collections from all over the eastern United States and the Mississippi Valley, and considering samples from Arizona (near base of Huachuca Mts., R. G. Wesson leg.) and Iowa (W. F. Buren leg.), it appears that the characters thought in 1949 to be diagnostic of a distinct species are in fact only average differences, connected by clinal variation to the eastern characters. Actually, the differences are slight; the underlying pigmentation affects the appearance of the fine sculpture. Samples from the Plains are frequently lighter in color than those from the eastern forests, but even some samples from the eastern coastal areas are medium brownish-ferruginous in color.

Although it may be that the distribution of *Amblyopone* is continuous between Arizona and the Plains and the Pacific Coast, we have no records between Arizona and northern California, where the population of *oregonensis* commences and runs northward through the moist coniferous forest belt. Although *oregonensis* has been considered to be a subspecies of *pallipes,* the differences between the two remain constant so far as known, and I shall call *oregonensis* a species until we have more information on possible range contacts between it and *pallipes.*

On several occasions in eastern Massachusetts, *A. pallipes* has been observed under stones in hardwood forest together with dead centipedes, usually lithobiids or geophilomorphs. The association in each case left no doubt that the ants were using chilopods for food; usually larvae were attached to the centipedes and appeared to be feeding actively. In another case, W. L. Nutting found *A. pallipes* workers attacking an asilid larva in leaf litter. Most observers agree, however, that chilopods are the main source of food for this species. In my experience, the centipedes used for food showed considerable variability in size and form, and lithobiids many times the size of the ant are found with the ants as often as smaller prey. It is assumed that the long, sharp sting of *A. pallipes*, which can penetrate even the human skin in some places, is used to subdue living prey, but we do not know all of the details of hunting behavior. *A. pallipes* workers in the artificial nest are very timid, and can scarcely be stimulated to attack centipedes of any kind enclosed with them.

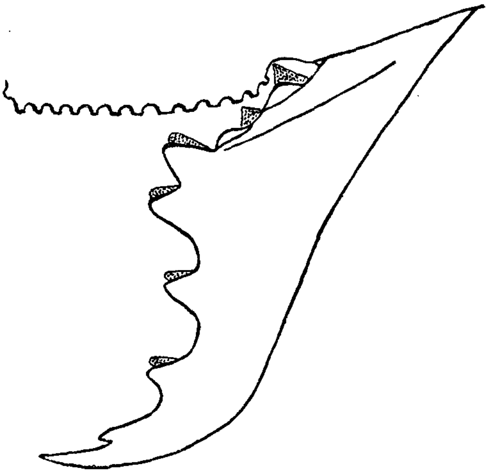


Figure 18. *Amblyopone trigonignatha,* holotype worker, dorsal view of left mandible and anterior clypeal apron.

When the ants are found with dead centipedes in the field, it usually is in a situation under a stone such that transport of the prey by the ants seems unlikely. I believe that the larvae are often brought to the spot where the larger sort of prey dies, and that they feed there for considerable lengths of time, rather than the reverse situation usual for ants, where the food is brought by the ants into more or less central brood chambers.

[3] *A. trigonignatha* was described in 1949 from a single worker taken in a leaf mold berlesate from Concord, North Carolina. It is very distinctive in the form of the clypeus and mandibles (Fig. 18). More than 200 separate collections of *Amblyopone* from all over the eastern half of the United States have been examined since 1949, but all these proved to be the common *A. pallipes*. *A. trigonignatha* still remains known only from the holotype [MCZ].

[4] AMBLYOPONE MYSTRIOPS sp. nov.

(Fig. 19)

Holotype female (alate): TL 7.2 (gaster expanded), HL 1.47, HW 1.38 (CI 94), WL 2.21, petiole L 0.66, petiole W 0.76, scape L (without basal neck) 0.91, straightline outside L left mandible 1.50, forewing L 4.3 mm.

Habitus and details of head, mandibles and scape as in Figure 19. Frontal lobes distinctly separated by an extension of the clypeus and the pit-like "frontal area." Genal teeth reduced to low rounded eminences. Clypeal apron short, convex, with 8 slender oblique teeth. Mandibles as shown in the figure; broken line on each shaft represents a rather indefinite dorsal carina or costa; between this and the tooth rows, the surface is concave. Viewed from the side edge-on, the mandibles are seen to be markedly flattened in an oblique ventrolateral direction, and the apical quarter is incrassate. Note the low, inconspicuous basal lamella, the small size of the apical tooth, and the convex ridge or swelling formed ventral to the subapical teeth, near the apex; the principal (median) teeth on the blade are in two separate ranks.

Antennal scapes curved and arched, slightly narrowed toward their midlength. Funiculus slightly but gradually thickened toward apex; segments I through VI longer than broad, I (pedicel) about 1½ times as long as II through X, which are approximately equal among themselves in length; VII and VIII about as long as broad; IX and X slightly broader than long;

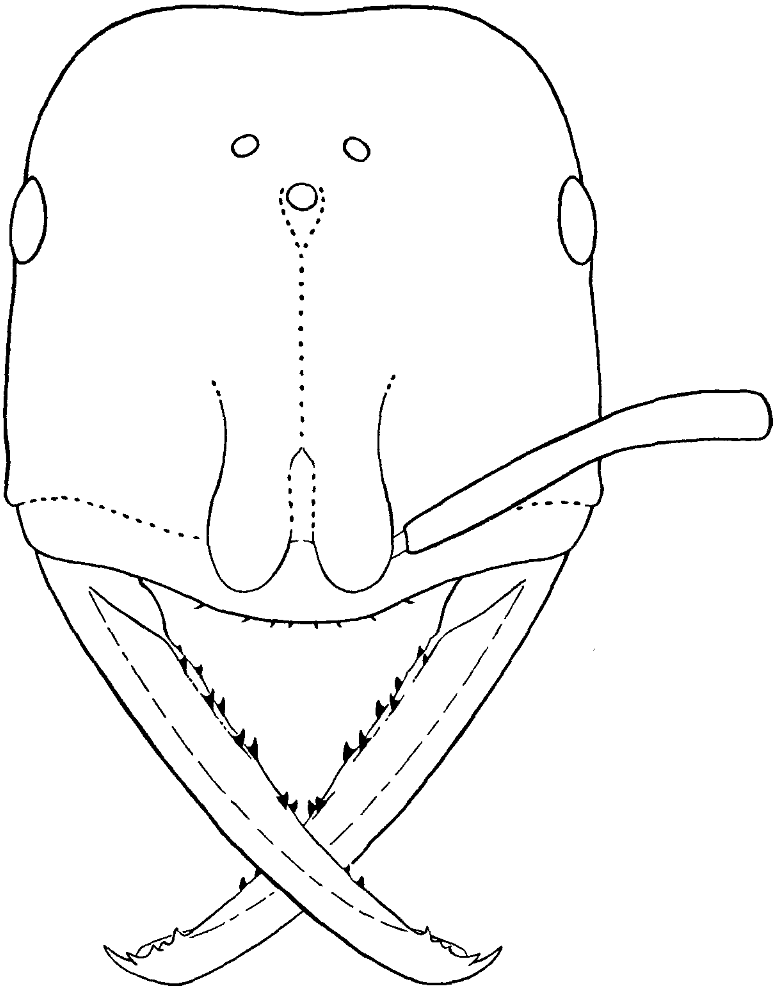


Figure 19. *Amblyopone mystriops*, holotype female, full-face view of head, including mandibles and left antennal scape.

XI (apical) twice as long as X. Under-mouthparts retracted, but 3 segments of the maxillary palpi and a single segment of each labial palpus are exposed; probably there are more basal segments hidden beneath the folded labrum.

Alitrunk very similar to that of large females of *A. pallipes.* Petiole also similar, but a little broader, with a nearly vertical anterior face, slightly concave in profile, rounding sharply into the gently convex dorsal face. Seen from above, the front and side outlines of the node are convex, although the front is slightly indented in the middle. Ventral process as in *A. pallipes.* The (normally exposed portion of the) postpetiole is a little longer than the petiolar node, and distinctly wider; abdominal segment IV is slightly longer and wider than III (postpetiole). Apex of gaster slightly laterally compressed; sting slender, curved.

Sculpture of head much like that of *A. pallipes,* reticulate-punctate and predominantly opaque; on anterior half of head, some of the interpunctural ridges form fine, parallel costulae on the lower, inner genae and on the frontal carinae, but these less distinct and extensive than those of *pallipes.* Cervical face of occiput shining, punctate. Clypeus longitudinally striate; "frontal area" a round-bottomed pit, smooth and shining, as is also a small impression in front of the anterior ocellus. Mandibles coarsely oblique-longitudinally striate, moderately shining. Antennae, tibiae and tarsi densely punctulate, subopaque. Alitrunk densely punctulate, shining (punctures not contiguous), the punctures rare on the pleura; lower half of lateral propodeal surfaces coarsely longitudinally striate; declivity smooth. Petiole, gaster and femora smooth, shining, with spaced punctures, those on the postpetiolar disc trailing shallow sulci.

Pilosity consisting mainly of soft, reclinate to oblique, pubescence-like hairs, densest on head, legs and gaster, but not hiding sculpture. Longer fine hairs on mandibles (especially inner surfaces), front of head, antennae (including scapes), legs and apex of gaster. Head and body dark reddish brown to piceous; mandibles, antennae and legs sordid yellow.

Wings hyaline, with yellowish veins and dark brown pterostigma in forewing. Venation of forewing of the "complete" type, without first radial crossvein. Rs joining wing margin ("radial cell closed"), Mf4 short, Mf2 present but short.

Holotype [MCZ] a unique female found among unidentified miscellany; labelled: "Guatemala:/Los Amates/Kellerman." Presumably this refers to Los Amates in the valley of the Rio Motagua, near the Honduras border.

In the form of its mandibles and their dentition, this species differs widely from all other *Amblyopone* species, and makes an approach to the condition in *Mystrium* (compare Figs. 4 and 19). The pilosity and other characters are, however, typical for *Amblyopone* rather than *Mystrium*. Whether this aberrant species represents a phyletically transitional form, or merely a New World convergence toward the *Mystrium* type, I cannot say. It would be interesting to know more about the habits and ecology of this odd species.

[5] Amblyopone monrosi sp. nov.

(Fig. 20)

Holotype worker: TL 4.3, HL 0.92, HW 0.77 (CI 84), WL 1.19, petiolar node L as seen from above 0.47, petiole W 0.43, scape L without basal neck 0.51, exposed straight-line outside L of left mandible 0.54 mm.

Amblyopone species, dorsal views of anterior border of clypeal apron. Figure 20. *A. monrosi,* paratype worker. Figure 21. *A. bruni,* holotype of synonymous *A. bruni juergi.*

A rather typical-appearing smallish *Amblyopone* of the "*Fulakora* group," with sides of head gently convex, posterior border weakly concave, greatest width of head at about the anterior third. Genal teeth acute, but small and almost hidden in pilosity. Compound eyes represented by a small patch of unpigmented, indistinct facets in the usual position. Frontal lobes small, contiguous, the line of separation deeply impressed. Clypeal apron with corner teeth unusually large and broad, blunt at apices and projecting over the masticatory borders of the closed mandibles (Fig. 20). Between the corner teeth are 6 smaller, obliquely truncate teeth socketed on low tubercles, the two median teeth about even with the apices of the corner teeth. (One or both of the outer small teeth may be fused to the corner tooth adjacent in different specimens.)

Mandibles basically of the typical *Amblyopone* pattern, but shorter and broader than usual, especially the thick, blunt-tipped apical tooth. Inner margin convex. Basal quarter or so of masticatory border occupied by a round-edged translucent lamella, about as high as the acute double teeth. The right mandible (crossed above the left in both holotype and paratype) has a small single tooth following the lamella, and after this, at the midlength of the mandible, a large, slightly retrorse double tooth; after this three large, apparently single teeth before the apical tooth. The left mandible, after the basal lamella, has three moderate-sized double teeth, followed by two subapical single teeth. (The paratype has similar dentition.)

Antennal scapes short, thick, only very slightly curved and feebly incrassate toward apex. Funiculus 11-segmented, strongly incrassate toward apex, but thickened gradually from segment II on to apex. All segments except the pedicel (I) and the apical (XI) appear to be broader than long, though VI, VII, VIII and IX are only slightly so. Apical segment almost as long as the preceding 3 segments taken together.

Alitrunk slender, straight in dorsal profile, rounded downward gently at the front of the pronotum and, posteriorly, into the plane, sloping declivity. Mesonotum almost twice as broad as long; promesonotal suture impressed; metanotal groove present but not conspicuous. Seen from above, the mesonotal area is gently constricted. Petiole seen from above subcircular, truncate behind. Seen from side, anterior face steep, curving broadly into gently convex dorsum. Ventral lobe rounded, with a long posterior slope. Postpetiole only a little longer than petiole, and only a little wider in its posterior part. Next segment (abdominal IV) slightly longer than postpetiole, and slightly wider, making the widest part of the gaster. Remainder of segments tapering caudad, subconical; sting stout, curved.

Body with head predominantly smooth and shining; head with abundant, small, close but not contiguous punctures, becoming much feebler and fewer on alitrunk and especially on gaster. Lower 2/3 of sides of propodeum and most of upper mandibular surfaces longitudinally striolate. Antennae very finely and densely punctulate, opaque.

Erect pilosity generally distributed, rather sparse and short, becoming a little longer and more abundant near gastric apex. Accompanying the longer pilosity, and replacing it on the legs, is a short fine reclinate pubescence. Color yellowish ferruginous.

The holotype [California Academy of Sciences] and the very similar paratype worker [MCZ] were taken together about 10 miles northeast of Pucon, Chile, by E. S. Ross and A. E. Michelbacher. This species is readily separated from *A. chilensis* by the shining sculpture of the head and the different clypeal and mandibular armament. Differences from other New World species are given in the key. This is the second species to be found in Chile.

The name is given in memory of my late good friend, Dr. Francisco de Asis Monrós, of Tucumân, Argentina, whose tragic death has deprived the world of a gifted and devoted scientist.

[6] AMBLYOPONE ORIZABANA sp. nov.

Holotype worker: TL 2.7, HL 0.58, HW 0.48 (CI 83), WL 0.74, petiole L 0.26, petiole W 0.29, scape L (without basal neck) 0.31, straightline outside L of left mandible 0.34 mm. A very small, yellow member of the "*Fulakora* group" with dorsum of head densely and evenly reticulate-punctate and opaque or nearly so. The habitus and shape of head, body and appendages are all substantially as in *A. smithi* [**17**, Fig. 40], although the posterior occipital border is more strongly concave in the middle in *orizabana*. Also, the mandibles are more slender in *orizabana,* and can close tightly against the clypeal apron (as in the holotype). Clypeal apron convex, with 4 truncate teeth socketed on low tubercles in the middle (median pair smaller, bases fused), flanked by broader corner teeth on each side; the latter cannot be seen clearly, and may possibly be subdivided. The mandibular dentition is difficult to see, but it appears to consist of a triangular basal tooth or lamella, 4 sharp double teeth, and a reclinate, acute subapical tooth in addition to the slender apical tooth. The inner borders are convex. Antennae much as in *A. smithi.*

Alitrunk constricted at the narrow, transverse mesonotum, which is continuous with the propodeal dorsum; metanotal groove almost obsolete, visible only in certain lights. Petiolar node with a vertical anterior face, convex in both directions;

dorsum only weakly convex. Petiole and postpetiole about equal in length; abdominal IV slightly longer. Ventral process of petiole with a small angular anterior lobe and a larger, bluntly subtriangular posterior lobe that slopes upward gradually posteriad. Gastric apex not compressed; sting stout.

Mandibles and lower sides of posterior half of alitrunk longitudinally striolate. Underside of head densely reticulate-punctate, but weakly shining. Rest of body, including legs, scapes and frontal groove, smooth and shining, with numerous, spaced small piligerous punctures, best seen on pronotum and petiole. Pilosity fairly abundant, but very short and mostly oblique; longer hairs on mandibles and gastric apex. Color light ferruginous yellow.

The holotype, a unique [MCZ], was taken by E. O. Wilson on Pico Orizaba, Veracruz, Mexico, on August 24, 1953. The worker was found under a large mossy rock in an open grassy strip along the trail between La Perla and Rancho Somecla, on the southern slope of the mountain, at about 2700 to 2800 m. altitude. At this altitude, the original forest cover is mainly broadleaf temperate trees, with *Carpinus* abundant and some pines. This rather ordinary small *Amblyopone* is easily distinguished from all the American species by its small size and yellow color; only *A. degenerata* is smaller, and this is very different in antennae and sculpture.

[7] *Key to the New World Species of Amblyopone — Workers and Females*

1. Antennae 7-segmented; worker eyeless, minute, yellow in color (holotype only 1.7 mm. total outstretched length) (se. Brazil) *degenerata* Borgmeier
   Antennae 12-segmented; worker larger, usually over 2 mm. in outstretched length .... 2.

2. Lobes of frontal carinae separated by a distinct gap (Fig. 19) ..... 3.
   Lobes of frontal carinae contiguous or fused, as in Figure 40 ...... 6.

3. Mandibles on inner surfaces each with two sparse separate rows of small, sharp teeth (Fig. 19, Guatemala) .... *mystriops* Brown
   Mandibles on inner surfaces with much larger teeth, those near the midlength fused at their bases so as to form heavy double teeth (Figs. 18, 40) .... 4.

4. Inner borders of mandibles angulately produced, so that the blades are triangular in shape without the apices; large double teeth with rounded apices; genal teeth reduced to inconspicuous obtuse angles (Fig. 18; Piedmont of North Carolina) . . . . *trigonignatha* Brown
Inner borders of mandibles straight to convex, not angulately produced, the blades linear; large double teeth predominantly acute; genal teeth acute and projecting . . . . 5.

5. Inner borders of mandibles and anterior clypeal apron straight, or at most only feebly convex (n. California to Brit. Columbia)
oregonensis (Wheeler)
Inner borders of mandibles, and usually also the anterior clypeal apron, decidedly convex in outline (temperate N. America w. at least to Iowa and Arizona) . . . . *pallipes* (Haldeman)

6. At least the anterior 3/5 of the head (as seen in full-face view) predominantly densely sculptured and opaque . . . . 7.
Entire or nearly entire dorsal surface of head smooth and shining, with spaced punctures . . . . 10.

7. Anterior 3/5 to 3/4 of dorsum of head coarsely longitudinally striate with intermixed punctures, occiput smooth and shining, with spaced punctures; full adult color piceous or black (se. Brazil to n. Argentina)
armigera Mayr
Dorsum of head densely and uniformly punctate or striolate-punctate and opaque throughout, except that the cervical border or median frontal groove may be shining in some cases; full color of worker yellow to ferruginous . . . . 8.

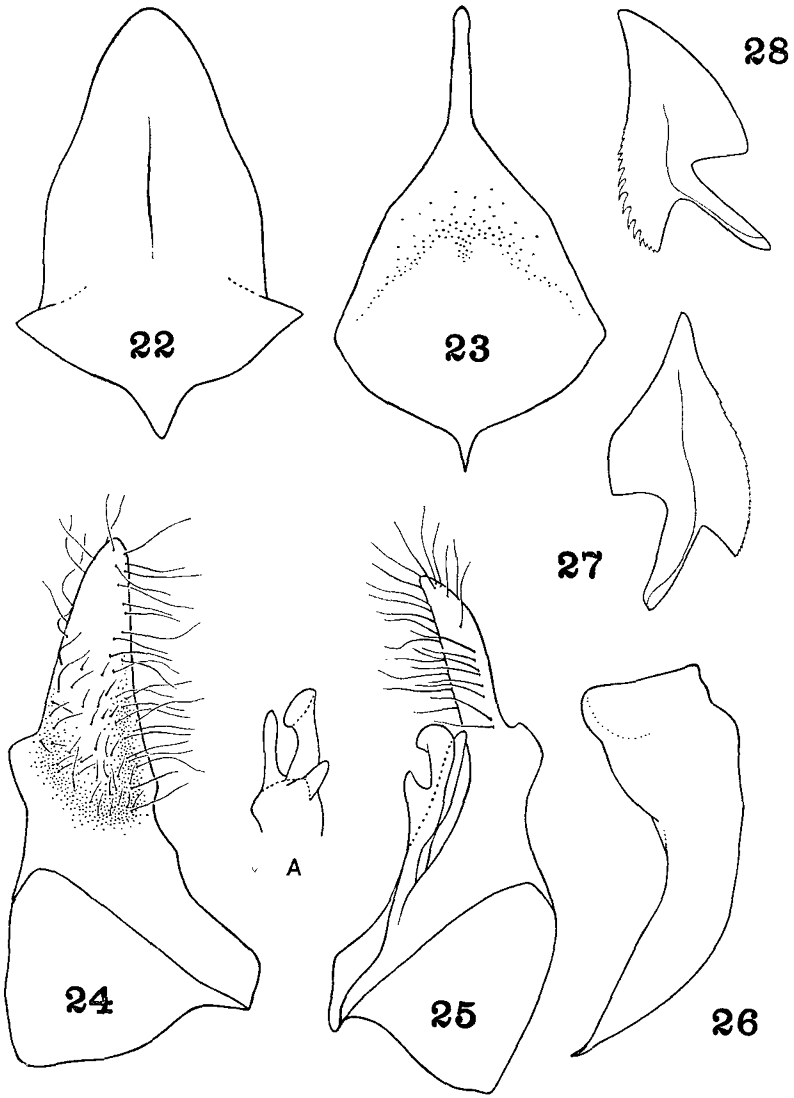
8. Size very small (TL of holotype worker 2.7 mm.); alitrunk very smooth, punctation sparse; propodeum with very few punctures on the dorsum, and its lateral striation restricted to the lower third of the sides; color of worker yellow (Mexico: Mt. Orizaba) . . . . *orizabana* Brown
Size larger, TL of worker > 3.0 mm.; punctures more abundant and distinct on alitrunk; sculpture of lateral faces of propodeum covering half or more of these surfaces . . . . 9.

9. Size larger; unique holotype worker 4.5 mm. long (according to the original description) (Cuba) . . . . *bierigi* (Santschi)
Size smaller; worker TL 3.0-4.1 mm., female TL 4.1-4.5 mm. (Chile)
chilensis Mayr

10. Larger and more robust, worker head width > 0.70 mm.; clypeal apron having the middle teeth small and not advanced beyond the much larger teeth that form the lateral corners (Fig. 20, Chile) . . . . *monrosi* Brown
Smaller and more slender, worker head width < 0.60 mm.; clypeal apron convex in outline, the middle teeth distinctly advanced beyond the corner teeth (se. Brazil to n. Argentina) . . . . *elongata* (Santschi)

[8] The large, relatively large-eyed, dark-colored workers with retrorse mandibular teeth in double rows (Fig. 3) form the group of *A. reclinata*. Belonging to this group are the nominal forms *reclinata, feai, rothneyi, bellii* and *quadrata.* I have been able to examine and compare directly the types of *rothneyi* and *bellii,* and I find them to differ scarcely at all. Forel's description of *bellii* is in error on several crucial points. First of all, the *bellii* types have denticulae on the anterior clypeal margin that are approximately as distinct as in the *rothneyi* type, and similar in form. The eyes of the *rothneyi* type are slightly larger (0.22 mm. greatest diam.) than in *bellii* (0.18 mm. greatest diam.), but not nearly so much so as Forel claims. I count about 70-90 facets in the *rothneyi* type before me (here designated and labeled as lectotype); though the count is very difficult, I find the two *bellii* syntypes to have almost as many facets (50-70) as *rothneyi.* In fact, under the best circumstances of counting, I seriously doubt whether the difference is significant.

The *bellii* types are slightly more coarsely and quite opaquely sculptured over head, alitrunk, petiole and postpetiole; in the *rothneyi* type, these areas are very densely punctate and nearly opaque, but many of the punctures do have narrow shining spaces between them, and the postpetiole is more definitely shining. Both of these species have the anterior genal angles bluntly subrectangular, and not projecting. The palpal count for both of the *bellii* syntypes is maxillary 4; labial 3 (not 2 and 3, as Forel states); the palpi cannot be seen in the *rothneyi* type. These two species may well be geographical variants; *bellii* is from Kanara, on the western side of the Peninsula south of Bombay, while *rothneyi* is from Barrackpore, near Calcutta. From Poona, central Madras Presidency, and Orissa, all on the Indian Peninsula, I have numbers of large males that probably belong to *bellii* and/or *rothneyi.* These males have distinctive genitalia and a long, narrow caudal process on the subgenital plate. The whole terminalia most resemble those of a series of large males of another species from Formosa (Figs. 23, 25), probably the same as the male doubtfully attributed to *bruni* by Forel (1913, Arch. Naturg., 79 (A6): 183), but which is more likely a member of the *reclinata* group.



Males of two indeterminate species of the *reclinata* group. Figure 22. Subgenital plate, specimen from Los Baños, Luzon (wings shown in Figure 5). Figure 23. Same, specimen from Chipon, Formosa (wings shown in Figure 6). Figure 24. Right paramere, mesial surface, and A, detached volsella in oblique view, Los Baños specimen. Figure 25. Left paramere with volsella attached, oblique dorsal view, Chipon specimen. Figure 26. Left mandible, Chipon specimen. Figure 27. Aedeagal valve, Los Baños specimen. Figure 28. Same, Chipon specimen.

There are several other series in the *reclinata* group in the MCZ. A series of workers from Mt. Makiling, Luzon (L. Uichanco leg.), and another accompanied by males from virtually the same locality (Los Banos, Luzon, F. X. Williams leg.) have small but protruding genal teeth, the apices of which are blunt or truncate. The sculpture of these two series is coarse and opaque, somewhat like that of the *bellii* types, and the eyes are about the size of *bellii*. However, the accompanying males have different terminalia; the subgenital plate (Fig. 22) has a broad, narrowly rounded lobe instead of the long, slender process of the males discussed above from India, which I take to be *A. bellii* on circumstantial evidence. A single male from San Carlos, Philippines, resembles the other Philippine males. The Philippine samples, and a series of workers of this same kind from Macao, were referred to *A. rothneyi* by Wheeler, but I think it is more likely that they are another species. Workers from both the Philippine and Macao series prove to have 5 segments in the maxillary palpi and 3 in the labial palpi, in comparison with the 4,3 count in the *bellii* types. A worker from the Cuernos Mts., near Dumaguete, Negros, Philippines, has small, protruding genal teeth, but the sculpture is somewhat lighter than in the Luzon and Macao series, more as in the *rothneyi* type. This specimen is smaller and has smaller eyes (greatest diameter about 0.14 mm.) with perhaps 35-40 facets, and agrees in this, in its smaller size, its sculpture, etc. with the description of *feai* by Emery.

Another small worker with rather small eyes, but this time with blunt genal angles like those of *bellii,* comes from Mao Marroe, 450 m., Soemba Island. This specimen is weakly shining over the alitrunk and quite shining over the petiolar node and postpetiole, these parts being cribrately punctate.

It is obvious that differences in eye size, petiolar width and so on are allometrically variable, and hence untrustworthy as species characters in the absence of more detailed information based on large series. Judging from the material before me, and taking into account the male characters, I would guess that the *reclinata* group consists of not less than two, and probably not more than three or four species. How the names are applied will of course have to be left to future revisers.

[9] Of the two forms described as *bruni* and *bruni* subsp. *juergi,* I have seen only the latter (holotype worker). When he described *juergi* in his "Glanures" paper, Forel apparently did not have before him the *bruni* type, and he probably used only the *bruni* description for the comparison. At any rate, he was wrong in describing the anterior clypeal margin of *juergi* as without denticulation; actually, very fine denticles are present. Of the other differences cited, at least some are allometric characters. Thus, relatively greater width of head and petiole and larger eye size are only to be expected of a larger worker as compared to a smaller one, as in this case. Since both of the types came from Pilam, Formosa (H. Sauter leg.), I think it likely that they are conspecific. This species has blunt double teeth on the mandibles, and the clypeal apron is characteristic in shape (Fig. 21).

[10] Two syntypes of *A. minuta* (type locality: Soengei Bamban, Sumatra, in termite nest) were examined through the courtesy of Dr. Besuchet. This is a very small species (TL 2.7 mm.) with slender mandibles; inner border feebly convex, teeth short, 3 double teeth with sharp retrorse points; apex slender. Clypeal apron nearly straight, with 6 separated teeth, inner two largest, outer two smallest. Head finely and densely reticulate-punctulate, opaque; alitrunk, petiole and gaster densely punctulate (apex of gaster less so), only moderately shining; the alitrunk subopaque. Color brown; appendages etc. yellowish.

A very small, dark brown male [MCZ] from Sandakan, Borneo (Baker leg.) may belong to this or a related species.

[11] Although they differ in size, the types of *luzonica* and *williamsi* in the Museum of Comparative Zoology are otherwise much more similar than the original characterizations and faulty figures indicate. In addition to the types, we now have further series from the Cuernos Mts. and vicinity, near Dumaguete, Negros Island, collected by J. W. Chapman and D. Empeso. This additional material, while closest to the *luzonica* type in size, somewhat bridges the gap between the two species. Considering the similarities, I cannot see that *williamsi* is more than a large "nest variety" of *luzonica.* Size differences of greater magnitude occur between series in other species of the genus (e.g., *australis, denticulata, pallipes*). *A. luzonica* is related to *A. silvestrii* and *A. amblyops,* but has the clypeal teeth in a distinctive pattern. In all three of these species, four subequal truncate teeth occur between a pair of larger ''corner teeth,'' which may themselves be more or less subdivided. In *silvestrii* and *amblyops,* the four middle teeth are more or less separate and autonomous, but in *luzonica* they are grouped into two partially fused pairs, one pair on each side of the midline. The frontal lobes are very close together, though not completely contiguous, so that this species is intermediate between the ''*Fulakora*'' and ''*Stigmatomma*'' groups in this respect. The worker of *luzonica* has the palpi segmented 4,3. Apparently this is the common small *Amblyopone* of the Philippines.

A. silvestrii has the four middle teeth very regular, equal in size, and close-set, separated by a wide gap on each side from the blunt, bipartite corner tooth. This gap is absent or weakly developed in *amblyops,* according to Karawajew's figure. *A. silvestrii* also has a densely punctate and more or less opaque alitrunk (petiole and postpetiole subopaque); the sculpture may not be quite so dense in *amblyops;* in *silvestrii,* the propodeal declivity is finely transversely striolate or shagreened, whereas in *amblyops* it is said to be ''very smooth and shining.''

[12] A group of species, related to *A. denticulatum,* from Europe, the Near East and North Africa, has workers medium to small in size, with very small eyes and reduced pigmentation in the worker. All of these species have the frontal lobes separated, if only narrowly so, and the clypeal apron normally has 5 truncate teeth, all socketed on tubercles, between the large ''corner teeth;'' the latter often bipartite. Santschi (1915) gives a reasonable key to the known species of the Mediterranean area. In *A. denticulata* the palpi are segmented 4,3.

The variety of *denticulata* called *gracilicornis* is only a small variant common in the Balkans and the Aegean region; I have seen the series in the Finzi Collection [MCZ] mentioned in the original description by Menozzi. I agree with Emery (1916) that *gheorghieffi* is only the male of *denticulatum.*

It seems likely that *A. santschii,* from Senegal, belongs with the *denticulatum* group, although the description is too sketchy to make this certain.

Dr. Kenneth Christiansen has given me some interesting small yellowish males with light brown heads, which he took in July and August, 1952 and 1953, in NW Tripoli Province, Lebanon, at 1100 m. altitude, and below the Turkish border, Latakia, Syria, at 800 m.; presumably both collections were made at light. These may be the males of an undescribed *Amblyopone* or of one of the species known from workers in North Africa.

[13] The variation, distribution and synonymy of *A. australis* and its close relatives has been discussed by Wheeler (1927: 1-20), Brown (1958b: 13-15) and Wilson (1958a: 142-143). *A. australis* shows strong geographical variation in several characters, some of which can be summarized in brief.

Sculpture of dorsum of head. In samples from southwestern and southeastern Australia, the longitudinal costulation of the front of the head usually extends only to near the level of the eyes or a little beyond. In New South Wales and Queensland the costulation varies widely by locality. A large proportion of the samples from the subtropical forests of northeastern New South Wales and southeastern Queensland have the costulation very extensive, reaching well beyond the eyes and often extending almost to the posterior cephalic border. This is also the condition in the Lord Howe and Norfolk Island populations, and in the New Zealand lots; presumably these populations represent historical introductions from eastern Australia. In samples from northern Queensland and New Guinea, the costulation is well developed, but does not usually extend very far beyond the eye; at least, it is distinctly shorter than in the southeastern Queensland samples. In southwestern Australia the costulae and punctures tend to be much coarser ("race *foveolata*") than elsewhere, but samples I collected in South Australia (Kangaroo Island — Kingscote, Rocky River and Ravine des Casoars; Lofty Range—Aldgate; Northern Flinders Ranges—Wilpena Pound) approach the Western Australian material in this respect, and make transition to the Victorian samples. Series from Tasmania, south central Victoria and the Australian Alps tend to have both the costulae and the punctures reduced.

Sculpture of mandibles. In southwestern Australia, South Australia, Tasmania, Victoria and the Alps generally, the dorsal and lateral surfaces of the mandibles are normally completely and regularly coarsely longitudinally striate. New Hebridean specimens are mostly of this type. In eastern New South Wales, one notes that some samples show a weakening of the striation along the external margin of the mandible, and in series from the New South Wales-Queensland border (National Park), many specimens have almost entirely smooth and shining mandibles, with scattered punctures. These may occur together in the same nests with specimens having nearly or quite completely striate dorsal and lateral mandibular surfaces. Such specimens look much like the sibling species *A. michaelseni,* which has predominantly smooth mandibles, and some of them further converge toward *michaelseni* in having the head slightly longer than broad and the genal tooth small in size. This extreme intranidal variation more or less matches the extensive variation in cephalic sculpture of the same series.

Farther north in Queensland, one finds a more consistent progression from largely striate to almost wholly smooth mandibles, the latter type prevailing in northern Queensland and New Guinea. The Lord Howe-Norfolk Island-New Zealand populations are of the intermediate type, with mandibles predominantly striate, but tending to be smooth along the outer borders.

Color. Pigmentation is difficult to evaluate in insects having as long a callow period as this species has, but the abundant material available does indicate some broad trends. In general, populations from most forested areas in southwestern Australia, Tasmania, Victoria, and the mountains of New South Wales have more or less reddish workers, although associated females may be much darker. However, in intermediate areas that are drier or without many trees, such as the western districts of Victoria, Kangaroo Island, and the Lofty and Flinders Ranges of South Australia, the workers are usually dark brown. In New South Wales and southern Queensland the color darkens, and most workers from Queensland, as well as all the mature individuals of New Guinea, Lord Howe, Norfolk Island and New Zealand, are dark brown or piceous, with lighter appendages. The New Hebrides series are intermediate on the reddish side. Some series taken from rotten logs in wet forests near Melbourne (Dandenong Range) are uniformly very light, and more yellowish than red. Most red series come from beneath stones. In Queensland, where nearly all *australis* come from rotten logs, the prevailing color is dark brown.

Size. The workers show extreme size variation, even at single localities or within single nest series. The only trend that I can see in the available material is one toward a wider spread of variation on the mainland of Australia, particularly in the southeastern areas. Perhaps much of this variation is phenotypic in origin.

Other characters: There is considerable variation in the mandibular dentition, but it is in large part ''random'' and difficult to analyze. New Guinea specimens often tend to form a blunt tooth between the two largest teeth, and in Australia there may be one, two or even three teeth basad of the largest tooth; however, these always decrease in size toward the mandibular insertions. Variation in compound eye size is partly regional, partly allometric. Even in the smallest workers, however, there are 12-15 or more facets backed by pigment, and usually more than 20. In the New Zealand (*''cephalotes''*) populations, the second and third funicular segments are unusually slender, but can be matched more or less closely by samples from eastern New South Wales.

Without detailing other variation in minor characters, I think it can be seen that variation in this species, whether individual or geographical, shows a high degree of discordance among the different character-systems. Certainly a character-by-character analysis in this case shows up the essential lack of a realistic basis for the old system of ''races'' and ''varieties,'' which is here discarded. Aside from the possibility of cryptic allopatric species, always a consideration to be respected in wide-ranging forms, *A. australis* looks in its totality like one species.

The two obscure forms *A. michaelseni* and *A. leai* appear to be peripheral siblings of *A. australis* now undergoing displacement pressure from *A. australis* after an expansion of this species into their respective ranges.

As might be expected from elementary considerations of character displacement (see Brown and Wilson, 1956), *A. australis* shows the maximum amount of difference from each of the siblings where it overlaps their respective ranges. Outside the zone of sympatry, *australis* sometimes displays some characteristics of the siblings, e.g., the very smooth mandibles of many Queensland *australis,* away from the range of *A. michaelseni,* which has predominantly smooth mandibles.

A. michaelseni was described from southwestern Australia, and I have seen a topotypic specimen collected there (Jarrahdale, J. Clark leg.). Clark also recorded samples from Victoria and New South Wales, but I have never seen any *michaelseni* from these eastern states, despite intensive collecting in Victoria and the close examination of several hundred nests of what all proved to be *australis.* Wheeler saw a specimen from Lucindale, South Australia. Apparently *michaelseni* is very rare and local, especially in the southeast, and its similarity in the field to *australis* makes it hard to spot. It has a slightly longer head than *australis,* the eyes are smaller (15 facets or less, not or scarcely pigmented), the genal teeth are completely lacking, and the costulae and punctures are much reduced.

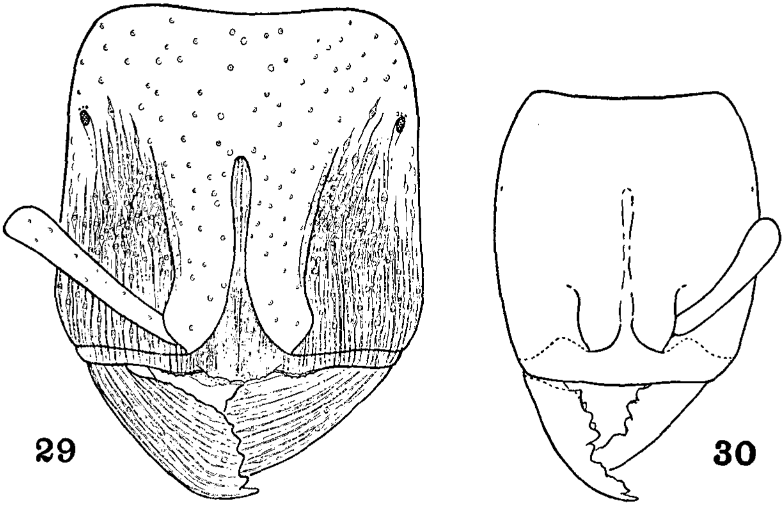
The Lord Howe sibling, *A. leai,* is known from two series from the island, of which I have seen three syntype workers from the summit of Mt. Gervis. As compared to the *australis* (*"howensis"*) populations from the same island, the *leai* sample is reddish-yellow in color (vs. dark reddish-brown), has smaller eyes with fewer and coarser facets (11-12 pigmented facets vs. 18-25), has short cephalic costulation, not or barely reaching beyond the eyes (vs. reaching nearly to posterior border), has slender second and third funicular segments (vs. segments II and III nearly or quite as broad as long), and has two well-developed subequal teeth basad of the large median mandibular tooth, while the latter tooth and its large distal neighbor are rather close together (vs. one distinct tooth basad of large median tooth, with sometimes an indistinct denticle basad of this; two large median teeth of mandible widely separated). It would be most interesting to investigate the relationship between these two species on Lord Howe, if they both still exist there.

[14] AMBLYOPONE MERCOVICHI sp. nov.

(Figs. 29, 32)

Holotype worker: TL 11.0, HL 2.04, HW 1.92 (CI 94), WL 2.98, petiole L 0.95, petiole W 1.11, scape L 1.12, exposed straightline L of mandible 1.19 mm. In general size, color and shape of body resembling at first glance *A. australis* samples from the Victorian Alps, but with entirely different mandibles and other divergent characters.

Head as shown in Figure 29. Cheeks shallowly impressed in region outside frontal carinae and anterior to compound eyes. Eyes much reduced, with 6-7 facets in greatest diameter. Frontal lobes broad, nearly horizontal, separated by a narrow median groove. Clypeus with a short but distinct median lobe, its apex rounded and denticulate, slightly overhanging the ventral or free clypeal border, which is also denticulate and is weakly concave in the middle. Genal angles rounded, unarmed. Labrum with the usual bilobed free margin, but also having a prominent transverse, bilobate ridge or welt near its middle, half of which is shown in Figure 29 as the stippled area below the clypeal margin. Mandibles subtriangular, much broader than those of



Two new species of *Amblyopone* from Australia, heads in full-face view. Figure 29. *A. mercovichi,* paratype worker. Figure 30. *A. gingivalis,* holotype worker. Drawn to same scale.

other *Amblyopone* species, the apical (masticatory) margin curving evenly into the basal margin. Apical margin with 5 distinct teeth, the apical largest, size of teeth decreasing basad; in approximate region of basal angle, the teeth are continued as a series of 5-6 low rounded teeth or crenulations passing onto the basal margin. The teeth and crenulations are single-ranked along the thin free inner mandibular margins.

Antennal scapes slightly incrassate apically, almost straight in dorsal view, but strongly curved to fit the genal curvature; when extended back, just barely reaching the compound eyes. Funiculi gradually incrassate toward apex, but without a distinct club; funicular segment II (counting pedicel as I) small, distinctly broader than long, the segments gradually increasing in length apicad to X, which is slightly longer than broad. Apical segment (XI) approximately twice as long as X. None of the specimens has the under-mouthparts opened out, but the apical segments of the maxillary palpi are visible in two specimens; this segment is flattened, curved and apically tapered; its length and position suggest that it is one of two segments in the maxillary palpus. The labial palpus is not visible, indicating that it is short and probably not more than 2-segmented.

Alitrunk rather narrow, with horizontal dorsal surface; anterior face of pronotum and sides of alitrunk steep; inferior pronotal angles acutely pointed. Alitruncal profile horizontal; pronotum and propodeum weakly convex (nearly plane), mesonotum weakly convex; metanotal groove distinct and impressed, with the slightly elevated mesonotum breaking an otherwise nearly straight alitruncal profile. Mesonotum from above subcircular, slightly broader than long, its boundaries distinct; constriction of alitrunk distinct, centered at metanotum; sides of propodeum diverging slightly caudad. Declivity of propodeum steep, flat, on each side with a low, rounded margin. Petiolar node with vertical, concave anterior face, meeting the almost flat (gently convex from side to side) dorsal face at an acutely rounded angle (Fig. 32).

Postpetiole a little shorter than the (normally exposed and pilosity-bearing part of the) succeeding segment, abdominal IV. Terminal segment of gaster conical, not compressed.

Body and appendages chiefly smooth and shining, with numerous piligerous punctures over upper part of head, dorsum of alitrunk, sides of pronotum, petiole, postpetiole (where strongest and most numerous) and abdominal segment IV. The cheeks anterior to the eyes, the gula, and the mandibles are rather coarsely longitudinally striate, with coarse interspersed punctures. Median lobe of clypeus more finely striate. Sides of posterior alitrunk finely striolate-punctate, chiefly longitudinally. Anterior coxae shagreened subopaque.

Most surfaces of body, especially gaster and dorsal surfaces elsewhere, with a thin pubescence of rather coarse, short, reclinate hairs. Longer, more erect tapered hairs, mostly on anterior dorsum of head and clypeus, masticatory and ventrolateral borders of mandibles, gula, antennae, and apical and ventral parts of gaster; also a few of these longer hairs on pronotum and fore coxae.

Color rich ferruginous red; slightly infuscate spot on vertex.

The holotype, with three paratype workers, was taken by Father C. Mercovich at Kinglake West (="Tommy's Hut"), Victoria, on November 15, 1951. The four workers were taken from the heart rot of a large, rather dry eucalypt log lying on the forest floor. One of the workers was found in what appeared to be the ants' midden, containing large numbers of heads of termites, which may possibly therefore have been a main item of food. In this connection, it is interesting to note that *A. mercovichi* bears certain resemblances to presumed cryptic termite-predators in other ant groups (e.g., *Cylindromyrmex* Mayr, *Metapone* Forel, *Gnamptogenys* of the *mordax* group).

This large and curious ant, although it occurs in country near Melbourne, is known only from the type collection. Father Mercovich's finds, in this and the case of *A. gingivalis* sp. nov. (below) prove that even the relatively well-collected parts of Australia hold many a surprise for the enterprising and persistent collector.

A. mercovichi is so different from all other *Amblyopone* known that it almost warrants being placed in a new genus. Still, its affinities with the *australis* and *saundersi* groups seem clear enough, despite the aberrant mandibles. We need to know more about this species.

The holotype and 2 paratypes (one with no head) have been returned to Father Mercovich for deposit in an Australian collection. (Smallest paratype: TL 9.3, HL 1.80, HW 1.72 (CI 96), WL 2.64, petiole L 0.83, petiole W 0.95, scape L 1.02, exposed straightline L mandible 1.05 mm.). One paratype in MCZ.

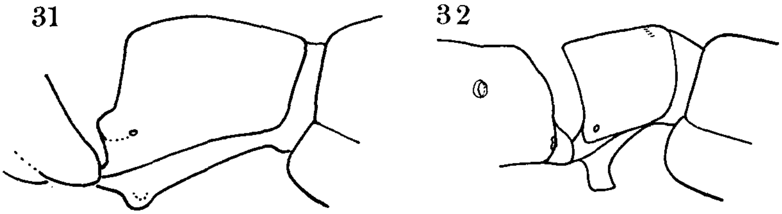
[15] AMBLYOPONE GINGIVALIS sp. nov.
(Figs. 30, 31)

This new species is known from a single worker collected by Father C. Mercovich, S.J., at Calga, New South Wales, during April, 1956. Father Mercovich sent me the specimen together with the sample of *A. mercovichi,* described as new above, and Mrs. Buffler prepared figures of the head (Fig. 30) and petiole (Fig. 31) under my supervision. I then returned these specimens to Father Mercovich in Australia, after which, learning of my progressing revision of the tribe, he very generously returned them to me so that I might present the description with the rest of the material on the amblyoponines. Unfortunately, the shipment suffered damage in transit, and the sole worker of *gingivalis* lost its entire head and the anterior part of the prothorax. It might seem wiser to forego description of a unique holotype missing its most important parts, but in this case we do have a good drawing of the head available, and the species is of such particular interest in connection with the limits of variation within the genus, that I have decided to give it a name.

Holotype worker: TL 8.6 (estimated), HL 1.5 (estimated), HW 1.4 (estimated) (CI 91 from drawing); WL 2.1 (estimated), petiole L 0.82, petiole W 0.68 mm. Estimated straightline L of mandible 0.9 mm. Form of head shown in drawing. Note extremely reduced eyes and clypeal apron, the latter completely unarmed, and the subtriangular mandibles, with fairly distinct basal border and mostly blunt teeth, partly double-ranked. Scapes short, subclavate; genal angles unarmed.

Remainder of body typically amblyoponine in form, slender; alitrunk constricted at metanotum (seen from above). Mesonotum nearly three times as broad as long, bounded behind by a distinct, shallowly impressed metanotal groove. Alitruncal dorsum in profile horizontal; promesonotum and propodeal dorsum forming separate feeble convexities. Propodeal declivity sloping caudad, forming on obtuse angle with the dorsum, into which it is gently rounded. Petiolar node longer than high and longer than broad (Fig. 31). Postpetiole nearly as long as the succeeding segment; last visible segment (abdom. VII) laterally compressed; extruded sting very long, slender, curved.

Sculpture of head (as recalled) densely and finely punctate or reticulate-punctate and predominantly opaque. Alitrunk, petiole and gaster mainly smooth and shining, with sparse punctures. Sides of alitrunk and anterior sides of petiole finely striate with scattered punctures, the striae principally longitudinal. Body overall with numerous fine, short, obliquely erect hairs and smaller, reclinate, pubescence-like hairs, not obscuring the sculpture. Color medium reddish-brown, head more brownish, appendages lighter.



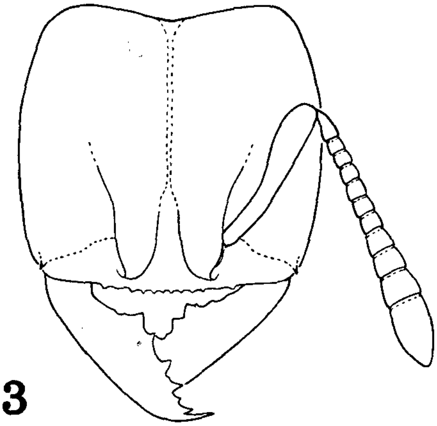
Two new species of *Amblyopone* from Australia, petioles and adjacent parts in side view. Figure 31. *A. gingivalis*, holotype worker. Figure 32. *A. mercovichi* paratype worker. Not drawn to same scale.

This species is so distinct in the shape of its clypeus and mandibles that there should be no chance of confusing it with any other *Amblyopone*. Undoubtedly it is a specialized relict, probably local in distribution. Father Mercovich took the sole worker under a stone in a gully with *Angophora* and scribbly gum (*Eucalyptus haemastoma*) trees as cover. The holotype will be returned to Father Mercovich for deposit in one of the Australian collections.

[16] The *ferruginea* group as presently known includes five Australian species: *aberrans, clarki, ferruginea, hackeri* and *longidens,* the first two of which are southwestern and the last three southeastern. The workers of all are stoutly built, small-eyed, yellow forms, smaller than *A. australis* and relatives, but not much different in general habitus. In fact, the *ferruginea* group occupies a position intermediate between the *saundersi* and *australis* groups in size, structure and presumably in biology, and may well represent the descendants of the line that led from *saundersi*-like ancestors to *A. australis*. Like both contiguous groups the members of the *ferruginea* group have a palpal formula of 2,2 in the workers, while the clypeal apron, its dentition, and the male-female wing venation are reduced as in *australis*. The females, where known, are distinctly larger than the workers and have the head, alitrunk and petiole more or less dark brown or blackish. The males are smaller and blackish. The species are all strongly cryptic in habits, and normally nest and forage below the soil surface, so that they are rarely seen except when flooding forces them to the surface, or in the cold of winter, when they may rise beneath stones to seek the heat stored there from solar radiation. There are no good observations known to me on nest size, behavior or food preferences, but I think that some colonies must attain a large size. Like many subterranean ants, members of this group are found in a great variety of habitats, including wet forest, alpine scrub, and arid woodland. The systematics of the group were partly clarified by Brown (1952), who showed that Clark's *mandibularis* was the same as *ferruginea* Smith (Fig. 36), and that *ferruginea* is a local species, so far found only in Melbourne and vicinity. Forel's variety *longidens* is really a good species (Fig. 34) (confused by Wheeler in 1927 with *ferruginea*), widespread but local in southeastern Australia.

A. hackeri (Fig. 39), the most "*Fulakora*-like" of the *ferruginea* group, occurs in the country on the border between southeastern Queensland and northeastern New South Wales. Portions of a dismembered chilopod were found in a nest of this species taken by P. F. Darlington in southeastern Queensland.

Of the southwestern forms, *aberrans* (Fig. 35) and *clarki* seem distinct enough in mandible type, despite the considerable variation in dentition shown by *clarki* (Figs. 33, 37, 38). In addition, samples having the general *clarki* habitus (Fig. 33) show unusually strong geographical variation in sculpture, which may in fact represent differences between two or even three separate species. Specimens from the type series (Ludlow, W. A.) (Fig. 37) and a series from Busselton, W. A. (J. Clark



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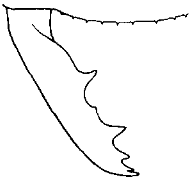

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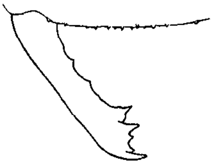

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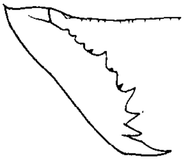

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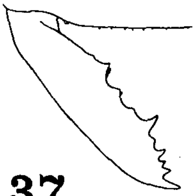

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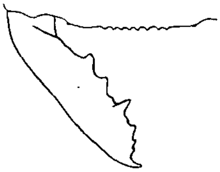

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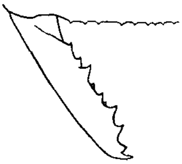

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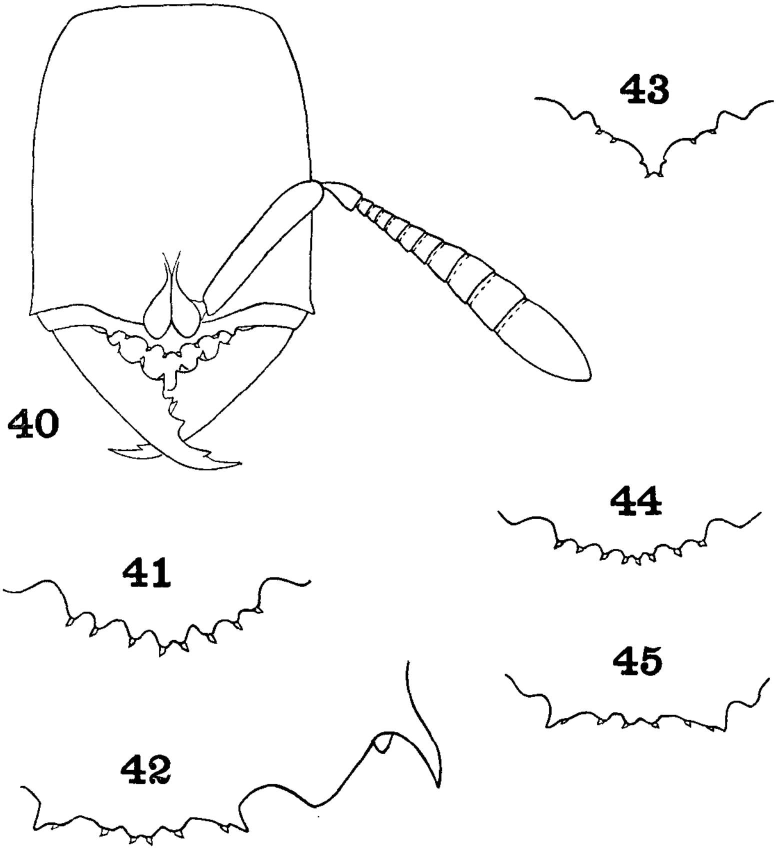
Australian *Amblyopone* of the *ferruginea* group, workers. Figure 33. *A. clarki* or near, Norseman, W. A., full-face view of head and mandibles. Figure 34. Right mandible and anterior clypeal margin, *A. longidens*, Grampians Range, Vict. Figure 35. Same, *A. aberrans* syntype, Mundaring, W. A. Figure 36. Same, *A. ferruginea*, specimen compared with type, Research, Vict. Figure 37. Same, *A. clarki* syntype, Ludlow, W. A. Figure 38. Same, *A. clarki* or near, Perth, W. A. Figure 39. Same, *A. hackeri* syntype, National Park, Queensland.

leg.) have the coarse, longitudinally striate or costulate sculpture of head and pronotum usual in species of the group. A worker taken by C. P. Haskins under a log in the National Park, W. A., of which the mandible and clypeal margin are shown in Figure 38, has the upper half of the head and the pronotum with numerous coarse, separated punctures in place of the costulae. Three workers (Fig. 33) taken by E. O. Wilson in arid woodland at Norseman, W. A. (which is far inland from the other *clarki* localities) have even more reduced sculpture; the punctures are much finer than in the National Park specimen, and the interspaces smooth and shining. More material is needed from southwestern Australia in order to clarify this situation.

[17] A number of small forms occurring in southeastern Australia and New Zealand are placed in the *saundersi* group. Already described as species are *exigua, wilsoni, lucida, punctulata* and *gracilis* from Australia, and *saundersi* from New Zealand. These forms all have the "*Fulakora* habitus;" i.e., they are small and slender, depigmented and with eyes much reduced or absent in the worker; the mandibles, clypeus and genal teeth are of the "typical *Stigmatomma*" pattern, and the lobes of the frontal carinae are fused or contiguous at the midline of the head. All have dense, fine punctate sculpture of the head. The palpi are apparently all segmented 2,2 (rarely 1,2).

It seems impossible for the time being to say how many good species there really are in this group. I am adding a new species that is quite distinct from any of the others (*A. smithi* sp. nov., described below). Only for *saundersi* do I have material from more than two or three localities, and this species is so variable that doubts must remain as to whether it may not represent two or more sibling species existing in New Zealand (Brown, 1958b).

There are differences among the species in head shape (especially CI), mandibular dentition, overall size and sculpture, but the best character is often the form and dentition of the anterior clypeal apron. In two series I have from Wallaby Creek in the Hume Range, central Victoria (D. Ashton leg.), and from Sherbrooke Forest in the Dandenong Range, Victoria (Brown leg.), the center of the clypeal apron is produced into



Australian *Amblyopone* of the *saundersi* group, workers. Figure 40. *A. smithi* sp. nov., paratype, full-face view of head. Figure 41. Anterior margin of clypeal apron, *A. gracilis* syntype. Figure 42. Same, *A.* sp. from Binna Burra, southeastern Queensland (left anterior corner of head with genal tooth also shown). Figure 43. Same, *A.* sp. from the Hume Range, central Victoria. Figure 44. Same, *A. exigua* from Kallista, Victoria, determined by Clark. Figure 45. Same, *A. lucida* syntype.

a definite median lobe (Fig. 43), while in paratypes of *A. lucida* from Coree (or Corrie) Creek in the Alps of the Capital Territory (G. Hill leg.) and a series from Bonang, Victoria, also in the eastern Alps (P. F. Darlington leg.), the apron is very nearly straight and has a differently arranged dentition (Fig. 45).

Most samples from Australia have clypeal aprons intermediate between these last two types (Figs. 41, 44). I have specimens of *exigua* Clark (Fig. 44), collected and determined by Clark himself, from Kallista, Victoria, which is adjacent to the type locality (Belgrave) and close to Ferntree Gully, where I collected another series of this same species. It should be noted here that Sherbrooke Forest, where the specimens (noted above) with the mesally lobate clypeal apron were found, is immediately adjacent to Belgrave and Kallista, and it seems likely that all of the specimens came from the same wet forest that clothes this limited area. That we are dealing here with a pair of sympatric species seems assured. Possibly the lobate form from Sherbrooke Forest and Wallaby Creek is an undescribed species, but since Clark's descriptions and figures are so vague, I cannot be sure that this form does not match his *A. wilsoni,* of which I have seen no authentic specimens.

Paratypes of *gracilis* (from Beech Forest on the Otway Peninsula of Victoria) are larger in size, but have a clypeal apron (Fig. 41) similar to that of *exigua.* A series matching the *gracilis* paratypes very well was taken by P. F. Darlington at Corinna, Tasmania. Another series taken by the same collector at Corinna is similar, but the insects are smaller in size; about half of them are ergatoid females with larger eyes.

This last collection agrees well with Clark's characterization of *punctulata.* In spite of their similarity, the two Corinna samples may belong to different species (*gracilis* and *punctulata*).

One more series, this from Binna Burra, near Beechmont in southeastern Queensland (P. F. Darlington leg.), is similar in size to *gracilis,* but has much larger genal teeth (Fig. 42), and the sides of the propodeum are largely smooth and shining (striolate, opaque in *gracilis, saundersi* and other similar species). Possibly this species is undescribed. It is clear that we need much more material of this group in order to be sure of the species.

AMBLYOPONE SMITHI sp. nov.
(Fig. 40)

Holotype worker: TL 2.6, HL 0.56, HW 0.44 (CI 79), WL 0.69, petiole L 0.29, petiole W 0.29, scape L (without basal neck) 0.26, exposed straightline L left mandible measured from lateral insertion 0.36 mm. Habitus of *saundersi* group, but much smaller than any of the other species known, and with *ca.* posterior 2/5 of the head distinctly shining, the punctures here coarse and numerous, but separated by predominantly smooth and shining interspaces; a median smooth strip extends forward to about the center of the head. The anterior half or slightly more of the head is densely punctulate, with intermixed indistinct longitudinal-oblique striolation, nearly or quite opaque.

The general shape of head, mandibles and antennae is shown in Figure 40. The eyes are reduced to minute, indistinct pigmented spots, each backing 2 or 3 indistinct facets. Mesonotum transverse, its posterior limits marked only by a feeble constriction; metanotal groove obsolete, a faint trace visible in certain lights. Propodeal dorsum meeting declivity through an obtuse, rounded angle; declivity plane, oblique, broader than high. Petiolar node sessile, a little longer than high; ventral process subquadrate, with rounded anterior corner and sharply rectangular posterior corner. Anterior face of node vertical, rounding into horizontal, weakly convex dorsum; seen from above, the node is approximately square, with rounded anterior corners. Postpetiole about as long as petiole, and only slightly wider; succeeding segment (abdominal IV) about as long as postpetiole, but slightly wider. Apex of gaster conical; sting stout, curved.

Sculpture, apart from head, predominantly smooth and shining, with scattered piligerous punctures. Lower mesepisterna and almost all of sides of propodeum, as well as mandibles, longitudinally striolate, but still moderately shining. Clypeus longitudinally striate. Pilosity as described for *A. monrosi.* Color ferruginous yellow.

Holotype [MCZ] and one very similar paratype worker [to be deposited in a major Australian collection] collected together from under a stone in clayey soil in dry eucalypt forest (predominantly *Eucalyptus Baxteri, E. obliqua* and *E. cosmophylla*) at Aldgate, near Mt. Lofty in the Lofty Ranges of South Australia, altitude about 550 m., December 8, 1950 (leg. W. L. Brown, Jr.). The weather at the time of collecting was very hot and dry; much digging turned up no further specimens.

This species is named for my long-time friend and adviser in myrmecology, Dr. Marion R. Smith.

[18] *A. celata* is a small yellow species, widespread in the Solomons. I was able to count only the maxillary palpal segments: there are four. Mann found that the pupae are naked, as in myrmicines. Apparently this species is replaced on New Guinea by *Prionopelta.*

[19] *A. zwaluwenburgi* is a minute species (under 2 mm. total length) that was found in the soil of a sugar cane field at the Hawaiian Sugar Planters Association Experiment Station, Honolulu. I think it is likely that the species has been introduced into Hawaii from Melanesia or the East Indies.

[20] Wilson (1958a) has discussed the variation of *Myopopone castanea* in some detail, emphasizing the Melanesian populations. He has synonymized five of the species, all described by Donisthorpe from 1938 to 1949, and there is every reason to accept his synonymy. Wilson's study extended only incidentally to the more western populations of *M. castanea,* which fall outside Melanesia proper, and it is now possible to study these in the light of additional material from the Philippines and elsewhere. Most of this material is included in the collection of Dr. J. W. Chapman, and comes principally from the vicinity of Dumaguete on Negros, Leyte, Palawan and southern Luzon (collected by Chapman, Baker, Williams, Brues and McGregor). Other material comes from northern Borneo (Mjöberg), Sumatra (Brues), etc.

The varieties *bakeri* Viehmeyer and *proxima* Stitz are represented by type material in the Museum of Comparative Zoology; comparison of these with the rest of the Philippine series shows that they are both part of the intraspecific variation of the *castanea* of that area. The characters of sculpture, and especially the shape of the subpetiolar process, show wide variation overlapping that of the New Guinea-Solomons samples.

The females, which are even more variable than the workers in sculptural characters, and which differ considerably from the workers of the same series, have been a source of synonymy even dating back beyond Donisthorpe's time. Bingham described *moelleri* from Sikkimese examples taken at light, and Stitz added a variety *striatifrons* based on females from Lombok and western Sumatra; the latter were compared only with Bingham's very sketchy description. Neither description mentions any features outside the usual variation of the sample of *castanea* in the Museum of Comparative Zoology.

Roger described *M. rufula* from Batjan, thinking even then that it was "perhaps only a local variety" of *M. maculata*, described from Ceylon; later (1863, Verzeichniss der Formiciden Arten und Gattungen, Berlin, p. 20) he synonymized *rufula* with Smith's *castanea*. Probably the *rufula* and *castanea* types came from the same series collected on Batjan. Emery (1911) considered *maculata* to be a subspecies of *castanea*, which is more in line with the present conception of geographical and individual nest variation within a single species. Since we know that the "diagnostic" characters of these forms vary discordantly among themselves, there seems little reason to recognize a Ceylonese or a more widespread variant under a formal name. The variety *bugnioni* Forel, described from Ceylon, was never satisfactorily separated from *maculata*, and is undoubtedly the same geographical variant.

There remains only *Myopopone beccarii* Emery, described from worker material from Ternate. According to the original description, *M. beccarii* is supposed to differ from *M. castanea* chiefly in having the mesonotum and petiole longitudinally rugulose and subopaque. In view of his qualifying remarks following the diagnosis, it seems that Emery may have meant "metanotum" instead of "mesonotum." A sample of workers from central Cape York Peninsula, Queensland, has faint striation or longitudinal rugulation between the coarse punctures of the propodeum (="metanotum") and petiolar dorsum, and the striation of the sides extends farther up onto the dorsum than in many other *castanea* samples. It seems that this may represent an approach to the condition Emery found in *beccarii*. In any case, *beccarii* comes from the middle of the range of *castanea*, and it seems unlikely that it is more than an extreme sculptural variant of the latter. Emery himself apparently lost some confidence in the distinctness of *beccarii*, because his Genera Insectorum entry (1911) rates *beccarii* as a mere subspecies of *castanea,* along with *moelleri* and *maculata.* Wilson (1958a) made no attempt to evaluate *beccarii,* and recognized it provisionally as a species only on the basis of the original description and grounds of virtual sympatry with *castanea.* Although I have not myself examined the types, I feel that the study of the variation in both eastern and western populations of *castanea* reveals sculptural extremes that are probably about as aberrant as described by Emery for *beccarii,* and I therefore consider that *beccarii* should be placed provisionally in the synonymy of *castanea.*

I have listed below the synonyms of *M. castanea* in chronological order. In those cases where the date is enclosed in parenthesis, Wilson (1958a: 144) has already given the full reference in indicating the synonymy, and the details will accordingly be omitted here. (T) before the entry indicates that either Wilson or myself has reviewed type material.

(T) *castanea* (Fr. Smith) (1860).
  maculata Roger, 1861:50, worker, female. Type loc.: Ceylon. N. syn.
  rufula Roger, 1861:52, worker. Type loc.: Batjan. Syn. Roger, 1863.
  beccarii Emery, 1887, Ann. Mus. Civ. Stor. Nat. Genova, (2)4:447, worker. Type loc.: Ternate. N. syn.
  moelleri Bingham, 1903:34, female. Type loc.: Sikkim, 7000 ft. N. syn.
  bugnioni Forel, 1913, Zool. Jahrb. Syst., 36:5, nota, worker, female, male. Type loc.: Peradeniya, Ceylon. N. syn.
(T) *bakeri* Viehmeyer, 1916, Ent. Mitt., 5:283, worker. Type loc.: Tacloban, Leyte, P. I. N. syn.
(T) *proxima* Stitz, 1925, Sitzb. Ges. naturf. Freunde, Berlin, 1923, p. 110, *nomen nudum;* descr. Wilson, 1958a:145. N. syn.
  striatifrons Stitz, 1925, Sitzb. Ges. naturf. Freunde, Berlin, 1923, p. 110, female. Type locs.: Lombok and w. Sumatra. N. syn.
(T) *picea* Donisthorpe (1938)
(T) *wollastoni* Donisthorpe (1942)
  smithi Donisthorpe (1946)
(T) *rossi* Donisthorpe (1947)
(T) *similis* Donisthorpe (1949)

[21] The species-level taxonomy of the Neotropical *Prionopelta* has been much confused. Mayr described the holotype female of *P. punctulata* as having 11 antennal segments. In his generic diagnosis of 1911, Emery noted that *Prionopelta* (so far as he personally was acquainted with the species) had 12 antennal segments in worker and female, and he felt that Mayr had been misled by an "anomaly." But material now available proves that southeastern Brazil and northern Argentina are inhabited by a species having 11 segments and corresponding reasonably well to Mayr's description of the type female and his later (1887) description to the worker. This species, which I consider to be *P. punctulata,* varies somewhat both inter- and intranidally in size, strength of sculpture, and intensity of the yellow pigment. Forel, utilizing differences he supposed to exist on the basis of a comparison of Mayr's two (female and worker) descriptions, gave the name *mayri* to the worker from Santa Catarina. The differences cited are in minor sculptural and pilosity features, and it seems best to accept Mayr's original opinion that his worker and female belong to the same species, rather than Forel's judgment based on the descriptions. Santschi described *P. bruchi* in 1923 from Alta Gracia, Córdoba, Argentina, apparently from the worker caste, although the description is headed by the symbol " ♀ " — probably a typographical error. Santschi's description is in the form of a comparison with "*mayri,*" although he does not state how he verified the determination of the *mayri* specimens used for the comparison. The differences mentioned are minor ones, subject for the most part to differences of viewing angle and interpretation, as well as to allometric variation. Santschi does not give a count of the antennal segmentation, the most important diagnostic character in this case. Samples taken since in Argentina by Kusnezov and others are all 11-segmented and appear to represent a single species, which I refer to *P. punctulata.* I myself have seen workers and males from Tucumán, Argentina (N. Kusnezov, P. Wygodzinsky leg.), and from Loreto, Misiones, Argentina (A. Ogloblin leg.). Kusnezov has determined the males from Tucumán as *bruchi.* It seems to me that there is no reason any longer to doubt the synonymy of *bruchi* with *punctulata.* Two workers from Agudos, S. Paulo, Brazil (W. W. Kempf leg.) belong to this species also.

Two other Neotropical *Prionopelta* species have already been eliminated from consideration: *P. mocsaryi* Forel, supposedly from Paraguay, appears to be a mislabeled sample of the Melanesian *P. opaca* Emery (Wilson, 1958a :149) ; *P. marthae*

Forel is a synonym of *Typhlomyrmex rogenhoferi* Mayr, according to Brown, 1953a.

All of the other forms of *Prionopelta* from the Americas have 12-segmented antennae in worker and female. They may be divided on the basis of cephalic sculpture into two groups. One kind corresponds to the first lug of couplet 2 in the short key below; this is the clearcut species *P. modesta,* with coarsely punctulate and opaque head. E. O. Wilson collected it at Las Hamacas, 17 km. north of Santiago Tuxtla, Veracruz, and at Pueblo Nuevo, near Tetzonapa, in the same state. At both localities, it was a common ant in the leaf litter of tropical evergreen forest; notes on the ecology and behavior of this species are given below. Other samples of *modesta* in the Museum of Comparative Zoology come from Finca El Real, Ocosingo Valley, Chiapas (C. and M. Goodnight and L. J. Stannard leg.), and from the vicinity of Guatemala City in orchid plants intercepted by U. S. Plant Quarantine at San Francisco. A series from Barro Colorado Island, Panama Canal Zone (J. Zetek leg.) is the only sample of *modesta* known from outside the Guatemala-southern Mexico area.

The remainder of the twelve-segmented forms, including types of the two nominal species *antillana* and *amabilis,* form a rather heterogeneous lot. The *antillana* type (St. Vincent, B. W. I.) in the Museum of Comparative Zoology has the anterior clypeal margin projecting somewhat forward and bluntly subangulate in the middle, and the cephalic sculpture is weak and subopaque, with sparsely punctulate, smooth and shining areas just mesad of the eyes. Specimens from Tumupasa, in the Amazon watershed of Bolivia (W. M. Mann leg.) agree well with the *antillana* type. Other series from Colombia, Costa Rica, Honduras, Guatemala, and even (one worker) Pueblo Nuevo, Veracruz, are very variable in cephalic sculpture, ranging from sparsely punctulate and shining to densely but very indistinctly punctulate and subopaque. In some of these specimens, the anterior clypeal margin can be seen, and is gently and evenly rounded; in other cases the anterior clypeal margin cannot be seen satisfactorily because the mandibles have not been opened. The relationship of *antillana* to *amabilis* remains obscure as far as I am concerned; much more material will be needed to decide the variation and limits of these two species.

The present distinctions among the American *Prionopelta* species are summarized in the following key to the workers and females:

Key to Neotropical species of Prionopelta based primarily on workers

1. Antennae 11-segmented (n. Argentina, se. Brazil) .... *punctulata* Mayr
Antennae 12-segmented .... 2.

2. Punctulation of head coarse, uniform over entire dorsum, deep and densely arranged, rendering the whole surface nearly or quite opaque (s. Mexico, common; C. America) .... ***modesta*** Forel
Punctulation of dorsum of head fine and shallow, often varying in distinctness and density from area to area; either spaced, with smooth, shining intervals, or combined in an indefinite, subopaque roughening of the surface (s. Mexico, C. America) .... ***amabilis*** Borgmeier
(Lesser Antilles, Bolivia, ?C. America) .... ***antillana*** Forel

[22] A colony of *P. modesta,* taken at Pueblo Nuevo, Veracruz, by E. O. Wilson, was studied for several weeks in a glass-topped plaster nest in the laboratory. The colony contained eggs, which hatched in the laboratory, but the dealate female apparently was not fertilized, and was not the colony queen. At the time of capture, other females were found in the colony with wings, as also in other colonies found at the same locality (August, 1953). The colonies often appear to be split into sections separated more or less from one another, and occupying small bits of rotting wood or bark in the leaf litter. Some of the fragments contain only workers, or workers and larvae, indicating that the colonies may be very loosely organized (like those of *Amblyopone*) and more or less nomadic.

Newly hatched larvae in the laboratory nest spent much time raising and moving about the anterior part of the body, possibly an activity functioning to attract workers with food. Several attempts were made to get the *Prionopelta* workers to accept various kinds of live and dead arthropods, but the workers are exceedingly timid foragers, and almost always recoiled violently when their antennae came into contact with the potential prey. Even such delicate animals as live *Tomocerus* (Collembola) and fresh-killed *Drosophila* adults were treated in this way by the ants. After repeated contacts within a very cramped foraging chamber, the ants finally killed a partly-grown geophilomorph centipede about 15 mm. in length — that is, much longer than the ants, which are about 2 mm. long. The ants grasped the centipede by a leg with a very rapid lunge of body and mandibular closure too quick to be observed in detail, and immediately doubled up and attempted to sting in the leg joints or body of the centipede. The centipede showed obvious agitation each time it was stung, and raced about, doubling and redoubling its body until the ant was finally dislodged. After being stung, the centipede showed impairment of locomotor activity of the segments behind the point where the ant had been attached, and ran rather crookedly, but after a few minutes showed partial recovery. Discontinuous observations covered several more individual attacks by different ants, and the following day, the ants were found to have removed the centipede, now motionless and apparently dead, to the brood chamber, where some larvae were now attached and feeding. Other later trials with small centipedes were made at a time when the colony was in its final stages of disintegration, and the ants simply fled upon the slightest movement of the centipedes.

The general impression gained from these observations was that *P. modesta* is capable of biting, hanging onto, and stinging into immobility even relatively large arthropods (such as a geophilomorph of the size indicated), but that such large prey animals would not normally be available in circumstances of confinement allowing the *Prionopelta* to attack them. Especially is this indicated when one considers that the usual result of physical contact between centipede and ant was the hasty retreat of both. Perhaps the usual prey will be found to include even smaller, juvenal centipedes or symphylans; search of the nests should be made to determine what *Prionopelta* feeds upon.

[23] The *Prionopelta* of the Old World occur in Madagascar, southeastern Africa and the Indo-Australian region. The Madagascan species (*descarpentriesi*) and the one from the mainland of Africa (*aethiopica*) are both known from single collections. They have not been compared directly with each other or with most other species of the genus, and the characters separating them as species are not clear from the descriptions. Since I have seen no material from these regions, I am merely placing the two names in the list as species without judging them further.

In the Indo-Australian region there are four nominal species, of which *brocha,* isolated on New Caledonia, is a very distinct relict (Fig. 15). The other three species are *majuscula* (New Guinea), *opaca* (New Guinea) and *kraepelini* (Java). *P. majuscula* and its synonymy have been discussed by Brown (1953b) and Wilson (1958a). So far as known, it is confined to northern New Guinea. It has moderately punctate, shining workers, yellowish in color and somewhat larger than *kraepelini* and *opaca* workers. Its females are distinctly larger than its own workers, and are a contrasting dark brown in color.

In *kraepelini* and *opaca,* the queens are scarcely larger than the workers and tend to have similar sculpture and color if from the same nest or locality. I have now seen a great deal of new material of these two forms, and the distinction between them is becoming blurred. Together, they turn out to have a vast range, from northern Queensland (at least) in the southeast to Java and the Philippines to the west and north. The typical *opaca* come chiefly from New Guinea and parts of Micronesia. They are usually brownish in color and have coarse, dense punctation over the body from head onto the first gastric segment at least. Workers and females of *kraepelini* usually have much less dense punctation, and the alitrunk and gaster are predominantly smooth and shining. I have seen samples more or less closely agreeing with *kraepelini* from several Micronesian localities; from Buitenzorg, Java (the *kraepelini* type locality) ; from Dumaguete, Negros, and Mt. Makiling, Luzon in the Philippines (J. W. Chapman Coll.) ; and from Mt. Bartle Frere, 1000-1600 m. (P. J. and P. F. Darlington leg.) and the Elliot Range, *ca.* 1000 m., near Townsville (Darlingtons leg.) in Queensland. Father J. J. McAreavey also sent me a couple of workers of this species which, he wrote me, came from the Grampians Range in western Victoria. I questioned this range at the time (which was before the Queensland records were available), but Father McAreavey has assured me (*in. litt.*) that the Grampians record is not based on a labelling error. Still, the Grampians record remains so astonishingly far beyond the other localities that only further collections there will remove all doubts about a possible mixup. The specimens are very similar to some in the Museum of Comparative Zoology from Dumaguete in the Philippines. Perhaps in favor of the Grampians record is the fact that the two Queensland collections both came from rather high levels on mountains.

In Micronesia, there are found forms intergradient between *opaca* and *kraepelini.* While I have not studied the Micronesian material at any length, I believe that probably most of the *kraepelini* specimens really are only smoother, light-colored variants of *opaca,* situated peripherally to New Guinea. It is interesting to note that the workers of *majuscula* have the smooth integument and light color approached by *kraepelini* outside New Guinea; many extra-New Guinea workers also appear to be more robust, in this tending toward *majuscula.* Apparently we have in *opaca* another case of centrifugal variation based on New Guinea, and involving character displacement against the parapatric species *majuscula.*

The relationship of *kraepelini* to *opaca* needs to be reviewed with more and better material than I now have before me. Also to be considered is the relationship of these species to the neotropical species; the *kraepelini* topotypes, although not well-preserved, are rather smooth and unusually pale, and do resemble *P. antillana.* It is not beyond possibility that this population may have reached Buitenzorg from the New World in plantings for the Botanical Gardens there. The Dumaguete samples were taken in an "Old Cemetery," and this and other circumstances suggest strongly that *Prionopelta* species like this one are often transferred accidentally by human commerce.

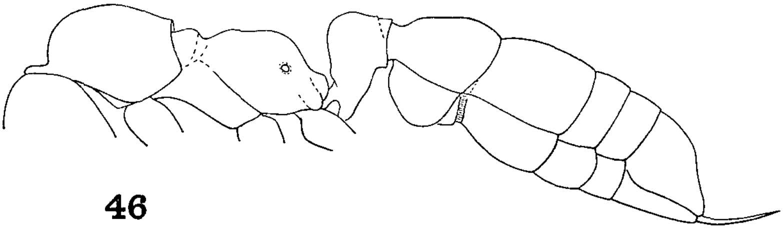
*Key to Indo-Australian species of Prionopelta, based primarily on workers**

1. Genal teeth well developed and acute (Fig. 15), more than 0.02 mm. long; size larger, head width of holotype worker 0.64 mm. (New Caledonia) *brocha* Wilson

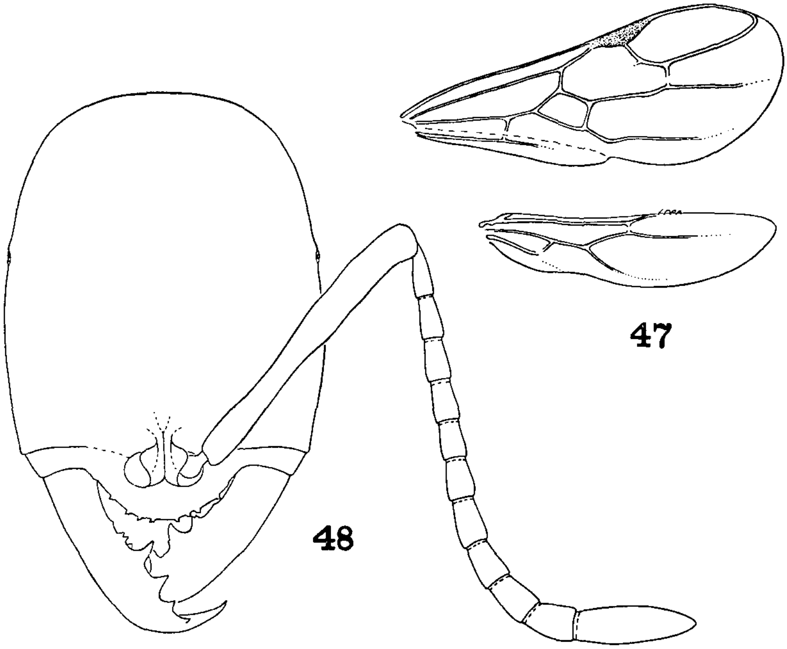
   Genal teeth minute to obsolete, never more than 0.01 mm. long; smaller spp., head width not exceeding 0.55 mm. in worker .... 2.

**Dorylozelus mjoebergi* Forel, from Queensland, may possibly be a *Prionopelta.* It is supposed to have only 11 antennal segments, which should separate it from the species in the key, all 12-segmented.

2. Size larger; head width > 0.47 mm. in worker; worker feebly sculptured, shining, yellowish in color; female distinctly larger than worker, dark brown (New Guinea) .... *majuscula* Emery
Size smaller; head width < 0.47 mm. in worker; color pale yellow to brown; female nearly same color and size as workers from same nest; sculpture variable, but always coarse on New Guinea (e. Australia, New Guinea, Micronesia, Java, Philippines)
opaca Emery and *kraepelini* Forel



46



47

48

Onychomyrmex. Figure 46. *O. hedleyi,* worker, outline of body from side view. Figure 47. Male wings, probably *O. mjoebergi,* specimen from the National Park, southeastern Queensland. Figure 48. *O. hedleyi* worker, full-face view of head.

[24] The known ranges of the three *Onychomyrmex* species have been increased in eastern Queensland in recent years, mainly through the activities of P. J. Darlington, Jr. (PJD) in 1932 and 1957-1958, and his son, P. F. Darlington (PFD) in 1957-1958. I (WLB) made a few collections in northern Queensland in 1950.

O. doddi: western slope of the Macalister Range, east of the Black Mountain Road running north from Kuranda, about 100 workers in a small rotten log in rain forest (WLB). This is only a few miles from Kuranda, the type locality.

O. mjoebergi: Mt. Spec Plateau, 2000-3000 feet altitude, about 40 miles north of Townsville (PFD). National Park, in McPherson Range, on the southern border of Queensland, 3000-4000 feet (PJD); workers and males were taken separately. The petiole of the workers from southern Queensland differs slightly from that of northern samples, but not enough to convince me that they are separate species.

O. hedleyi: Mt. Bellenden Ker, east side, 3000-4500 feet (PJD). Mt. Spec Plateau, 2000-3000 feet (PFD). Malanda, 2200 feet (WLB). Kuranda, 1100 feet (WLB). Mt. Spurgeon, 3500-4000 feet (PJD). Thornton Peak, near Daintree, 1000-4000 feet (PFD). Eungella Range, west of MacKay (PFD).

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the manuscript and added valuable biological observations, but this is not meant to imply their responsibility for any of the views expressed in this paper.

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INDEX

Included here are names of ant species, genera and higher categories mentioned in the body of this paper. Names cited in the Appendix and captions to figures are excluded where reference is made to them through bracketed numbers at the primary (species-list) reference. The pages of the primary references are given in boldface below. Abbreviations for generic names are as follows: A. = Amblyopone, Myop. = Myopopone, Myst. = Mystrium, O. = Onychomyrmex, P. = Prionopelta.

aberrans, A., 155, **167**
Aenictus, 152, 180
aethiopica, P., **177**
amabilis, P., **177**
Amblyopone, 145, 146, 148, 149, 150-153, **155-169**, 170-179 181, 188, 198, 218
Amblyoponini, **145-153**, 156, 181
amblyops, A., **167**
antillana, P., **177**
arizonensis, A., **169**
armigera, A., **167**, 192
Arotropus, **155**
australis, A., 150-152, 155, 159, 162-164, **167**, 170-173

bakeri, Myop., 213, **215**
barretoi, A., **168**
beccarii, Myop., 214, **215**
bellii, A., 165, **167**
bierigi, A., **167**, 192
binodosus, A., 155, **169**
brocha, P., 174, 176, **177**
bruchi, P., **178**
bruni, A., 165, **167**
bugnioni, Myop., 214, **215**

camillae, Myst., **170**
castanea, Myop., 149, 152, 170, 173, **213-215**
celata, A., 149, 155, **168**, 176
cephalotes, A., **167**
Cerapachyinae, 149
chilensis, A., **168**, 192
churchilli, P., **177**
clarki, A., 155, **168**

degenerata, A., 158, 161, 164, 165, **168**, 181, 191
denticulata, A., 155, **168**
descarpentriesi, P., **177**
doddi, O., 180, **181**
Dorylinae, 149, 178
Dorylozelus, 146, 154, 177, **181-182**
Dorylus, 182

Ectatommini, 145, 149, 153, 173
egregia, A., 156, 164, **168**
elongata, A., 164, **168**, 192
emeryi, A., **168**
Ericapelta, **156**
Examblyopone, **173**
exigua, A., **168**

fallax, Myst., **170**
feai, A., **168**
ferruginea, A., 164, **168**
fortis, A., **167**
foveolata, A., **167**
Fulakora, 152, **155**, 164, 174, 176, 188, 190, 197, 207, 209

gheorghieffi, A., **168**
gingivalis, A., 165, **168**
glauerti, A., 156, 166, **168**, 179
gracilicornis, A., **168**
gracilis, A., **168**

hackeri, A., **168**
hedleyi, O., 178, 180, **181**
howensis, A., **167**

impressifrons, A., 158, **168**

javana, Myst., **170**
juergi, A., **168**

kraepelini, P., 175, **177**

laevidens, A., **167**
leai, A., **168**
Leptogenys, 180
Lithomyrmex, **156**, 166, 179
longidens, A., **168**
lucida, A., **168**
luzonica, A., **168**

maculata, A., **167**
maculata, Myop., 170, 214, **215**
majuscula, P., 173, 175, 176, **177**
mandibularis, A., **168**
mayri, P., **178**
mercovichi, A., 165, **168**
michaelseni, A., **168**
minima, Paraprionopelta, 146, **181**
minor, A., **167**, **168**
minuta, A., **168**
mjoebergi, Dorylozelus, 146, **181-182**
mjoebergi, O., 149, 179, 180, **181**
mocsaryi, P., **178**
modesta, P., **178**
moelleri, Myop., 214, **215**
Monomorium (Notomyrmex), 166
monrosi, A., **168**, 192
montigena, A., **169**
mutica, A., 155, 156, 165, **168**
Myopopone, 145, 154, **170-173**, 213-215
Myrmecia, 149, 150
Myrmica, 148
mysticum, Myst., 169, **170**
mystriops, A., **169**, 191
Mystrium, 145, 148, 151, 153, 155, **169-170**, 188

nana, A., **167**
Neoamblyopone, **155**
nidifex, Strumigenys, **152**
norfolkensis, A., **167**
normandi, A., 164, **169**

oberthueri, Myst., **170**
obscura, A., **167**
Onychomyrmex, 145, 146, 148, 149, 150, 152, 155, 166, **178-181**
Onychomyrmicini, 145
opaca, P., 177, **178**
oregonensis, A., **169**, 192
orizabana, A., **169**, 192

pallens, A., **167**
pallipes, A., 148, 149, 150, 166, 167, **169**, 192
paranensis, A., **168**
Paraprionopelta, 146, 161, **181**
picea, Myop., **215**
Ponera, 182
Ponerinae, 146, 149, 178
Ponerini, 145, 182
poultoni, P., **177**
Prionopelta, 145, 148, 149, 151, 153, 154, **173-178**, 182
Protamblyopone, **155**
proxima, Myop., 213, **215**
punctulata, A., **169**
punctulata, P., 173, **178**

quadrata, A., **169**
queenslandica, A., **167**

reclinata, A., 158, 165, 166, 167, **169**
Renea, **173**
rogeri, Myst., 169, **170**
rossi, Myop., **215**
rothneyi, A., 165, **169**
rufula, Myop., 214, **215**

santschii, A., **169**
saundersi, A., 158, 165, **169**

serrata, A., **169**
silvestrii, A., 166, **169**
silvestrii, Myst., **170**
similis, Myop., **215**
simillima, P., **177**
smithi, A., **169**, 174
smithi, Myop., **215**
stadelmanni, Myst., **170**
Stigmatomma, 145, **155**, 164, 165, 197, 209
striatifrons, Myop., 214, **215**
subterranea, A., **169**
testacea, P., **177**
trigonignatha, A., **169**, 192

voeltzkowi, Myst., **170**

wheeleri, A., **169**
williamsi, A., **168**
wilsoni, A., **169**
wollastoni, Myop., **215**

Xymmer, **155**, 164, 165

zwaluwenburgi, A., **169**