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CHARACTERS AND SYNONYMIES AMONG THE GENERA OF ANTS.

PART III. SOME MEMBERS OF THE TRIBE PONERINI (PONERINAE, FORMICIDAE)

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INTRODUCTION

The present part¹ is concerned with some genera and species in the tribe Ponerini of subfamily Ponerinae. It consists mainly of the justification for some rather radical revisionary changes in the tribe at the generic level. It is felt that these findings should be presented here in order that they should not distract from the "final" reclassification results eventually to be presented in synoptic form for the Ponerinae and for all Formicidae. This paper by no means exhausts the necessary changes that must be made in the generic classification of the Ponerini, but it deals with some of the most fundamental ones that require more than summary proposal. Some synonymies proposed or suggested at the species level are to be considered a by-product of the research into generic limits. At various stages during the last two years, the work on ponerine reclassification has been supported by grants from the Bache Fund of the National Academy of Sciences, from the Society of the Sigma Xi, and from the National Science Foundation (G-23680). This help is gratefully acknowledged.

SOME OLD AND NEW GENERIC CHARACTERS OF PONERINI

Tribe Ponerini, the largest in subfamily Ponerinae, has undergone no basic classificatory changes since the appearance of

¹ Part I. *Breviora*, Mus. Comp. Zool., no. 11: 1-13 (1953).
Part II. *Ibid.*, no. 18: 1-8 (1953).

Emery's fascicle covering the subfamily in the *Genera Insectorum* in 1911. Emery's treatment was really a refinement of his earlier reclassification of the ponerines published in 1901. In his well-known key to the genera of ants, Wheeler (1922) followed Emery's classification of the Ponerini for the most part, but worked in the additional genera described up to 1922.

The Emery classification employed a number of characters of worker and female in distinguishing his genera of tribe Ponerini, but the two most stressed were (1) the number of segments in the maxillary and labial palpi, and (2) the number of tibial spurs on the middle and hind legs.

Unfortunately, the palpal character saw extensive use only during some of the early years of ant systematics. Emery, Mayr, and even Frederick Smith often gave the count of segments in their descriptions, but curiously, after Emery used the palpal counts as a foundation stone of his 1901 classification, these appendages were almost completely ignored by most later describers of ponerine species, probably due to the fact that the smaller mouthparts are so small and difficult of access. Later authors seem to have relied more on habitus than on truly diagnostic characters when they placed new (or supposed new) species to genus. As a result, some species have been described as new over and over again in different genera and subgenera (consult the case of "*Trachymesopus*" *brunoi* and its synonyms, discussed below). The primitive number of worker-female palpal segments appears to be 4, 4 (4 maxillary, 4 labial — the formula always stated in that order); in the male it is 6, 4, the basic number for all ants. In many Ponerini, especially the smaller or cryptobiotic species and their derivatives, the number is much reduced, and reaches as low as 0, 1 in the worker, while less consistent reduction occurs in the male. Palpal segmentation is undoubtedly important in generic classification and in the analysis of phyletic trends, but due to its neglect in species descriptions, it remains unknown for a majority of forms. Work is now going forward to correct this deficiency, and some results are incorporated in the present paper.

The other major character in question is the number and state of development of the tibial spurs. The trait is an ambiguous one, as can be seen from its employment in keys. Wheeler's 1922 key to the genera of the Ponerini states it this way in the very first couplet:

- Middle and hind tibiae with two spurs 2.
 Middle and hind tibiae with a single, well-developed spur, which is always pectinate; the lateral spur is rudimentary or absent 19.

This couplet really expresses the difference thought to separate the "lower" Ponerini, mostly large in size, from the "higher" members, which tend to be smaller (e.g., *Ponera*, *Cryptopone*). Generally speaking, the genera with smaller-sized species do tend to lose the lateral spurs of the middle and hind tibiae, while genera having larger-sized species normally retain the extra spur, although usually in a more or less reduced condition. The difficulty, of course, lies with distinguishing between the condition "two spurs" and "lateral spur rudimentary," especially when one finds that in most species the lateral spur is considerably smaller than its mate. Furthermore, the threshold at which a "vestigial spur" becomes just another apical seta of the tibia is unspecified along a gradual morphocline of species. In short, the lateral tibial spur, as an allometric character, cannot be used to split the Ponerini into two main groups, and in fact probably cannot even be used by itself as a diagnostic character at the generic level.

Other adult characters of value in classification still remain: the shape of the clypeus has been and still is an important generic character. The tarsal claws may be simple, or may have one or more teeth, or may even be pectinate, as in the case of most *Leptogenys* species. I consider the pectination of the claws, imperfect in some African species of the genus, to be insufficient as a tribal character in view of the several other strong characters shared by both adult and larval Ponerini and *Leptogenys*, and accordingly I am placing tribe Leptogenyini as an included synonym of Ponerini (**new synonymy**).

Another character of some importance is the presence of heavy, conical, spine-like setae on the extensor surfaces of the middle tibiae and tarsi. These structures, which appear to promote movement through soil or rotten wood by improving traction, are found in certain cryptobiotic genera (e. g., *Centromyrmex*, *Wadeura*, *Cryptopone*, *Promyopias*) as well as in a number of fossorial wasps (many pristocerine Bethyridae, most non-parasitic Scoliodea, for instance), all of which seek their prey underground or in other confined circumstances. Emery cited the presence of such spine-like, as well as merely bristle-like, setae as characteristic of *Euponera* subgenus *Trachymesopus*, which he named (in 1911) accordingly. The heterogeneity of *Trachymesopus* in this regard, as well as in other respects, made it a perfect catch-all for miscellaneous species of medium-to-small Ponerini from the very beginning, and it has continued in this role right down to the present. As a matter of fact,

heavy, conical spine-like setae that arise over half or more of the mid-tibial extensor surface are found only in a particular group of "*Trachymesopus*," and this group (*ochracea* and allies) shares this and several other characters with the members of *Cryptopone*. The relationship between *Trachymesopus* and *Cryptopone* has long been discussed by E. O. Wilson and myself (see Wilson, 1958: 352), and now the discovery of the concordance between the tibial armament and other characters, particularly the basal mandibular pit, makes the solution of this problem obvious. The "*Trachymesopus*" species with these characters are all really *Cryptopone*, and are transferred accordingly, as discussed under that genus below.

One of the chief *Cryptopone* characters just mentioned is a particularly interesting one; this is a prominent oval pit or fovea near the base of the mandible in its dorsolateral surface. This pit, or its obvious homolog, is also found in all *Brachyponera*, in the members of the "*Trachymesopus*" *sharpi* group, in *Hagensia*, in *Euponera sikorae* Forel (type species of *Euponera*!), and in a few other African species formerly placed in *Euponera* or other genera, but is lacking in *T. stigma*, the type species of *Trachymesopus*, and its closest relatives. All known species with the basal pit are from the Old World, and chiefly from Africa, with the exception of *Cryptopone gũlva* and (perhaps) *C. guatemalensis*, which apparently represent a *Cryptopone* invasion of the New World that has spread through North America and reached Central America. In the other direction, *Cryptopone* has reached southeastern Australia and New Caledonia, but curiously, no true *Cryptopone* are known to occur in Ethiopian Africa.

The basal mandibular pit in ponerine species was early noted as a character by Gustav Mayr and occasionally mentioned by later authors in species descriptions, but only Arnold used it as a generic character in his 1951 review of *Hagensia*, a genus in which the pits are unusually distinct. In most species that have it, the pit has been overlooked completely in descriptions, particularly after 1900. Many Ponerini, especially among the larger and presumably more primitive species, bear another character in the form of an oblique groove across the dorsal face of the mandible, curving outward from the inner base and usually continuing into the lateral longitudinal mandibular sulcus that runs to the apex. This channel, which may be functioning to

distribute some product from the mandibular glands, is probably not homologous with the basal pit. It is oriented differently, and at least one species of "*Bothroponera*" has both the pit and the groove.

In the former *Trachymesopus*, species without the truly spine-like mid-tibial setae (except for 2-3 of these setae at the tibial apex) are divided into three groups: the *stigma* and *darwini* groups, which have no basal mandibular pit and no anal lobe on the hind wing of the sexes, and the *sharpi* group, which has the pit, and the lobe in the male only, so far as known. The *sharpi* group is close to *Brachyponera*, with which it shares the pit and the lobe, but further information may dictate a separate genus for each of these groups.

In what remains of *Trachymesopus*, the *stigma* group (e. g., *stigma*, *cautus*, *pachynodus*, *rufonigrus*) has palpal segmentation 3, 3, while *darwini* has 4, 3. Thus, it may be seen that *Trachymesopus* is a heterogeneous grouping even after the removal of the *Cryptopone* species; its reclassification will have to await the study of more of the larvae and adult winged forms.

Among the most promising of characters to be used in ponerine systematics are those of the larvae. The Wheelers (1952) have laid the groundwork for a comparative study of the larvae of the genera of Ponerini, but for the great majority of species of the tribe, the larvae have never been studied. The larvae of Ponerini are usually covered with peculiar medullate projections, called by the Wheelers "tubercles." In consonance with the morphological terminology applied to other holometabolous larvae, particularly Lepidoptera, I propose that these projections be called by the more specifically descriptive term *chalaza* (sing.), *chalazae* (pl.). The chalazae of Ponerini are matched by apparently homologous structures in tribes Thaumatomyrmicini and Odontomachini, which are close to Ponerini on the basis of adult characters as well. Some of the smaller ponerine genera bear special paired mushroom-shaped chalazae on one or more abdominal tergites; these have long been known to function as "hangers" by which the larvae are stuck to the ceiling and walls of the nest by a glutinous substance covering the head of the chalaza. The number and placement of these fungiform chalazae is important in generic taxonomy, but they must be used with care owing to the fact that they may change in number and form, or be lost altogether, as the instars metamorphose one into another.

REVISIONARY OBSERVATIONS ON SOME
PARTICULAR GENERA

CRYPTOPONE Emery

Worker: Small in size, generally under 4 mm total length, depigmented (ferruginous or yellowish); eyes absent or extremely reduced, body compact; mandibles downcurved, with a few (4-6) coarse teeth set on more or less oblique masticatory borders. Dorsolateral mandibular surface with a conspicuous basal pit or fovea, circular or elliptical in outline. Middle tibiae with stout spinules covering about $\frac{2}{3}$ or more of their extensor surfaces. Palpal segmentation 2, 2 or less.

Female: Aside from well-developed compound eyes, ocelli, thorax and the other obviously female characters, fit the worker diagnosis. Hind wings without anal lobe, but with two basal cells.

Male: Small, slender, dark-colored, with pygidial spine so common among Ponerini. Hind wing without anal lobe.

Species: Those placed here by Wilson (1958), plus the former *Trachymesopus* species *crassicornis* (Emery), *gilva* (Roger), probably *guatemalensis* (Forel), *ochracea* (Mayr), *rotundiceps* (Emery), *sauteri* (Wheeler), *taivanae* (Forel) and its probable junior synonym *takahashii* (Wheeler). Of species formerly placed in *Ponera*, *P. typhla* (Karawajew) is clearly a *Cryptopone*, and is probably a synonym of *C. testacea* (Emery); the Australian *P. mjobergi* Forel is a junior synonym of *C. rotundiceps* (**new synonymy**). Among species to be deleted from the *Cryptopone* roll, *C. rufotestaceus* Donisthorpe belongs in *Trachymesopus* as that genus is presently constituted, and is the same as the large variant of *T. darwini* hitherto known as *T. lamarki* Santschi (**new synonymy**). True *Cryptopone* has not been taken in Africa south of the Sahara, and *C. angustata* Santschi (type examined) and *C. hartwigi* Arnold should be transferred to *Ponera* as that genus is currently constituted. I have not checked this list of species for exhaustiveness, but it should serve to give a general idea of *Cryptopone* in the sense of the present work.

TRACHYMESOPUS Emery

As already explained above, *Trachymesopus* (without the *Cryptopone* species) contains at least three groups of species. The type species, *T. stigma*, is common and widespread in both the Indo-Australian region and in the warmer parts of the New World. The Old World synonymy is extensive, and has been

dealt with by Wilson (1958:355). In the New World, the synonymy of *stigma* is not yet clear. *T. cognata* (Emery) has never been differentiated satisfactorily, and *T. succedanea* (Roger) could be either *stigma* or the closely related *cautus* Mann. *T. compressinodis* Borgmeier is a synonym of *T. cautus* Mann (types compared; **new synonymy**). Agreeing with *stigma* and *cautus* in palpal segmentation (3, 3) and in the lack of an anal lobe on the hind wings of both sexes, are two Australian species, *rufonigra* (Clark), transferred from *Brachyponera*, and *pachynodus* Clark (wings unknown in the latter). Two other species that apparently are close to this group are *lunaris* (Emery) and *ferrugineus* (F. Smith), though so little is known about these forms now that they cannot be confidently assigned.

The second group consists of *darwini* and relatives. These are medium-small species known only from the ferruginous-colored females, which are taken commonly at light throughout wide areas of the Old World tropics. These females lack an anal lobe on the hind wing, and their palpal formula is 4, 3. They lack a mandibular pit and have no spine-like setae on the outer face of the middle tibia. They are found from northern Australia, Indonesia and the Philippines westward through India to tropical Africa. They vary considerably in size, but the variation may be continuous; in fact, all of these forms may well represent a single species. As mentioned above, the species described as *Cryptopone rufotestacea* by Donisthorpe belongs here and is a synonym of *T. lamarki* Santschi, which in all likelihood is only a size variant of *darwini*. It seems likely also that Motschulsky's *Amblyopone testacea* belongs in this complex.

The third group is the group of *sharpi* Forel, which consists of medium-small species, all castes blackish in color, with a distinct elliptical mandibular pit; palpal segmentation (as seen in 2 African specimens of *brunoi* only) is 4, 4. Anal lobe lacking in 2 *brunoi* females from Liberia, but present (though separated by a relatively shallow cleft) in a single male from Southern Rhodesia; perhaps in this group the character is variable or sexually dimorphic. Mid-tibiae without spine-like setae on extensor faces.

Some of the species (*brunoi*, *malayanus*, *katangana*) were described originally in *Ectomomyrmex*, or were placed in that genus later. Actually, these species are all very close to *sharpi*—in fact, *malayanus* is almost certainly a straight synonym of *sharpi*. The form of *sharpi* from China and Japan has the propodeum

wider and more opaque above; it was described by Wheeler as subspecies *pilosior*, but should be considered as a good species until more is known about the variation in this complex, which, if it matches the variation found in *brunoi* in Africa, may be considerable. *T. pilosior* occurs westward to the scarp of the Tibetan Plateau, where I collected a worker on Mt. Omei, Szechuan Province, in 1945; *Euponera* (*Trachymesopus*) *chosonensis* Teranishi, 1940, from Osaka, Japan, is its **new synonym**. The Oriental and African forms of this group are also very close, and deserve careful comparison. The *sharpi* group does not really belong to *Trachymesopus*, and will eventually have to be moved out. But in order to avoid one additional round of name changes, I am leaving it where it is until the limits of other closely related groups, especially *Brachyponera*, are clarified.

TRACHYMESOPUS BRUNOI comb. nov.

Pachycondyla (*Ectomomyrmex*) *brunoi* Forel, 1913, Deutsche ent. Zeitschr., beih., p. 205, worker. Type loc.: Bulawayo, S. Rhodesia. Syntype examined.

Euponera (*Trachymesopus*) *nigeriensis* Santschi, 1914, Boll. Lab. Zool. Portici, 8: 316, worker. Type loc.: Olokomeji, Nigeria; also from Aburi, Gold Coast. Syntype examined. **New synonymy**.

Euponera (*Trachymesopus*) *bayoni* Menozzi, 1932, Ann. Mus. Civ. Stor. Nat. Genova, 56: 97-98, worker. Type loc.: Kome, Sesse Archipelago, Victoria Nyanza, Uganda. **New synonymy**.

Ectomomyrmex nigeriensis var. *katangana* Santschi, 1933, Bull. Ann. Soc. Ent. Belg., 73: 96, Type loc.: Pweto, Elisabethville, Belgian Congo. Syntype examined. **New synonymy**.

Euponera (*Mesoponera*) *dentis* Weber, 1942, Proc. Ent. Soc. Wash., 44: 43, fig. 9, dealate female. Type loc.: Lotti Forest, Imatong Mts., Sudan. Type examined. **New synonymy**.

Euponera (*Trachymesopus*) *lamottci* Bernard, 1953, Mem. Inst. Fr. Afrique Noire, 19 (1): 195, fig. 2g, h, i, dealate female. Type loc.: Keoulenta Savannah, French Guinea. **New synonymy**.

This species occurs widely in Africa south of the Sahara. In addition to the types mentioned above, I have seen samples from Liberia, Cameroons and the Kalahari Desert. There is some small variation among these samples in relative head width and in strength and opacity of the sculpture, but this appears to be both size-linked (allometric) and continuous.

ECTOMOMYRMEX Mayr

The taxonomy of this genus has been considerably simplified at the species level by the partial revisions of Wilson (1958) and Yasumatsu (1962), but an even more fundamental change needed is the removal of the species *brunoi* and *malayanus*. These, as has been demonstrated above, are members of the *sharpi* group of "*Trachymesopus*." With these deletions, *Ectomomyrmex* is once more restored to the status of a strictly Indo-Pacific genus, ranging from India and northwestern China eastward to Japan and Korea, Samoa and northern Queensland. It is now also possible to define the genus.

Ectomomyrmex consists of medium-sized to large, usually basically black-colored forms, the workers and females of which tend to have the posterior cranium somewhat prismatic, and the posterior face of the petiolar node strongly striate, or at least rugose-punctate. Worker-female palpi segmented, so far as is known, 4, 4; mandibles without basal pit, the oblique basal groove present and weak, or absent. The oblique mesepisternal suture is present and reasonably distinct in the worker. Compound eyes fairly to rather well developed and multifaceted in the worker.

CENTROMYRMEX Mayr

Centromyrmex Mayr, 1866, Verh. zool.-bot. Ges. Wien, 16: 894. Type:

Centromyrmex bohemanni Mayr, 1866, monobasic.

Spalacomyrmex Emery, 1889, Ann. Mus. Civ. Stor. Nat. Genova, 27: 489.

Type: *Spalacomyrmex feae* Emery, 1889, monobasic.

Typhloteras Karawajew, 1925, Konowia, 4: 128. Type: *Typhloteras hamulatum* Karawajew, 1925, monobasic.

Glyphopone Forel, 1913, Rev. Zool. Afr. 2: 308. Type: *Glyphopone bequaerti* Forel, 1913, monobasic. **New synonymy.**

Glyphopone subgenus *Leptopone* Arnold, 1916, Ann. S. Afr. Mus., 14: 163.

Type: *Glyphopone (Leptopone) rufigaster* Arnold, 1916, monobasic.

New synonymy.

The type female of *Glyphopone bequaerti* has been compared directly with a winged female kindly sent by Dr. Arnold (Abercorn, Northern Rhodesia, 10-12-1943, Arnold leg. et det.). These two specimens are virtually identical and are surely conspecific, as indicated in the formal synonymy expressed below. The median lobe of the clypeus is hardly to be considered "bicarinate," but the median portion of its surface is very slightly concave when viewed in the proper light. Although these are

large females, with dark forebody and rufous gaster, they bear the general characters of *Centromyrmex*, and in any case, they are probably no larger or darker than the female of *C. gigas*, judging from the workers of *gigas* I have seen. It seems best to consider *Glyphopone* a synonym of *Centromyrmex* until the worker of *G. bequaerti* is found and we are able to determine whether it has the definitive characters.

CENTROMYRMEX BEQUAERTI Forel comb. nov.

- Glyphopone Bequaerti* Forel, 1913, Rev. Zool. Afr., 2: 308, fig. 1, alate female. Type loc.: Kibombo, Belgian Congo; examined.
Glyphopone (Leptopone) rufigaster Arnold, 1916, Ann. S. Afr. Mus., 14: 163, figs. 10, 10a, alate female. **New synonymy.**

PROMYOPIAS SILVESTRII Santschi

- Myopias (Promyopias) Silvestrii* Santschi, 1914: 324, fig. 10, worker. Type loc.: Mamou, French Guinea; one syntype worker examined.
Promyopias asili Crawley, 1916, Entomologist, London, p. 30, fig., alate female. Type loc.: "Nyasaland," [according to label on holotype: Mlanje, Nyasaland, 15-IV-1913, S. A. Neave leg.]. Holotype in British Museum, examined. **New synonymy.**

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