Phylogenetic relationships and classification of ectatommine ants (Hymenoptera: Formicidae)

JOHN E. LATTKE

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The phylogenetic relationships between the genera of ants considered until now as ectatommines are investigated using cladistic methods. They are found polyphyletic and a new arrangement is proposed. Paraponerini is reinstated for *Paraponera;* Proceratiini is reinstated for *Proceratium* and *Discothyrea.* The tribe Ectatommini is reduced to the following genera: *Ectatomma, Rhytidoponera, Gnamptogenys, Heteroponera* and *Acanthoponera. Aulacopone* is placed in an informal genus group. Most fossils though to be ectatommines can not be reliably determined as such and probably belong to other formicid groups. Palaeogeography coupled with the present distribution of the taxa supports an origin of Ectatommini sometime about the early Oligocene.

John E. Lattke, Instituto de Zoología Agrícola, Universidad Central de Venezuela, Apartado 4579, Maracay 2101-A, Venezuela.

Introduction

The primitive ponerine tribe Ectatommini as we know it is the result of an exhaustive study by Brown (1958). An extensive and mostly well justified series of generic synonymies reduced a confusing array of names to 9 genera with the following distributions:

Acanthoponera Mayr - Neotropical
Heteroponera Mayr - Australian and Neotropical
Rhytidoponera Mayr - Australian and Oriental
Paraponera F. Smith - Neotropical
Ectatomma F. Smith - Neotropical
Aulacopone Arnoldi - Palearctic
Gnamptogenys Roger - Neotropical, Australian, Oriental and Nearctic
Proceratium Roger - Cosmopolitan
Discothyrea Roger - Cosmopolitan

Brown (1958: 178) discussed the likely relations among these genera and points out *Acanthoponera* as the genus presenting the most primitive characters. From this group he considered *Heteroponera* as a directly derived genus, and standing close to *Heteroponera* is *Rhytidoponera* and possibly *Aulacopone.* Also placed tentatively close to *Heteroponera* were *Proceratium* and *Discothyrea.* Thus, these genera represented for Brown a separate lineage from *Paraponera* and *Ectatomma. Gnamptogenys* posed a problem in its relation to other groups but Brown favored its proximity with *Heteroponera.* Taylor (1980) studied *Aulacopone* and considered it nearest to *Heteroponera.* He also discussed some of the ties among other ectatommine genera and supported Brown's conclusions. More recently Kugler (1991) studied the sting apparatus of six ectatommine genera and his conclusions diverge from the aforementioned studies. His findings will be taken up further along in this text.

Recent studies of the internal phylogeny of ants (Baroni Urbani et al. 1992) divide extant formicids into two groups, with the Ponerinae and Cerapachyinae in the same clade, and the Myrmeciini in another clade. According to their schema the cerapachyines bear a closer relation to ponerines than the myrmecines, so in the present study the genus *Cerapachys* F. Smith of Cerapachyinae was chosen as an outgroup. Additionally the genus *Myrmecia* Fabricius of Myrmeciinae, was also used as an outgroup for comparative purposes. Since the monophyly of Ectatommini was to be put to the test other ponerine genera were also considered: *Pachycondyla* F. Smith, *Amblyopone* Erichson, *Typhlomyrmex* Mayr, *Platythyrea* Roger, *Centromyrmex* Mayr, and *Harpegnathos* Jerden. Information for these genera was gleaned from the following literature, besides the dissection of speci-

Table 1. Taxa and character state data used in the cladistic analysis of ectatommine genera. A "?" signifies unknown or not applicable (e.g., polymorphic). Characters 1, 7, 9, 15, 33 & 35 were treated as unordered.

	1	1111111112	2222222223	333333
Charact. nos	1234567890	1234567890	1234567890	123456
Cerapachys	0121011102	0011010000	0011101000	012110
Myrmecia	0?00000000	0000001000	0000000000	000000
Paraponera	0011000102	0000001110	0010001101	004001
Proceratium	0121021102	1011110110	0011001110	012120
Discothyrea	2120032102	1021010110	0012101100	012110
Rhytidoponera	0132111111	0011200111	0010001101	113120
Ectatomma	0142111111	0011200111	0010001101	013020
Gnamptogenys	1142111112	1111200111	101000110?	?13120
Heteroponera	1121112021	1111210001	0100001100	011100
Acanthoponera	1100112001	1011210001	0100001100	011100
Pachycondyla	2120041001	0000010002	000001110?	001000
Amblyopone	2?11011001	0000110002	0010001100	002100
Typhlomyrmex	1152111000	0100210000	0010001100	012100
Platythyrea	2100010002	1100001001	0000001101	012000
Centromyrmex	2121011001	0100210000	0000001100	002000
Harpegnathos	2120010000	000010?10	0000001101	000000

mens: Baroni Urbani et al. (1992); Bolton (1990); Brown (1958, 1960, 1965, 1975); Kempf (1967); Ward (1990). The most parsimonious trees were obtained and then used for generating a strict consensus tree using the "ie" and "nelsen" options of Steve Farris' Hennig 86 phylogenetic inference program. The following characters, except where noted, are valid for the worker caste. When a genus shows variation for a meristic character state (e.g. palpal formula, number of spurs, etc.) the maximum known count was used. Characters polymorphic within terminal taxa were scored as unknown, as well as when it was not possible to distinguish the character. No specimen of *Aulacopone* was studied, and all comments about the genus depend upon the descriptions of Arnoldi (1930), and Taylor (1980). Due to the poor knowledge of *Aulacopone* (only 14 characters available out of 36) it was not included within the character matrix. The character matrix can be consulted in Table 1.

1. The degree of fusion between the basal antennal sclerites and frontal carinae was discerned in the following way: (0) antennal sclerite relatively independent of frontal carina, recognizable as a lobe at the base of the frontal carina; (1) antennal sclerite apparently fused with frontal carina, recognizable as a separate ridge along the outer margin of the frontal carina; (2) Antennal sclerite not recognizable. The last character state could represent a total fusion of the antennal sclerite with the frontal carina or simple disappearance of the ridge.
2. Mandibular proximal basal tooth: 0 = present, 1 = absent. This is character 1 of Ward (1990).
3. Maxillary palp no: 0 = 6, 1 = 5, 2 = 4, 3 = 3, 4 = 2, 5 = 1 segment.
4. Labial palp no: 0 = 4, 1 = 3, 2 = 2, 3 = 1 segment.
5. Anterior clypeal lamella, 0 = absent, 1 = present. This is a thin and narrow lamella that is found along the anterior edge of the clypeus in some ants. Its most apparent representation is found in the genus *Gnamptogenys*.
6. Anterior clypeal shape: 0 = medianly excised, 1 = medianly convex to straight, 2 = with a prominent anteromedian projection, not overhanging the mandible, 3 = with a prominent anteromedian projection overhanging the mandibles, 4 = variable. Only the general shape is taken into account, thus denticles, such as in *Amblyopone*, are not considered.
7. Funiculus: 0 = filiform or subfiliform, 1 = incrassate, 2 = clubbed.
8. Promesonotal suture: 0 = flexible, 1 = rigidly fused.
9. Shape of the prosternal process: 0 = unilobed and triangular (Fig. 1a-b), 1 = posteriorly bifurcate (Fig. 1c-e), 2 = variable. This process is best viewed after removing the forecoxae. Apparently, in some previously bifurcate processes, a lobe has developed between the apical denticles, giving the process a unilobed look.
10. Number of stout moveable setae on the foretibial apex: 0 = 2, 1 = 1 (Fig. 2a), 2 = none (Fig. 2b).
11. Row of stout setae present at the anterior edge of the foretarsal basal notch: 0 = present (Fig. 2a), 1 = absent (Fig. 2b). This region of the foretarsus is usually covered with a dense row of pilosity but the setae, when present, are quite distinct appearing as a comb.
12. Prominent seta on the foretarsal base (opposite the strigil): 0 = absent (Fig. 2a), 1 = present (Fig. 2b). In some cases the presence of the seta was easily ascertained, but sometimes careful manipulation of the lighting and specimen was necessary in order to distinguish the seta from the surrounding pilosity.
13. Number of mesotibial apical spurs: 0 = 2, 1 = 1, 2 = none.
14. Number of metatibial apical spurs: 0 = 2, 1 = 1, 2 = none.
15. Empodia: 0 = present, 1 = variable, 2 = absent. Freeland et al. (1982) briefly surveyed this trait in some ant groups and found it had a useful potential.
16. Metacoxal cavities: 0 = open, 1 = closed. This character has been used by Ward (1990), Bolton (1990) and Baroni Urbani et al. (1992).
17. Metabasitarsal sulcus (0) present; (1) absent. This is character 23 of Ward (1990) and 15 of Baroni Urbani et al. (1992). In *Platythyrea* this area presents an oval pit on the opposite side of the tarsus as the sulcus, and was not considered homologous.
18. Petiole (0) with a laterotergite; 1 = without a laterotergite. This is character 30 of Ward (1990).
19. Second abdominal tergum and sternum (petiole): 0 = not fully fused, 1 = completely fused.
20. Opening of metapleural gland directed (0) laterally; (1) obliquely or posterolaterad; (2) posterad. In cladistic studies of ants this character has been considered by Ward (1990) and Baroni Urbani et al. (1992). The frequent cuticular processes and flanges that surround this opening vary such that it is difficult to characterize the dorsal or ventral orientation of the

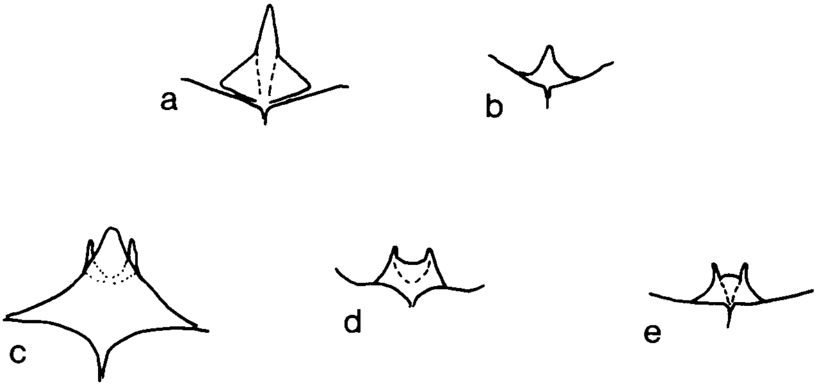


Fig. 1. Ventral view of prosternal process: (a) *Paraponera clavata,* (b) *Acanthoponera mucronata,* (c) *Ectatomma tuberculatum,* (d) *Gnamptogenys gracilis,* (e) *Heteroponera dolo.*

opening within some terminal groups (e.g., *Ectatomma*).

21. Metacoxal armature: 0 = lacking, 1 = present. An autapomorphy of *Gnamptogenys.*
22. Anterior face of third abdominal segment (0) without a carina or ridge that arches dorsad and laterad of the helcium; 1 = with such a carina. The presence of this carina is apparently an autapomorphy of acanthoponerines.
23. Posterior border of petiolar sternite (0) with lateral lobes (Figs 3a-c), 1 = without lateral lobes (Fig. 3d).
24. Helcium: 0 = protruding from abdominal segment (Fig. 5a), 1 = variable, protruding to slightly depressed, 2 = sunk within a depression, (Fig. 5b).
25. Sternum of helcium: 0 = small and inconspicuous, overlapped by tergum (Fig. 5a); 1 = large and prominent (Fig. 5b). This character has found use by Ward (1990), Bolton (1990) and Baroni Urbani et al. (1992).
26. Helcium (0) occupying a median position on the anterior face of abdominal segment III, 1 = occupying a ventral position on the anterior face of abdominal segment III. This is best appreciated in a lateral view.
27. Third abdominal tergum and sternum (0) not fully fused; 1 = completely fused and incapable of independent movement. Character 22 of Baroni Urbani et al. (1992), its use is also discussed in this reference.
28. Fourth abdominal tergum and sternum (0) not fully fused; 1 = completely fused.
29. Edge of posterior petiolar foramen, where sternite meets tergite: 0 = invaginated (Fig. 4b), 1 = straight (Fig. 4a). An apparent autapomorphy of *Proceratium.*
30. Dorsal stridulatory organ on pretergite of abdominal segment IV absent (0) or (1) present. This character is polymorphic in *Pachycondyla.*
31. Ventral stridulatory organ on presternite of abdominal segment IV absent (0) or (1) present. The stridulitra on presclerites of abdominal segment IV and its use in ant studies is discussed in Baroni Urbani et al. (1992). In the present study the existence of a stridulitrum was considered positive if a determined area of the presclerites refracted light into rainbow colors.
32. Abdominal segment IV presclerites (0) separated from rest of segment by a constriction or slightly thickening; (1) thickened as a distinct collar which along its posterior edge slightly overlaps the rest of the segment. The shape and form of the presclerites of abdominal segment IV has found varied use and definition amongst myrmecologists, see Baroni Urbani et al. (1992: 309) for a discussion.
33. Postpetiolar process in lateral view: 0 = with a vertical anterior face and a sharp ventral edge which curves concavely posterad to join the rest of the gaster (Fig. 7a), 1 = with a vertical anterior face that forms an acute angle with the ventral border (in ventral view this type of process projects anterad as a bluntly pointed triangle or lobe, Fig. 7b), 2 = process made up of low carina(e) and not outstanding, anterior face of second abdominal segment forms a right angle with its ventral border (Fig. 7c), 3 = projects anterad as a more or less broad shelf (Fig. 7d), 4 = absent (Fig. 7e).
34. Jugal lobe of hind wing: 0 = present, 1 = absent.

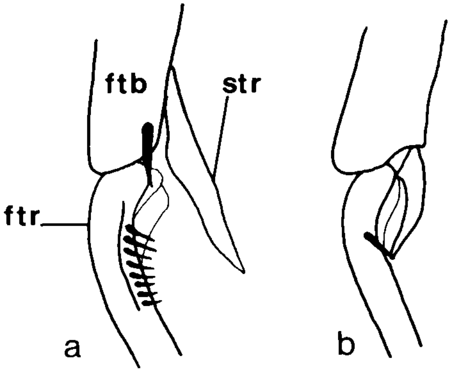


Fig. 2. Outside lateral view of foretibial-tarsal junction: (a) *Ectatomma tuberculatum,* (b) *Gnamptogenys bispinosa.* ftb = foretibial apex, ftr = foretarsal base, str = strigil.

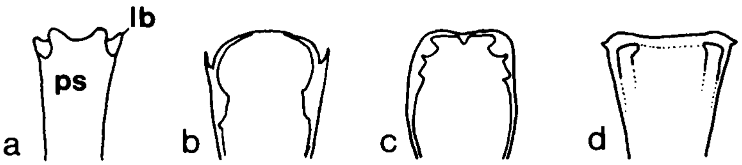


Fig. 3. Dorsal (internal) view of sterna of abdominal segment two: (a) *Myrmecia forficulata,* (b) *Cerapachys* cf. *augustae,* (c) *Platythyrea angusta,* (d) *Amblyopone lurilabes.* lb = lateral lobe, ps = petiolar sternite.

35. Curvature of the gaster is: 0 = nil to barely noticeable, 1 = noticeably arched ventrad by curvature of either abdominal segments III or IV, 2 = noticeably arched ventrad by curvature of abdominal segment IV only.
36. Lateral hypopygidial margins: 0 = without stout setae, 1 = with stout setae.

The characters as mentioned for each tribe follow the same enumeration as above.

Tribe Ectatommini

Ectatommii Emery, 1895: 767; 1901: 36. Type genus: *Ectatomma* F. Smith, 1858: 102.

Ectatommini: Ashmead 1905: 382; Forel 1916: 236; Brown 1958: 178; Kempf 1972: 262; Wheeler & Wheeler 1985: 259.

Pachycondylini: Ashmead 1905: 382 (in part).

Worker synopsis for tribe Ectatommini

1. Frontal carinae expanded laterally and covering antennal sclerite.
2. No mandibular proximal basal tooth.
3. Maximum maxillary palp count: 6.
4. Maximum labial palp count: 4.
5. Thin and narrow lamella bordering anterior clypeal margin.
6. Anterior clypeal margin convex to straight.
7. Shape of flagellum variable; from filiform to clubbed.
8. Degree of fusion of promesonotal suture variable.
9. Prosternal process posteriorly bidentate or with a lobe between the teeth, giving it a unilobed aspect.
10. Maximum number of stout setae on foretibial apex: 1.
11. Row of stout setae present or absent along anterior edge of foretibial basal notch.
12. Prominent seta on foretarsal base present or absent.
13. Mesotibial apex with one spur.
14. Metatibial apex with one spur.
15. Empodia absent.
16. Metacoxal cavities open or closed.
17. Basitarsal sulcus lacking.
18. Laterotergite on second abdominal segment absent or present.
19. Tergum and sternum of petiole rigidly fused or unfused.
20. Metapleural gland opening directed posterolaterally.
21. Metacoxae armed or unarmed.
22. Anterior face of postpetiole with or (usually) without ridge partially about the helcium.
23. Sternum of second abdominal segment with or without posterolateral lobes.
24. Helcium usually protruding from anterior face of postpetiole.
25. Sternum of helcium smaller than tergum.
26. Helcium medianly placed on postpetiolar face.
27. Postpetiolar sternum and tergum fused.
28. Fourth abdominal tergum and sternum completely fused.
29. Edge of posterior petiolar foramen invaginated.
30. Stridulitrum on pretergite of abdominal segment IV present or absent.
31. Stridulitrum on presternite of abdominal segment IV usually absent.
32. Presclerites of abdominal segment IV collar-like and slightly overlapping rest of segment.
33. Postpetiolar process variable.
34. Hind wing jugal lobe absent (except *Ectatomma*).
35. Fourth abdominal segment usually arched ventrad sometimes straight.
36. Hypopygidium unarmed.

Fig. 4. Ventral view of abdominal segment two (petiole), posterior half: (a) *Proceratium goliath,* (b) *Gnamptogenys porcata.* ps = petiolar sternite, pt = petiolar tergite.

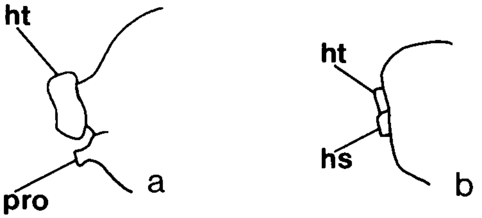


Fig. 5. Lateral view of anterior half of abdominal segment three: (a) *Rhytidoponera purpurea,* (b) *Discothyrea* sp. hs = helcium sternite, ht = helcium tergite, pro = postpetiolar process.

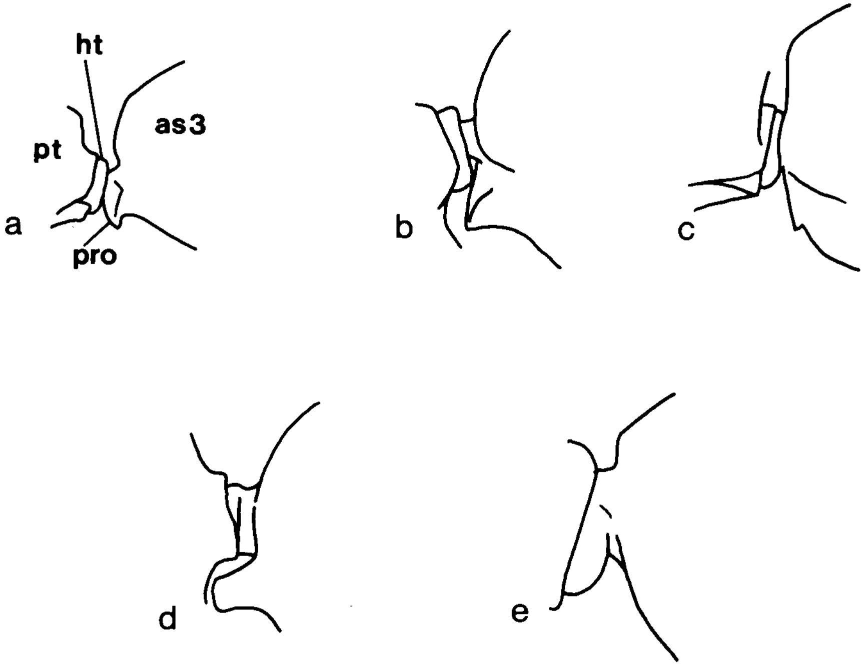


Fig. 6. Lateral view of junction abdominal segments 2 and 3: (a) *Harpegnathos saltator,* (b) *Heteroponera dolo,* (c) *Platythyrea quadridens,* (d) *Gnamptogenys gracilis,* (e) *Paraponera clavata.* as3 = abdominal segment 3, ht = helcium tergite, pro = postpetiolar process, pt = petiolar tergite.

Additional traits:

a. Median longitudinal cephalic carinae developed to varying degrees (lost or indistinct in *Gnamptogenys*).
b. Anterior (free) mesepisternal margin bordered by a thin lamella.

The tribe as presently defined can be divided into two groups: Group I includes the genera *Ectatomma* (6 species studied, 4 dissected), *Rhytidoponera* (14 species studied, 3 dissected), and *Gnamptogenys* (64 species studied, 28 dissected); Group II includes *Heteroponera* (5 species studied and 3 dissected), and *Acanthoponera* (2 species studied, 1 dissected).

Characters separating ectatommines from proceratines are as follows: 5, 9, 33. Characters that divide ectatommines from paraponerines are: 5, 6, 13-5, 17, 32, 33, 36. The following set of ectatommine characters are all considered derived: 5, 9, 15, 18-9, 34. The following characters are considered synapomorphies for the group: 5, 15.

Worker synopsis for the *Ectatomma* group

3. Maximum maxillary palp count: 3.
4. Maximum labial palp count: 2.
7. No distinct antennal club.
8. Promesonotal connection rigidly fused.
9. Prosternal process posteriorly bidentate or with a lobe between the teeth.
16. Metacoxal cavities open.
18. Petiolar laterotergite absent or indistinct.
19. Tergum and sternum of petiole rigidly fused.
20. Metapleural gland opening directed posterolaterad (obliquely).
22. Anterior face of postpetiole without ridge partially surrounding helcium.
23. Sternum of second abdominal segment without posterolateral lobes.
33. Postpetiolar process tends to project anterad as a shelf (Fig. 7d) and in ventral view is relatively broad (weakly developed in *Ectatomma*).
35. Fourth abdominal segment moderately to strongly arched ventrad (except some *Gnamptogenys* species).

Characters that can be considered derived for the group are: 3, 4, 8, 9, 18-20, 33, 35. Most of these character states can also found in other ponerine taxa, though the shape of the postpetiolar process does appear to unique to this group.

The following discussion will try to establish relationships between each genus taking into account the degree of development of characters considered in the matrix and a few others not included. In treating *Gnamptogenys* for this analysis only the *Holcoponera* and *Stictoponera* species groups were accounted for, since they represent the more primitive groups closest to the ancestral stock. Other species groups within *Gnamptogenys* represent lineages derived of relatively recent adaptive radiations and have developed a series of apomorphies, including reversals, which would encumber the considerations (Lattke, in press).

Of the three genera *Ectatomma* conserves the greatest number of plesiomorphies: the clypeal lamella can be lacking or is poorly developed in comparison with most species of *Gnamptogenys* and *Rhytidoponera.* The propodeal spiracles are well separated from the declivitous propodeal face and a modest anterior petiolar peduncle is also present in this genus. The hind wings of sexual forms still conserve the jugal lobe.

Autapomorphies for *Ectatomma* are the development of tuberculate prominences on the pronotal dorsum. Additionally, a convex lobe is produced over and between the bidentate prosternal process giving it a unilobular aspect if not examined carefully (Fig. 1). A short basal length of the outer foretibial strigil has longer and denser hairs than the rest of the strigil comb. In the other genera examined the comb is either uniformly pectinate or interrupted by short lengths of velum (sensu Schoenitzer 1987). Denticles are found on the humeri of *Gnamptogenys sinensis* Wu Jian (1987), but they certainly represent an independent development.

Rhytidoponera and *Gnamptogenys* exhibit the following synapomorphies as compared with *Ectatomma:* well developed anterior clypeal lamella in most species, spiracles shifted posterad towards the declivitous propodeal face, and winged forms lack the jugal lobe of the posterior wings. *Rhytidoponera* presents a stridulitrum on the presternite of abdominal segment IV, but this stridulitrum is absent in most *Gnamptogenys.*

For *Rhytidoponera* plesiomorphies are less than in *Ectatomma,* and of interest is the *impressa* group of species, which is considered to be the most primitive group of *Rhytidoponera* (Brown 1953: 4) and has been revised by Ward (1980). The mesonotum forms a convexity on the mesosomal dorsum, but not as prominent as in *Ectatomma.* The moveable foretarsal seta is retained, as well as the foretarsal row of setae opposite the calcar. The prosternal process usually appears unilobular but below the lobe the teeth can be observed. The petiolar peduncle is variable but at its longest it is longer than in *Gnamptogenys. Rhytidoponera* has as its distinctive apomorphy the denticle on the lateral pronotal corner.

In *Gnamptogenys* the mesonotum is sometimes quite indistinct and many species have lost the petiolar peduncle. The apical foretibial moveable setae are lost as well as the row of stout setae on the foretarsal base. Mention should be made of the single prominent foretarsal seta. In his description of the fossil *Gnamptogenys pristina* Baroni Urbani (1980: 5) reports a prominent seta interrupting the foretarsal pectinate convexity. Although failed to locate it in other species of the genus, a study of specimens at hand revealed the seta's consistent presence in members of the genus. It can be difficult to observe due to surrounding pilosity, but viewing the lateral foretarsal base with posterior lighting will usually make it visible.

Worker synopsis for the *Acanthoponera* group

3. Maxillary palp number: 6 or 4.
4. Labial palp number: 4 or 3.
7. Antennae clubbed (3 or 4 segments) or incrassate.
8. Promesonotal connection flexible.
9. Prosternal process is bifurcate or unilobed in *Heteroponera,* unilobed in *Acanthoponera.*
16. Metacoxal fossae enclosed.
18. Second abdominal segment with laterotergite.
19. Tergum and sternum of second abdominal segment unfused.
22. A carina or ridge on the anterior face of the third abdominal segment arches dorsolaterad around the helcium and is separated from it by a shallow sulcus. (Apparently lost in some *Heteroponera*).
23. Sternum of second abdominal segment with posterolateral lobes.
24. Helcium protruding from or slightly depressed in abdominal segment.
33. Postpetiolar process with a vertical anterior face that forms an acute angle with the ventral border.
35. Gaster with no pronounced ventral curvature.

Additional characters:

a. A median longitudinal cephalic carina is present.
b. Shallow antennal scrobe poorly to well developed.
c. No petiolar peduncle. The node is very close to the propodeum and it is not posible to observe the insertion of the petiole into the propodeum.

Out of the aforementioned traits the following can be considered derived: 7, 22, 33, as well as a-c. Character 22 appears to be unique for this group.

Heteroponera usually lacks a median tarsal claw, though some neotropical species have a modest median tooth. In a lateral view the mesosomal dorsum of *Heteroponera* can usually be divided into two broad convexities divided by the promesonotal suture. The mesometapleural sulcus is narrow compared with *Acanthoponera* and the antennal club has three segments. Both Brown (1958: 180) and Taylor (1979: 356) suggested *Rhytidoponera*'s closeness to *Heteroponera* due to a species of the latter genus with denticles on its lateral pronotal corners. But the apomorphies separating these two groups indicate the denticles are convergent, as well the auriculate occipital lobes of *Heteroponera inca* Brown and those of *Gnamptogenys costata* (Emery) and *G. menadensis* (Mayr).

The following suite of characters distinguish *Acanthoponera* from *Heteroponera:* strikingly large eyes, elongate palpi, antennal club of 4 segments, a long and somewhat protuberant clypeus, lack of a prominent seta along the concavity of the foretarsal base, tarsal claws with a prominent median tooth and basal lobe, long acute spines on the propodeum and node apex, and slight ventral displacement of the helcium along the anterior postpetiolar face. In a lateral view the dorsal mesosomal margin is evenly flat to weakly convex, with no trace of sutural impressions. The elongate palpi with the primitive 6,4 formula would conceivably favor their greater mobility and radius of action. This could be a response to critical conditions associated with nocturnal arboreal foraging. The presence of a prominent median tarsal tooth probably facilitates its frequent foraging on leaf surfaces. It is interesting to note hat this group develops prominent basal lobes on the tarsal claws as a probable answer for negotiating smooth leaf surfaces and did not retain nor develop empodia de novo. Of these two genera, *Acanthoponera* can be considered the most derived.

Tribe Paraponerini, trib.rev.

Paraponerini Emery, 1901: 35; Forel 1916: 236. Type-genus: *Paraponera* F. Smith, 1858: 110.
Ponerii: Forel 1893: 163 (in part).
Ectatommii: Emery 1895: 767 (in part).
Ectatommini: Brown 1958; Kempf 1972: 262; Wheeler & Wheeler 1985: 256 (in part).

Worker synopsis (unless noted) for tribe Paraponerini

1. Antennal basal sclerite with distinct ridge at base of frontal carina.
2. Mandibular proximal basal tooth present.
3. Maxillary palp 5 segments.
4. Labial palp 3 segments.
5. No anterior clypeal lamella.
6. Anterior clypeal margin medianly excised and with a denticle at each side of excision.
7. Funiculus filiform.
8. Promesonotal connection rigidly fused.
9. Prosternal process unilobed and triangular.
10. No stout moveable setae on foretibial apex.
11. Row of stout setae present on foretibial base.
12. No single prominent seta on foretarsal base.
13. Mesotibial apex with 2 apical spurs.
14. Metatibial apex with 2 apical spurs.
15. Empodia present.
16. Metacoxal fossae open.
17. Basal sulcus present on first metatarsomere.
18. Petiole without a laterotergite.
19. Tergum and sternum of second abdominal segment fused and rigid.
20. Metapleural gland opening directed laterally.
21. Metacoxa unarmed.
22. Helcium not partially surrounded by ridge.
23. Posterior border of petiolar sternite without lateral lobes.
24. Helcium protruding from abdominal segment.
25. Sternum of helcium small and inconspicuous.
26. Helcium situated medianly on postpetiole anterior face.
27. Postpetiolar tergum and sternum fused.
28. Fourth abdominal tergum and sternum fused.
29. Edge of postpetiolar foramen evaginated.
30. Stridulitrum present on pretergite of abdominal segment IV.
31. No stridulitrum on abdominal segment IV presternite.
32. Presclerites of abdominal segment IV slightly elevated above rest of segment, but not collarlike nor overlapping rest of segment.
33. Anteroventral postpetiolar process absent.
34. Hind wings of male and female with jugal lobe.
35. Gaster with no sharp anteroventral curvature.
36. Hypopygidial margins with lateral row of stout setae.

Other traits:

a. Petiole with a long peduncle.
b. Antennal scrobe well developed.
c. Anterior mesepisternal margin bordered by a low crest, not lamellate.
d. Pronotum with lateral tumosities.

This distinctive tribe harbors the sole species *Paraponera clavata.* The following traits divide paraponerines from ectatommines: 2, 5, 6, 13-15, 17, 33-2, 36. The following characters separate paraponerines from proceratines: 2, 6, 13, 14, 16-7, 30, 32-6. The whole set of derived paraponerine characters are: 8, 10, 17, 19, 30, 33, 36. Out of these 33, b, and d are autapomorphies. Even though antennal scrobes have been developed a myriad of times in different ant taxa, the shape of the scrobes in paraponerines is quite distinct and makes independent development of the attribute likely.

The opening that connects the metacoxal fossae with the metasternal incision is extremely narrow and the integument around this zone appears to be very thin as compared with *Ectatomma.* A slight angle or low tubercle is frequently found on the metacoxal dorsum, it is more round and uniform than in *Gnamptogenys* and is undoubtably convergent. Another case of convergence are pronotal prominences which can be found in most *Ectatomma,* but usually in this genus they are poorly developed and the anteromedian prominence (totally lacking in *Paraponera*) is more noticeable. Similar prominences in *Odontoponera* Mayr, a "higher ponerine", can also be considered convergent. Despite the impressive differences of adult *Paraponera,* the larvae are similar to those of the *Ectatomma* and *Heteroponera* groups, differing noticeably in the lack of spinules on the mandibles (Wheeler 1971). Pygidial but not hypopygidial spines are found in cerapachyine ants and unrelated taxa such as *Ophthalmopone berthoudi, Amblyopone* of the *reclinata* group, and *Pachycondyla crassinoda* (Bolton 1990: 65). Within the studied taxa, absence of a postpetiolar process was found to be unique, though as a final note of curiosity, the anteroventral postpetiolar process is apparently missing in the Argentine fossil ant *Ameghinoa piatnitzkyi.* The illustrations in Viana & Rossi (1957) show a postpetiolar ventral profile that tapers directly to the junction with the petiole. Unfortunately the state of preservation of these fossils makes it unwise to venture any opinions.

Tribe Proceratiini, trib. rev.

Proceratii Emery, 1885: 765; 1901: 36. Type genus *Proceratium* Roger, 1863: 171.
Proceratiini: Ashmead 1905: 382; Emery 1911: 49; Forel 1916: 236.
Ectatommini: Brown 1958: 178; Kempf 1973: 262; Wheeler & Wheeler 1985: 259 (in part).

Worker synopsis (unless noted) for tribe Proceratiini

1. Antennal insertions totally exposed, basal antennal sclerite with a ridge at base of frontal carina or not.
2. Mandibular proximal basal tooth absent.
3. Maximum maxillary palp number: 5.
4. Maximum labial palp number: 4.
5. No anterior clypeal lamella.
6. Clypeus with an anterior median projection.
7. Funiculus apically incrassate to clubbed.
8. Promesonotal suture rigidly fused.
9. Prosternal process unilobed.
10. No stout moveable setae on foretibial apex.
11. No row of stout setae along foretarsal base.
12. No prominent seta on foretarsal base.
13. Maximum mesotibial spurs: 1.
14. Maximum metatibial spurs: 1.
15. Empodia absent or present.
16. Metacoxal fossae totally enclosed by integument.
17. No metabasitarsal sulcus.
18. Laterotergite of second abdominal segment absent.
19. Tergum and sternum of second abdominal segment rigidly fused.
20. Metasternal gland opening directed laterally.
21. Metacoxa unarmed.
22. Helcium not partially surrounded by ridge.
23. Posterior border of petiolar sternite without lateral lobes.
24. Helcium protruding or sunk within a depression.
25. Sternum of helcium small or large.
26. Helcium situated medianly on anterior postpetiole.
27. Postpetiolar tergum and sternum fused.
28. Fourth abdominal tergum and sternum fused.
29. Edge of postpetiolar foramen invaginated or not.
30. No stridulatory organ on fourth abdominal pretergite.
31. No stridulitrum on fourth abdominal presternite.
32. Fourth abdominal presclerites collar-like and slightly overhanging rest of segment.
33. Postpetiolar process Y or V shaped, sometimes broadly convex.
34. No jugal lobe on hind wing.
35. Gaster strongly arched ventrad, either on account of the third or fourth abdominal segment.
36. Hypopygidium unarmed.

Species of *Proceratium* studied: 5, dissected 3. Species of *Discothyrea* studied: 5, dissected 2. Characters that separate proceratines from ectatommines are: 1, 3, 5, 9, 20. Characters separating proceratines from Paraponerini are: 1, 2, 4, 11, 13-4, 16, 36.

The study and interpretation of the character states of *Proceratium* and *Discothyrea* is problematic due to their extreme specialization and derived character states, not only is this manifest in the adult, but in the known larvae as well (Wheeler & Wheeler 1971: 1214).

Many character states are shared by cryptobiotic leaflitter species, and others appear frequently enough in obviously unrelated groups as to make such characters extremely unreliable if considered individually. A case in point is the weakly to strongly reflected gaster found in many of the aforementioned groups. This trait has apparently arisen independently a number of times and should be viewed cautiously in pointing out links between genera. The same constraint should be exercised with the following recurring convergent syndrome in small hypogeic forms of *Gnamptogenys, Heter-*

oponera, Discothyrea, and *Proceratium:* shortening of the scapes, incrassate to clubbed funicular apex, reduced pigmentation, small eyes, smoothening of the integument, fusion of mesosomal sutures, sharply angled propodeal corners, anteroposteriorly compressed node (into a disciform or scale-like shape), and a truncate anterior postpetiolar face. Also frequent is anterior displacement of the lobes of the frontal carinae, and the clypeus forming almost a right angle with the dorsal cephalic margin if the head is observed laterally.

The following lists contrast the two genera character by character.

Attributes of *Proceratium:*

a. Antennal insertions not on a clypeal prominence, which rarely overhangs the mandibles, and if so, only negligibly.
b. Clypeus frequently bluntly bidentate and occasionally bicarinate.
c. Mandibles toothed or denticulate.
e. Empodia present or absent.
f. Petiole with or without an anterior peduncle.
g. Posterior foramen of petiole with invaginations where the tergum and sternum meet.
h. Helcium weakly sunk or protruding from postpetiolar anterior face.
i. Sternum of helcium small and overlapped by tergum.
j. Fourth abdominal segment more strongly curved than III.

Attributes of *Discothyrea:*

a. Antennal insertions on a shelf-like prominence of the clypeus which overhangs the mandibles.
b. Clypeus never bidentate nor bicarinate.
c. Funiculus apically clubbed.
d. Mandibles edentate.
e. Empodia well developed.
f. Petiole sessile, never with an anterior peduncle.
g. Posterior petiolar foramen without an invagination where the tergum meets the sternum.
h. Helcium sunk within the anterior postpetiolar face, surrounded by a well defined sulcus.
i. Sternum of helcium as large as tergum.
j. Curvature of gaster can be attributed to either abdominal segment III or IV, depending upon the species.

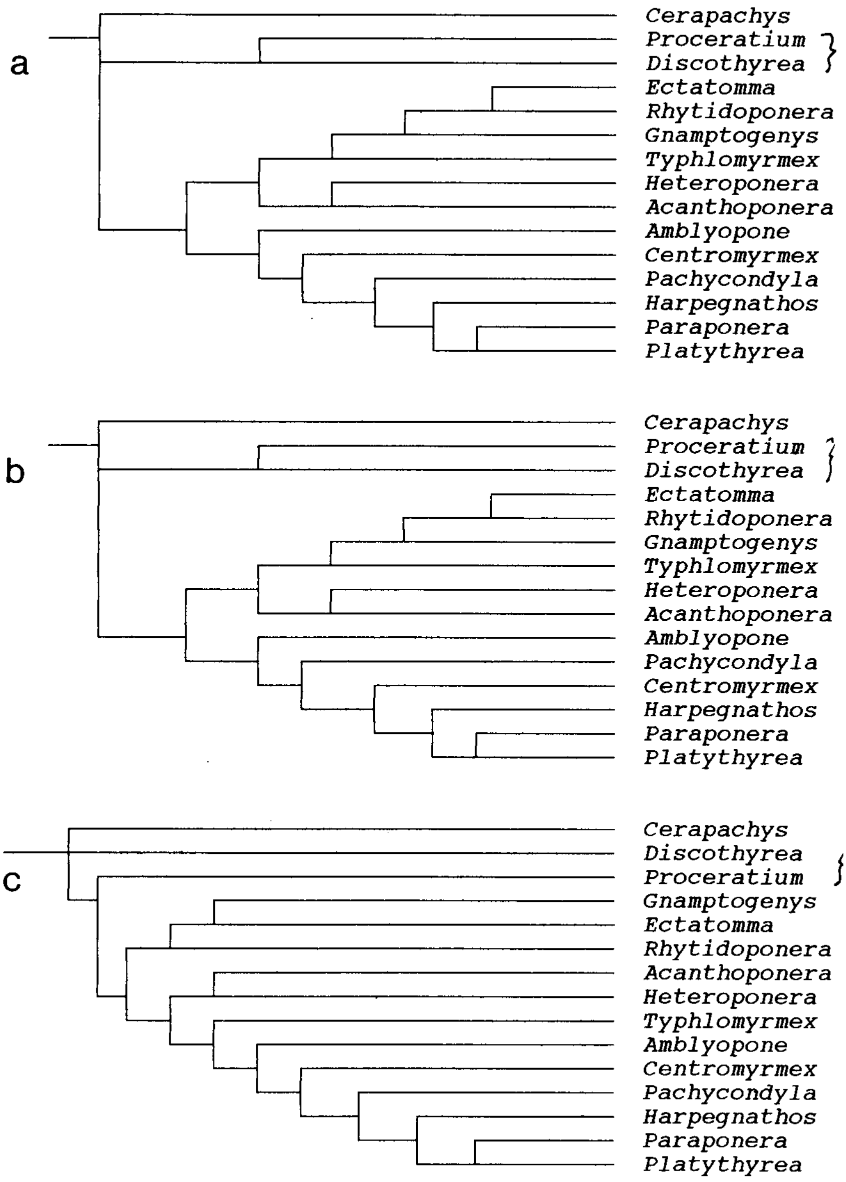
One surprise is the bulging presternite of abdominal segment III in *Discothyrea* as opposed to its state in *Proceratium* and in the rest of Ponerinae according to Baroni Urbani et al. (1992: 308). Their study includes two species of *Discothyrea* but characterizes Ponerinae as having a reduced presternite. The state of the petiolar foramen in *Discothyrea* is probably related to the structure of the helcium. The evaginations usually seen in other genera apparently permit greater movement of the overdeveloped tergum of the helcium, thus granting greater mobility to the gaster as a whole. If the helcium sternite is almost as large as the tergum, then such invaginations are not practical. Greater gastric mobility is apparently achieved in *Discothyrea* through the development of a sulcus around the helcium which gives it a longer neck while maintaining a close distance between abdominal segments II and III. The added distance to the neck of the helcium conceivably permits greater movement between the postpetiole and the posterior border of the petiole. In other ants with well developed helcium sternites, the development of the presclerites of abdominal segment IV into a ball joint grants additional mobility to the gaster.

Genus *Aulacopone*

The relations of the genus *Aulacopone* remain unknown despite Taylor's (1980) study and conclusions. The lack of empodia in workers and females is not an exclusivity of Ectatomini, and *Aulacopone*'s supposed closeness to *Heteroponera* is unfortunately grounded upon insufficient evidence. The anteriorly pronounced scape insertions, narrow clypeus and its anterior process are similar to that found in *Discothyrea* and *Proceratium,* but the structure of the anterior process and lobes are different. In some *Discothyrea* species the frontal lobes are fused behind the antennal insertions, forming a flat median area that bounds an antennal scrobe. The petiole is broadly connected to the gaster in *Aulacopone* and a similar situation is found in some *Discothyrea* but not in *Heteroponera.* As in many *Proceratium* females (and only one Australian species of *Heteroponera*) the eyes have erect pilosity. Without the consideration of other characters, including some obliging dissections, the affinities of *Aulacopone* will remain shrouded in mystery. For this reason the genus *Aulacopone* is best left in its own informal genus group until decisive data is available.

The fossil record

The "ectatommine" fossil record is open to question. This is specially true of those preserved in sedimentary deposits. Carpenter (1930) reports *Archiponera wheeleri* from the Oligocene Florissant shales of Colorado and Wheeler (1930) finds in the specimen similarities with the *Gnamptogenys* *schmitti* group. Yet Brown (1958) admits that the state of preservation of Florissant shale fossils is less than desirable. Dlusskiy (1981: 66) described? *Rhytidoponera kirghizorum* from Miocene of Kirghizia but it is apparent from the brief description and illustration that the state of preservation of the fossil is rather poor. It is hard to justify its being an ectatommine, and even more so assigning it to that extant genus, a determination which even leaves Dlusskiy unconvinced. Mayr (1868: 75) described *Ectatomma europaeum* from a winged female in Oligocene Baltic amber. Brown (1958: 181) later tentatively combined it to *Gnamptogenys europaea* based upon the original description. The confusion probably stems from the sculpture, which is mostly foveolate with costulate (kielchen) areas, an arched



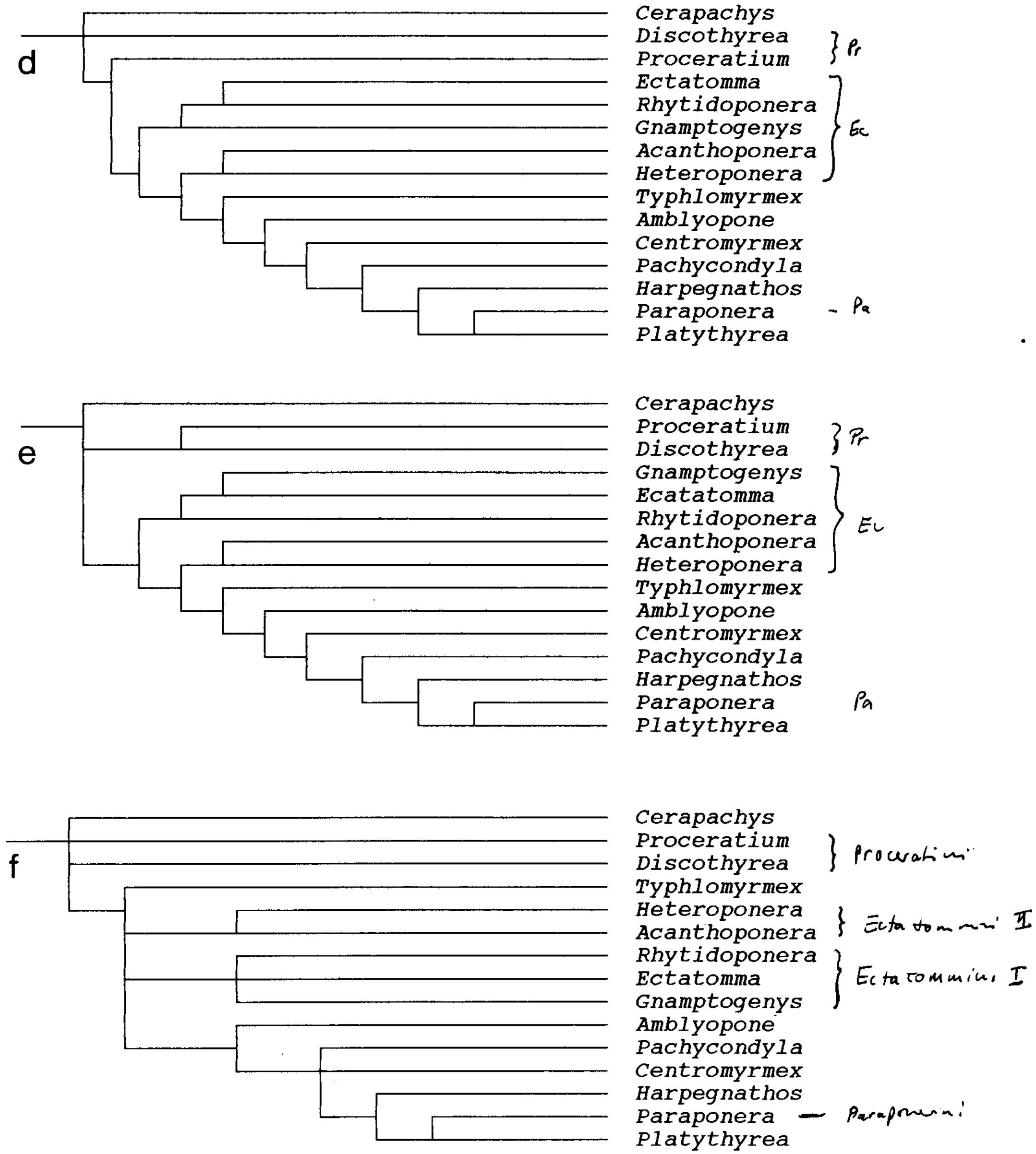


Fig. 7. Phylogenetic relations of the ectatommine genera along with other ponerine genera using as an outgroup the poneroid genus *Cerapachys*. For all trees: length 103, consistency index .53, and retention index .62. (a-e) shortest trees found, (f) Nelsen consensus tree.

anterior clypeal border, filiform funiculus, subparallel frontal carinae; an erect and slightly pedunculate petiolar node. Other than that it seems an unlikely ectatommine, and its present classification is injustified. It combines short triangular mostly punctate mandibles, scapes inserted close to the anterior cephalic border, a prominent ridge between the two propodeal faces, unarmed metacoxae, a bluntly pointed anteroventral postpetiolar process and uncurved second gastric segment. Unfor-

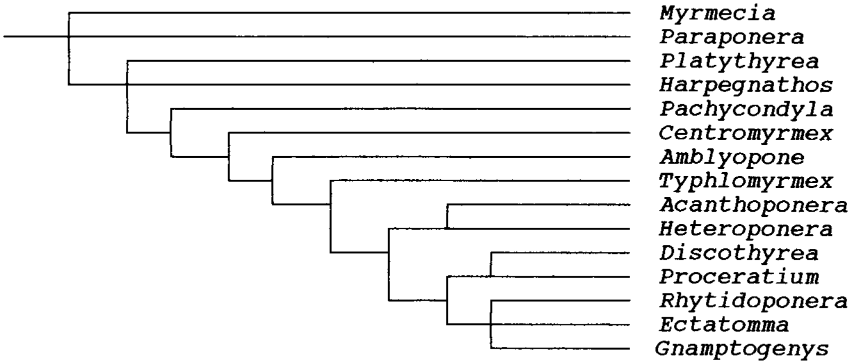


Fig. 8. Phylogenetic relations of the ectatommine genera along with other ponerine genera using as an outgroup the genus *Myrmecia*. Nelsen consensus tree calculated upon 4 shortest trees. For all trees length 105, consistency index .53 and retention index .63.

tunately the description lacks details which could have clarified the matter further and most of the Koenigsberg amber collection was dispersed elsewhere or lost during WWII. The same can be said of *Electroponera,* described by Wheeler (1915: 34) from a Baltic amber specimen mostly hidden behind an air film and thus presenting little that could justify it as an ectatommine. Wheeler (1915: 33) described the supposed male of *Gnamptogenys europaea* from another piece of Baltic amber and Emery (1891: 571) describes *Ectatomma gracile* from a male embedded in Miocene Sicilian amber. Brown & Kugler (*in* Brown & Carpenter 1978: 417) find Emery's species assignable to *Gnamptogenys* based upon the original description. Subsequent study of other Sicilian amber fossils revealed them to be so badly shrivelled and distorted that correct placement is difficult, if not impossible (Brown, pers. comm.). Taylor (1978: 360) reports seeing an ectatommine male from Kirghizian deposits. Formicid males are generally morphologically conservative and within the ectatomines, with few exceptions, do not furnish clear generic distinctions (Brown 1958: 178). Another Baltic amber species, *Bradoponera meieri* (Mayr 1868: 73; Wheeler 1914: 32) has been pointed out as a possible link between *Proceratium* and *Heteroponera* (Brown 1958: 180). A study of Mayr's careful description and Wheeler's subsequent notes in the light of the above discussion makes this genus a likely ancestral form of *Discothyrea,* with unprobable *Heteroponera* affinities. Early Miocene specimens of *Gnamptogenys* from Dominican amber (Baroni Urbani 1980) are the only reliable ectatommine fossils. These fossil *Gnamptogenys* can be placed in extant species groups, thus demonstrating a diverse fauna for the genus by this time period (Lattke, in press). Also known from Dominican amber are *Paraponera* (Wilson 1985) and *Proceratium* (Lattke 1991).

Palaeogeography and distribution

Large epigaeic ectatommines are absent from Eurasia, North America and Africa. Brown (1958: 183) explains this vacuum as a product of competitive displacement or extinction, taking into account the presence of "ectatommine" fossils in Baltic amber and Florissant shales, and the presence of *Aulacopone* in Azerbaydzhan. Baroni Urbani (1980: 9) and Taylor (1980: 360) also support this explanation. While it is not difficult to accept their extinction from Eurasia and North America, it is harder to suppose this for the total absence of ectatommines from Africa. The phylogenetic analysis of the Ectatommini coupled with their geographical distributions suggest another alternative. Taking into account palaeogeographical data of Barker & Burrell (1977), and Tarling (1980), an origin, or at least dispersal, of these groups can be hypothesized sometimes during the early Oligocene, after the separation of Africa from Gondwana (85 × 10 years B.P.), but before the separation of South America from Palaeoantarctica (34-35 × 10 years B.P.). The cosmopolitan distribution of *Proceratium* and *Discothyrea* imply an older origin for these two genera. It has been suggested that their widespread distribution is a consequence of the unobtrusive niche they occupy as predators of arthropod eggs (Brown 1958: 182). But taking into account our yet meagre knowledge of hypogaeic arthropod biology it seems premature to presume that such specialization implies reduced competitive pressures. The rich leaf litter fauna could well abound in organisms that will feed on arthropod eggs, behavior already reported for other ants (Brown 1979: 344).

Phylogenetic relations

Figure 7f is the strict consensus tree calculated from the five shortest trees found (Figs 7a-e). A basal polytomy arises involving *Proceratium, Discothyrea* and the rest of the examined genera. The next polytomy involved each of the two ectatommine groups, *Typhlomyrmex,* and the rest of the genera. There is agreement in the close relationships within the ectatommine genera of groups 1 and 2, respectively, and the separation of *Paraponera* from Ectatommini. Kugler (1991) supports the close relation of *Acanthoponera* to *Gnamptogenys* and *Ectatomma,* though with some reservation. Given the unclear relation between the acanthoponerine group and the ectatommine group they are left within the Ectatommini until further evidence can be marshalled.

The results provide sufficient base for the separation of *Paraponera* from Ectatommini and the resurrection of Emery's tribe Paraponerini. Additional support comes from Kugler's (1991) study of the ectatommine sting apparatus, which also recognizes the distinctness of *Paraponera.* Also well founded is the separation of *Discothyrea* and *Proceratium* from Ectatommini. In Kugler's (1991: 160) study of the sting apparatus two characters were found to link *Proceratium* and *Discothyrea* with the other ectatommine genera, yet they are prone to convergence, thus weakening their value. But he did find 8 synapomorphies linking the two proceratine genera as sister groups. Hashimoto's (1991) study of the sensilla of the antennal and labial palpi reveals great differences from the ectatommine genera *Gnamptogenys* and *Rhytidoponera.* These two genera are then placed within their old tribe Proceratini since they apparently bear more in common with each other than with other ponerines. Even taking this into account the differences between the two genera are surprising. Relations between *Discothyrea* and *Proceratium* need further scrutinizing as it may be possible that they are not as related as the present day evidence shows. Both taxa appear to have a long history and the shared traits found between them could be the result of prolonged similar selective pressures.

Figure 8 is a strict consensus tree derived from the four most parsimonious trees found using *Myrmecia* as an outgroup. The most important differences involving the ectatommine genera is the basal polytomy, which involves *Paraponera* and the rest of the considered taxa, and the sister-group relation of Proceratini with the *Ectatomma* group of genera. *Typhlomyrmex* is placed in a sister-group relation with Ectatommini. The results in this case support the closeness of the genera within each of the two ectatommine groups and the separation of *Paraponera* from Ectatommini.

The relative closeness of *Typhlomyrmex* to the Ectatommini is another situation that merits furter research. The genus was considered by Emery (1911) a part of a subtribe of Ectatommini and in the course of Brown's revisionary work it was left alone and elevated to tribal status, Brown (1965). In a discussion of its affinities with other groups, Brown (1965) points out some similarities with Amblyoponini and Ectatommini, but then argues against such relations. Though convinced that there was nothing in common with the amblyoponines, he did not totally rule out the possibility of ectatommine ancestors for *Typhlomyrmex.*

Most of the genera treated here can be pointed out as relatively primitive amongst the ponerines due to the median position occupied by the helcium on the anterior postpetiolar face. This character state is present in both the Myrmeciinae and Cerapachyinae and can be considered plesiomorphic. In higher ponerines, such Poneriini, the helcium has been ventrally displaced on the anterior postpetiolar face, the apparently derived state. Exceptional in this case is one *Acanthoponera* species, whose ventrally displaced helcium is an independent development.

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References

Arnoldi, K. V. 1930. Studien über die Systematik der Ameisen. IV. *Aulacopone,* einen neue Ponerinengattung in Russland. *Zoologische Anzeiger* 89: 139-144.

Ashmead, R. 1905. A skeleton of a new arrangement of the families, subfamilies, tribes and genera of the ants, or the superfamily Formicoidea. *Canadian Entomologist* 27: 381-384.

Barker, P. F. & Burrell, J. 1977. The opening of Drake Passage. *Marine Geology* 25: 15-34.

Baroni Urbani, C. 1980. The ant genus *Gnamptogenys* in Dominican amber. *Stuttgarter Beiträge zur Naturkunde* (Ser. B) 67: 1-10.

- Phylogeny and behavioural evolution in ants, with a discussion of the role of behaviour in evolutionary processes. *Ethology, Ecology & Evolution* 1: 137-168.

Baroni Urbani, C., Bolton, B. & Ward, P. S. 1992. The internal phylogeny of ants. *Systematic Entomology* 17: 301-329.

Bolton, B. 1990. Abdominal characters and status of the cerapachyine ants. *Journal of Natural History* 24: 53-68.

Brandão, C. R. & Lattke, J. 1990. Description of a new Ecuadorean *Gnamptogenys* species, with a discussion of the *Alfaria* group. *Journal of the New York Entomological Society* 98: 489-494.

Brown, W. L. 1953. Characters and synonymies among the genera of ants. I. *Breviora* 11: 1-13.

- 1958. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini. *Bulletin of the Museum of Comparative Zoology* 118: 175-362.
- 1960. Contributions toward a reclassification of the Formicidae. III. Tribe Amblyoponini. *Ibidem* 122: 143-230.
- 1965. Contributions toward a reclassification of the Formicidae. IV. Tribe Typhlomyrmecini. *Psyche* 72: 65-78.
- 1975. Contributions toward a reclassification of the Formicidae. V. Ponerinae, Tribes Platythyreini, Cerapachyini, Cylindromyrmecini, Acanthostichini and Aenictogitini. *Search, Ithaca* 5: 1-115.
- 1979. A remarkable new species of *Proceratium* with dietary and other notes on the genus. *Psyche* 86: 337-346.

Brown, W. L. & Carpenter, F. 1978. A restudy of two ants from the Sicilian amber. *Ibidem* 85: 417-423.

Carpenter, F. 1930. Fossil ants of North America. *Bulletin of the Museum of Comparative Zoology* 70: 3-66.

Clark, J. 1951. The Formicidae of Australia. I. Myrmeciinae. C.S.I.R.O., Melbourne, 230 pp.

Dlusskiy, G. M. 1981. Miocene ants of the U.S.S.R., pp. 64-83 *in* Vishnyakova et al.: New fossil insects of the U.S.S.R. *Trudy Paleontologicheskogo Institute* 183: 1-88.

Emery, C. 1891. Le formiche dell'Ambra Siciliana nel Museo Mineralogico dell'Universita di Bologna. *Memoria della R. Accademia delle Science dell' Instituto di Bologna* 1: 568-591.

- 1895. Die Gattung *Dorylus* Fab. und die systematische Einteilung der Formiciden. *Zoologisches Jahrbuch für Systematik* 8: 685-774.
- 1901. Notes sur les sous-families des dorylines et ponerines. *Annals de la Société Entomologique Belge* 45: 32-54.

Forel, A. 1893. Sur la classification de la famille des Formicides, avec remarques synonymiques. *Annals de la Société Entomologique Belge* 37: 161-167, 285-286 (not seen).

- 1916. Cadre synoptique actuel de la faune universelle des fourmis. *Bulletin de la Société Vaudoise des Sciences Naturelles* 51: 229-253.

Freeland, J., Crozier, R. H. & Marc, J. 1982. On the occurrence of arolia in ant feet. *Journal of the Australian Entomological Society* 21: 257-262.

Hashimoto, Y. 1991. Phylogenetic study of the family Formicidae based on the sensillus structures on the antennae and labial palpi. *Japanese Journal of Entomology* 59: 125-140.

Kempf, W. W. 1962. Retoques a classificação das formigas do genero *Heteroponera* Mayr. *Papeis Avulsos de Zoologia, São Paulo* 15: 29-47.

- 1967. A synopsis of the neotropical ants of the genus *Centromyrmex* Mayr. *Studia Entomologica* 9: 401-410.
- 1972. Catálogo abreviado das formigas da região neotropical. *Ibidem* 15: 1-344.

Kugler, C. 1991. Stings of ants of the tribe Ectatommini. *Insecta Mundi* 5: 153-166.

Lattke, J. 1991. The genus *Proceratium* in Dominican amber. *Caribbean Journal of Science* 26: 101-103.

- (in press). Revision of the ant genus *Gnamptogenys* in the New World. *Journal of Hymenoptera Research.*

Mayr, G. L. 1862. Myrmekologische Studien. *Verhandlungen der Zoologisch-Botanischen Verein in Wien* 12: 649-766.

- 1868. Die Ameisen des baltischen Bernsteins. *Beitraege zur Naturkunde Preussens Koeniglichen physikalisch-oekonomischen Gesellschaft zur Koenigsberg* 1: 1-102.

Schoenitzer, K. & Lawitsky, G. 1987. A phylogenetic study of the antenna cleaner in the Formicidae, Mutillidae, & Tiphiidae. *Zoomorphology* 107: 273-285.

Smith, F. 1858. Catalogue of hymenopterous insects in the British Museum. VI. Formicidae. 216 pp.

Tarling, D. H. 1980. The geologic evolution of South America with special reference to the last 200 million years. Pp. 1-14 *in* Ciochon & Chiarelli (Eds): Evolutionary biology of New World monkeys and continental drift. Plenum. 528 pp.

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

- 1980. Notes on the Russian endemic ant genus *Aulacopone* Arnoldi. *Psyche* 86: 353-361.

Viana, M. J. & Rossi, J. A. 1957. Primer hallazgo en el Hemisferio Sur de Formicidae extinguidos y catálogo mundial de los Formicidae fósiles. *Ameghiniana* 1: 108-113.

Ward, P. S. 1980. A systematic revision of the *Rhytidoponera impressa* group in Australia and New Guinea. *Australian Journal of Zoology* 28: 475-498.

- 1984. A revision of the ant genus *Rhytidoponera* in New Caledonia. *Ibidem* 32: 131-175.
- 1990. The ant subfamily Pseudomyrmecinae: generic revision and relationship to other formicids. *Systematic Entomology* 15: 449-489.

Weber, N. 1946. Two common ponerine ants of possible economic significance. *Proceedings of the Entomological Society of Washington* 48: 1-16.

Wilson, E. O. 1985. Ants of the Dominican amber 4. A giant ponerine in the genus *Paraponera. Israel Journal of Entomology* 19: 197-200.

Wheeler, G. C. & Wheeler, J. 1971. Ant larvae of the subfamily Ponerinae: second supplement. *Annals of the Entomological Society of America* 64: 1197-1217.

- 1976. Ant larvae: Review and synthesis. *Memoirs of the Entomological Society of Washington* 7: 1-108.

- 1985. A simplified conspectus of the Formicidae. *Transactions of the American Entomological Society* 111: 255-264.

Wheeler, W. M. 1915. The ants of the Baltic amber. *Schriften der physikalisch-oekonomischen Gesellschaft zu Koenigsberg* 55 (1914): 1-142.

- 1922. Ants of the American Museum Congo Expedition. VII. Keys to the genera and subgenera of ants. VIII. A synonymic list of the ants of the Ethiopian Region. *Bulletin of the American Museum of Natural History* 45: 631-1004.

- 1930. A new *Emeryella* from Panama. *Proceedings of the New England Zoological Club* 12: 9-13.

Wu Jian, X. G. 1987. A new species of the genus *Gnamptogenys* from China. *Scientia Sinicae* 23: 303-305.

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