

STUDIES ON THE ANT FAUNA OF MELANESIA

VI The Tribe Cerapachyini¹

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INTRODUCTION

The Cerapachyini have been noted chiefly for the fact that some, and perhaps all, of the member species are robber ants, i.e., they raid the nests of other ants for food². Melanesia contains a rich diversity of these myrmecophagous ants, with a total of four genera and 25 species known at the present time. In the following list the species have been provisionally divided into groups on the basis of characters in external morphology.

LIST OF THE MELANESIAN SPECIES OF CERAPACHYINI, ARRANGED INTO SPECIES GROUPS AND WITH NEW SYNONYMY

Genus *Cerapachys* Fr. SmithGroup of *C. dohertyi* Emery

<i>desposyne</i> Wilson	<i>lindrothi</i> Wilson
<i>dominula</i> Wilson	<i>majuscula</i> Mann
<i>flavaclavata</i> Donisthorpe	<i>polynikes</i> Wilson
<i>inconspicua</i> Emery	<i>sculpturata</i> Mann
= <i>terricola</i> Mann	<i>vitiensis</i> Mann
= <i>terricola</i> subsp. <i>tulagi</i> Mann	<i>zimmermani</i> Wilson

Group of *C. opaca* Emery

<i>opaca</i> Emery	<i>superata</i> Wilson
= <i>opaca</i> subsp. <i>longicornis</i> Viehmeyer	

Group of *C. papuana* Emery(Subgenus *Syscia* Roger)

<i>crypta</i> Mann	<i>pawa</i> Mann
<i>fuscior</i> Mann	<i>pusilla</i> (Emery)
<i>papuaua</i> (Emery)	

1 Previous parts of this series appeared in Mus. Comp. Zool., Bull. **118**: 101-153 (1958); **119**: 303-371 (1958); **120**: 483-510 (1959). Measurements used in the present part have been defined in full in the same journal, **116**: 357-358 (1957) and a gazetteer of the author's collecting localities in Melanesia is in **118**: 102-110.

2 Wilson, E. O. "Observations on the behavior of the cerapachyine ants", *Insectes Sociaux* **5**: 129-140 (1958).

Species of Uncertain Position

nitens DonisthorpeGenus **Phyracaces** Emery*cohici* Wilson*krombeini* Donisthorpe*dumbletoni* Wilson*marginata* (Emery)Genus **Sphinctomyrmex** Mayr*caledonicus* Wilson*cribratus* EmeryGenus **Lioponera** Mayr*versicolor* Donisthorpe

The 12 known species of *Cerapachys* (*Cerapachys*), comprising the chief segment of the cerapachyine fauna, have evidently been derived from stocks originating in southeastern Asia. They do not seem to contain much phyletic diversity; indeed, it is even possible that all have been derived from only two invading species. Two of the species (*opaca*, *superata*) form a group apparently peculiar to New Guinea. The other species belong to what can be termed the *dohertyi* group, which is also richly represented in southeastern Asia. In the following list are given all of the known Indo-Australian species of *Cerapachys* (*Cerapachys*), tentatively arranged into groups chiefly on the basis of body sculpturing, the character which is the most variable (and hence most useful taxonomically) in the genus.

LIST OF THE INDO-AUSTRALIAN SPECIES OF *Cerapachys* (*Cerapachys*),
ARRANGED INTO TENTATIVE SPECIES GROUPS

Group of *C. antennata* Fr. Smith

Probably closely allied to group of *sulcinodis*; body almost entirely smooth and shining.

antennata Fr. Smith (Borneo)**Group of *C. butteli* Forel**

Dorsum completely costate.

butteli Forel (Sumatra)**Group of *C. dohertyi* Emery**

Embracing a morphocline: foveate or grossly punctate to smooth and shining.

aitkeni Forel (India)*manni* Crawley (Sumatra)*bryanti* Wheeler (Borneo)*muii* Wheeler & Chapman (Philippines)*desposyne* Wilson (New Guinea)*polynikes* Wilson (New Guinea)*dohertyi* Emery (Borneo, Sumatra)*reticulata* Emery (Formosa)*dominula* Wilson (New Guinea)*rufithorax* Wheeler & Chapman (Philippines)*flavaclavata* Donisthorpe (New Guinea)*salimani* Karawajew (Java)*inconspicua* Emery (New Guinea, Solomons)*sculpturata* Mann (Fiji)*lindrothi* Wilson (Fiji)*vitiensis* Mann (Fiji)*majuscula* Mann (Fiji)*zimmermani* Wilson (Fiji)

Group of *C. opaca* Emery

Head rugo-reticulate. Dorsum of remainder of body showing morphocline: densely punctate-striate to smooth.

opaca Emery (New Guinea)

superata Wilson (New Guinea)

Group of *C. sulcinodis* Forel

Incompletely costate.

jacobsoni Forel (Java, Sumatra)

sulcinodis Forel (Burma)

risi Forel (Hongkong)

sumatrensis Crawley (Sumatra)

sauteri Forel (Formosa)

Species of Uncertain Position

conservata Viehmeyer (Celebes, in copal)

nitens Donisthorpe (New Guinea)

It will be noted that of the 27 species included in these provisional groupings (excluding *conservata* and *nitens*), 18 belong to the *dohertyi* group. In size, body form, sculpturing, and color, the Oriental representatives show greater interspecific variability than the Melanesian species. Several, e.g., *dohertyi*, *manni*, *rufithorax*, *salimani*, appear close to the presumptive "primitive" Melanesian species, *inconspicua*. (A redescription of *dohertyi* has been presented in the Appendix.) In the hypothetical phylogeny of the Melanesian species to follow, it will be postulated that one or more of these *inconspicua*-like populations served as the ultimate stem of all of the Melanesian representatives of the *dohertyi* group.

EVOLUTION OF THE CERAPACHYS DOHERTYI GROUP IN MELANESIA

The ten known Melanesian members of the *dohertyi* group show considerable interspecific variation on their own, but this variation can be resolved into several unilateral trends (morphoclines) along which the individual species can be arranged stepwise. Figure 1 shows a conventional phylogenetic tree linking the species on the basis of the morphoclines. Four phyletic lines are postulated: (1) pre-*inconspicua-dominula*, involving the morphoclines of decreasing size and loss of sculpturing; (2) *inconspicua-desposyne*, involving the morphocline of reduction of dorsal pedicel sculpturing from oreate-punctate to finely and densely punctate; (3) *inconspicua-polynikes*, involving the morphocline of the spread of dense sternopetiolear pubescence to cover the sides of the petiolear tergite; (4) *inconspicua-zimmermani*, involving the morphoclines of increasing size and general loss of sculpturing. All of the morphoclines concerned in the known diagnostic characters separating the Melanesian *dohertyi* group species converge on *inconspicua*, thus indicating it as the species closest to the ancestral stock.³ *Inconspicua* is also the most widespread member of the genus in Melanesia; in fact, *sculpturata* of Fiji is little more than a local (but clearly distinct) variant of this species. Finally, *inconspicua* appears closest to the majority of the Oriental members of the *dohertyi* group.

3. For a theoretical discussion of this type of evolutionary analysis, see the excellent article by T. P. Maslin, "Morphological criteria of phyletic relationships", *Syst. Zool.* **1**: 49-70 (1952).

These considerations, if valid, lead to a curious conclusion. The species *inconspicua* appears to be the most primitive Melanesian member of the *dohertyi* group, yet on purely zoogeographic evidence it appears to have achieved its present wide distribution in Melanesia only relatively recently. Judging from dispersal and speciation patterns preponderant in the better known genera of Ponerinae (Wilson, 1959, *Evolution* 13: 122-144), *inconspicua* is a "Stage-II" species that has just passed through an initial period of expansion throughout most of Melanesia (Stage I). The endemic Fijian species *sculpturata* almost certainly represents the outermost population established by this emigratory wave. Whether *inconspicua-sculpturata* entered Melanesia from southeastern Asia (Stage I, primary) or spread outward secondarily from a headquarters on New Guinea (Stage II, secondary) is uncertain, but its affinity with some of the modern Oriental species seems to indicate that it could have been a relatively recent invader into New Guinea.

In either case, the evident fact that *inconspicua sculpturata* has only relatively recently arrived on Fiji, where its apparent descendent species exist as old endemics, is curious indeed. But the paradox might be easily removed if speciation in the *dohertyi* group is conceived as the outcome of several successive waves of *inconspicua*-like forms into New

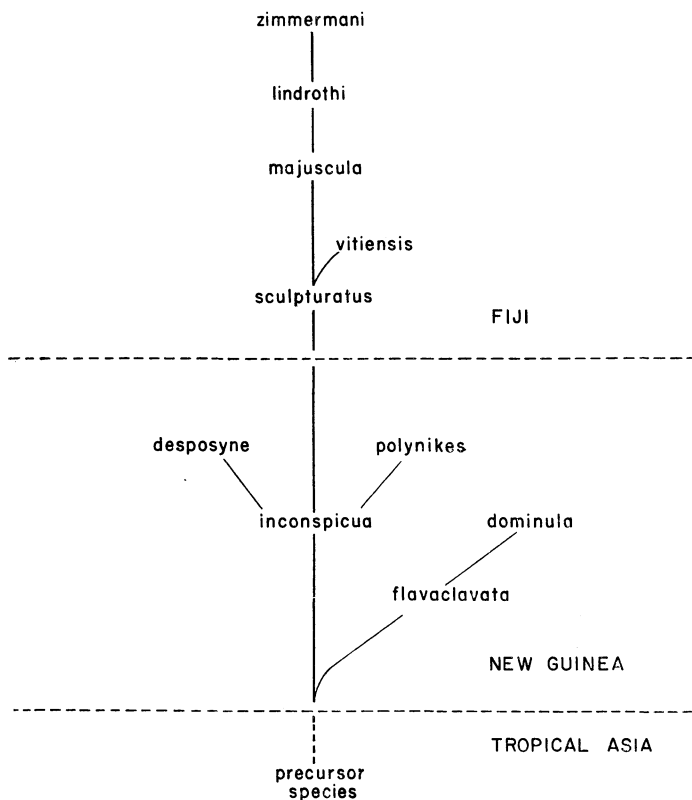


Fig. 1. Conventional phylogenetic diagram showing the hypothesized relationships of the Melanesian members of the *Cerapachys dohertyi* group.

Guinea, with some of the waves extending on as far as Fiji. The simplest possible hypothesis to account for the phylogeny and dispersal of the *dohertyi* group, as represented in figure 1, would seem to be as follows. No more than three invasions need be postulated (see fig. 2). It is hypothesized that the "*flavaclavata* subgroup" (*flavaclavata*, *dominula*) was derived from an early invading population of a *dohertyi* group species from southeastern Asia into New Guinea. The divergence of this subgroup was perhaps hastened after a time by interaction with a second invading population, which was destined to become *desposyne*

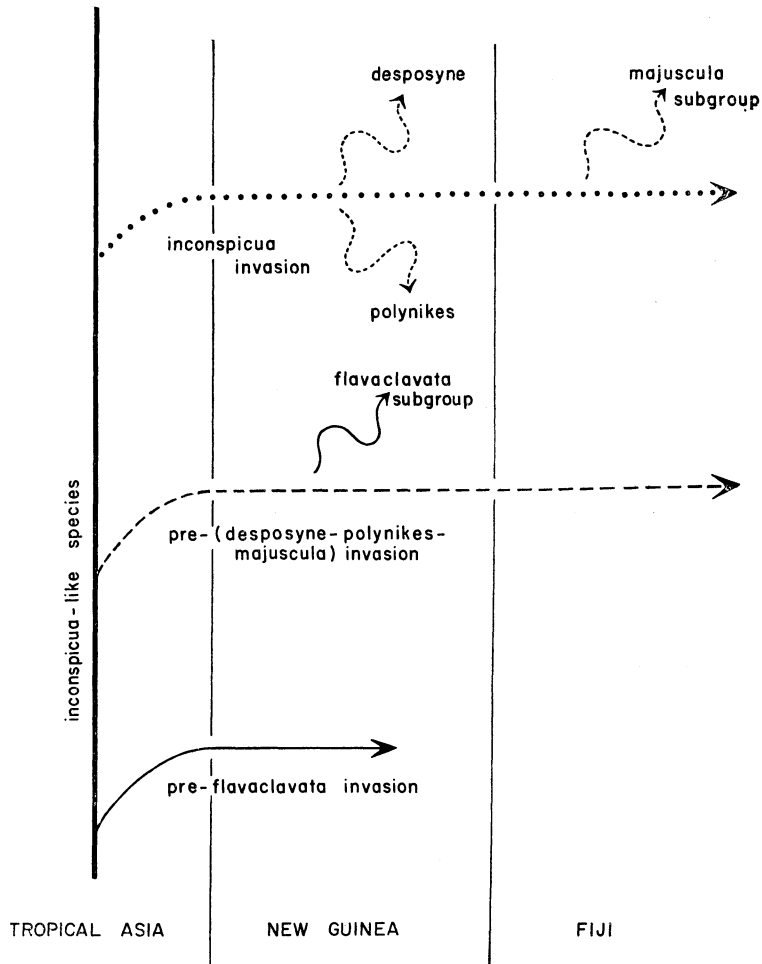


Fig. 2. Diagram schematizing in extreme form the hypothesis of multiple invasion and displacement advanced to explain the phylogeny of the Melanesian members of the *dohertyi* group. The straight arrows, solid and broken, represent the successive waves of invasion into Melanesia from persistent Oriental stocks. The wavy arrows represent the evolutionary displacement of resident Melanesian species by more recently invading populations. It is suggested that displacement was a principal factor in divergence, but not the only one operating. Further explanation in text.

and *polynikes* on New Guinea and the *majuscula* subgroup (*majuscula*, *lindrothi*, *zimmermani*) on Fiji. These last three elements are assumed to have evolved to their present state at least in part through interaction with the third and final invasion wave, which has given rise to the modern *inconspicua* subgroup (*inconspicua*, *sculpturata*, *vitiensis*). In addition, there exists evidence, from the pattern of geographic variation in *inconspicua*, that displacement has occurred between *inconspicua* and the *flavaclavata* subgroup. This will be treated in more detail in a later part of the paper. If we may deduce this much from the general pattern exhibited by other Ponerinae, each invading population has reached its maximum range in Melanesia during the early period of its residency there. The first two waves have since "broken", i. e., the populations have been fragmented and displaced at least in part through the agency of interaction of populations invading in later times.

ORIGIN OF OTHER CERAPACHYINE SPECIES IN MELANESIA

The *opaca* group of *Cerapachys* appears to be peculiar to New Guinea. It probably originated ultimately from an Oriental source fauna, since no member of the subgenus *Cerapachys* is known from Australia. A different consideration holds for the members of the *papuana* group, comprising the subgenus *Syscia*. The western Melanesian species are closely related to *australis* of eastern Australia, although there is no way of determining which is the source and which the derivative species. *C. crypta* and *C. fuscior* are giant versions of *australis-papuana* that are precinctive to Fiji.

Sphinctomyrmex papuanus is evidently close to *steinheili* of eastern Australia and *caledonicus* of New Caledonia. Since *steinheili* is a wide spread, abundant species of a genus well developed in Australia, it seems reasonable to guess that *papuanus* and *caledonicus* were derived from it by independent invasions of New Guinea and New Caledonia. The same consideration holds with respect to *Phyracaces marginata* of New Guinea and *P. cohici* and *P. dumbletoni* of New Caledonia. These three species are allied to the *adamus* group of Queensland. The relationships of *P. krombeini* of New Guinea have not been determined, but judging from the description alone it appears likely to be closest to one of the many large, bicolorous species of Australia.

SYSTEMATICS

The types of the new species described herein are deposited at the Museum of Comparative Zoology (MCZ), U. S. National Museum, Washington, D. C. (USNM), California Academy of Sciences, San Francisco (CAS) and B. P. Bishop Museum, Honolulu (BISHOP).

Genus *Cerapachys* Fr. Smith

KEY TO SPECIES OF CERAPACHYS OF WESTERN MELANESIA

Worker Caste

- | | |
|--|---|
| 1. Antenna 9-segmented (subg. <i>Syscia</i>)..... | 2 |
| Antenna 12-segmented (subg. <i>Cerapachys</i>)..... | 4 |

- 2 (1). Postpetiole slightly broader than long (New Guinea)..... 8. **papuana**
 Postpetiole slightly longer than broad..... 3
- 3 (2). Head coarsely and irregularly rugose and punctate (Solomon Is.)..... 9. **pawa**
 Head bearing punctures only, and these are regularly distributed..... 10. **pusilla**
- 4 (1). Dorsa of alitrunk and gastric tergite 1 entirely covered by dense, fine, longitudinal striae; robust, medium-sized species (pronotal width about 0.6 mm)...
 5. **opaca**
 Dorsa of alitrunk and gastric tergite 1 lacking striae..... 5
- 5 (4). Dorsa of postpetiole and gaster densely and finely punctate and subopaque, their pilosity at least as dense as that of appendages and predominantly appressed-subappressed1. **desposyne**
 Dorsa of postpetiole and gaster at most bearing scattered foveolae or punctures, their surfaces shining; pilosity of these sclerites notably less dense than that of appendages and predominantly erect-suberect..... 6
- 6 (5). Head roughly sculptured, rugose-reticulate to contiguously foveate; larger species, with head width (across and including eyes) 0.90 mm or more..... 7. **superata**
 Head relatively smooth, at most bearing scattered foveolae or punctures; smaller species, with head width (across and including eyes) not exceeding 0.77 mm 7
- 7 (6). Sides of petiolar tergite shagreened and opaque to subopaque, and densely clothed with relatively short, appressed-subappressed, greyish hairs; thus contrasting with sides of postpetiolar tergite, which are smooth and shining and bear predominantly standing pilosity no denser than that on sides of adjacent gastric tergite 1.....6. **polynikes**
 Sides of petiolar and postpetiolar tergites with sculpturing and pilosity variable among 3 remaining species, but in none do surfaces of 2 adjacent tergites contrast with each other as described above..... 8
- 8 (7). Larger species, with head width (across and including eyes) never less than 0.61 mm; color intranidally variable, ranging from yellowish red to dark reddish brown commonly in small nest series; cephalic sculpturing varying internidally from sparsely punctate to densely foveolate.....4. **inconspicua**
 Smaller species, with head width (across and including eyes) never exceeding 0.59 mm; color blackish brown to medium reddish brown; head sparsely punctate and mostly smooth and shining..... 9
- 9 (8). Head width of unique type specimen only 0.36 mm; body concolorous medium reddish brown2. **dominula**
 Head width of extensive study series 0.46-0.54 mm; body concolorous piceous brown3. **flavaclavata**

1. *Cerapachys* (*C.*) *desposyne* Wilson, n. sp.

Worker: Resembling *inconspicua* Emery and *polynikes* Wilson of New Guinea in general form but differing from these and all other known Melanesian species in having exposed surfaces of petiole, postpetiole, and gaster densely punctate and opaque. Also resembling

dohertyi Emery of southeastern Asia but differing in lacking foveae on dorsal surface of body posterior to head and in having much denser puncturation over most of body.

Holotype worker: HW 0.80 mm, HL 0.94 mm, SL 0.59 mm, CI 85, SI 74, EL 0.26 mm, PW 0.60 mm, width of petiole 0.55 mm, maximum length of petiole 0.52 mm (this measurement was made from the level of the anteriormost part of the anterior border to the level of the posteriormost part of the posterior border), width of postpetiole 0.67 mm, maximum length of postpetiole 0.59 mm, width of first gastric tergite 0.85 mm.

Dorsal surface of head covered by contiguous foveolae approximately 0.06 mm in diameter; foveolar spaces and interspaces in addition densely shagreened. Laterad, beyond level of inner margin of eye, foveolae diminish in size to become punctures only 0.03 mm in diameter or less; these are mostly separated by spaces greater than their diameters. Gula bearing only few, fine, widely scattered punctures. Entire dorsum of thorax, and entire exposed surfaces of propodeum, pedicel, and gaster, densely, irregularly punctate and subopaque. Sides of thorax bearing only few scattered punctures, its surface mostly strongly shining.

Entire body and appendages covered by moderately long (0.06–0.20 mm), oblique (forming an angle of approximately 45° with sclerital surface), pale yellowish pilosity. In addition, most of body covered by shorter, appressed, pale yellowish pubescence, densest on dorsa of alitrunk, pedicel, and gaster, but only feebly developed on gula and sides of head and thorax.

Body uniformly deep piceous brown; appendages mostly a lighter shade of dark reddish brown.

Paratype worker, HW 0.80 mm. In size and other external features this specimen appears nearly identical to holotype.

Holotype, worker, (MCZ), Bisianumu, 500 m, near Sogeri, Papua, holotype nest series, Wilson, acc. no. 658. Paratype, worker, same data.

DISTRIBUTION: New Guinea.

The two type workers were found foraging close together during the day on the floor of disturbed foothills rain forest.

2. *Cerapachys* (C.) *dominula* Wilson, n. sp.

Worker: Most closely resembling *C. flavaclavata* Donisthorpe but easily distinguished from this and all other known Melanesian species by its exceptionally small size and elongate body form. It differs further from *flavaclavata* in its distinctly lighter body coloration (concolorous medium reddish brown as opposed to concolorous piceous brown in *flavaclavata*).

Holotype worker: HW 0.36 mm, HL 0.49 mm, SL 0.20 mm, CI 76, SI 56, EL 0.09 mm, PW 0.26 mm, width of petiole 0.21 mm, maximum length of petiole 0.26 mm, width of postpetiole 0.29 mm, maximum length of postpetiole 0.25 mm, width of first gastric tergite 0.35 mm.

Sides of propodeum and petiolar node weakly shagreened and feebly shining. Entire remainder of body bearing only scattered, fine punctures, surface almost entirely moderately to strongly shining.

Pilosity as in *flavaclavata*: entire body covered with abundant, medium length (0.01–0.06 mm), predominantly suberect, pale yellowish hairs; pilosity of appendages similar but sparser and predominantly oblique. In addition, sparse, appressed, pale yellowish pubescence covers most of petiole and entire postpetiolar and gastric sterna.

Body concolorous medium reddish brown, appendages a lighter shade of light reddish brown.

Holotype, worker (CAS), Maffin Bay, Neth. New Guinea, 1 July 1944, E. S. Ross.

DISTRIBUTION: New Guinea.

3. *Cerapachys* (C.) *flavaclavata* Donisthorpe

Cerapachys (*Cerapachys*) *flavaclavata* Donisthorpe, 1938, Ann. Mag. Nat. Hist. ser. 11, 2: 499 (worker; type locality: Sabron, 400 m, Cyclops Mts., Neth. New Guinea).—Wilson, 1958, Insectes Sociaux 5: 129 (behavior).

DISTRIBUTION: New Guinea.

NETH. NEW GUINEA: Sabron (syntype examined, MCZ). NE NEW GUINEA: lower Busu River, Wilson, nos. 939, 985.

Both of my collections of this distinctive little species were made from the floor of primary lowland rain forest. The raid of a colony (no. 985) against a colony of *Pheidole* sp. has been reported (Wilson, 1958).

4. *Cerapachys* (C.) *inconspicua* Emery

Cerapachys inconspicua Emery, 1902, Termész. Füzet. 25: 153 (worker; type locality: Sattelberg, NE New Guinea).

Cerapachys terricola Mann, 1919, Mus. Comp. Zool., Bull. 63: 277 [worker, male; type locality: Malapaina, Three Sisters Group, Solomons (by present restriction)]. **New Synonymy.**

Cerapachys terricola subsp. *tulagi* Mann, 1919, *op. cit.*, p. 279 (worker, male; type locality: Tulagi, Florida I., Solomons). **New Synonymy.**

DISTRIBUTION: New Guinea, Solomon Is.

NETH. NEW GUINEA: Maffin Bay, E. S. Ross. NE NEW GUINEA: Sattelberg (syntype examined, Emery coll.); lower Busu River, Wilson, no. 930. SOLOMON IS.: Malapaina (*terricola* syntypes examined, MCZ); Tulagi, Florida I. (*tulagi* syntypes examined, MCZ).

This widespread species seems to be most closely related to *muiri* Wheeler and Chapman of the Philippines, *flavaclavata* Donisthorpe of New Guinea, and *vitiensis* Mann of Fiji. In describing *terricola* and *tulagi*, Mann used as an example of "*inconspicua*" a single worker from Fulakora, Santa Isabel. His comparative diagnosis seems to suggest that the latter specimen, which I have not seen, may belong to an undescribed species differing from the true *inconspicua* by characters in mandibular sculpturing and antennal form.

C. inconspicua shows marked internidal variation in the limited samples thus far examined. This variation is "bipolar" in nature, i.e. ranges between two extreme forms that encompass all of the extreme characters and includes a gradient of intermediate forms. In the sections below the principal variable characters are described briefly with reference to individual nest series.

Maffin Bay, Neth. New Guinea. HW 0.49–0.50 mm. Thoracic dorsum bearing scattered, well developed foveolae; sides of propodeum covered with irregular sculpturing dense enough to scatter reflected light; dorsa of petiole and postpetiole covered by foveolae separated from one another by spaces approximately equal in width to foveolar diameters

sides of petiole and postpetiole irregularly and coarsely sculptured; gastric tergite 1 with scattered but well formed and evenly distributed punctures, prominent enough to scatter reflected light.

Busu River, NE New Guinea. HW 0.57–0.64 mm. Sculpturing as in Maffin Bay workers.

Sattelberg, NE New Guinea. HW not measured: estimated to be within range of Busu River series. Sculpturing similar to that of Maffin Bay workers except that thoracic dorsum completely lacks foveolae.

Malapaina, Solomon Is. HW 0.51–0.58 mm. Foveolae present on thoracic dorsum but much sparser than in Maffin Bay workers; foveolae of petiole and postpetiole separated by spaces roughly twice as wide as foveolar diameters; punctures of gastric tergite 1 distinctly sparser than in Maffin Bay workers; sculpturing otherwise similar to that described for Maffin Bay workers.

Tulagi, Solomon Is. HW 0.57–0.62 mm. Foveolae lacking on thoracic dorsum; sculpturing of sides of propodeum notably weaker than in other material examined; dorsa of petiole and postpetiole almost completely smooth and shining; sculpturing of gastric tergite 1 as in *Malapaina* workers.

It is noteworthy that in the diagnostic feature of sculpturing the Solomons material of *inconspicua* converges toward the related New Guinea species *flavaclavata*. On New Guinea, where *inconspicua* and *flavaclavata* occur in intimate sympatry, the two species are much more distinct. Thus the pattern of geographic variation of *inconspicua* falls into the special category of "character displacement" (see W. L. Brown and E. O. Wilson, 1956, *Syst. Zool.* 5: 49–64).

Striking intranidal color variation occurs in series no. 930. The workers range from reddish yellow (callows?) to dark reddish brown. A large minority of the workers belonged to the former extreme.

Accession no. 930 (Busu River) was made on May 4, 1955, from a colony of 100–200 workers and an undetermined number of males found nesting under the bark of the lower surface of a "zorapteran-stage" log. The log was partly buried in leaf litter on the floor of undisturbed lowland rain forest.

5. *Cerapachys* (C.) *opaca* Emery Fig. 3, A.

Cerapachys opaca Emery, 1902, Termész. Fü. 25: 153 (worker; type locality: Sattelberg, NE New Guinea).

Cerapachys (C.) *opacus* subsp. *longicornis* Viehmeyer, 1914, Arch. Naturg. 79 A (12): 27 (worker; type locality: Wareo, NE New Guinea). **New Synonymy.**

DISTRIBUTION: New Guinea.

NE NEW GUINEA: Sattelberg (holotype examined, Emery coll.); lower Busu River, Wilson, no. 921; Didiman Creek, Lae, Wilson, no. 694; Gemeheng, 1300 m, Wilson, no. 772.

This species is easily distinguished by its distinctive sculpturing. The alitruncal dorsum and first gastric tergite are almost entirely covered by dense, fine, longitudinal striae. The head and pedicel are covered by a coarse rugoreticulum, with dense fine punctures (or "shagreening") occupying the interspaces. Most of the lateral surfaces of the alitrunk are relatively smooth and shining.

The characters cited by Viehmeyer to distinguish his subsp. *longicornis* appear to be trivial in nature: "Etwas grösser (4.5 mm) und dunkler. Kopf hinter der Augen stärker

und gerader verengt. Hinterecken schärfer. Fühler länger; der Scapus überragt den Hinterrand der Augen beträchtlich; keins der Geißelglieder kürzer als breit . . . Die Skulptur sehr ähnlich, aber die Grubenpunkte mehr ausgebildet; auf dem Kopf sehr stark und dicht, fast netzmaschig, auf dem Thorax nur seicht und weitläufig. . .”

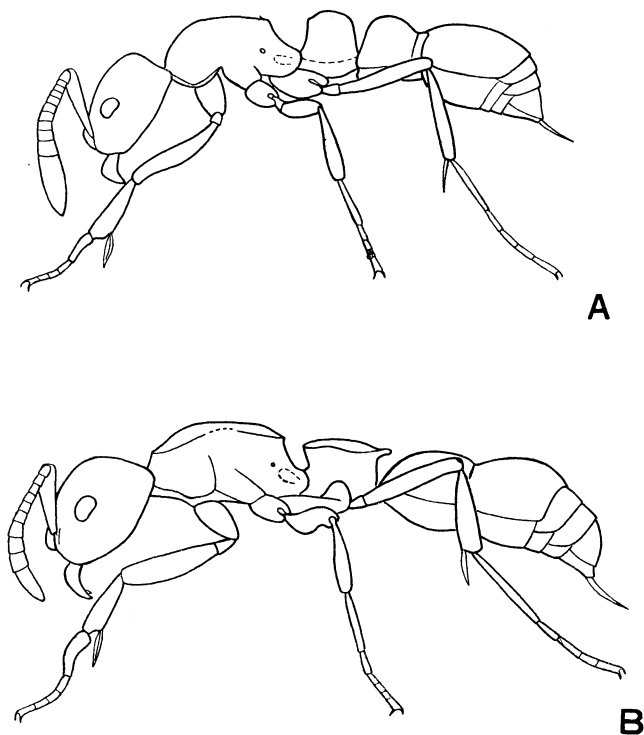


Fig. 3. The worker caste of two Melanesian cerapachyine species. A, *Cerapachys opaca* Emery, Gemeheng, NE. New Guinea. B, *Phyracaces cohici* Wilson, Ciu, New Caledonia.

At Gemeheng, workers were found crossing a native trail in file during the afternoon. A single ergatogyne was running in the file, and it seemed clear that the colony was in the process of emigration. Some of the workers were carrying what appeared to be their own larvae, slung beneath their bodies in a fashion often described as characterizing the Dorylinae. The determination of the larvae has been kindly checked for the author by Prof. G. C. Wheeler, who states, "We find no reason for doubting that the larvae . . . are *Cerapachys opaca*. They are definitely in the subfamily Cerapachyinae. They show as much affinity with *Eusphinctus* as with the *Cerapachys* in our collection, but that signifies nothing, for our *Cerapachys* material is inadequate." It is noteworthy that the larvae are all of approximately the same growth stage. The association of a synchronous larval brood and frequent emigration is well known in the Dorylinae. There is an excellent chance that a similar social control mechanism will eventually be demonstrated in some of the Cerapachyinae.

6. *Cerapachys* (C.) *polynikes* Wilson, n. sp.

Worker: Resembling *inconspicua* Emery, especially in size and body form, but differing from this and all other known Papuan species by the following distinctive combination of characters: sides of petiolar tergite densely clothed with short greyish hairs, which contrast sharply with longer, sparser yellowish hairs that cover the sides of postpetiolar tergite; sides of petiolar tergite densely shagreened and opaque, contrasting sharply with smooth and shining sides of postpetiolar tergite.

Holotype worker: HW 0.66 mm, HL 0.79 mm, SL 0.48 mm, CI 84, SI 73, EL 0.18 mm, PW 0.49 mm, width of petiole 0.42 mm, maximum length of petiole (viewed from directly above) 0.41 mm, width of postpetiole 0.50 mm, width of first gastric tergite 0.67 mm.

Sculpturing of head, alitrunk, postpetiole, and gaster consisting only of a few scattered piligerous punctures; remainder of surface of these tagmata almost completely smooth and shining, except for portions of mesopleuron and some segmental margins, which are shagreened. Petiole densely and finely punctate, sides opaque, dorsum subopaque to feebly shining.

Entire body and appendages clothed with abundant, long (0.06–0.32 mm), suberect yellowish hairs. Entire postpetiole and postpetiolar and gastric sterna in addition densely clothed with shorter, appressed, greyish hairs.

Body uniformly rich dark reddish brown in color, appendages medium reddish brown.

Paratype variation: HW 0.52–0.64 mm. Six of seven paratypes have HW ranging 0.63–0.64 mm, these individuals nearly identical to holotype in body form, sculpturing, and pilosity. Single nanitic worker in series has a HW of only 0.52 mm and further departs from remainder of type series in several characters commonly subject to allometric variation, viz.: body form more slender; CI only 77; sides of head more flattened; alitruncal dorsum more flattened; puncturation and pilosity overall sparser.

Holotype, worker (MCZ), Lower Busu River, near Lae, NE New Guinea, 4 May 1955, holotype nest series, Wilson acc. no. 936. Parantidotypes, 7 workers, same data.

DISTRIBUTION: New Guinea.

The type colony was found under the bark of a "zorapteran stage" log on the floor of primary rain forest. The colony was small, containing less than twenty workers. It may have been incipient, a condition that is further indicated by the presence of the nanitic worker described above.

7. *Cerapachys* (C.) *superata* Wilson, n. sp.

Worker: Closely resembling *opaca* Emery, with which it is intimately sympatric in NE New Guinea, but differing from that species markedly by its overall lighter body sculpturing. In particular, *superata* completely lacks striae on dorsum of thorax and gastric tergite 1, with the result that these surfaces are mostly smooth and shining in reflected light. *Superata* also differs from *opaca* in shape of gastric tergite 1, which is somewhat more slender and less flattened dorsally.

Holotype worker: HW 0.91 mm, HL 1.05 mm, SL 0.74 mm, CI 87, SI 81, EL 0.26 mm, PW 0.64 mm, width of petiole 0.60 mm, maximum length of petiole 0.56 mm, width of postpetiole 0.71 mm, width of first gastric tergite 0.92 mm.

Entire dorsal surface of head, from level of antennal insertion to occipital border, covered by a coarse rugoreticulum, interspaces of which densely and finely punctate-shagreened. In limited area approximately 0.12 mm across, just laterad to posterior limit

of frontal carina, reticulum obsolete and interspace sculpturing relatively feeble. On sides of head, laterad to level of eye, reticulum progressively reduced to a system of scattered piligerous foveae, which become further reduced on gula to small piligerous punctures. Pronotal dorsum covered by moderately abundant piligerous foveae; posterior face of propodeum very feebly shagreened and feebly shining; remainder of alitrunk bearing scattered piligerous punctures, its surface mostly smooth and moderately shining. Petiolar dorsum rugose-reticulate, with finely punctate reticular interspaces; reticulum grading into piligerous foveolae on sides. Postpetiole and gaster bearing scattered piligerous punctures, which are distinctly more abundant on postpetiole; most of surface of these tagmata smooth and moderately shining.

Entire body uniformly covered with long (mostly 0.06–0.30 mm), coarse, suberect, yellowish brown hairs. Appendages covered with somewhat sparser, predominantly oblique, but otherwise similar, pilosity. Petiolar and postpetiolar sternites, and anterior and posterior faces of petiole covered in addition by an appressed, greyish pubescence.

Body uniformly piceous brown. Appendages a lighter shade of dark reddish brown.

Paratype, worker: HW 0.85 mm. In external morphology this specimen nearly identical to holotype.

Holotype, worker (MCZ), Lower Busu River, near Lae, NE New Guinea, 28 April 1955, Wilson acc. no. 884. Paratype, worker, same locality, 3 May 1955, acc. no. 914.

DISTRIBUTION: New Guinea.

The two type workers were collected as strays from the floor of primary lowland rain forest.

8. *Cerapachys (Syscia) papuana* (Emery)

Ooceraea papuana Emery, 1897, Termész. Füz. **20**: 594, pl. 15, figs. 42, 43 [worker; original localities: Mt. Hansemann and Berlinhafen (Aitape), NE New Guinea].

DISTRIBUTION: New Guinea.

The supposed distinction between *papuana* and the closely related *pusilla* (Emery) (New Guinea) and *pawa* Mann (Solomons) cited in the key are derived from the original descriptions and may prove invalid when more material is available. The diagnostic characters involving petiolar proportions and extent of cephalic sculpturing may be simply expressions of intraspecific allometric variation.

9. *Cerapachys (Syscia) pawa* Mann, NEW STATUS

Cerapachys (Syscia) pusilla subsp. *pawa* Mann, 1919, Mus. Comp. Zool., Bull. **63**: 277 (worker; type locality: Ugi I., Solomons).
(See under *papuana*).

10. *Cerapachys (Syscia) pusilla* (Emery)

Ooceraea pusilla Emery, 1897, Termész. Füz. **20**: 595 (worker; type locality: Mt. Hansemann, NE New Guinea).
(See under *papuana*).

Species Inquirenda

11. *Cerapachys* (C.) *nitens* Donisthorpe, 1949, Ann. Mag. Nat. Hist. ser. 12, 1: 487 (male; type locality: Maffin Bay, Neth. New Guinea).

KEY TO SPECIES OF CERAPACHYS OF THE FIJI ISLANDS

Worker Caste

1. Antenna 9-segmented (subg. *Syscia*)..... 2
 Antenna 12-segmented (subg. *Cerapachys*)..... 3
- 2 (1). Foveolae of central portion of postpetiolar dorsum 0.02–0.03 mm in diameter; color pale reddish brown (Viti Levu).....17. **crypta**
 Foveolae of central portion of postpetiolar dorsum 0.04–0.05 mm in diameter; color dark reddish brown (Taveuni)..... 18. **fuscior**
- 3 (1). Dorsum of postpetiole covered by foveolae that are approximately 0.03 mm in diameter and separated from each other by spaces of approximately same magnitude; smaller species, with HW less than 0.67 mm..... 4
 Dorsum of postpetiole smooth and shining, at most with scattered fine punctures; larger species, with HW ordinarily greater than 0.70 mm and less than this only in occasional nanitics..... 5
- 4 (3). Entire thoracic dorsum covered with abundant foveae approximately 0.03 mm in diameter.....14. **sculpturata**
 Most of central portion of thoracic dorsum smooth and shining.....15. **vitiensis**
- 5 (3). Lateral surface of petiole covered by contiguous foveolae approximately 0.06 mm in diameter; petiole (including peduncles) distinctly broader than long.....
13. **majuscula**
 Lateral surface of petiole bearing only scattered fine punctures, most of its area smooth and shining; petiole (including peduncles) distinctly longer than broad 6
- 6 (5). Sterna of petiole and postpetiole completely covered by subcontiguous foveolae approximately 0.06 mm in diameter.....12. **lindrothi**
 Sterna of petiole and postpetiole lacking foveolae, their surfaces almost completely smooth and shining..... 16. **zimmermani**

12. *Cerapachys* (C.) *lindrothi* Wilson, n. sp.

Worker: Along with *zimmermani* Wilson, *lindrothi* differs from closely related Fijian “stem” species *majuscula* Emery by following distinctive characters: (1) lateral surfaces of head, propodeum, and petiole sparsely and finely punctate, as opposed to densely foveolate in *majuscula*: (2) petiole, seen from directly above, distinctly longer than broad in *lindrothi* and *zimmermani* but about equally as broad as long in *majuscula*. *Lindrothi* differs from *zimmermani* in its densely foveolate petiolar and postpetiolar sterna; these surfaces almost completely smooth and shining in latter species. *Lindrothi* differs from the other two known Fijian *Cerapachys*, *sculpturata* Mann and *vitiensis* Mann, as well as from the putative “stem”

species of New Guinea, *inconspicua* Emery, by its larger size and overall lighter sculpturing.

Holotype worker: HW 0.74 mm, HL 0.96 mm, SL 0.62 mm, CI 77, SI 84, EL 0.20 mm, PW 0.59 mm, width of petiole 0.46 mm, maximum length of petiole 0.52 mm, width of postpetiole 0.62 mm, maximum length of postpetiole 0.54 mm, width of first gastric tergite 0.88 mm.

Ventral surfaces of petiole and postpetiole covered by abundant foveolae, which are separated from each other by spaces approximately equal in width to foveolar diameters. A limited area immediately around metapleural gland bulla roughly shagreened. Remainder of body mostly smooth and shining, bearing only a few scattered piligerous punctures.

All of body covered by abundant, long (mostly 0.09–0.23 mm), pale yellowish, suberect hairs. Appendages bearing somewhat less abundant, pale yellowish, predominantly oblique hairs. Pubescence present only on anterior face of petiole.

Body uniformly rich, medium reddish brown; appendages a paler shade of reddish brown.

Worker paratype variation: HW 0.69–0.75 mm. Paranidotype series relatively invariable in external morphology.

Ergatogyne: HW 0.76 mm, HL 0.94–0.97 mm, SL 0.59–0.60 mm, CI 79–81, SI 78–79, EL 0.22 mm, PW 0.58–0.59 mm, width of petiole 0.52–0.53 mm, maximum length of petiole 0.50–0.53 mm, width of postpetiole 0.71–0.75 mm, maximum length of postpetiole 0.56–0.59 mm, width of first gastric tergite 1.05 mm. Lateral and median ocelli small but well developed. Pedicel and gaster distinctly proportionately thicker than in worker caste, as shown by the measurements just given. In these 2 characters (presence of ocelli, larger pedicel and gaster) ergatogynes resemble one another closely and differ from worker caste. Otherwise, exceedingly worker-like. Associated with increased pedicel size, alitrunk is somewhat higher in region of propodeum, but alitruncal saturation is identical to that of worker.

Holotype, worker (MCZ), Nadala, 880 m, near Nadarivatu, Viti Levu, Fiji Islands, Wilson acc. no. 28. Paranidotypes: 10 workers, 2 ergatogynes, same data.

DISTRIBUTION: Fiji.

The type colony was collected in a partly disturbed midmountain rain forest. It was nesting in a small rotting tree limb, approximately ten centimeters in diameter, found on the deeply shaded forest floor next to a stream.

This species is named in honor of Prof. Carl Lindroth, the distinguished Swedish entomologist and zoogeographer.

13. *Cerapachys* (C.) *majuscula* Mann

Cerapachys (*Cerapachys*) *majusculus* Mann, 1921, Mus. Comp. Zool., Bull. 64: 408 (worker; type locality: Nadarivatu, Viti Levu).

DISTRIBUTION: Fiji.

Mann (1921) states that the type colonies of this species were found nesting beneath stones in midmountain rain forest. Syntype examined, MCZ.

14. *Cerapachys* (C.) *sculpturata* Mann, NEW STATUS

Cerapachys (*Cerapachys*) *vitiensis* subsp. *sculpturatus* Mann, 1921, Mus. Comp. Zool., Bull. 64: 407 (worker; type locality: Nasoqo, Viti Levu).

DISTRIBUTION: Fiji.

This small, heavily sculptured form is evidently closely related to *inconspicua* Emery of western Melanesia. Along with *vitiensis*, it appears to form the link between *inconspicua* and the more highly evolved Fijian members of the *majuscula* subgroup.

15. *Cerapachys* (C.) *vitiensis* Mann

Cerapachys (*Cerapachys*) *vitiensis* Mann, 1921, Mus. Comp. Zool., Bull. 64: 406 (worker; type locality: Lasema, Vanua Levu).

DISTRIBUTION: Fiji.

Mann (1921) states that the type specimens were collected from beneath a stone in a mountain bog. Syntypes examined, MCZ.

16. *Cerapachys* (C.) *zimmermani* Wilson, n. sp.

Worker: Closely related to *lindrothi* Wilson of Fiji, differing in much sparser body sculpturing. Body puncturation generally sparser and finer than in *lindrothi*, and petiolar and postpetiolar sterna almost completely smooth and shining, lacking foveolae that characterize type series of *lindrothi*.

Holotype worker: HW 0.87 mm, HL 1.00 mm, SL 0.64 mm, C1 87, SI 74, EL 0.26 mm, PW 0.62 mm, width of petiole 0.53 mm, maximum length of petiole 0.59 mm, width of postpetiole 0.66 mm, maximum length of postpetiole 0.64 mm, width of first gastric tergite 1.00 mm. Entire body, including pleura and sterna of petiole, postpetiole, and gaster smooth and strongly shining, its sculpturing limited to scattered, fine, piligerous punctures. Pilosity and color as described for holotype of *lindrothi* Wilson.

Paratype variation: HW 0.83 mm (paratopotype) and 0.66 mm (Navai Mill). Both specimens closely resemble holotype in body form, sculpturing, and pilosity. Navai Mill worker is overall more slender in body shape, as would be expected in such a distinctly smaller individual.

Holotype, worker (BISHOP 2827), Mt. Korombamba, Viti Levu, Fiji, 400 m, 1 Aug. 1938, E. C. Zimmerman. Paratypes: paranidotype worker, same data (MCZ); worker, Navai Mill, near Nadarivatu, Viti Levu, 850 m, 7 Sept. 1938, Zimmerman (USNM).

DISTRIBUTION: Fiji.

The Mt. Korombamba specimens were collected, according to Dr. Zimmerman's note, by "beating shrubs"; the Navai Mill worker was also captured by "beating." If *zimmermani* is indeed a low arboreal forager, as these notes suggest, it is exceptional in this respect among the Melanesian cerapachyines whose habits are known.

This species is named after the collector, Dr. E. C. Zimmerman, an outstanding modern student of Pacific entomology.

17. *Cerapachys* (*Syscia*) *crypta* Mann

Cerapachys (*Syscia*) *crypta* Mann, 1921, Mus. Comp. Zool., Bull. 64: 408 fig. 1 (worker, ergatogyne; type locality: Nadarivatu, Viti Levu).

DISTRIBUTION: Fiji.

This species and the closely related *fuscior* Mann are the largest of the Indo-Australian *Syscia*. They appear to have been derived phylogenetically from the *australis-papuana* stock of Australia and western Melanesia. The ergatogyne of *crypta* is considerably larger than the

worker, and its pedicel and gaster are greatly broadened with respect to the rest of the body. The ocelli are well developed, and small compound eyes are present. The alitrunk is typically worker-like. Syntypes examined, MCZ.

18. *Cerapachys (Syscia) fuscior* Mann, NEW STATUS

Cerapachys (Syscia) cryptus subsp. *fuscior* Mann, 1921, Mus. Comp. Zool., Bull. **64**: 410-411 (worker; type locality: Somo Somo, Taveuni).

DISTRIBUTION: Fiji.

The differences in color and sculpturing between this form and *crypta* (cited in the key) seem ample to warrant treating the two as distinct species, although further collecting may show them to be no more than insular variants of the same species. Syntypes examined, MCZ.

Mann (1921) makes the following note concerning the type series: "Several small colonies were found beneath stones after rains. When disturbed the workers roll up and feign death, making no attempt to sting when picked up."

Genus **Phyracaces** Emery

KEY TO SPECIES OF PHYRACACES OF NEW GUINEA

Worker Caste

Head, alitrunk, and petiole dark red, gaster black; larger species, with pronotal width exceeding 0.59 mm..... 19. **krombeini**
Entire body black; smaller species, with pronotal width 0.50 mm or less..... 20. **marginata**

19. *Phyracaces krombeini* Donisthorpe

Phyracaces krombeini Donisthorpe, 1946, Ann. Mag. Nat. Hist. ser. 11, **13**: 580 (worker; type locality: Port Moresby, Papua).

DISTRIBUTION: New Guinea.

This species is known only from the type material. Judging from the description, it is one of the most distinctive of the Melanesian cerapachyines and can be easily identified by the characters cited in the key. Its relationship to the numerous bicolored *Phyracaces* species of eastern Australia has not been determined.

20. *Phyracaces marginata* (Emery)

Cerapachys marginata Emery, 1897, Termész. Füzet. **20**: 594, pl. 15, fig. 41 [worker; type locality: Lemien Forest, near Berlinhafen (Aitape), NE New Guinea].
Phyracaces marginata, Emery, 1911, Genera Ins. **118**: 11, pl. 1, fig. 2.

DISTRIBUTION: New Guinea.

NE New Guinea: Wamuki, 800 m, Mongi R. Watershed, Wilson, no. 854; lower Busu River, Wilson, no. 1030.

This is a small black species belonging to the *adamus* group, which has its headquarters in eastern Australia. Several related species (e.g., *adamus*, *binodis*) occur in Queensland, while two (*cohici*, *dumbletoni*) are known from New Caledonia. The Papuan and New

Caledonian species are not closely related, however, and the evidence seems to suggest that they were derived independently from an Australian source fauna.

KEY TO SPECIES OF PHYRACACES OF NEW CALEDONIA

Worker Caste

Large species (HW 1.16–1.25 mm) with unusually long scapes (scape index greater than 90); greatest width of petiole well forward of its transverse midline 22. **dumbletoni**
 Smaller species (HW 0.88–1.01 mm) with distinctly shorter scapes (scape index less than 70); greatest width of petiole at about its transverse midline..... 21. **cohici**

21. **Phyracaces cohici** Wilson Fig. 3, B.

Phyracaces cohici Wilson, 1957, *Breviora* 74: 1 fig. (worker, male; type locality: Ciu, New Caledonia); 1958, *Insectes Sociaux* 5: 131 (behavior).

DISTRIBUTION: New Caledonia.

22. **Phyracaces dumbletoni** Wilson

Phyracaces dumbletoni Wilson, 1957, *Breviora* 74: 5 fig. (worker, ergatogyne; type locality: Chapeau Gendarme, New Caledonia); 1958, *Insectes Sociaux* 5: 133–134 (behavior).

DISTRIBUTION: New Caledonia.

Genus **Sphinctomyrmex** Mayr

23. **Sphinctomyrmex caledonicus** Wilson

Sphinctomyrmex caledonicus Wilson, 1957, *Breviora* 74: 8 (worker, ergatogyne; type locality: Ciu, New Caledonia); 1958, *Insectes Sociaux* 5: 136 (behavior).

DISTRIBUTION: New Caledonia.

24. **Sphinctomyrmex cribratus** Emery

Sphinctomyrmex (Eusphinctus) cribratus Emery, 1897, *Termész. Füz.* 20: 594 [worker; type locality: Lemien Forest, near Berlinhafen (Aitape), NE New Guinea].

DISTRIBUTION: New Guinea.

This species is evidently closely related to *steinheili* Forel of eastern Australia and *caledonicus* Wilson of New Caledonia. Whether it is conspecific with either of these cognate forms cannot be determined without a direct comparison of authentic samples, and its present treatment here as a distinct entity is no more than an "educated guess."

Genus **Lioponera** Mayr

25. **Lioponera versicolor** Donisthorpe

Lioponera versicolor Donisthorpe, 1948, *Ann. Mag. Nat. Hist.* ser. 11, 14: 589 (male; type locality: Maffin Bay, Neth. New Guinea).

DISTRIBUTION: New Guinea.

The occurrence of *Lioponera* in New Guinea should not be too surprising, since the genus is widespread in southeastern Asia and is represented by at least one species (*australis* Forel) in Queensland. However, since Donisthorpe's *versicolor* is based on the male alone, its generic allocation needs to be verified.

APPENDIX

Through the kindness of Dott. Delfa Guiglia, of the Museo Civico di Storia Naturale, Genova, I have been able to examine the holotype of *C. dohertyi* Emery, a key form with reference to the large and complex Indo-Australian *dohertyi* group, along with that of its nanitic variety *parvula* Emery.

26. *Cerapachys* (C.) *dohertyi* Emery

Cerapachys (C.) *Dohertyi* Emery, 1902, Rend. Accad. Sci. Ist. Bologna 6: 25 (worker; type locality: Pulo Laut, Borneo).

Cerapachys (C.) *Dohertyi* var. *parvula* Emery, 1902, *loc. cit.* (worker; type locality: Pulo Laut, Borneo). **New Synonymy.**

Holotype worker: HW 0.95 mm, HL 1.08 mm, SL 0.67 mm, CI 88, SI 71, EL 0.29 mm, PW 0.70 mm, width of petiole 0.66 mm, maximum length of petiole 0.56 mm, width of post-petiole 0.80 mm, width of first gastric tergite 0.97 mm.

Entire head coarsely and evenly rugo-reticulate, reticular interspaces remarkably uniform in size, diameters almost all between 0.05 and 0.07 mm. Interspace surfaces finely shagreened, subopaque to feebly shining. Entire pronotum and lateral face of propodeum similarly rugoreticulate. Approaching midline on dorsa of mesonotum and propodeum, reticulum grades into an area of scattered isolated foveolae. Foveolae in vicinity of midline have diameters of only 0.03–0.06 mm, separated by shining interspaces equal in breadth to their diameters or greater. Propodeum posteriorly marginate, its posterior face mostly smooth and shining. Petiole with similar sculpturing to that of head, except that interspaces somewhat more heavily shagreened. Postpetiole also rugoreticulate, but reticulum less regular and reticular interspaces narrower and shallower; interspace surfaces shagreened as on petiole. Gastric tergite 1 variably punctate: punctures of anterior 1/4 of tergite are coarsest (diameters approximately 0.33 mm) and densest, being separated by interspaces only about as wide as punctures themselves. Posteriorly punctures become progressively smaller and more scattered; near posterior tergal border only about 0.06 mm in diameter and separated by distances of approximately 0.03 mm.

Entire body covered by abundant erect-suberect, pale yellowish hairs ranging from 0.08 to 0.20 mm in length. In addition, a second layer of similar but shorter hairs (pubescence) ranging between 0.03 and 0.06 mm in length. Pubescence almost absent on head and relatively sparse over most of alitrunk but strongly developed on pedicel and gaster. Appendages bearing similar pilosity and pubescence, but generally sparser and less erect.

Body concolorous dark reddish brown; appendages pale reddish brown.

A series of workers from Wai Lima, southern Sumatra (MCZ), appear nearly identical to the holotype. The holotype of Emery's variety *parvula* is almost certainly nothing but a nanitic worker of *dohertyi*. It originated from the type locality of *dohertyi* and is nearly identical to the *dohertyi* holotype in body form, sculpturing, and pilosity. It apparently differs only in its smaller size (HW 0.62 mm) and paler coloration (body concolorous pale reddish brown).