December 1991

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Abstract

The sting apparatus anatomy is described and compared for 24 species in six of the 9 extant genera of Ectatommini: *Paraponera*, *Acanthoponera*, *Gnamptogenys*, *Ectatomma*, *Proceratium*, and *Discothyrea*. Phylogenetic analysis sorts 15 species of *Gnamptogenys* into four species groups. Phylogenetic analyses on the six ectatommine genera suggest that: 1) *Gnamptogenys* and *Ectatomma* are sister genera, 2) *Proceratium* and *Discothyrea* are sister genera, 3) *Acanthoponera* may be more related to *Gnamptogenys* and *Ectatomma* than to the others, and 4) *Paraponera* may not belong with the other five genera.

Introduction

The sting apparatus is a complex set of sclerites derived from abdominal segments 8, 9, and 10 and enclosed in a chamber formed by the 7th tergum (pygidium) and sternum (hypopygium). Because these sclerites have been internalized, they have not been used in taxonomic or phylogenetic studies until relatively recently. Studies on the Myrmicinae, Myrmeciinae and *Nothomyrmecia* (Kugler 1978a, 1978b, 1980, 1986) have shown that the sting apparatus has many characters that vary at different taxonomic levels and thus can be used to infer relationships between genera.

In this paper I turn my attention to the ponerines. The tribe Ectatommini as presently constituted (Brown, 1958; Hölldobler and Wilson, 1990) contains nine extant genera. Here I describe and compare the sting apparatuses, pygidium and hypopygium of six genera: five species of *Ectatomma*, 15 species of *Gnamptogenys*, and one species each of *Paraponera*, *Proceratium*, *Discothyrea*, and *Acanthoponera*. Phylogenetic analysis is employed to infer relationships between these genera and between the 15 species of *Gnamptogenys*. The resulting dendrograms are compared with other classifications.

Methods

Sting apparatuses were dissected from the ants, cleared in hot lactophenol solution, and usually dissected further into two halves and a separate sting. The stings were mounted in glycerin jelly for ease of precise positioning and repositioning for different views. The other sclerites were usually mounted in Canada balsam. Occasionally whole apparatuses were mounted in glycerin jelly if specimens were few and very fragile.

Voucher specimens identified with the label "Kugler 1990 Dissection voucher" are deposited in the Kugler collection.

Most preparations were drawn and measured using a Zeiss KF-2 phase contrast microscope with an ocular grid. Accuracy is estimated at ± 0.001mm at 400X magnification. The very large *Paraponera* apparatus was measured and drawn with a Zeiss dissection microscope and ocular grid; estimated accuracy ± 0.025mm at 50X magnification.

Measurements of the sting are shown in Figure 6. The boundary between the sting shaft and the valve chamber is the point where the inner wall of the sting shaft touches the outer sting wall at the anterior end of the sting shaft. In some *Gnamptogenys* species where the inner wall is displaced ventrad (Figs. 20, 24, 26, 29, 31), the boundary is the midpoint of the upper curve in the sigmoid shape of the inner wall. The boundary between the valve chamber and the sting bulb is the point where the inner and outer walls of the sting separate. **StingL** is the sum of the lengths of the

three sting regions. The **Index of Reduction (IR)** is a measure of the length of the sting relative to the size of the ant (sting shaft L / pronotal W).

Hopefully, most other terms will be clear from the labeled illustrations, but some need further illustration (See also Kugler, 1978a). **Intervalvifer sensilla** are a cluster of trichodea on the oblong plate just anterior to the articulation of triangular and oblong plates, the intervalvifer articulation. **Ramal sensilla** are a row of trichodea inside the ramus of the oblong plate. The **fulcral arm sensilla** are in two clusters of campaniformia(?) along the ventral edge of the oblong plate: one cluster just anterior to the fulcral arm, the other in the base of the fulcral arm (a + b respectively in setal counts). The **dorsoterminal chaeta** of the gonostylus is a conspicuous chaeta located on the dorsal surface at the tip of the gonostylus. The **companion seta** is longer than other setae and located adjacent to the dorsoterminal chaeta.

Phylogenetic analyses were performed with Swofford's PAUP 3.0 program for Macintosh. The *Gnamptogenys* phylogenetic analysis used eleven sting apparatus characters that varied among species. The Ectatommini phylogenetic analysis used seven characters that varied among genera. Correlated characters were avoided. Polarity was assigned to all character states *a piori* by outgroup comparison with sting apparatuses of the primitive ponerine genus *Amblyopone*. Characters were scored as "Dollo" if it seemed unlikely that a derived character state evolved more than once. Characters were scored as "irreversible" if it seemed unlikely that a derived state would have reverted to an ancestral condition. Characters were scored as "ordered" if derived states could have reversed or have arisen more than once. No characters were weighted. Trees were produced by an exhaustive branch-and-bound search with the default options.

Results

A. Descriptions

1. *Paraponera*

Specimens examined: *P. clavata*, 2 workers, Ecuador, Piedrero, 16-I-69, M. Deyrup; 2 workers, Peru, Putumayo, La Chorrera to La Sombra, 21-VIII-1920, Cornell Univ. Expedition.

Spiracular Plate (Fig. 3). Body oval, ringed with wide ridges; dorsal half of posterior edge excavated somewhat, as in *Discothyrea* and *Procer-atium*. Large dorsal notch. Medial connection a wide band narrower at midline than on either side.

Quadrate Plate (Fig. 4; some terms in Fig. 9). Body much larger than apodeme and extending over much of the posterior arm of the oblong plate; narrower dorsally to accommodate a lateral anal plate. Apodeme with medial lobe and large lateral lobe that extends a third of the way down the posterior edge of the apodeme.

Anal Plates (Fig. 4). Medial plate subtrapezoidal with about 14-16 large marginal setae. Lateral plates more or less Y-shaped and fitting around the corners of the medial plate; posterior edges ill defined; no sensilla.

Oblong Plate (Fig. 4; some terms in Figs. 11, 19, 23). Anterior apodeme short, rounded. Dorsal ridge with a dorsally projecting tubercle anterior to intervalvifer articulation. Posterior arm with narrow median lobe along whole length; no subterminal tubercle or medial projection at apex. Ventral arm separated by a large postincision that extends to dorsal ridge; fulcral arm large, triangular, heavily sclerotized on anterior and ventral edges. Plate with about 10-15 intervalvifer, 32-39 ramal, and 5+15-18 fulcral arm sensilla

Gonostylus (Fig. 4; some terms in Figs. 12, 13). Long, slender, two-segmented; distal segment much shorter than proximal; apex notched. Proximal segment with setae and chaetae scattered along sides, then densely setose posteroventrally. Distal segment densely set with longer setae dorsad and shorter setae ventrad; no dorsoterminal chaeta nor an especially long terminal seta.

Triangular Plate (Fig. 4; some terms in Fig. 14). Thick, subrectangular body constricts abruptly at junction with ramus. Dorsoapical and ventroapical processes short; no dorsal tubercle; medial tubercle large.

Lancet (Fig. 5). Long, very slender, heavily sclerotized, with two equally large valves. Apex strong, acute, with about 12 well developed dorsal barbs.

Sting (Figs. 6, 7; some terms in Figs. 15, 16, 29). Long, slender, more or less evenly tapered to apex, heavily sclerotized. Sting shaft long (62-63% of StingL; IR 0.64-0.66), slender, upturned except at tip, which is wider than high and without barbs; hemocoel small. Valve chamber 24-27% of StingL; low; not differentiated externally from base of sting shaft. Sting bulb shorter than valve chamber; sting base transversely arched, with heavy basal ridge.

Furcula (Figs. 6, 7). Dorsal arm with large lateral lobes. Ventral arms short, not fused to sting.

Pygidium. No visible pygidial glands, ducts, or reservoir; no emargination or sculpture of anterior edge of tergum often associated with pygidial glands. Simple hairs on posterior half of plate with median bare strip. No spines, tubercles or emargination on apex.

Hypopygium. Apex not notched; with median and two larger lateral spines, then with a row of blunt, thick bristles lateral to spines. Median strip without pilosity.

2. *Acanthoponera*

Specimens examined: *A. minor*, 1 worker, Costa Rica, Heredia, La Selva Field Station, III-74, C. Kugler.

Spiracular Plate. Lost in preparation.

Quadrate Plate. Like that of *Proceratium* (Fig. 36) in shape, proportions of body and apodeme, sizes of medial and lateral lobes, and medial connection.

Anal Plate. Subtriangular, with 4 long marginal setae plus one seta and 3 basiconica (or broken setae) in middle of plate. Seems to be space for a lateral plate, but cannot distinguish its outline.

Oblong Plate. Both preparations lack fulcral arms, but rest of plate seems like that of *Ectatomma ruidum* (Fig. 11). Anterior apodeme short, subacute; long postincision up to dorsal ridge; posterior arm long, slender, with no median lobe, but small tubercle at apex. Plate with 2-3 intervalvifer and 12-13 ramal sensilla (fulcral arm sensilla unknown).

Gonostylus (Fig. 8). Similar to that of *Ectatomma* (Figs. 11-13), but longer and with different setation. Apex with small notch. Proximal segment with 6 setae/chaetae and 1-2 campaniformia(?) spread along lateral surface; distal segment with 1 seta and 3-4 campaniformia anteriorly, apex with two isolated setae.

Triangular Plate. Like that of *Ectatomma* (Fig. 14), including thick body and medial tubercle, but no clear lateral tubercle.

Lancet. Well sclerotized, knife-like, caudal half weakly upcurved, lacking barbs. Two valves per lancet: anterior one moderately large, caudal one very small and weak.

Sting. Anterior half not clear, but seems similar to sting of *Proceratium* (Fig. 37), only much longer. Sting shaft well sclerotized, acute, only slightly upcurved; hemocoel large. Dorsum of valve chamber and sting bulb seem nearly membranous and little, if any, higher than base of sting shaft; can not distinguish boundaries in this preparation.

Furcula. Not discernable in poor preparation.

Pygidium and hypopygium. Not mounted.

3. *Ectatomma*

Specimens examined: *E. lugens*, 1 worker, Colombia, Putumayo, 5 km S. Mocoa, 7-I-77, C. Kugler. *E. permagnum*, 2 workers, Bolivia, Caranavi, 800m, 24-26-VI-81, Kugler and Lambert. *E. ruidum*, 3 workers, Colombia, Gairaca, 6-V-77, C. Kugler; 2 workers, Costa Rica, Heredia, La Selva Field Station, III-74, C. Kugler. *E. tuberculatum*, 2 workers, Bolivia, Caranavi, 800m, 24-26-VI-81, Kugler and Lambert. *E. quadridens*, 1 worker, Colombia, Meta, Villavicencio, 22-X-77, W. W. Lamar; 1 queen, Colombia: Meta, Trocha Quinta, 21 km N. San Juan de Arama, 600m, 24-IV-76, C. Kugler.

All workers nearly identical, except for numbers of setae and arrangement of sensilla on gonostyli. The queen of *quadridens* is the same as the worker, except for more sensilla on anal plate, oblong plates, and gonostyli.

Spiracular Plate (Fig. 10). Large, subrectangular. Spiracle small, near posterior edge in posteroventral quadrant. Anterior apodeme not enlarged. Posteroventral corner slightly more sclerotized than body of plate. Medial connection widest at midline. Deep dorsal notches.

Quadrate Plate (Fig. 9). Both apodeme and body large. Apodeme with narrow lateral and medial lobes and short anterodorsal corner; lateral lobe not extending down posterior edge of apodeme. Body with a large, rectangular, posteroventral lobe that completely overlaps the posterior arm of the oblong plate and articulates with the lateral extremities of the anal plates. Anal arc wide with thickened, well sclerotized posterior margin.

Anal Plates (Fig. 9). Median plate triangular with 9-15 long setae, mostly marginal, but a few submarginal; 1-3 submarginal basiconica. Y-shaped lateral plates articulate with corners of median plate and with posteroventral lobes of quadrate plate.

Oblong Plate (Fig. 11). Anterior apodeme very short, wide. Dorsal ridge lacking a tubercle anterior to the intervalvifer articulation; medial lobe small, confined to apex of arm. Postincision

extends to dorsal ridge. Ventral arm with two abrupt changes in thickness; thickest along ramus, which is paralleled by a thinner band, then an even thinner band leading to the fulcral arm. Fulcral arm short, linear; may partially overlap posterior arm in some preparations. Plate with 7-9 intervalvifer, 24-29 ramal, 3-4 + 0 fulcral arm sensilla in workers of all species, except the larger *tuberculatum*, which has 8-11 intervalvifer, 39-45 ramal and 3 + 0 fulcral arm sensilla.

Gonostylus (Figs. 11-13). Distinctly 2-segmented. Proximal segment in the four smaller species with 10-14 setae/chaetae ranging from very short to long and arranged in two more or less distinct patches: a posterodorsal patch containing the longest setae and a posteroventral patch generally with very short chaetae/setae. Proximal segment in the larger *tuberculatum* (Fig. 12) with an additional, more or less distinct anterior patch. Distal segment in all species with 1-4 setae or chaetae anterodorsally and 3-7 campaniform sensilla dorsad. Apex of distal segment with a short dorsoterminal chaeta and long companion seta in *permagnum*, *lugens*, and *quadridens* (Fig. 13), but with only the dorsoterminal chaeta in *tuberculatum* (Fig. 12), and no terminal sensillum in *ruidum* (Fig. 11). Apex not notched.

Triangular Plate (Fig. 14). Large, compact, with short dorsoapical and ventroapical processes. Medial tubercle on ventral process. Large lateral tubercle on body of plate.

Lancet (Fig. 14). Short, heavily sclerotized, with two large valves; distal smaller. Apex narrowed to a stiff spine; no apical barbs.

Sting (Figs. 15, 16). Short and heavily sclerotized. Sting shaft very short (43-45% of StingL; IR 0.26-0.29), deep, with large hemocoel; apex acute, about as wide as deep, without appendages. Valve chamber markedly higher than base of sting shaft and almost as long (36-40% of StingL). Sting bulb short; sting base with large basal ridge not strongly arched in anterior view; truncate in ventral view; anterolateral corners moderately prominent. In ventral view the sting tapers almost uniformly from base to apex.

Furcula (Figs. 15, 16). Weakly arched, no dorsal arm. Ventral arms overlapping sting base but not fused to it.

Pygidium. No sign of reservoir, ductules, characteristic sculpture or emargination of pygidium that might indicate presence of pygidial glands. Apex blunt, lined with short hairs. Lateral pilosity on posterior half of plate.

Hypopygium. Apex notched and lined with stiff hairs; no spines or blunt bristles. Pilosity on posterior half of plate, including along midline.

4. *Gnamptogenys*

Specimens examined: *G. annulata*, 2 workers, Venezuela, Amazonas, Alto Río Saipa, 530m, 4-II-89, J. Lattke 1258. *G. bispinosa*, 2 workers, Costa Rica, Río Reventazón, 4 km E. Turrialba, 18-22-I-73, W. L. Brown. *G. brunnea*, 2 workers, Colombia, Chocó, Finca Los Guaduales, 760 m, 2-VII-78, C. Kugler. *G. continua*, 2 workers, Venezuela, Táchira, San Cristóbal, Quebrada La Parada, 1100m, 13-IX-89, J. Lattke 598. *G. gracilis*, 2 workers, Venezuela, Bolívar, vía El Dorado-Santa Elena km 155, 1200m, 20-V-85, J. Lattke 671. *G. horni*, 2 workers, Venezuela, Bolivar, Isla Ratón, Cañón del Diablo, 500m, 18-IV-89, J. Lattke 1439. *G. interrupta*, 1 worker, Venezuela, Aragua, Parque Nacional Henri Pittier, Rancho Grande, 1000m, J. Lattke. *G. moelleri*, 2 workers, Venezuela, Barinas, Res. For. Ticoporo, 240m, 26-VIII-87, J. Lattke 1145. *G. mordax*, 2 workers, Venezuela, Zulia, El Tucuco, 6-IX-84, J. Lattke 598. *G. porcata*, 2 workers, Venezuela, Táchira, Siberia, 39.7 km WNW San Cristóbal, 1200m, 28-VIII-88, J. Lattke 1204. *G. nr. strigata*, 2 workers, Ecuador, Bolivar, 20 km vic. Balzapamba, 1850m, 18-IX-86, N. Zalaba. *G. sulcata*, 2 workers, Venezuela, Táchira, vía San Cristóbal-La Fría, Quebrada La Blanca, 550m, 9-VIII-83, J. Lattke 356. *G. tornata*, 2 workers, Venezuela, Aragua cr. Cumboto, 90 km N. Maracay, 50m, 23-VI-84, J. Lattke 521. *G. tortuolosa*, 2 workers, Venezuela, Amazonas, Alto Río Mavaca, 200m, 5-II-89, J. Lattke 1279. *G. triangularis*, 1 queen 1 worker, Venezuela, Miranda, Parque, Los Mariches, 1200m, 19-IV-86, J. Lattke. 905.

Spiracular Plate (Figs. 17, 21, 30, 32). In all species well developed, with spiracle small, positioned at or very near posterior edge; dorsal notch deep; median connection band-like, widest mesad. Plate shape varies continuously from nearly square (Fig. 17) to somewhat parallelogram-shaped (Fig. 21), to a narrow oval due to reduction of posteroventral corner (Figs. 30, 32).

Quadrate Plate (Figs. 23, 33). Larger than spiracular plate. Apodeme with thick anterior edge and well developed medial and lateral lobes on dorsal edge; lateral lobe in most species also

extending a short distance down posterior edge of apodeme, but varies in development from almost membranous and imperceptible to moderately wide and well sclerotized; anterodorsal corner prominent, acute in lateral view. Body of plate less sclerotized than apodeme, but wider; strongly produced ventrad, subtending anal plates and overlapping the oblong plates. Anal arc a band with thickened, well sclerotized posterior edge.

Anal Plates (Figs. 23, 33). Weakly sclerotized and defined. Median plate more or less oval in shape, varies from wider than long to longer than wide; with 3-11 long marginal and sometimes submarginal setae. Lateral anal plates very poorly sclerotized and lacking sensilla.

Oblong Plate (Figs. 19, 23, 27, 33). Anterior apodeme short, wide, heavily sclerotized. Dorsal ridge of posterior arm with median lobe absent (Fig. 27) or present; when present, varying from a small prominence at distal end (Fig. 19) to a wide shelf that may be flat (Fig. 23) or proximally downcurved (Fig. 33). Postincision present (Fig. 19) or absent (Figs. 23, 27, 33). Fulcral arm basically triangular, but variable in length; in some species its dorsal extremity overlaps the posterior arm of the oblong plate (Figs. 27, 33). Numbers of intervalvifer, ramal and fulcral sensilla vary intra- and interspecifically; generally more in larger ants. For example, small *brunnea* with 6 intervalvifer, 8-9 ramal, and 0 + 1 fulcral arm sensilla; largest *mordax* with 12-14 intervalvifer, 26-30 ramal, and 3-5 + 3-6 fulcral arm sensilla.

Gonostylus (Figs. 23, 33). Arises subapically from posterior arm of oblong plate; not strongly sclerotized and with few sensilla; apex not notched. Proximal segment about half to two-thirds the length of the distal segment. Proximal segment with 0-3 dorsal campaniformia(?), and caudad with either 2-3 short chaetae (Fig. 23) or 1-2 long setae plus 1-2 chaetae (Fig. 33). Distal segment always with dorsoterminal chaeta and companion seta at apex and 3-9 campaniformia(?) spaced in a line along the dorsum. In *sulcata* and some *mordax* the distal segment has an additional seta at its anterior end.

Triangular Plate (Figs. 22, 23, 33). Body compact and triangular; corners not greatly produced. Medial tubercle present, sometimes prominent, on ventoapical process; no dorsal tubercles present. Lateral face of body with a depression near the posteroventral edge; size and shape of depression varies from small and oval in some species (Fig. 33) to triangular and much larger in other species (Fig. 22). In some the depression is bounded dorsally by a narrow ridge (Fig. 22).

Lancet (Figs. 18, 23, 28, 33). Short, well sclerotized, with larger proximal and smaller distal valve in all species. Valve sizes vary from large (Fig. 23) to very small (Fig. 18). Apex abruptly spinate in some species (Fig. 18, 23), more gradually tapered in other species (Fig. 28, 33), but always acute and moderately to strongly sclerotized.

Sting (Figs. 20, 24-26, 29, 31, 34). More or less evenly tapered from base to apex in both lateral and ventral views; the three regions of the sting not indicated by distinctly different heights or widths. Sting shaft short (42%-53% of StingL; IR 0.24-0.40), wide, and deep with large hemocoel. Apex of sting shaft more acute in side view than in ventral view; in some species with a pair of small to minute lateral flanges (Figs. 24, 26, 29, 31, 34). Valve chamber quite variable in length (25%-41% of StingL) but never markedly higher than base of sting shaft. Inner wall of valve chamber lowered by a thickening of the dorsal wall of the sting, causing the hemocoel in the sting shaft to continue over the posterior portion of the valve chamber in all species except *interrupta* (Fig. 34), *continua*, and *mordax*. The length of the thickened dorsal wall varies (cf. Figs. 24, 26 with Figs. 20, 29, 31). Sting bulb relatively short; dorsal wall thin and weak just anterior to valve chamber. Sting base with a moderately thick basal ridge, which is nearly straight across, except at its slightly prominent lateral corners. Height of sting base in lateral view varies, as do shapes of basal notches (cf. Figs. 24, 26, 31, 34). Articular processes large and thick.

Furcula (Figs. 20, 24-26, 29, 31, 34). An inverted Y-shape; dorsal arm short to long, but less than length of lateral arms in side view. Not fused to sting base.

Pygidium. In at least ten species intersegmental membrane with two clusters of pygidial gland cells, one cluster on each side. Each gland cell empties into the intersegmental membrane by its own ductule. Any reservoir, if present, is not large enough for me to be confident of its existence. Anterior border of pygidium lacks the characteristic sculpture or emargination often associated with pygidial glands in other genera. Similar glands may be present in the other *Gnamptogenys* species, but lost in preparation.

Hypopygium. Apex narrowly to widely notched or truncate. Posterior half of plate densely set with long hairs, including along midline. No spines or blunt bristles.

5. *Proceratium*

Specimens examined: *P. micrommatum*, 2 workers, Honduras, Lancetilla, III-79, W. L. Brown; 1 worker, Colombia, Guajira, Río Don Diego, 5m, 9-VII-77, C. Kugler.

Spiracular Plate (Fig. 35). Posterior edge excavated in dorsal half. Spiracle small, next to posterior edge. Medial connection band-shaped, widest mesad. No dorsal notch.

Quadrate Plate (Fig. 36). Apodeme with medial and lateral lobes; lateral lobe large, extending well down the posterior edge of the apodeme. Body about twice as large as apodeme; notched posterodorsally as if to accommodate a lateral anal plate.

Anal Plate (Fig. 36). Preparation somewhat folded, but appears to have a broadly rounded posterior edge with 4-6 long marginal setae. Lateral plates, if present, very weakly sclerotized.

Oblong Plate (Fig. 36). Anterior apodeme wide, truncate. Dorsal ridge with tendon, but no tubercle anterior to intervalvifer articulation; no medial lobe on posterior arm. Large postincision separates posterior and ventral arms. Fulcral arm linear. Sensilla: 2-4 intervalvifer, 9-11 ramal, 2-3 + 0 fulcral arm.

Gonostylus (Fig. 36). Short, club-shaped, single-segmented. Distal portion with 23-28 setae and 2-3 campaniformia(?); no distinct dorsoterminal chaeta or companion seta. Apex blunt, not notched.

Triangular Plate (Fig. 36). Body, ventroapical process slender; no medial tubercle.

Lancet (Fig. 36). Single, small, membranous valve faintly visible in only one preparation. Apex acute, moderately well sclerotized, with two vestigial barbs that are not visible in lateral view preparations.

Sting (Figs. 37, 38). Sting shaft of moderate length (59% of StingL; IR 0.40), upcurved, well sclerotized and acute; hemocoel large. Valve chamber 21% of StingL, not higher than base of sting shaft; dorsal wall very thick. Sting bulb short; sting base weakly arched transversely, with strong basal ridge. Sting in ventral view narrow, almost evenly tapered from articular processes to apex; sting bulb narrows cephalad.

Furcula (Figs. 37, 38). Y-shaped with long dorsal arm. Not fused to sting base.

Pygidium. Anterior edge with strong, V-shaped medial emargination surrounded by a small patch of concentric striation. A possible reservoir visible in one preparation.

Hypopygium. Apex weakly and narrowly notched. Posterior half of plate with dense pilosity, except in a median strip.

6. *Discothyrea*

Specimens examined: *D. sexarticulata*, 1 worker, Colombia, Magdalena, El Campano, 16-V-76, C. Kugler; 2 workers, Colombia, Magdalena, San Pedro de la Sierra, 1300m, 10-II-77, C. Kugler.

Spiracular Plate (Fig. 39). Posterior edge weakly excavated dorsad; no dorsal notch. Spiracle not at caudal edge.

Quadrate Plate (Fig. 40). Similar to that of *Proceratium*, but lateral lobe of apodeme not as greatly expanded.

Anal Plate. With 5 long marginal setae. Shape distorted in preparation. No apparent lateral plates.

Oblong Plate (Fig. 40). Shape as in *Proceratium*, including unusual anterior apodeme, but fulcral arm more club-shaped. Sensilla: 3-5 intervalvifer, 6-7 ramal, 2 + 0 fulcral arm.

Gonostylus (Fig. 40). Like that of *Proceratium*, except for more acute apex. Distal portion with 24-27 setae, 0-2 campaniformia.

Triangular Plate (Fig. 40). Like that of *Proceratium*.

Lancet. Shape and sclerotization like that of *Proceratium*, but with two small, weakly sclerotized valves and no detectable barbs on apex.

Sting (Figs. 40, 41). Proportions and overall shape similar to that of *Proceratium*, but sting shaft not as cuneiform in lateral view, valve chamber higher internally, basal notch larger and sting base narrower, not arched. Sting shaft 52-54% of StingL; IR 0.40-0.41. Valve chamber 25% of StingL.

Furcula (Figs. 41, 42). Reduced to a small, flat sclerite fused to sting base.

Pygidium. Anterior edge broadly V-shaped. Anterior third of pygidium with fine, concentric striations around the median notch of the anterior edge.

Hypopygium. As in *Proceratium*.

Discussion

A. *Gnamptogenys*

Figure 1 shows the single most parsimonious tree produced the characters and assumptions in Appendix 1 (Tree Length 24; Consistency Index 0.71; Homoplasy Index 0.29). The analysis suggests four species groups among the 15 species examined. Within these groups, some species have nearly identical sting apparatuses, varying slightly in such size-related characters as length of sting and numbers of sensilla. In the list that follows, those species with nearly identical apparatuses are underlined.

Group 1: *triangularis-bispinosa*. Synapomorphies: a) lancet valves small, b) sting apex dorsoventrally compressed.

Synapomorphies of groups 2, 3, and 4: a) Spiracular plate longer than wide, rectangular to oval, b) postincision of oblong plate absent, fulcral arm short, subtriangular, c) sting shaft flanges present.

Group 2: *tortuolosa-horni-tornata-annulata-sulcata*. Synapomorphies: a) triangular plate with diagonal ridge, b) sting hemocoel in side view extends over 15-25% of the valve chamber.

Synapomorphies of groups 3 and 4: a) spiracular plate oval, b) sting shaft with apical flanges large enough to see clearly in ventral view.

Group 3: *brunnea*-nr. *strigata-porcata-moelleri-gracilis*. Synapomorphies: a) no obvious median lobe on posterior arm of oblong plate (a reversal from median lobe present in all other species), b) basal segment of gonostylus without long setae (independently evolved from group 1 according to this dendrogram).

Group 4: *continua-mordax-interrupta*. Synapomorphies: a) median lobe of oblong plate posterior arm down-curved, b) sting hemocoel limited to sting shaft (reversal from extending above valve chamber in all other species).

Characters 1, 4, and 7 have derived states that could result from sting reduction and therefore could be convergent in different groups, but all groups defined by the derived states of these characters are also defined by other characters as well.

This analysis was completed without reference to Lattke's (1991a) classification based on external anatomy. The following similarities were found: 1) group 1 species are all members of Lattke's *rastrata* group, 2) group 3 species are all members of his *striatula* group, 3) group 4 species are all members of the *mordax* subgroup within the *mordax* group, 4) three species in group 2 (*tortuolosa*, *tornata*, *sulcata*) are members of Lattke's *tornata* group, the first two being sister species. Differences are: 1) Lattke's *mordax* group contains all group 4 species plus group 2 members *horni* and *annulata*, and 2) relationships among species in my group 3 and Lattke's *striatula* group are different. In short, there is substantial concurrence between the two classifications.

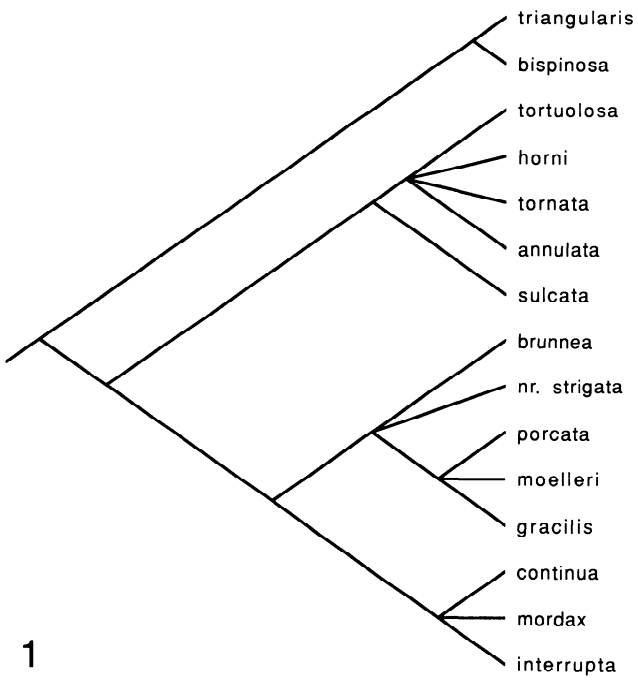

Figure 1. Shortest cladogram for 15 species of *Gnamptogenys*, based on the sting apparatus.

The results also concur with aspects of Emery's (1911, pp. 35-46) classification, which was also not consulted in advance: 1) Members of Emery's erstwhile subgenera *Parectatomma* and *Poneracantha* (*triangularis* and *bispinosa*, respectively), also separate out from all other species in my analysis. 2) All species that would be placed in Emery's genus *Holcoponera* are the five species in group 3. 3) groups 2 and 4 only contain species that would be placed in Emery's subgenus *Gnamptogenys*. However, the monophyly in my analysis of group 3 (Emery's genus *Holcoponera*) with groups 2 and 4 (Emery's subgenus *Gnamptogenys*)

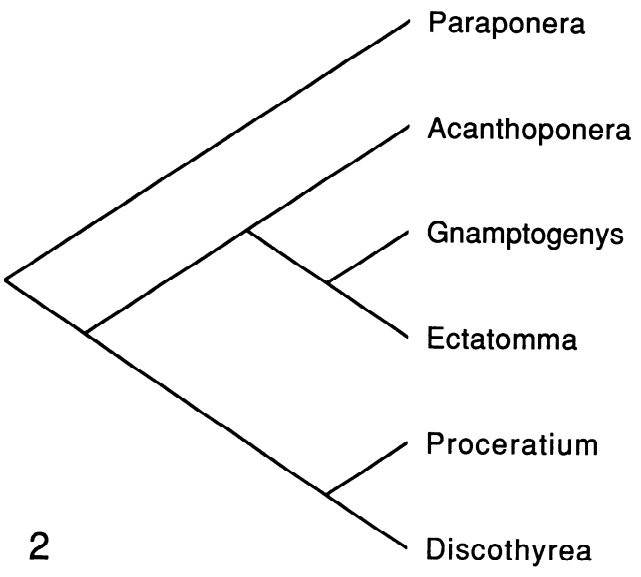

Figure 2. Shortest cladogram for six genera of Ectatommini, based on the sting apparatus.

supports Brown's (1958, pp. 216-219) view that *Holcoponera* is not a distinct genus.

B. Ectatommini

Figure 2 shows the single most parsimonious tree produced using the characters and assumptions given in Appendix 2 (Tree Length 10, Consistency Index 0.89, Homoplasy Index 0.11)

The apparatus of *Paraponera* is quite different from those of other ectatommine genera. The characteristics it shares with them are probably symplesiomorphies: 1) spiracular plate with wide medial connection and posterodorsal notch, 2) quadrate plate with distinct medial and lateral lobes and wide medial connection, 3) quadrate plate with large body extending ventral to articulation with triangular plate, 4) lateral plates present, or if not visible (*Proceratium*, *Discothyrea*), a notch in quadrate plate indicates possible presence, 5) oblong plate postincision extends to dorsal ridge at least in some species (not in most *Gnamptogenys*), 6) sting shaft with relatively long valve chamber and short sting bulb; both little wider than base of sting shaft, 7) no barbs on sting shaft. One potential synapomorphy I find with other ectatommine genera is a similar excavation of posterior edge of the spiracular plate, which is shared with *Proceratium* and *Discothyrea*. Another possible synapomorphy may be the basically triangular shape of the fulcral arm of the oblong plate, which is unlike that of *Amblyopone*. However, *Nothomyrmecia* has a fulcral arm like that of *Paraponera*, which could mean that the triangular shape is a primitive condition and this similarity among ectatommines may also be symplesiomorphic. The only potential autapomorphy of *Paraponera* is the undulating and dorsoventrally compressed shape of sting shaft, but this trait is also seen in *Nothomyrmecia* (Kugler, 1980). Until I better understand the distribution of these characters in ants and potential ant ancestors, I can not say how *Paraponera* may be related to other ant genera, except that it is not clearly linked to other ectatommines.

The other five ectatommine genera are linked in this dendrogram by the reduction in sting length and the loss of the large lateral lobes of the furcula's dorsal arm. However, these are states that often result from sting apparatus reduction and thus are prone to convergence. If the simple dorsal arm of the furcula (character 6) and the shorter sting length (character 7) were independently derived, then *Proceratium* and *Discothyrea* may not be monophyletic with *Acanthoponera*, *Gnamptogenys*, and *Ectatomma*.

The position of *Acanthoponera* in Figure 2 should be taken lightly. Several of the characters used in the analysis had unknown states in this genus because I had only a single specimen to work with and because parts of the apparatus were lost in the preparation process. Its synapomorphies with *Ectatomma* and *Gnamptogenys* are: 1) triangular plate thick-bodied, almost equilaterally triangular plates, and 2) sparse pilosity on distal segment of the gonostylus. The pair of isolated sensilla on the end of the gonostylus may also be seen as a similarity, though they are both setiform in *Acanthoponera*, whereas one is chaetiform in *Gnamptogenys* and *Ectatomma*.

Ectatomma and *Gnamptogenys* are linked in the phylogenetic analysis by a single synapomorphy, the spine-like lancet apex. This synapomorphy assumes that the spine-like lancet apex was acquired by the ancestor of *Gnamptogenys* and *Ectatomma*, but has subsequently been lost in some *Gnamptogenys* species. In addition, the spiracular plates of *Ectatomma* are very much like the plates of some *Gnamptogenys* species, but this might be symplesiomorphic. Unlike the other genera, the gonostyli of some species of *Ectatomma* and all *Gnamptogenys* bear dorsoterminal chaetae and companion setae. The sting shaft, though

strong and acute, is short (IR 0.24-0.40 in *Gnamptogenys*; 0.26-0.30 in *Ectatomma*), but *Proceratium* (IR 0.40) and *Discothyrea* (IR 0.40-0.41) are similar. Autapomorphic features of *Gnamptogenys* are: 1) spiracle very near posterior edge of spiracular plate, 2) distal segment of gonostylus much longer than proximal segment (subequal in *Ectatomma* and *Acanthoponera*; much shorter in *Paraponera*), and 3) lateral flanges on sting apex in many *Gnamptogenys* species. Autapomorphic features of *Ectatomma* are: 1) ventral arm of oblong plate with thickened band, and 2) furcula not fused to sting base, but with dorsal arm absent.

Proceratium and *Discothyrea* are clearly sister genera. At least eight synapomorphies link these two genera: 1) abrupt reduction in width of the dorsal portion of the spiracular plate, 2) lateral anal plates apparently absent, 3) fulcral arm of oblong plate extending all the way to the dorsal ridge, 4) gonostylus single-segmented, club-shaped, and with similar pilosity, 5) triangular plate with slender body and long ventroapical process, 6) lancet valves highly reduced (also present, probably convergently, in some *Gnamptogenys*), 7) sting bulb sides more strongly convergent than in other genera, and 8) anterior edge or the pygidium V-shaped and with concentric striations. They differ shape of the spiracular plates, height of the sting valve chamber, and construction of the sting base and furcula.

In conclusion, the grouping of genera produced by phylogenetic analysis closely reflects relationships implicit in the classification of Emery (1911, pp. 4-5, 27-52), even though I purposely did not consult his classification until after my analysis was finished. Emery treated *Paraponera* as a separate, monotypic Tribe Paraponerini. His Tribe Ectatommini contained four subtribes. The subtribe Ectatommini contained (among others) *Acanthoponera* and *Ectatomma*, with *Gnamptogenys* treated as a subgenus of *Ectatomma*. His subtribe Proceratiini contained (among others) *Proceratium* and *Discothyrea*. Wheeler (1922, pp. 636-645) employed the same classification with respect to these taxa, except for elevating the Proceratiini to full tribal status, a move that my analysis does not support.

Unlike Emery's classification, however, erstwhile *Holcoponera* species are clearly members of the the genus *Gnamptogenys*, rather than a separate genus. Also, the clear affinity of Emery's *Ectatomma Parectatomma triangularis* and *Ectatomma Poneracantha bispinosa* with *Gnamptogenys sensu stricto* supports Brown's (1958) synonymy of *Parectatomma* and *Poneracantha* with *Gnamptogenys* and the elevation of *Gnamptogenys* to a full genus.

Although the sting apparatus of *Paraponera* does not seem especially related to those of other ectatommines examined, we should not necessarily resurrect Emery's Tribe Paraponerini for two reasons. First, it is still possible that if the whole subfamily Ponerinae were considered, *Paraponera* would have a greater affinity to *Ectatomma* and its relatives than to other taxa. Second, it should be stressed that my conclusions are based on single character system. A more inclusive analysis including external characters may yield different results. Indeed, an alternative classification based on phylogenetic analysis of numerous, often new, external characters is being prepared by Lattke (1991b).

These results, therefore, should not be construed as a classification scheme, but rather, as an alternative hypothesis that should be tested by phylogenetic analysis in the context of the Ponerinae as a whole and using multiple character systems.

Acknowledgments

I am deeply grateful to John E. Lattke for supplying identified specimens of all *Gnamptogenys* species and for showing me his unpublished manuscripts.

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Appendix 1
Phylogenetic Analysis of *Gnamptogenys*: Characters and Transformation Assumptions

In the list below, the ancestral character state is assumed to be 0. Character state transformation assumptions follow the list of states for each character.

1. Spiracular plate shape: (0) square, with distinct anteroventral and posteroventral corners, (1) clearly longer than wide, with distinct anteroventral and posteroventral corners, (2) oval, with posteroventral corner reduced to broad curve (Irreversible).
2. Median lobe of oblong plate's dorsal arm: (0) not clearly present, (1) a straight shelf of variable length and width, (2) shelf-like, but curved ventrad at its proximal end (Dollo).
3. Oblong Plate: (0) postincision present and fulcral arm long, narrow, strongly angled, (1) postincision absent and fulcral arm short, subtriangular, erect, not overlapping posterior arm, (2) postincision absent and fulcral arm short, subtriangular, erect, and with narrow dorsal lobe that overlaps posterior arm (Dollo).
4. Gonostylus basal segment: (0) with 1 or 2 long setae, (1) without long setae (Irreversible).
5. Triangular plate ridge (0): absent, (1) present (Dollo).
6. Lancet apex: (0) gradually tapered, (1) abruptly spine-like (Dollo).
7. Lancet valves: (0) large, (1) small (Irreversible).
8. Sting apex: (0) not compressed dorsoventrally, (1) compressed dorsoventrally (Dollo).
9. Sting flanges: (0) absent, (1) present, but tiny and not visible in full ventral view, (2) present and clearly visible in full ventral view (Dollo).
10. Sting hemocoel: (0) limited to sting shaft (in side view), (1) extended anteriad over 25% of valve chamber, (2) extended anteriad over 25-50% of valve chamber, (3) extended anteriad over more than 50% of valve chamber (Dollo).
11. Basal notch of sting: (0) distinctly concave from articular process to sting base, (1) not distinctly concave throughout (Ordered).

	CHARACTERS										
	1	2	3	4	5	6	7	8	9	10	11
G. triangularis	0	1	0	1	0	1	1	1	0	3	1
G. bispinosa	0	1	0	1	0	1	1	1	0	3	1
G. tortuolosa	1	1	1	0	1	0	1	0	1	1	1
G. horni	1	1	1	0	1	1	0	0	1	1	1
G. tornata	1	1	1	0	1	1	0	0	1	1	1
G. sulcata	1	1	2	0	1	1	0	0	1	1	0
G. annulata	1	1	1	0	1	1	0	0	1	1	0
G. brunnea	2	0	2	1	0	0	0	0	2	3	0
G. nr strigata	2	0	2	1	0	0	0	0	2	3	0
G. porcata	2	0	2	1	0	0	0	0	2	2	0
G. moelleri	2	0	2	1	0	0	0	0	2	2	0
G. gracilis	2	0	2	1	0	0	0	0	2	2	0
G. continua	2	2	2	0	0	0	0	0	2	0	0
G. mordax	2	2	2	0	0	0	0	0	2	0	0
G. interrupta	2	2	2	0	0	0	0	0	2	0	0

Table 1. *Gnamptogenys* phylogenetic analysis data matrix.

Appendix 2
Phylogenetic Analysis of Ectatommini: Characters and Transformation Assumptions

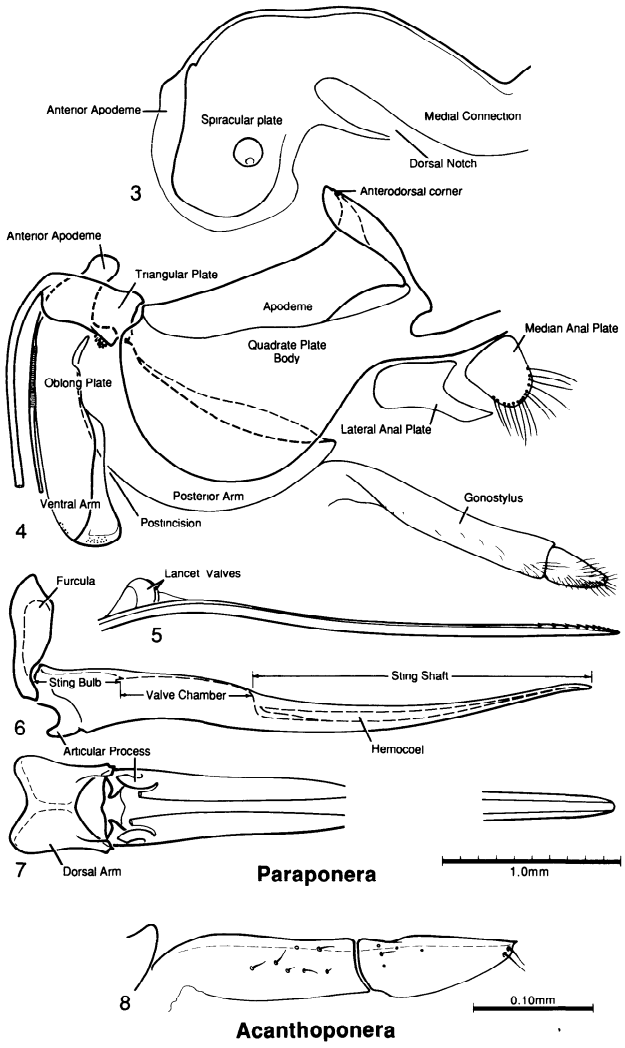
In the list below, the ancestral character state is assumed to be 0. Character state transformation

assumptions follow the list of states for each character.

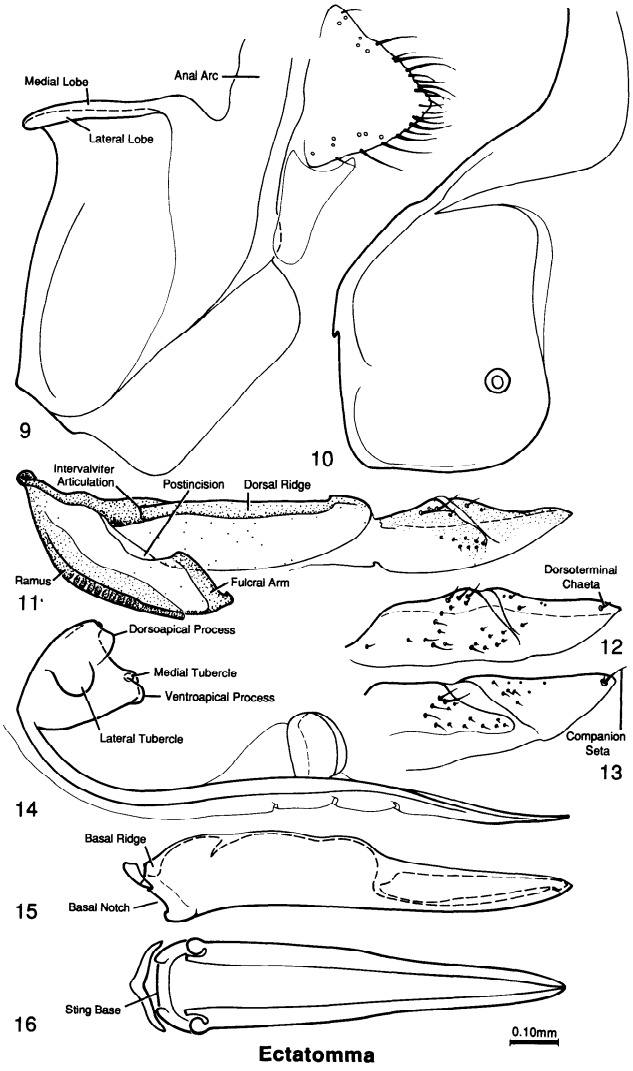
1. Spiracular plate posterior edge: (0) not reduced, (1) abruptly reduced in dorsal half (Ordered).
2. Oblong plate fulcral arm: (0) not extending along entire postincision, (1) extending along entire postincision to dorsal ridge of oblong plate (Ordered).
3. Gonostyli: (0) two segmented, (1) single segmented and club-shaped (Irreversible).
4. Gonostylus pilosity: (0) abundant on distal segment (or distal half of single segment), (1) sparse on distal segment or half (Irreversible).
5. Lancet apex: (0) not spine-like, (1) spine-like in at least some species (Dollo).
6. Furcula dorsal arm: (0) large, with lateral flanges, (1) a distinct, simple shaft, without flanges, (2) reduced to a small tubercle, or absent, (3) furcula fused to sting base (or lost entirely); no dorsal arm (Irreversible).
7. Index of Reduction: (0) > 0.60, (1) < 0.60 (Irreversible).

	CHARACTERS						
	1	2	3	4	5	6	7
Paraponera	1	0	0	0	0	0	0
Acanthoponera	?	0	0	1	0	?	1
Gnamptogenys	0	0	0	1	1	1	1
Ectatomma	0	0	0	1	1	2	1
Proceratium	1	1	1	0	0	1	1
Discothyrea	1	1	1	0	0	3	1

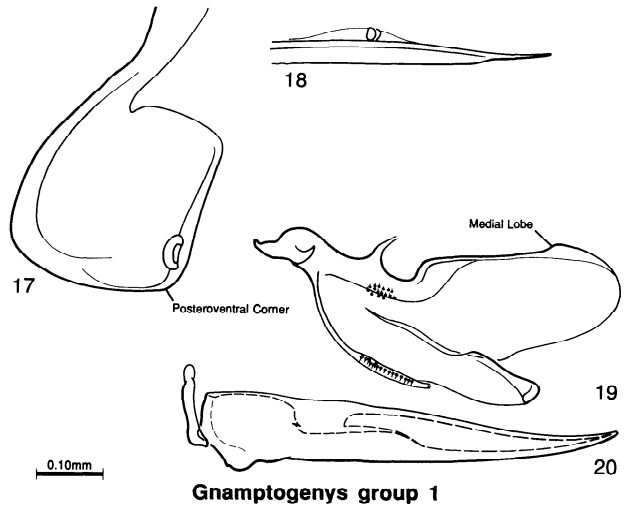
Table 2. Ectatommini phylogenetic analysis data matrix.



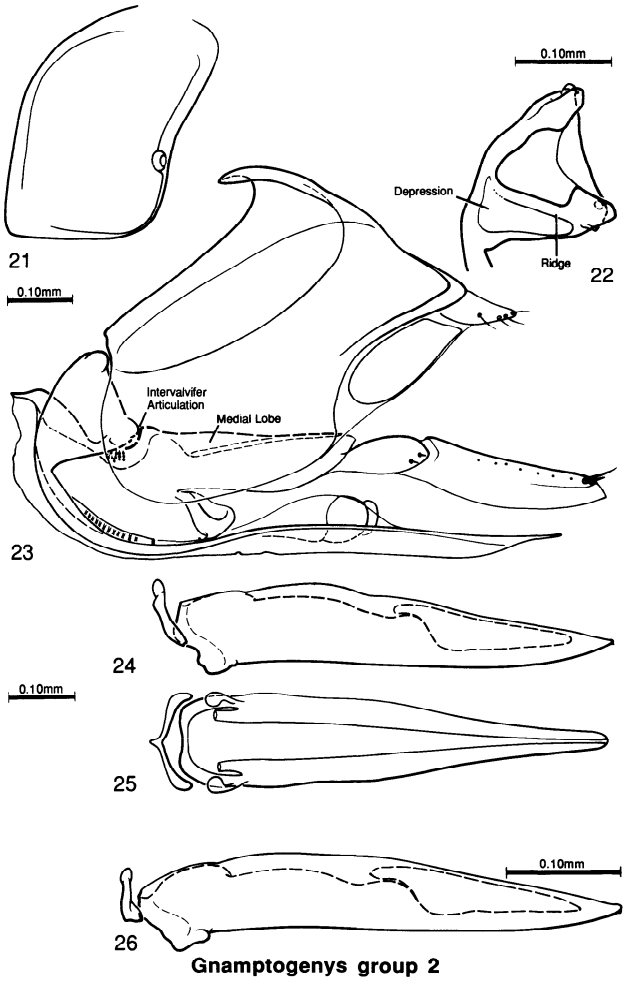
Figures 3-8. *Paraponera clavata*. 3. Lateral view spiracular plate; dorsal view medial connection. 4. Lateral views quadrate plate, lateral anal plate, oblong plate, gonostylus, triangular plate; dorsal view median anal plate. 5. Lateral view lancet. 6-7. Lateral and ventral views sting, furcula. 8. *Acanthoponera minor*, lateral view gonostylus.

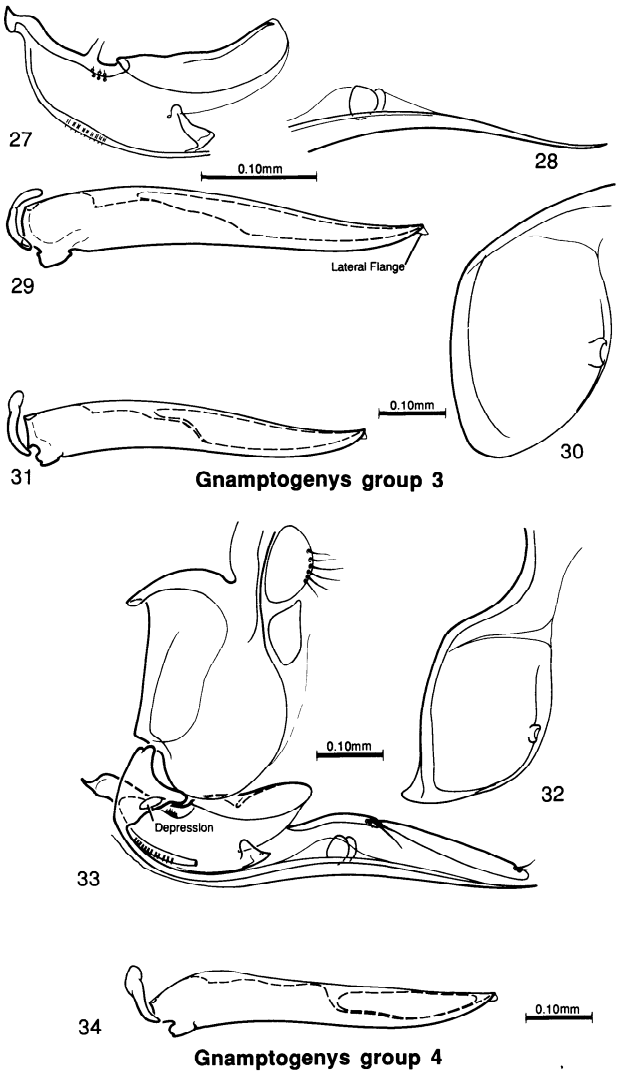


Figures 9-16. *Ectatomma*. 9. *E. lugens*, lateral views quadrate plate, lateral anal plate; dorsal view median anal plate. 10. *E. ruidum*, lateral view spiracular plate; dorsal view medial connection. 11. *E. ruidum*, lateral views oblong plate, gonostylus. 12. *E. tuberculatum*, lateral view gonostylus. 13.*E. quadridens*, lateral view gonostylus. 14. *E. ruidum*, lateral views triangular plate, lancet. 15-16. *E. ruidum*, lateral and ventral views sting, furcula.



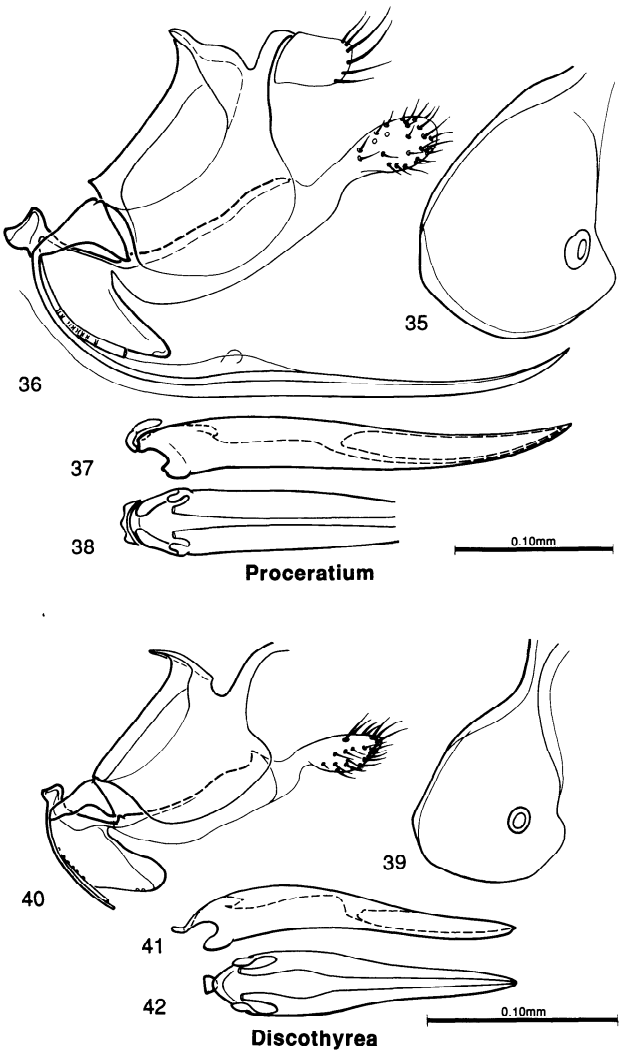
Figures 17-20. Representatives of *Gnamptogenys* group 1. 17. *G. triangularis*, lateral view spiracular plate. 18. *G. triangularis*, lateral view lancet. 19. *G. bispinosa*, lateral view oblong plate. 20. *G. bispinosa*, lateral views sting, furcula.





Figures 21-26. Representatives of *Gnamptogenys* group 2. 21. *G. sulcata*, lateral view spiracular plate. 22. *G. annulata*, detail of triangular plate. 23. *G. annulata*, lateral views quadrate plate, anal plates, oblong plate, gonostylus, triangular plate, lancet. 24-25. *G. annulata*, lateral and ventral views sting, furcula. 26. *G. horni*, lateral views sting, furcula.

Figures 27-34. Representatives of *Gnamptogenys* group 3. 27. *G. brunnea*, lateral view oblong plate. 28. *G. brunnea*, lateral view lancet. 29. *G. brunnea*, lateral views sting, furcula. 30. *G. moelleri*, lateral view spiracular plate. 31. *G. moelleri*, lateral views sting, furcula. Figs. 32-34. Representatives of *Gnamptogenys* group 4. 32. *G. continua*, lateral view spiracular plate; dorsal view medial connection. 33. *G. continua*, dorsal view median anal plate; lateral views quadrate plate, lateral anal plate, oblong plate, gonostylus, triangular plate; lancet. 34. *G. interrupta*, lateral views sting, furcula.



Figures 35-38. *Proceratium micrommatum*. 35. Lateral view spiracular plate. 36. Lateral views quadrate plate, anal plate, oblong plate, gonostylus, triangular plate, lancet. 36. Lateral views sting, furcula. 37. Ventral views furcula, anterior portion of sting. Figs. 39-42. *Discothyrea sexarticulata*. 39. Lateral view spiracular plate; dorsal view medial connection. 40. Lateral views quadrate plate, oblong plate, gonostylus, triangular plate. 41-42. Lateral and ventral views sting, furcula.