A SIMPLIFIED CONSPECTUS OF THE FORMICIDAE

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From the Transactions of the American Entomological Society
Volume 111: 255–264

Issued July 30, 1985 1531

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ABSTRACT

The genera of living ants are listed alphabetically under tribes and the tribes phylogenetically under subfamilies. Ten subfamilies, 61 tribes and 303 genera are recognized. The authors' disagreements (based in part on larvae) with other current systems are explained in notes.

In the course of our study of ant larvae we have often needed to learn quickly the taxonomic location of a newly acquired and unfamiliar exotic genus. We had W.M. Wheeler's 1922 key to the subfamilies, tribes, genera and subgenera, but that was in no way a ready reference; nor was Emery's monumental "Genera Insectorum," which was spread throughout 15 years (1910-1925) and five fascicles.

Snelling (1981) published a key to subfamilies based on our 1972 key. He does not, however, divide the subfamilies into tribes, but he lists the genera in each subfamily and gives all the synonyms of each genus. This list occupies approximately 15 pages.

All we needed was a bare outline which showed the relations of taxa without characterizations or synonyms. So we have made one for ourselves and publish it herewith, hoping that it will be of use to others with similar needs. It is up-to-date according to our views. Our gospel for genera is Brown 1973, but we are apostates as to certain genera (marked with an asterisk) because of larval and/or adult characters. Our major disagreements with Brown involve higher taxa; these are explained in the numbered notes.

We have also included among those notes a revision of the characterization of Cerapachyinae in our 1972 conspectus of subfamilies.

Since we have studied the larvae of 758 species of ants in 194 genera representing 51 of the 61 tribes and all ten of the living subfamilies, and published a monograph (1976) on our results, perhaps we might be forgiven if we occasionally emphasize the importance

of larvae in ant taxonomy. Our sins might be considered venial when one considers that our latter-day systematists have repeatedly stated that classification should ultimately be based on all characters of organisms, including developmental. We have never maintained that larval characters should take precedence over adult characters but they can supplement the adult evidence in doubtful cases.

MYRMECIINAE

Nothomyrmeciini: *Nothomyrmecia* (1)
Myrmeciini: *Myrmecia*

PONERINAE

Amblyoponini: *Amblyopone, Apomyrma, Concoctio, Myopopone, Mystrium, Onychomyrmex, Prionopelta*
Cylindromyrmecini: *Cylindromyrmex*
Platythyreini: *Platythyrea, Probolomyrmex*
Typhlomyrmecini: *Typhlomyrmex*
Ectatommini: *Acanthoponera, Aulacopone, Ectatomma, Gnamptogenys, Heteroponera, Paraponera, Rhytidoponera*
Proceratiini (2): *Discothyrea, Proceratium*
Thaumatomyrmecini: *Thaumatomyrmex*
Ponerini (3): *Asphinctopone, Belonopelta, *Bothroponera, Brachyponera, Centromyrmex, Cryptopone, Diacamma, Dinoponera, Dolioponera, Emeryopone, Euponera, Hagensia, Harpegnathos, Hypoponera, Leptogenys, Megaponera, *Myopias, Odontoponera, Ophthalmopone, Pachycondyla, Paltothyreus, *Phrynoponera Plectroctena, Ponera, Prionogenys, Psalidomyrmex, Simopelta, Streblognathus, *Trapeziopelta*
Odontomachini (4): **Anochetus, Odontomachus*

CERAPACHYINAE (5)

Cerapachyini: *Cerapachys, *Lioponera, *Phyracaces, Simopone, Sphinctomyrmex*
Acanthostichini: *Acanthostichus*

DORYLINAE (6)

Cheliomyrmecini: *Cheliomyrmex*
Dorylini: *Dorylus*
Ecitonini: *Aenictus, Eciton, Labidus, Neivamyrmex, Nomamyrmex*

LEPTANILLINAE (7)

Leptanillini: *Leptanilla, Leptomesites, Noonilla, Phaulomyrma*

PSEUDOMYRMECINAE

Pseudomyrmecini: **Pachysima, Pseudomyrmex, Tetraponera, *Viticicola*

MYRMICINAE

Myrmicini: *Ephebomyrmex, Hylomyrma, Manica, Myrmica, *Paramyrmica, Pogonomyrmex*

Pheidolini: *Adlerzia, Ancyridris, Aphaenogaster, Goniomma, Machomyrma, Messor, Oxyopomyrmex, Pheidole, Stenamma, Veromessor*

Melissotarsini: *Melissotarsus, Rhopalomastix*

Metaponini: *Metapone*

Stereomyrmecini: *Stereomyrmex*

Myrmicariini: *Myrmicaria*

Cardiocondylini: *Cardiocondyla*

Crematogastrini: *Crematogaster*

Solenopsidini: *Allomerus, Anergates, Anergatides, Anillomyrma, Antichthonidris, Brownidris, Carebarella, Chelaner, Diplomorium, Hagioxenus, Huberia, Liomyrmex, Megalomyrmex, Monomorium, Nothidris, Oxyepoecus, Solenopsis, Syllophopsis, Tranopelta, Vollenhovia, Xenomyrmex*

Pheidologetini: *Anisopheidole, Carebara, Lophomyrmex, Oligomyrmex, Paedalgus, Pheidologeton, Trigonogaster*

Myrmecinini: *Acanthomyrmex, Atopomyrmex, Atopula, Dacryon, Dilobocondyla, Lordomyrma, Myrmecina, Perissomyrmex, Peronomyrmex, Podomyrma, Pristomyrmex, Terataner*

Meranoplini: *Ankylomyrma, Calyptomyrmex, Geognomicus, Mayriella, Meranoplus, Prodicroaspis, Promeranoplus, Romblonella, Willowsiella*

Leptothoracini: *Adelomyrmex, Dacetinops, Harpagoxenus, Lachnomyrmex, Leptothorax, *Macromischa, Macromischoides, Poecilomyrma, Rogeria (Chalepoxenus, Doronomyrmex, Epimyrma, Formicoxenus, Myrmoxenus* and *Symmyrmica* are probably synonyms of *Leptothorax)*

Ocymyrmecini: *Ocymyrmex*

Tetramoriini: *Decamorium, Eutetramorium, Ireneopone, Rhoptromyrmex, Stigmomyrmex, Strongylognathus, Teleutomyrmex, Tetramorium, Tetramyrma, Triglyphothrix, Xiphomyrmex*

Ochetomyrmecini: *Ochetomyrmex, *Wasmannia*

Cataulacini: *Cataulacus*

Cephalotini (8): *Cephalotes, *Eucryptocerus, Procryptocerus, *Zacryptocerus*

Basicerotini: *Aspididris, Basiceros, Creightonidris, Eurhopalothrix, Octostruma, Protalaridris, Rhopalothrix*

Dacetini: *Acanthognathus, Asketogenys, Cladarogenys, Codioxenus, Colobos-*

truma, Daceton, Dorisidris, Dysedrognathus, Epitritus, Epopostruma, Glamyromyrmex, Gymnomyrmex, Kyidris, Mesostruma, Miccostruma, Microdaceton, Neostruma, Orectognathus, Pentastruma, Quadristruma, Serrastruma, Smithistruma, Strumigenys, Tingimyrmex, Trichoscapa

Agroecomyrmecini: *Tatuidris*

Phalacromyrmecini: *Phalacromyrmex*

Stegomyrmecini: *Stegomyrmex*

Proattini: *Proatta*

Attini: *Acromyrmex, Apterostigma, Atta, Cyphomyrmex, Mycetarotes, Mycetophylax, Mycetosoritis, Mycocepurus, Myrmicocrypta, Sericomyrmex, Trachymyrmex*

ANEURETINAE (9)

Aneuretini: *Aneuretus*

DOLICHODERINAE

Dolichoderini: *Dolichoderus, Linepithema*

Leptomyrmecini: *Leptomyrmex*

Tapinomini: *Anillidris, Araucomyrmex, Azteca, Bothriomyrmex, Conomyrma, Dorymyrmex, Ecphorella, Engramma, Forelius, Froggattella, Iridomyrmex, Liometopum, Neoforelius, Semonius, Tapinoma, Technomyrmex, Turneria, Zatapinoma*

Axinidrini: *Axinidris*

FORMICINAE

Myrmoteratini: *Myrmoteras*

Santschiellini: *Santschiella*

Melophorini: **Diodontolepis, Lasiophanes, Melophorus, Notoncus, Prolasius, Pseudonotoncus*

Formicini: *Acanthomyops, Cataglyphis, Formica, Lasius, Myrmecocystus, Polyergus, Proformica, Pseudolasius, Rossomyrmex, Teratomyrmex*

Gesomyrmecini: *Gesomyrmex*

Gigantiopini: *Gigantiops*

Oecophyllini: *Oecophylla*

Myrmecorhynchini: *Myrmecorhynchus*

Plagiolepidini: *Acantholepis, Acropyga, Anoplolepis, Plagiolepis, Pseudaphomomyrmex*

Brachymyrmecini: *Aphomomyrmex, Brachymyrmex, Cladomyrma, Euprenolepis, Paratrechina, Petalomyrmex, Prenolepis, Stigmacros*

Myrmelachistini: *Andragnathus, Myrmelachista*

Camponotini: *Calomyrmex, Camponotus, *Colobopsis, Dendromyrmex, Echinopla, Forelophilus, Notostigma, Opisthopsis, Overbeckia, Phasmomyrmex, Polyrhachis*

GENERA INCERTAE SEDIS

Aenictogiton, Amyrmex, Bregmatomyrmex, Brunella, Ireneella, Leptanilloides, Paraprionopelta, Pilotrochus, Scyphodon, Tricytarus

NOTES

(1) We no longer agree with Taylor (1978) that *Nothomyrmecia* merits subfamilial status. Adult anatomy may warrant a separate tribe, but the larvae are not more than generically different and as Taylor himself has said (p. 284): "Thus, almost all behavioral characteristics of *Nothomyrmecia* are held in common with *Myrmecia,* further confirming the primitiveness of *Nothomyrmecia.*"

(2) In his revision of the ponerine tribe Ectatommini Brown (1958:179) stated that our "larval findings agree in most respects at the generic level with the new classification adopted here." On p. 176 he attempted to justify the lumping of the Proceratiini into the Ectatommini: "The only doubts here rest on the unusual nature of the proceratiine larvae, but then these are known for only a few species in one genus, *Proceratium,* and none of the *Heteroponera* species. [The larva of *H. relicta* had been known since 1915.] The Ectatommini appear to make up one reasonably clearcut tribe with these inclusions." Our answer to this argument: — We have now studied the larvae of 3 species of *Proceratium* and 2 species of *Dischothyrea,* which constitute one clearcut taxon (our Proceratiini). We have studied the larvae of 35 species in 5 genera forming another clearcut taxon (our Ectatommini). Brown is equally clearcut in his key to genera of workers in separating *Proceratium* and *Discothyrea* from the other Ectatommini (1958:185).

We protested vigorously (1971:1213) against Brown's inclusion of these two genera in the Ectatommini and we oppose it here.

(3) Brown (1973) lumped a dozen genera in the tribe Ponerini into *Pachycondyla.* Surely this must be one of the biggest lumps in the history of myrmecology: The larvae of *Ectomomyrmex, Phrynoponera, Pseudoneoponera, Pseudoponera, Termitopone* and *Wadeura* are unknown. We have already protested (1976:93) on behalf of *Bothroponera* and *Myopias.* We might compromise on *Bothroponera* and we offer no objection to lumping

Mesoponera and *Neoponera* with *Pachycondyla,* but if larval characters are to have any weight at all, we must insist on the integrity of *Myopias* and *Trapeziopelta.*

(4) Brown's next lumping was to reduce the tribe Odontomachini to a subtribe of Ponerini (1976). We object on the basis of both adult and larval characters. Brown himself admits (p. 72) that "the genera *Odontomachus* and *Anochetus* are among the most distinctive and easily recognized of all ants." The head and mandibles distinguish them from all other Ponerinae. In fact, they scarcely belong in the subfamily Ponerinae: they lack the characteristic ponerine constriction between the first and second gastric somites, although Brown said "(Constricted in some *Anochetus*)" (1976:74). Considering Brown's recognition of about 280 species in the two genera, a few exceptions should not invalidate the character. If the larvae were not tuberculate, we would place these two genera in a separate subfamily.

Brown bases his characterization of the larvae of his subtribe (1976:76) on our characterization of the larvae of the tribe Odontomachini (1971:1213). He minimizes the taxonomic importance of tubercles. Nevertheless we have reviewed our material and are prepared to re-affirm as distinctive of the tribe Odontomachini the typical tubercle described in our characterization: we have found it in all our species of *Anochetus* and *Odontomachus* but in no other genus of Ponerini. In summary, then, in our system the tribe Odontomachini stands as it has stood for 90 years.

(5) In 1976 (p. 90) we traced in detail the taxonomic wanderings of the cerapachyines, ending with W.M. Wheeler's placing them in a separate subfamily, using larval characters as partial justification. Brown (1975:13) did not think that larval characters supported the retention of the subfamily Cerapachyinae and reduced the taxon to a tribe in the subfamily Ponerinae, because the body shape of the larvae is an adaptive character. That shape is suited to transportation under the worker's body. This is an adaptation to a nomadic life in the Dorylinae, but the Cerapachyinae are not known to be nomadic. Anyway, what's wrong with adaptive characters above the species level? True, convergent adaptive characters deceive, but the deception may be exposed by other characters. We still consider the cerapachyines intermediate between the Dorylinae and Ponerinae, but not affiliated with either.

We will, therefore, continue to place them in a separate subfamily, the Cerapachyinae.

Recharacterization of Subfamily Cerapachyinae (1972:37-38)

Workers.—Body elongate, subcylindrical and heavily sclerotized; pedicel of one segment which is nearly as broad as thorax; with a distinct constriction between first and second gastric somites. Frontal carinae distinct from each other, projecting forward and not covering antennal insertions. Antennae exceptionally short and thick, inserted close together; antennal fossa marked by a lateral carina on cheek. Pygidium margined laterally and posteriorly with a row of spines. Sting powerful.

Pupae.—Enclosed in cocoons.

(6) In 1893 Dalla Torre put the army ants in the subfamily Dorylinae and there they abode for nearly a century. Recently several myrmecologists (e.g., Snelling 1981) decided that they were diphyletic and hence the Old World forms should be separated from the New World and named respectively Dorylinae and Ecitoninae. But Kistner (1972) spoiled that geographically logical partition by suggesting that the Old World *Aenictus* shared a common ancestry with the New World *Neivamyrmex* because of the relationship of their myrmecophilous staphylinids. That we can applaud, because we (1984) are unable to distinguish the larvae of these two genera. In 1975 Gotwald and Kupiec stated that geographic, morphological and behavioral evidence indicates a triphyletic origin resulting in three lineages (1) Ecitonini-Cheliomyrmecini, (2) Dorylini and (3) Aenictini, which still keeps the two Worlds separate and pleases everyone except us. Now on the basis of adult and larvae we might propose for the army ants a tetraphyletic origin of four subfamilies: (1) Dorylinae, (2) Aenictinae, (3) Cheliomyrmecinae and (4) Ecitoninae. But the support of this hypothesis will have to wait upon the discovery of fossils and we can't wait that long. Meanwhile we will continue to use Dorylinae for all true army ants. That at least is well supported by larval evidence.

(7) Urbani (1977:428) has stated that the larvae are the chief justification for separating the Leptanillinae from the Dorylinae.

Queens and workers show an indisputable doryline affinity and the alleged males have never been collected with workers.

(8) For this tribe we follow Kempf 1973:460.

(9) Using larval characters we helped establish (Wilson et al 1956) the subfamily Aneuretinae. Brown (1973) reverted to the Emery-Wheeler classification and returned it to the Dolichoderinae. We are not averse to a subfamily containing only one living genus and species.

On Lumping

We have been carrying on a friendly feud with Dr. Brown for many years — ever since he lumped Proceratiini into Ectatommini. We accuse him of using our larval studies when they support his conclusions based on adults and ignoring them when they contravene. It is unlikely that the controversy will ever be resolved.

So we nominate Dr. Brown for the position of Master Lumper of Myrmecology. He has lumped two subfamilies and four tribes in one subfamily; a rough estimate places the number of generic unions at more than 200. If he continues at this pace he may eventually attain the pinnacle reached by Dillon (1963), who placed all "living things" into one kingdom (Plantae). [This we consider *reductio ad absurdissimum*.] Our biological system of classification is designed to serve two purposes: (1) to indicate degrees of kinship; (2) as a convenience. It is a corollary of evolution that all organisms are related, but how convenient is it to have them all in the same taxon?

It is not that we disapprove of lumping *per se*. In fact, we regard much of it useful and correct. But some of Dr. Brown's lumps are not acceptable to us.

Since so many of these notes have dealt with Dr. Brown's changes, it may seem that we are attempting to denigrate his work. Let us invoke the vernacular and say with emphasis: NO WAY! We have the highest regard for his work; here we are merely disagreeing with a few of his conclusions that concern our studies. Our relations with Dr. Brown — both personal and professional — have been most cordial and, to us at least, beneficial. Let this paragraph serve as expression of our highest esteem.

LITERATURE CITED

BROWN, W.L. 1958. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini. Bull. Mus. Comp. Zool. Harvard College 118:175-362.

_____. 1973. A comparison of the Hylean and Congo-West African rain forest ant faunas. *In* "Tropical Forest Ecosystems in Africa and South America: A Comparative Review." Eds. E.J. Meggers, A.S. Ayensu and W.D. Duckworth. Smithsonian Inst. Press, Washington, D.C. p. 161-185.

_____. 1975. Contributions toward a reclassification of the Formicidae. V. Ponerinae, tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini, and Aenictogetini. Search 5:1-115

_____. 1976. Contributions toward a reclassification of the Formicidae. Part VI. Ponerinae, tribe Ponerini, subtribe Odontomachiti, Section A. Introduction, subtribal characters. Genus *Odontomachus*. Studia Entomol. (Rio de Janeiro) 19:67-171.

DALLA TORRE, K.W. 1893. Catalogus Hymenopterorum. VII. Formicidae. Leipzig. 289 p.

DILLON, L.S. 1963. A reclassification of the major groups of organisms based upon comparative cytology. Systematic Zool. 12:71-82

EMERY, C. 1910-1925. Hymenoptera. Fam. Formicidae. *In* Wytsman's "Genera Insectorum."

GOTWALD, W.H., AND B.M. KUPIEC. 1975. Taxonomic implications of doryline worker ant morphology: *Cheliomyrmex morosus*. Ann. Entomol. Soc. Amer. 68:961-971.

KEMPF, W.W. 1973. A new *Zacryptocerus* from Brazil, with remarks on the generic classification of the tribe Cephalotini. Studia Entomol. 16:449-462.

KISTNER, D.H. 1972. A new genus of the staphylinid tribe Dorylomimini from Africa and its possible significance to ant phylogeny. Entomol. News 83:85-91.

SNELLING, R.R. 1981. Systematics of social Hymenoptera. Chap. 5. *In* "Social Insects" Vol. II. H.R. Hermann ed. Academic Press, New York, p. 369-404.

TAYLOR, R.W. 1978. *Nothomyrmecia macrops:* a living-fossil ant rediscovered. Science 201:979-985.

URBANI, C.B. 1977. Materiali per una revisione della sottofamiglia Leptanillinae Emery. Entomol. Basiliensia 2:427-488.

WHEELER, G.C., AND JEANETTE WHEELER. 1971. Ant larvae of the subfamily Ponerinae: second supplement. Ann. Entomol. Soc. Amer. 64:1197-1217.

_____. 1972. The subfamilies of Formicidae. Proc. Entomol. Soc. Washington 74:35-45.

_____. 1976. Ant Larvae: Review and Synthesis. Mem. Entomol. Soc. Washington, No. 7, 108 p.

_____. 1984. The larvae of the army ants: a revision. J. Kansas Entomol. Soc. 57:263-275.

WHEELER, W.M. 1915. *Paranomopone*, a new genus of ponerine ants from Queensland. Psyche 22:117-120, 1 pl.

WHEELER, W.M. 1922. Keys to the genera and subgenera of ants. Bull. Amer. Mus. Nat. Hist. 45:631-710.

WILSON, E.O., T. EISNER, G.C. WHEELER AND JEANETTE WHEELER. 1956. *Aneuretus simoni* Emery, a major link in ant evolution. Bull. Mus. Comp. Zool. Harvard College 115:81-99, 3 pl.