

THE STING APPARATUS IN THE PRIMITIVE ANTS *NOTHOMYRMECIA* AND *MYRMECIA*

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Abstract

The skeletomusculatures of the sting apparatuses of *Nothomyrmecia macrops* Clark and several *Myrmecia* species are described and compared to each other, and to those of other ants and Hymenoptera. Although *Nothomyrmecia* is often considered the most primitive living ant, its sting apparatus is more derived than those of *Myrmecia* and the primitive ponerine *Amblyopone*. Stings of these three genera show no clear derivation from those of other Hymenoptera.

Introduction

Taylor's (1978) rediscovery of *Nothomyrmecia macrops* Clark, an ant regarded as a "living fossil," has kindled hopes that research now possible on all aspects of its biology will produce fresh insights into the origin and evolution of the ants. One facet deserving close scrutiny is its internal anatomy. Comparative studies of internal or internalised structures, such as the proventriculus (Eisner 1957 and references) and mouthparts (Gotwald 1969), have contributed significantly to hypotheses of formicid phylogeny and classification, and recently the sting apparatus has shown promise of becoming an important taxonomic tool (Foerster 1912; Hermann 1969; Blum and Hermann 1978; Kugler 1978, 1979a, b). This paper is an examination of the phylogenetic position of *Nothomyrmecia* within the Formicidae, as based on sting apparatus morphology, and secondarily, a further test of this character system.

I will first describe the sting apparatus in detail for *N. macrops* and several species of *Myrmecia* (bulldog ants), and then address three questions: 1) How closely related are *Nothomyrmecia* and *Myrmecia*? They have been split into two subfamilies (Clark 1952; Taylor 1978), or lumped into one (Brown 1954; Wilson *et al.* 1967). 2) Does the sting apparatus conform to the notion that *Nothomyrmecia* is the most primitive living ant (Wilson 1971; Taylor 1978)? 3) Does sting apparatus morphology give any clues to ant ancestry?

Methods

All dissections were performed on specimens preserved in 70% ethanol, or on rehydrated pinned specimens. Musculature was examined on whole preparations in alcohol. Skeletal structures were dissected, cleared, and slide-mounted. See Kugler (1978) for details of slide preparation and definitions of terms. Voucher specimens deposited in the Australian National Insect Collection, Canberra, and the Museum of Comparative Zoology, Harvard University, bear the label "Kugler Study 1979".

Results

Nothomyrmecia (Figs 1-6)

Species examined.—*N. macrops*, 4 ♀♀.

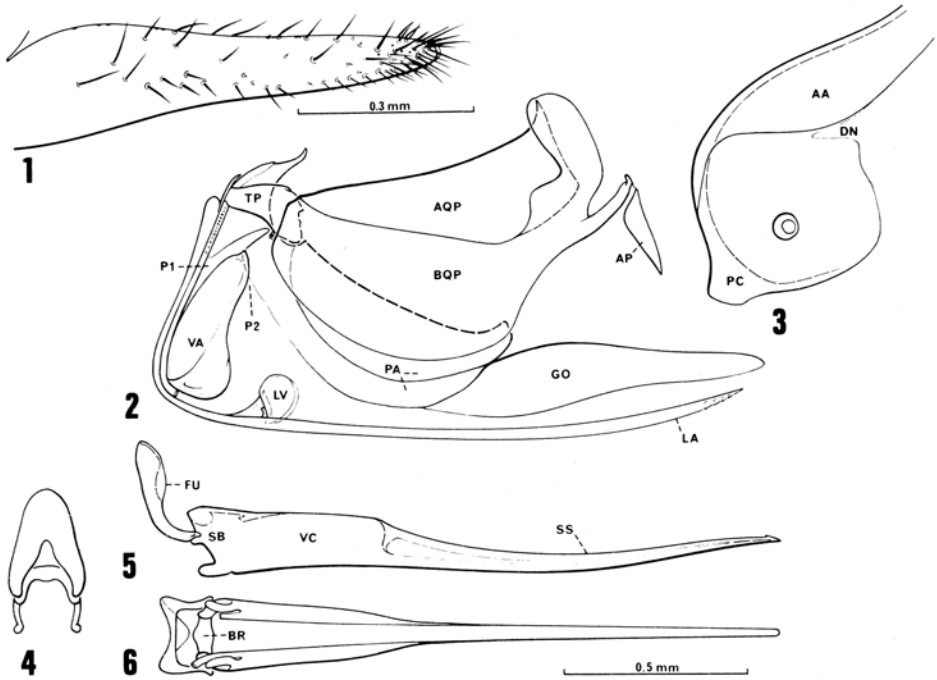
Spiracular plate (Fig. 3). Wide anterior apodeme connects two halves of plate; a heavy ridge borders leading, ventral and posterior margins. Posteroventral corner produced as a rounded lobe for muscle attachment. Narrow dorsal notch present; no posterodorsal lobe.

Quadrate plate (Fig. 2). Apodeme well sclerotised, subtriangular; topped by wide medial and lateral flanges, the latter extending part way down the apodeme's caudal border. Body of plate large, grading into membrane ventrad.

Anal plate (Fig. 2). Longer than wide in dorsal view, with rounded lateral and caudal margins and truncate anterior edge; perimeter well defined. All setae (13-15) located along edge of caudal half of plate; most are long, tapered, trichoid sensilla, but three near midline are chaetiform in all specimens.

Oblong plate (Fig. 2). Strongly subdivided by membranous pre- and postincisions that separate the ventral arm from the remainder of the plate, then join and extend to the dorsal ridge. Posterior arms of opposite plates connect apically by membrane only; dorsal ridge strong. Sensilla counts (ranges for single oblong plates): intervalvifer, 17-23; ramal, 13-17; fulcral, 13-15.

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FIGS 1-6—Sting apparatus sclerites of *Nothomyrmecia macrops*: (1) gonostylus, lateral view; (2) quadrate, anal, triangular and oblong plates, gonostylus and lancet, lateral view; (3) spiracular plate, flattened to show lateral and caudal aspects; (4) furcula, anterior view; (5) sting and furcula, lateral view; (6) sting and furcula, ventral view. Abbreviations: AA, anterior apodeme; AP, anal plate; AQP, apodeme of quadrate plate; BQP, body of quadrate plate; BR, basal ridge; DN, dorsal notch; FU, furcula; GO, gonostylus; LA, lancet; LV, lancet valves; P1, preincision; P2, postincision; PA, posterior arm of oblong plate; PC, posteroventral corner; SB, sting bulb; SS, sting shaft; TP, triangular plate; VA, ventral arm of oblong plate; VC, valve chamber. Figs 2-6 drawn to same scale.

Gonostylus (Figs 1, 2). One-segmented, but in some preparations I detect a very slight thinning of the dorsal wall at about four-fifths of its length, probably the vestige of an articulation. Sclerotisation on dorsal surface and apical quarter of lateral surface grades insensibly into membrane anteroventrad. Sensilla distribution does not reflect two segments; counts (ranges for single gonostyli): trichoid, 56-72; basiconic, 6-14; campaniform, 10-16. No dorsoterminal chaeta.

Triangular plate (Fig. 2). Dorsal edge shorter than ventral edge; base abruptly narrowed and attaching perpendicularly to first ramus. Dorsal and medial tubercles present.

Lancet (Fig. 2). Two equally large valves per lancet. Shaft well sclerotised, with strong dorsal ridge in caudal half and ventral ridge throughout; height increases slightly to near apex. Six barbs per lancet.

Sting (Figs 5, 6). Well sclerotised, exertile. Sting shaft 65-67% of sting length, upcurved, tapered evenly to fine apex endowed with one pair of dorsal barbs. Subapex of shaft slightly wider than high; not as high as exposed parts of lancets. Valve chamber long (23-24% of sting length), profile weakly differentiated from sting bulb and sting shaft; internal apophysis strong, but not markedly extending chamber length. Sting bulb short (9-11% of sting length), with large basal ridge and prominent, narrowly rounded anterolateral corners. Campaniform sensilla present from sting apex to about midlength on valve chamber. Index of reduction (sting shaft L/pronotal W) $\times 100$ 88-103; higher values are from smaller individuals.

Furcula (Figs 4-6). Dorsal arm thin, transversely arched. Ventral arms in side view narrow, strongly curved.

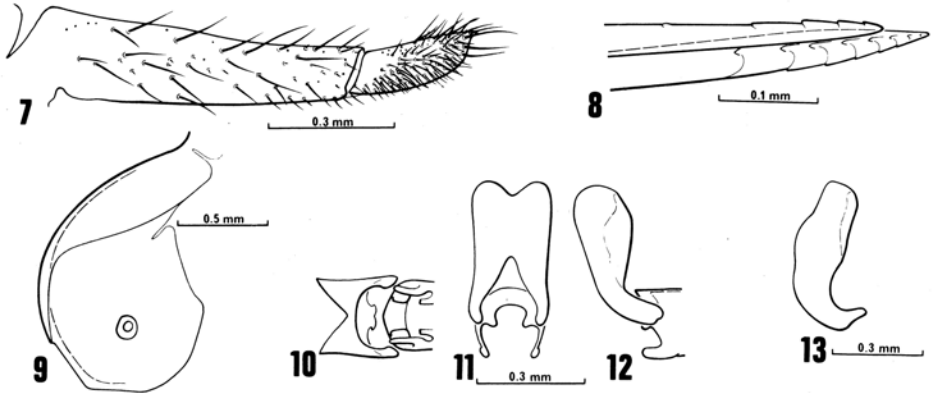
Musculature. As described and illustrated by Daly (1955) for *Paraponera clavata* F. (Ponerinae), with only minor exceptions. I could not find his muscles 6 (T7 to spiracular plate) or 10 (S7 to spiracular plate), but in *Nothomyrmecia* they may be used with the parallel and contiguous muscles 7 and 11, respectively. Instead of muscle 30 running from the dorsal end of the quadrate plate to the anal plate, there is a muscle with the same origin inserting on the wall of the hindgut, well before the anal plate. With that insertion, it is more like muscles Daly found in the Apidae (34, 36-38). In every other respect his descriptions check out perfectly, though in parts I wish they were more specific. For instance, the medial and lateral lobes of the quadrate plates provide extra surface area for the attachments of muscles 26 and 27 on the ventral surfaces, and muscle 12 on the upper surface; muscle 43 originates on all three parts of the oblong plate surrounding the junction of the pre- and postincisions (in *Nothomyrmecia*); and muscle 40 originates on the second ramus and anterior edge of the ventral arm. I should point out for future investigators that the account of *P. clavata* musculature

by Hermann and Blum (1966) contains several errors. Their summary of sting musculature in ants (Blum and Hermann 1978, Table 6) omits one muscle, and gives confusing composite descriptions of origins and insertions in various Hymenoptera for other muscles.

Myrmecia (Figs 7-13)

Species examined.—*M. mandibularis* F. Smith, 1 ♂; *M. nigrocincta* F. Smith, 1 ♀; *M. piliventris* F. Smith, 1 ♀; *M. pyriformis* F. Smith, 9 ♀♀; *M. vindex* F. Smith, 1 ♀.

Although the *Myrmecia* sting apparatus has been treated by others (Rietschel 1937; Cavill *et al.* 1964; Robertson 1968; Hermann 1975), their descriptions and figures are either very sketchy, or deal mainly with the sting-associated glands. None permit detailed comparisons of the skeletomusculature.



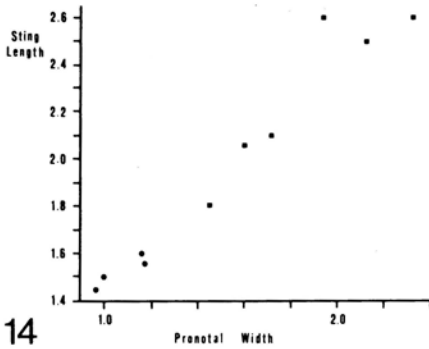
Figs 7-13—Sting apparatus sclerites of *Myrmecia* spp.: (7) gonostylus of *M. pyriformis*, lateral view; (8) end of sting and lancet of *M. nigrocincta*, lateral view; (9) spiracular plate of *M. pyriformis*, flattened; (10-12) furcula and sting base of *M. mandibularis*, ventral, anterior and lateral views, respectively; (13) furcula of *M. pyriformis*, lateral view.

The figures given for *Nothomyrmecia* largely suffice for *Myrmecia* as well, since the latter differ from *N. macrops* only in the following ways. All sclerites more strongly sclerotised. Posteroventral corner of spiracular plate in *piliventris* neither as broad nor as prominent as in *N. macrops*, and not at all salient in *pyriformis* (Fig. 9), *nigrocincta* or *vindex*. Medial connection of spiracular plate with median notch deep in *vindex* and some *pyriformis* (Fig. 9) to shallow or absent in other *pyriformis* (no correlation with size of ant) and other species. Anal plate in all *Myrmecia* with both marginal and submarginal sensilla (25-40), all trichoid. Gonostylus (Fig. 7) with two segments separated by a membranous articulation; distal segment very strongly sclerotised, especially in *mandibularis* and *piliventris*, but proximal segment with more or less distinct, irregular membranous area on proximal 30-70% of lateral surface. Gonostylar sensilla numerous: trichoid, 127-272; basiconic, 9-27; campaniform, 14-35. Each lancet (Fig. 8) with seven to 12 barbs, depending on the species. Index of reduction of sting 74 (*vindex*) to 94 (*piliventris*). Sting shaft with four to 12 pairs of dorsal barbs occupying 9-80% of sting shaft; only the terminal two to four pairs (Fig. 8) approximate *Nothomyrmecia* barb size, others visible only at 400 \times . Basal ridge of sting in all but *pyriformis* narrower mesad than in *N. macrops* (Figs 10, 12). Furcula (Figs 10-13) in all *Myrmecia* with wider, bilobed dorsal arm; *mandibularis* and *piliventris* also with more strongly developed caudal expansion of dorsal and ventral arms (Fig. 12). Musculature of *pyriformis* is like that of *Nothomyrmecia* in all respects. Other *Myrmecia* musculatures were not examined.

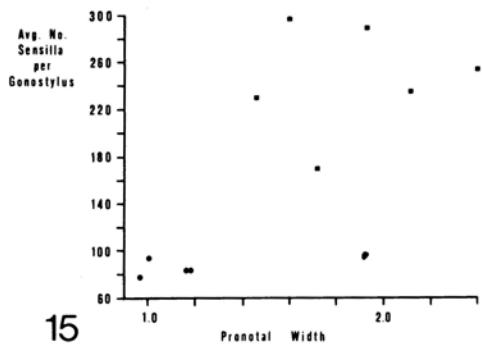
Aside from variation in numbers of sensilla, I find no consistent differences between the apparatuses of major and minor workers of *pyriformis*.

Discussion and conclusions

Most of the differences between the sting apparatuses of *Nothomyrmecia* and these *Myrmecia* species are probably due to the prevalingly smaller size of the former ants. For example, the reductions in sting lengths (Fig. 14) and sensilla counts (Fig. 15) with smaller body size may be continuations of trends within *Myrmecia*. Unfortunately, smaller species of *Myrmecia* were not available for study. Other characters not obviously related to size also intergrade, but four do seem constantly different in my sample (*Myrmecia* states given first): 1) anal plate with vs without submarginal sensilla, 2) anal plate without vs with chaetae, 3) dorsal arm of furcula bilobed vs unilobed, and 4) gonostyli two- vs one-segmented. It may reasonably be argued that these are size-related reductions also, but so far I detect no intermediate states, and such reductions of the gonostyli and furcula do not seem to be necessary consequences



14



15

FIGS 14-15—Examples of variation in sting apparatus with size (pronotal width) of individuals of *Nothomyrmecia macrops* (circles) and *Myrmecia* species (squares). *M. pyriformis* is represented by two individuals, a major and a minor. All measurements in millimetres. (14) Variation in sting length with pronotal width; (15) variation in average number of sensilla per gonostylus with pronotal width.

of smaller body size, since ants much smaller than *Nothomyrmecia* (e.g. *Amblyopone*) exhibit the *Myrmecia*-like characters. I judge the difference between the *Myrmecia* and *Nothomyrmecia* sting apparatuses to be at about the same level as that found between closely related myrmecine genera (Kugler 1978). Most characters are either identical or intergrade, but several characters that are apparently discontinuous and derived support their standing as distinct genera. In no way does the sting apparatus of *Nothomyrmecia* appear more primitive than that of *Myrmecia*.

Moreover, the *Nothomyrmecia* apparatus does not seem more primitive than that of the primitive ponerine, *Amblyopone pallipes* (Kugler 1978). *Amblyopone* has all the primitive characters found in *Myrmecia* and *Nothomyrmecia* (except for submarginal sensilla on the anal plate), plus a sting that I consider somewhat more primitive. The sting of *A. pallipes* is much longer relative to the size of the ant (index of reduction 119); the sting shaft is more strongly upcurved and takes up more of the total sting length (75-76%); and the valve chamber is shorter (17% of sting length), lower, and much less differentiated from the sting shaft in profile. A strongly curved sting is probably a derived state for the Hymenoptera in general (Brothers 1975), but not in the Formicidae where the tendency for reduction results in a shortening and/or straightening of the sting, especially the sting shaft (Foerster 1912; Kugler 1978). Size and shape of the valve chamber have not been considered in the Hymenoptera literature, but within the Myrmecinae I found both cases of dilation and cases of reduction of the chamber in the more advanced genera. Where reduction in size of the chamber had occurred, it was correlated with reduction in size and sclerotisation of many other parts of the sting apparatus. Since none of the rest of the *Amblyopone* apparatus is at all weak or foreshortened, its valve chamber is probably not either, and the latter's smaller size than in *Nothomyrmecia* more likely reflects the ancestral, rather than derived, condition.

Present knowledge of sting apparatus morphology in the Hymenoptera helps us little in deciding on the origins of the Formicidae. Only a fraction of the available characters in the aculeate apparatus have been catalogued (Daly 1955; Brothers 1975), and nearly all of those that resemble formicid characters are either symplesiomorphies or reduction convergences. This is the case for even the more recently proposed ancestors or sister groups of ants: bethylids (Wheeler 1928; Malyshev 1968), tiphiids (Wheeler 1928; Brown and Nutting 1950; Brown 1954; Wilson *et al.* 1967), scoliids (Wheeler 1928; Brothers 1975), sierolomorphids and vespids (Brothers 1975). Hermann (1975) however, has brought attention to several potential synapomorphies between the primitive ants and *Typhoctes peculiaris* Cresson (Bradyobaenidae of Brothers 1975; Mutillidae of others): 1) the gonostylus with distal segment shorter than proximal, and 2) the apically upcurved sting. But even these rather unusual characters for the Aculeata appear in taxa regarded as only distantly related to the typhoctids and formicids on other grounds. The pompilids and some sphecids have similar gonostyli, and the apids and some sphecids also have upcurved stings. In order to sort the

convergences from true synapomorphies, we need more detailed descriptions and more information on variation and function of the sting apparatus within the families of Hymenoptera. Perhaps then we could use this structure to help link the ants and wasps.

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References

- BLUM, M. S. and HERMANN, H. R. JR (1978).—Venoms and venom apparatuses of the Formicidae: Myrmeciinae, Ponerinae, Dorylinae, Pseudomyrmecinae, Myrmicinae, and Formicinae. Venoms and venom apparatuses of the Formicidae: Dolichoderinae and Aneuretinae. Chapters 25 and 26, pp 801-894, *In* Bettini, S. (Ed), "Arthropod Venoms". Springer-Verlag: Berlin, New York.
- BROTHERS, D. J. (1975).—Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *Univ. Kans Sci. Bull.* **50**: 483-648.
- BROWN, W. L. JR (1954).—Remarks on the internal phylogeny and subfamily classification of the family Formicidae. *Insectes Sociaux* **1**: 21-31.
- BROWN, W. L., JR and NUTTING, W. L. (1950).—Wing venation and the phylogeny of the Formicidae. *Trans. Am. ent. Soc.* **75**: 113-132 + 2 pl.
- CAVILL, G. W. K., ROBERTSON, P. L. and WHITFIELD, F. B. (1964).—Venom and venom apparatus of the bull ant, *Myrmecia gulosa* (Fabr.). *Science N.Y.* **146**: 79-80.
- CLARK, J. (1951) [1952].—"The Formicidae of Australia. Volume 1. Subfamily Myrmeciinae". Commonwealth Scientific and Industrial Research Organisation: Melbourne.
- DALY, H. V. JR (1955).—A comparative study of the sting of aculeate Hymenoptera. M.A. thesis, University of Kansas.
- EISNER, T. (1957).—A comparative morphological study of the proventriculus of ants (Hymenoptera: Formicidae). *Bull. Mus. Comp. Zool., Harv. Univ.* **116**: 439-490 + 25 pl.
- FOERSTER, E. (1912).—Vergleichend-anatomische Untersuchungen über den stechapparat der Ameisen. *Zool. Jahrb., Abt. Anat. Ontog. Tiere* **34**: 347-380.
- GOTWALD, W. H. JR (1969).—Comparative morphological studies of ants, with particular reference to the mouthparts (Hymenoptera: Formicidae). *Mem. Cornell Univ. Agric. Exper. Sta., Ithaca, N.Y.* **408**: 1-150.
- HERMANN, H. R. JR (1969).—The hymenopterous poison apparatus: Evolutionary trends in three closely related subfamilies of ants (Hymenoptera: Formicidae). *J. Ga. ent. Soc.* **4**: 123-141.
- HERMANN, H. R. JR (1975).—The ant-like venom apparatus of *Typhoctes peculiaris*, a primitive mutillid wasp. *Ann. ent. Soc. Am.* **68**: 882-884.
- HERMANN, H. R. JR and BLUM, M. S. (1966).—The morphology and histology of the hymenopterous poison apparatus. I. *Paraponera clavata* (Formicidae). *Ann. ent. Soc. Am.* **59**: 397-409.
- KUGLER, C. (1978).—A comparative study of the myrmicine sting apparatus (Hymenoptera, Formicidae). *Stud. Entomol.* **20**: 413-548.
- KUGLER, C. (1978) [1979a].—Further studies of the myrmicine sting apparatus: *Eutetramorium*, *Oxyopomyrmex*, and *Terataner* (Hymenoptera, Formicidae). *Psyche* **85**: 255-263.
- KUGLER, C. (1979b).—Evolution of the sting apparatus in the myrmicine ants. *Evolution* **33**: 117-130.
- MALYSHEV, S. I. (1968).—"Genesis of the Hymenoptera and the Phases of their Evolution". Haigh, B. (translator); Richards, O. W. and Uvarov, B. (Eds). Methuen: London.
- RIETSCHEL, P. (1937).—Bau und Funktion des Wehrstachels der staatenbildenden Bienen und Wespen. *Zeitschr. Morph. Ökol. Tiere.* **33**: 313-357.
- ROBERTSON, P. L. (1968).—A morphological and functional study of the venom apparatus in representatives of some major groups of Hymenoptera. *Aust. J. Zool.* **16**: 133-166.
- TAYLOR, R. W. (1978).—*Nothomyrmecia macrops*: A living-fossil ant rediscovered. *Science N.Y.* **201**: 979-985.
- WHEELER, W. M. (1928).—"The Social Insects: Their Origin and Evolution". Kegan Paul, Trench and Trubner: London.
- WILSON, E. O. (1971).—"The Insect Societies". Belknap/Harvard University Press: Cambridge.
- WILSON, E. O., CARPENTER, F. M. and BROWN, W. L. (1967).—The first Mesozoic ants, with the description of a new subfamily. *Psyche* **74**: 1-19.

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