

Nothomyrmecia macrops^o:
A Living-Fossil Ant Rediscovered

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The most primitive living ant, previously an enigma,
rediscovered and the subject of international study.

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The Australian ant *Nothomyrmecia macrops* was described by Clark in 1934 (1) from two worker specimens in the National Museum of Victoria, Melbourne. The species was classified in a new monotypic higher taxon, now tribe Nothomyrmecini of subfamily Myrmeciinae (1-3). Other myrmeciine genera are *Myrmecia* (Australia, about 65 species; New Caledonia, 1 species), *Prionomyrmex* (Oligocene, Baltic Amber, 1 species), and *Ameghinoa* (early Tertiary, Argentina, 1 species) (4). The myrmeciines are considered the most structurally generalized of all ants, apart from the North American Cretaceous fossil *Sphecomyrma freyi* (subfamily Sphecomyrminae) (5). *Myrmecia*, while fully eu-

social, has significantly primitive behavior (6, 7). *Nothomyrmecia* has been recognized as the most generalized of these insects and hence the most primitive known living ant, the descendent of a group important in formicid phylogeny (5, 7), and a likely near facsimile of species extant perhaps 60 million years ago or more. There has been speculation on the outside possibility that its behavior, when known, might represent an early stage in formicid social evolution (3, 7, 8). Study of the Melbourne specimens has been limited by their being dry-mounted, while the developmental stages and adult sexual forms have remained unknown. In the absence of further collections, *N. macrops* has be-

come, naturally enough, a "holy grail" to ant specialists, and its "rediscovery in the living condition" has been stated as "one of the principal challenges of modern Australian entomology" (8).

Clark's specimens were probably collected near the western end of the Great Australian Bight by an excursion party that traveled, in December 1931, southward from near Balladonia through mallee-type *Eucalyptus* woodland and forest and set up camp for several weeks at the Thomas River mouth, east of Esperance, in the extensive sand plain heath present there. Insects were collected, without precise data, for a local naturalist, Mrs. A. E. Crocker, who sent them to Clark. Many Australian and American collectors and expeditions have since unsuccessfully sought *Nothomyrmecia* in this area, especially in the sand plain heath, where a guild of similarly pale colored, large-eyed, nocturnally foraging ants is well represented (8).

Nothomyrmecia was rediscovered on 22 October 1977 southeast of Ceduna on the Eyre Peninsula of South Australia by a CSIRO field party that had camped overnight en route from Canberra to Western Australia (9). Workers and dealate queens were collected while foraging nocturnally on the ground and tree trunks in disturbed roadside mallee woodland, but colonies were not lo-

The author is a Principal Research Scientist and Curator of Hymenoptera (Formicidae) with the Australian National Insect Collection, Entomology Division, CSIRO, Canberra.

cated. The collection site is about 1000 kilometers east of the Balladonia-Thomson River Track, which the party later surveyed without finding the ant, despite knowledge of its likely habitat preferences. Another well-informed party has since worked the area south of Balladonia, without success (10). In a visit in

General Anatomy

Workers of *N. macrops* (Fig. 1, A to C) average about 10 millimeters in length. Although often likened superficially to *Myrmecia* (3, 7), they more closely recall the formicine weaver ants of genus *Oecophylla*. Their pale yellow-

mecia, is moderately heavily sculptured, and bears abundant long erect hairs. The first metasomal segment (abdominal II) forms a petiole, and, unlike *Myrmecia*, *Prionomyrmex* (11), or *Ameghinoa* (12), there is no constriction behind abdominal III, delimiting a postpetiole. The sting is prominent and effective, with moderately painful delivery. The metapleural glands each comprise a dense pad of very small cells, whereas most other ants investigated have many fewer, loosely scattered, large cells, as in *Myrmica* (Myrmicinae) (13). A large thin-walled apical extension of each metapleural bulla receives the numerous glandular ducts and apparently represents an expanded "sieve plate." *Myrmecia* has a similar metapleural gland structure, which might be unusual among ants.

Summary. The Australian *Nothomyrmecia macrops* is the most primitive living ant. Until recently rediscovered, it was known only from two 46-year-old specimens, both workers. All developmental stages and adult castes are now known. Adults have stridulatory organs placed ventrally, between abdominal sternites III (with plectrum) and IV (with stridulitrum), differing from all other Hymenoptera, where these organs are dorsal. The chromosome number is the highest recorded for Hymenoptera ($2n = 92$). Virgin queens are brachypterous. Other anatomical and behavioral features are reviewed. Most are primitive for ants, many being shared with *Myrmecia*, another primitive Australian genus. Fundamental differences in abdominal structure place *Myrmecia* near the base of the poneroid phylad of ant subfamilies, while *Nothomyrmecia* is a primitive formicoid.

mid-November to Eyre Peninsula Philip S. Ward and I began systematic field studies and secured several colonies, complete with queens, larvae, and pupae. These colonies have since yielded alate females and males.

This article provides a first summary of information accumulating about *Nothomyrmecia*.

ish-brown color and large eyes have been correctly interpreted as indicating nocturnality (8). The elongate-triangular mandibles, with spaced minute teeth, are less specialized than those of *Myrmecia*, and *Prionomyrmex* is intermediate (3). Ocelli are present but vestigial. The exoskeleton, especially that of the gaster, is less heavily sclerotized than in *Myr-*

Perhaps the most astonishing discovery of my investigation is the stridulatory organ of *Nothomyrmecia*. This organ consists of the usual plectrum and stridulitrum arrangement between abdominal segments III and IV. However, the organ is here uniquely positioned ventrally, involving the sternites (Fig. 1G). Stridulatory organs found among other ants are dorsal and tergal, and neither type is present in *Myrmecia* (14). Other hymenopterous abdominal stridulatory organs are always dorsal, with stridulitrum on either the IV or V tergite, and plectrum on the one preceding (15).

Females (Fig. 1, D to F) differ from workers in the expected features. They are slightly larger on average, with similar general structure, including that of abdominal segments III and IV, which also bear a ventral stridulatory organ. Ocelli are well developed, but the eyes are not significantly enlarged. The pterothoracic sclerites are structured as usual in flying ants, although they occupy less of the mesosomal bulk than is usual. This peculiarity relates to the unexpected and specialized brachyptery of the alate queens, the wings of which barely overlap the first gastral segment (abdominal III). They are not only scaled down relative to those of males, but they are also peculiarly trimmed, although a frenal fold and hamuli are retained (Fig. 2, B and C). The reduced mesosomal structure resembles that of some brachypterous *Myrmecia* species (16).

Males superficially resemble those of *Myrmecia* but have a single waist node. The wings (Fig. 2A) are long, with a full, primitive, venational complement. The median vein leaves the cubital proximal to the root of the cubito-anal cross vein, an unusual feature convergently developed in Dorylinae, Ecitoninae, and *Typhlomyrmex* (Ponerinae) (17). An anal

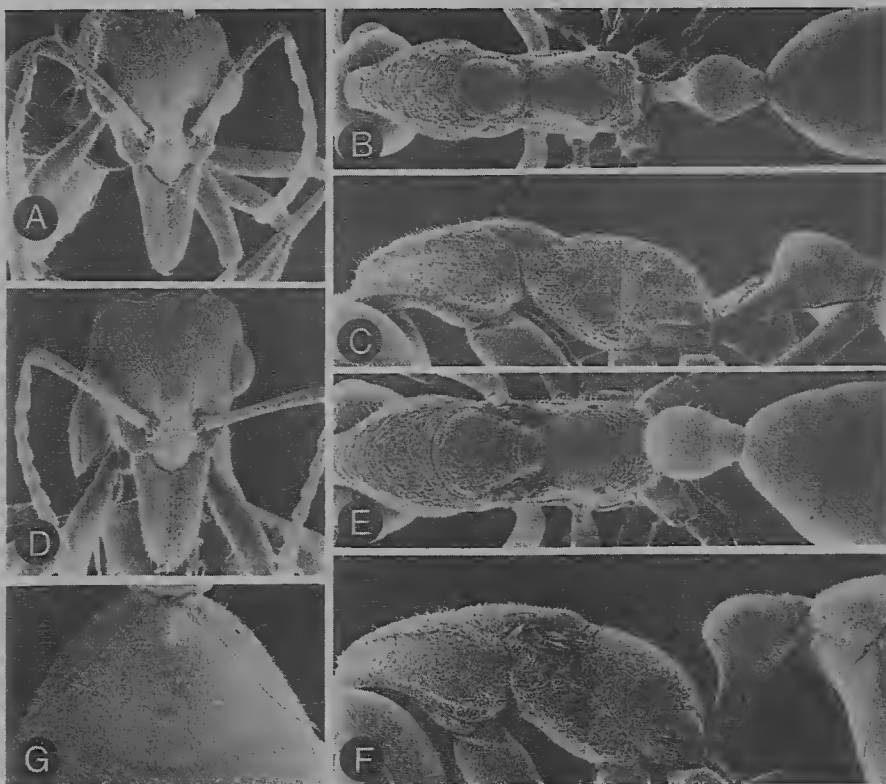


Fig. 1. Scanning electron micrographs of *Nothomyrmecia macrops* specimens. (A) Head of worker in front view; (B) mesosoma and petiole in dorsal view; and (C) in side view. (D to E) Equivalent views of dealate female. Note the very reduced section of the mesosoma devoted to structures associated with wings and flight. (G) The ventral stridulatory organ of a worker, with the sinuous posterior edge of sternite III overlaying the fine regular stridulitrum on the anterior portion of sternite IV.

(that is, jugal) lobe is present on the hind wing, as is the case in various primitive ants; but a series of basal hamuli in addition to the apical set occurs only in *Nothomyrmecia* among formicids and is a primitive character (15). The forelegs of most, but not every, male specimen each bear two apical tibial spurs, one a long calcar, the other a short thick cone. All other Hymenoptera, except some primitive Symphyta and Proctotrupeoidea and all Ceraphronoidea, have single foretibial spurs (18). Some illustrations of *Sphecomyrma freyi* (5) incorrectly depict paired spurs in that species. The mesoscutum carries parapsidal furrows, but notauli are lacking, a clearly derived condition. A functional ventral stridulatory organ, like that of the female castes, is present. Significance of genitalic structures cannot be estimated in the absence of comparative studies. Cerci are present; sternite IX has a bifid apex; the gonoforceps are divided into proximal and distal sections and lack the dorsal projection present in some *Myrmecia* species (19); the volsellae are unspecialized, and the penis valves are strikingly elaborate, with several denticulate apical processes.

Adult *Nothomyrmecia* and *Myrmecia* share other significant primitive features including a formula of six maxillary and four labial palpa in all sexes; 12 antennal segments in female castes and 13 in males; paired calcariae on the middle and hind tibiae; tarsal claws each having a strong median tooth; and a sting whose complete structure includes a furcula and two-jointed gonostyli, as in other primitive ants (20). The proventriculus of workers is actively dammed, with the cuticular structure relatively unspecialized, that of *Nothomyrmecia* being similar to *Pseudomyrmex* (Pseudomyrmecinae) (21). Most of these features are present in various other primitive ants of subfamilies Ponerinae and Pseudomyrmecinae.

Nothomyrmecia eggs, like those of *Myrmecia* (6) are subspherical and non-adhesive. The larvae lack specialized tubercles and have a primitive shape and general structure, sharing many features with *Myrmecia* (22) and with primitive prodoryline and proponerine Ponerinae (23), although the sensilla on the mouthparts are more abundant. The pupal cocoons are substantial, but have thinner walls than those of *Myrmecia* and most primitive ponerines; meconia are produced.

In short, the general structure of adults and developmental stages confirms the primitiveness of *Nothomyrmecia*. Clearly derived features include

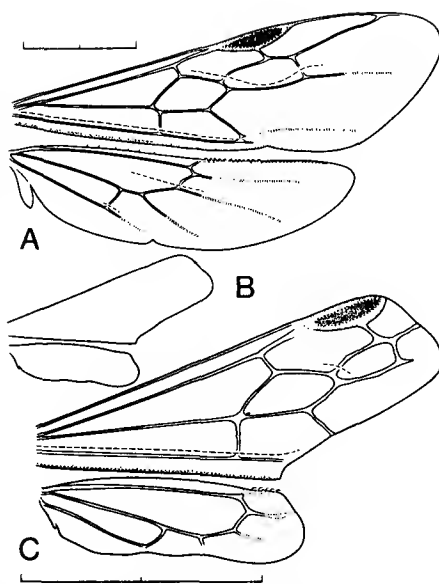


Fig. 2. *Nothomyrmecia* wings. (A) Male; (B) outline of female wing to same scale; and (C) detail of enlarged female wing to illustrate characteristics of its structural reduction. Scale bars, 2 mm.

the vestigial worker ocelli, female brachyptery, and male mesoscutal structure, whereas the abdominal and female mandibular structure, with the basal hamuli and two-segmented gonoforceps of the males, are features more primitive than those of *Myrmecia*. The stridulatory organ and supplementary male foretarsal spurs probably represent evolutionary novelties.

The differences in waist structure separating *Nothomyrmecia* and the advanced myrmecinae are neither superficial nor trivial. Abdominal segment IV of *Myrmecia* (Fig. 3B) is "tubulate" in

form, with its acrotergum and acrosternum each broadly expanded and separated from the body of its plate by a transverse construction and incised groove, presumably representing the antecostal suture (24). In addition, the lateral edges of these plates are aligned and intimately associated, especially in the anterior portion, which at rest is fully inserted into segment III (the postpetiole), the posterior edge of which embraces the antecostal constriction of segment IV to form a ball joint. Controlled telescopic and rotational movement at this node facilitates abdominal mobility. Similar tubulation of segment III was doubtless important in evolution of the petiole-postpetiole joint in ants and other Hymenoptera. Evolution of the mesosomal-metasomal waist in primitive Aprocrita apparently involved acrotergal expansion (25). Subfamily Pseudomyrmecinae has been related to the Myrmecinae (3) and has a *Myrmecia*-like metasoma. Tubulation of abdominal IV is found in workers, queens, and most males of subfamily Ponerinae (Fig. 3A), where full lateral fusion of the sclerites is frequent and the structure is sometimes further elaborated (26). Tubulation evidently functions as a preadaptation to postpetiole formation, which has been important in evolution within and beyond the Ponerinae (see below and 27).

In contrast, *Nothomyrmecia* (Fig. 3C) has the sclerites of segment IV freely articulated, with structure similar to that of succeeding segments. The acrotergite and acrosternite are probably represented only by the thickened anterior rims of the sclerites, and the portion of each plate which inserts into segment III is

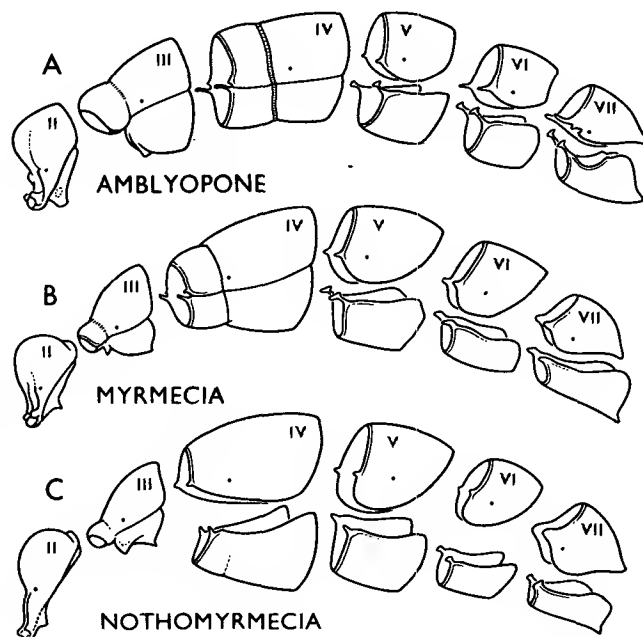


Fig. 3. Diagrams of exploded abdominal plates of primitive ants, illustrating anatomical differences in segment IV, which has its sclerites separate in *Nothomyrmecia* (C), but associated to form a tubulate structure in *Myrmecia* (B) and *Amblyopone* (A).

only feebly differentiated, by superficial sculpture (which includes the sternal stridulitrum) from the exposed part. The structure is here nontubulate, and a postpetiole is not differentiated. A generally *Nothomyrmecia*-like segment IV is considered primitive to that of *Myrmecia*, because this is the condition in most aculeates, and probably in *Sphecomyrma* (5).

Phylogenetic Implications

Current evolutionary models (3, 5, 7) recognize two ant phylads, the myrmecioid and poneroid complexes. *Nothomyrmecia* represents primitive Myrmeciinae, which stand near the base of the myrmecioid complex, linking the ancestral Sphecomyrminae and subfamily Aneuretinae (28), which apparently generated the major subfamilies Dolichoderinae and Formicinae. The advanced myrmeciines (*Myrmecia*, *Prionomyrmex*, *Ameghinoa*) and Pseudomyrmecinae are derived separately from *Nothomyrmecia*-grade stock. The Poneroid phylad includes the five other ant subfamilies, which are derived through the primitive Ponerinae, as possibly represented by *Amblyopone* (tribe Amblyoponini).

As indicated above, the advanced myrmeciines and the pseudomyrmecines have abdominal IV tubulate, like the Ponerinae. Also, the pseudomyrmecines, like ponerines and unlike *Nothomyrmecia* or *Myrmecia*, have dorsal stridulatory organs, which are found nowhere else in the myrmecioid complex

(14). If the structures concerned are truly homologous (that is, each uniquely evolved), the pseudomyrmecines and advanced myrmeciines must be dissociated from *Nothomyrmecia* by transfer to the poneroid complex, with derivation from a primitive poneroid ancestor shared with the Ponerinae and possessing a tubulate abdominal IV bearing a dorsal stridulatory organ. Loss of such an organ in the *Myrmecia* lineage could easily have occurred—it has within several ponerine and myrmecine genera (14). This hypothesis is summarized and extended in Fig. 4. *Nothomyrmecia* remains approximately annectent to the Aneuretinae, and the model requires reinstatement for it of Clark's subfamily Nothomyrmeciinae (2), which is probably desirable anyway on phenetic grounds. Also, the erstwhile "myrmecioid complex" would need renaming, as the "formicoid complex." This model collapses if ponerine-like tubulation and dorsal stridulatory organs arose convergently with the higher myrmeciines and pseudomyrmecines from a primitive *Nothomyrmecia*-related stock. The many similarities between *Nothomyrmecia* and *Myrmecia* do not invalidate the hypothesis. These ants would be expected to retain primitive characteristics in common, even if exemplifying different basal lineages with separate evolutionary potential which we, in hindsight, see realized among modern ants.

Formicoid trophic evolution has largely involved adaptations to liquid feeding by adults and larvae. These include convergent development, in both

Dolichoderinae and Formicinae, of elaborate proventriculi, to serve as passive valve dams, retaining liquid food in the greatly expandable crop (21, 29). This is often accompanied by gastral expansion, facilitated partly by free movement of the segment IV sclerites. These trends culminate in the separate development of replete ("honey pot") workers in several groups of both subfamilies (7). These are capable of enormous gastral expansion, and function as stationary liquid storage reservoirs for their colonies. The beginnings of this evolution could be represented by the crop and gastral expansion observed in *Nothomyrmecia* foragers (see below). Correlated trends include reduction in gastral sclerotization and convergent modification of sting structure and function (to either a spreading or a spraying device) in the two subfamilies.

These developments might have been forced by problems of mechanical operation of a piercing sting occasioned by crop expansion. No known formicoid except *Nothomyrmecia* has an abdominal stridulatory organ (14). The "primitive formicoids" of Fig. 4 need not have had such a structure; but if they did, the organ (whether dorsal or ventral) could have been lost in further evolution, in correlation with sclerotic reduction of the gaster. Also, its operation would likely have been compromised in groups with gastral expansion exceeding that of *Nothomyrmecia*. The *Sphecomyrma* fossils have been reported to lack a dorsal stridulatory organ (14), but they should be checked for the presence or absence of a ventral one. Abdominal tubulation is a preadaptation to postpetiolar development through strangulation of segment IV. Among ants this occurs only in the poneroid complex (as comprised here) and has occurred repeatedly (27). The only other known postpetiolate Hymenoptera (Bradynobaenidae-Apteryogyninae) (15) apparently also have abdominal IV tubulate (30). Tubulation aids controlled use of the sting, which is rarely degenerate in poneroids; it must, however, limit crop expansion and has perhaps restricted emphasis on liquid feeding in the complex (29). Repletes are unknown among poneroids; the proventriculus is seldom elaborated, and is reduced to a simple tube in some groups (21). The myrmecines especially have developed alternative trophic life-styles, utilizing nonliquid foods such as fungi, seeds, and plant material (7). Massive gastral expansion, comparable to that of formicoid repletes, occurs in several poneroid groups having physogastric queens, whose abdomens swell to an un-

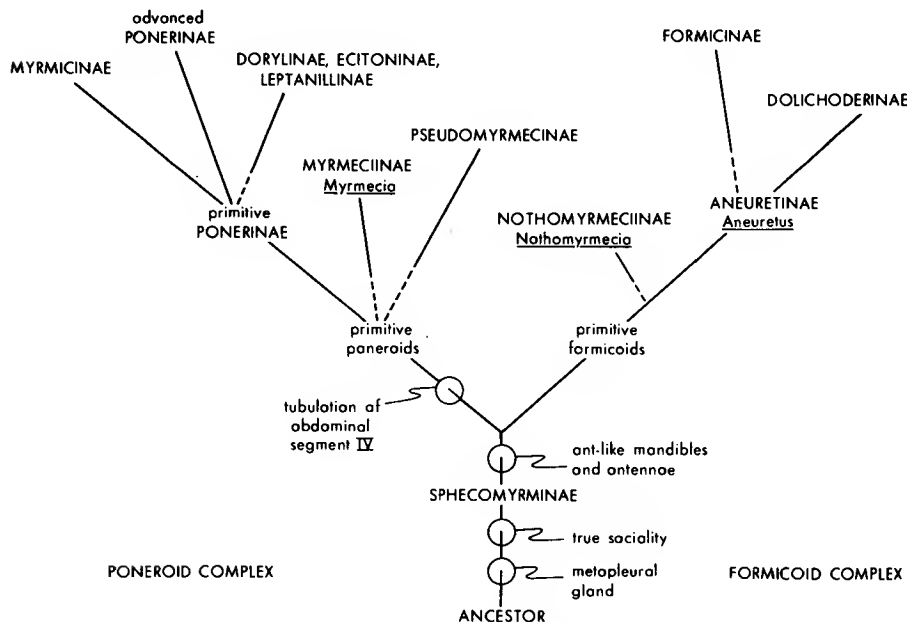


Fig. 4. A simple, hypothetical, branching phylogenetic diagram, illustrating the hypothesis developed here. *Nothomyrmecia* stands close to the ancestors of the formicoid phylad, and *Myrmecia* to the poneroid stock.

usual degree because of hypertrophy of the ovaries and fat body. In the minute European workerless parasite *Teleutomyrmex schneideri* (Myrmicinae), segment IV is not involved in this expansion (31). Queens of the various army ants *Aenictus* (Dorylinae), *Eciton*, *Labidus*, and *Neivamyrmex* (Ecitoninae), and probably those of Leptanillinae, oviposit intermittently and massively. Physogastry here does involve expansion of segment IV, which has separable sclerites; and these females, unlike their workers, have a single waist node (32). This apparently reversed evolutionary trend is doubtless an adaptation to physogastry. It neatly correlates free movement of the segment IV sclerites negatively with the presence of postpetioles and positively with gastral expansion, and explains the peculiar female metasomal dimorphism in these ants. Comparable reversal of gastral tubulation is seen in army ant males and in those of the advanced (euponerine) Ponerinae.

Many of the major characteristics of ant phylogeny (Fig. 4) which are reviewed above can thus be correlated with the structural modifications of abdominal segment IV which have profoundly influenced ant evolution.

Genetics

Preliminary investigations (33) show that *Nothomyrmecia* has a very high diploid chromosome number of about 92, the highest number known among Hymenoptera, where the range otherwise is $2n = 6$ to 84. This range is encompassed by the ants, and all Hymenoptera with $2n$ exceeding 52 are ants. Most are *Myrmecia* species, of which ten have been investigated yielding a $2n$ range of 9 to 84. Four species of *Myrmecia*, with $2n = 60, 66, 81,$ and 84 , have diploid numbers exceeding 52, and a *Bothroponera* species (Ponerinae) has $2n = 60$ (34). Most *Nothomyrmecia* chromosomes are dotlike acrocentrics, but some larger metacentrics are present.

Preliminary electrophoretic study (35) of 18 loci, in about 100 foraging workers, has revealed one polymorphic locus (amylase) showing substantial variation (four alleles at frequencies greater than .05). This suggests either a greater effective population size than field observations indicate or stabilizing selection at this or a closely linked locus. Marker genes at the amylase locus should provide information on the multiplicity of insemination of queens and the parentage of males.

Field Studies

The woodland at the Eyre Peninsula collection site seems similar to that in surrounding areas. *Eucalyptus oleosa* (Myrtaceae) forms an almost pure stand on fine textured, well drained, brown calcareous earth with low organic content. The presence of scattered *Callitris preissii* (Cupressaceae), which forms an almost pure stand nearby and is elsewhere very patchily distributed, might indicate soil or drainage peculiarities. The apparent absence of the otherwise locally common funnel ant *Aphaenogaster barbigula* (Myrmicinae), which builds easily collapsed, craterlike, pitfall trapnest entrances up to about 25 centimeters in diameter, might be related to soil type, and could be important in allowing access to the site by *Nothomyrmecia*. The plants present (36) are all widespread species found on both sides of the Bight; most range eastward into Victorian mallee woodland.

Nothomyrmecia workers were readily collected on *Eucalyptus* trunks at night, but they could not be found during daytime. Night search in surrounding areas shows that the population is apparently very local, occupying only several hectares. The ant seems absent from apparently similar adjacent sites. Nest entrances, when located, consisted of small (about 4 to 6 mm), unspecific holes in the ground under shallow leaf litter, without surrounding mounds or deposited soil. Location of further populations will almost certainly require night search, since the presence of *Nothomyrmecia* is not evidenced during the day. The ants forage singly and range to the tops of the trees, where they probably seek sweet substances and hunt for small arthropods. The remains of a small unidentifiable microlepidopteran and a spiderling have been taken from foragers. Workers feed avidly from baits of honey streaked on the tree trunks and imbibing for long periods, often exceeding 30 minutes. Their gasters visibly expand with crop expansion, although the sclerites do not separate sufficiently to expose the intersegmental membranes. After feeding, foragers continue to stray on the trees, apparently randomly, and observers experience great difficulty in tracking the return of the ants to nests, at least until around dawn. At first light, the ants begin to leave the trees, proceeding directly and positively across the surrounding leaf litter to the nest entrances, which are located in open ground and are evidently not associated with basal accumulations of bark litter and debris near trees. Incomplete observations, inter-

rupted by bad weather, suggest that there might be a considerable exodus from the nests at dusk, with few foragers returning until near dawn. If this is true, the position of the sun or light areas of the sky would be similarly related to the body axis on both journeys. There is no evidence that chemical trails are laid by foragers, and, unlike smaller *Myrmecia* species, they show no structured jumping or hopping behavior. Disturbed foragers sometimes adopt a stationary open-jawed threatening stance, but they usually fall abruptly to the ground and feign death in a cryptic, motionless pupal posture. A *Myrmecia* species, similar in size to *Nothomyrmecia*, is an equivalent diurnal forager, first appearing as *Nothomyrmecia* withdraws. A few dealate queens of *Nothomyrmecia* were encountered among the workers. When tracked to nests they proved to be colony founders, following the incompletely claustral mode of establishment, in which young queens leave their immature first brood in order to forage.

Bionomics

Five *Nothomyrmecia* nests were excavated on 17 to 18 November. In each a single gallery (diameter, 4 to 5 mm) descended steeply at about 60° to a terminal, subelliptical, horizontal chamber (diameter, 3 to 5 cm; height, 5 to 10 mm; depth below ground, ranging from 18 to 43 cm). Each shaft had three to five side chambers, one within 10 cm of the surface. The ants retreated timidly, most being captured with brood and queens (one in each nest) in the terminal galleries. The brood comprised numerous half-to full-sized larvae, all probably of a single generation, and a few pupae; eggs were not seen. Callow adults, alate queens, and males were absent. Mature nests probably contain 50 to 70 workers. A dense layer of calcrete rocks in the soil profile apparently limited nest depth. A sixth nest penetrated this, and excavation was abandoned.

By 9 March 1978, four colonies, two with queens, survived in laboratory culture. Additional larvae had not been produced, and all but a few in two nests had pupated. Workers began emerging from 24 December, males from 16 January, queens from 20 January. Callows are recognizable for about 2 days. Emergence seemed due for completion by mid-April. One colony produced males, and another males plus queens. The latter began emerging on 20 January and 3 March, respectively, possibly in a natural sequence. Both trophic and apparent-

ly reproductive eggs were laid occasionally, but consistently, by workers. These were fed mostly to larvae, but also to other adults, including mother queens and alate sexuals. Oviposition by queens was not observed. No reproductive eggs were accumulated. Two observation series of assembled foragers were collected on 23 October and 17 to 18 November. The first included a (presumably colony-founding) dealate female. Both of these groups accumulated many reproductive eggs from late December onward, and a few of these hatched by mid-February; pupation had not occurred by 9 March. It is not known whether the dealate female in the mixed group contributed eggs, but oviposition by workers was seen. Production of eggs is thus not inhibited by laboratory conditions. These events suggest that brood is normally not present in colonies during winter (say from late April to early September). As a result, foraging in this season is likely to be reduced, and nests possibly sealed, as in *Myrmecia tarsata*, which does not overwinter brood (personal observation).

A further nest, with a single terminal chamber 18 cm below ground, was also excavated. This contained two dealate queens. Brood was not seen and, if present, must have been small. This nest was located by tracking a foraging queen at dawn from a tree 4.5 meters away. One queen left the nest briefly at night in light rain to drink water from fallen leaves. These ants survived in culture without evident antagonism, and on 9 March were supporting a large larva and a cocoon, which was smaller than those in mature colonies and was spun on 28 February. Larvae were fed with insect fragments and apparently normal (reproductive as opposed to trophic) eggs by both queens. Founding thus may be pleometrotic with queens evidently reduced later to one (secondary monogyny). Mating flight details are unknown. The queens might flutter from vegetation, like some brachypterous *Myrmecia* (personal observation). None had undergone dealation as virgins in the nests by 9 March. Alates are presumably released by late summer or autumn (March or April) but might be overwintered in parent nests. Founding queens excavate to considerable depth; and, even if released in late summer, evidently mature no eggs until spring.

Aptery or brachyptery in *Myrmecia* queens is not uncommon (2, 16, 37); although its adaptiveness is unclear, it might sometimes involve premating isolating mechanisms. This seems unlikely in *Nothomyrmecia*, where brachyptery might relate to population structure, as

an adaptation developed in small scattered populations held in enclaves by competition with other ants, or by precise, unusual, ecological requirements. It might be inadaptative for queens to disperse and attempt to establish colonies away from enclaves. The situation could be compared to that of brachypterous mountaintop or island insects (38), and *Nothomyrmecia* could be dangerously overspecialized in this regard. Brachyptery might be recently evolved; female wings, if nonfunctional for dispersal, would probably quickly disappear altogether. Short-winged queens might be irregular products of drought-stressed colonies, as has been reported in some *Chelaner* (Myrmicinae) species in semiarid Australia (39, 40), but no available evidence suggests such dimorphism in *Nothomyrmecia*.

Adult *N. macrops* are largely nectarivorous but drink hemolymph from insect prey. The latter, with little dissection, is fed directly to larvae. Larvae can move independently toward food, and cannibalism among them seems rare. Pupae are used for larval food if forage is withheld. Eggs are scattered in observation nests, with larvae plus eggs and pupal cocoons only roughly segregated. Mature larvae swell anteriorly before spinning cocoons and are buried by workers to facilitate cocoon formation. Emergence from cocoons is often assisted by nurses, which tend to be the smaller, least aggressive workers. Occasional trophallaxis has been seen between workers, and with sexuals or larvae, which exude anal droplets imbibed by workers. Workers and females actively groom each other, with special attention to the posterior mesosoma (? metapleural glands). They will collapse tonically immobile in pupal posture if nests are jolted, or if dragged or carried by nest mates. Queens or workers may be dragged by antennae or limbs without tonic immobility, sometimes by counteracting workers, and appear from abdominal movements to stridulate if distressed by this. Stridulation occurs when workers, queens, or males are held; but it is neither easily induced nor is it continuous, especially in males. Digging is induced when nest soil is moistened. Refuse heaps, including food wastes, discarded cocoons, and dead immatures or adults, are accumulated away from the occupied sections of nests. Wastes are regularly deposited in the small (15 mm in diameter) dishes used for feeding honey, which are frequently filled with soil, even by colony-founding queens. These seem to be behaviorally totipotent compared with workers. Males are occasionally ob-

served riding for many minutes on alate female nest mates, without attempting copulation. All standard self-grooming routines (7) are actively practiced, except abdominal tip licking, which has not been seen. Alarm communication is slow and inefficient. The ants are generally nonaggressive, differing markedly from most *Myrmecia*. Territoriality between colonies is not evidenced in either field or laboratory. Allozyme markers suggest that several colonies can contribute foragers to single trees. Workers transferred to alien colonies are shown little aggression. Mixed foragers will settle to behave like queenless colony fragments and will adopt foraging queens.

Thus, almost all behavioral characteristics of *Nothomyrmecia* are held in common with *Myrmecia*, further confirming the primitiveness of *Nothomyrmecia*.

Retrospect

The resistance to collection for 46 years by *Nothomyrmecia* is explained by its apparently patchy, locally limited distribution, its nonspecific, insignificant nest entrances, its strict nocturnality of foraging, the likely restriction or cessation of aboveground activity in winter (correlating negatively with that of most insect collectors in Australian areas of severe summer climate), and the unlikely collection at light traps of the brachypterous queens (males in this context would probably not have been recognized). Doubts have been expressed about the true provenance of the original specimens, which I believe were very likely collected in mallee woodland south of Balladonia. The previously almost exclusive emphasis by would-be collectors in this area on heath rather than mallee sites could have been misdirected. The rediscovery of *Nothomyrmecia* in Western Australia remains a challenge to interested naturalists.

References and Notes

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 24. The areas identified here as acrosclerites might in fact be secondarily differentiated sections of the definitive tergite and sternite. This would not substantially affect the argument. The term "pretergital belt" was used for the anterior portion of the segment IV exoskeleton by W. L. Brown, *Search Agric. Geneva N.Y.* 15, 37 (1975).
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 26. Lateral fusion of segments III, IV, and V in ants was briefly reviewed by W. H. Gottwald [*Cornell Univ. Agric. Exp. Stn. Mem.* 408, 126 (1969)]. In species of *Heteroponera*, *Gnamptogenys*, *Proceratium*, *Discothyrea* (all Ectatommini), and *Psalidomyrmex* (Ponerini) abdominal IV is strongly fused laterally and arched or reflexed, turning the gastral apex ventrally or even anteriorly [W. L. Brown, *Bull. Mus. Comp. Zool. Harv. Univ.* 118, 175 (1958)]. *Asphinctopone* (Ponerinae) workers have segment IV tubulate, with laterally fused sclerites. However, the acrosclerites are (presumably through secondary reduction) mere ridges, with the insertion into segment III being only slight. *Sphinctomyrmex* (Cerapachyini) has serially repeated tubulation of segments IV, V, and VI, producing several gastral constrictions.
 27. Development of a strongly constricted postpetiole has independently occurred within several ponerine genera including *Proceratium* (Ectatommini) and *Cerapachys* (Cerapachyini), and in the evolution from primitive ponerine or poneroid stock of Dorylinae, Ectoninae, Leptanilinae, and Myrmicinae. The only ectonine genus usually said to lack a worker postpetiole is *Cheliomyrmex* (Ectoninae-Cheliomyrmecini); it has a tubulate but relatively unconstricted segment IV, resembling that of many ponerines (such as *Amblyopone australis*) (Fig. 3A) and exemplifying a condition presumably primitive for Ectoninae [see figure 4-29 of (7), p. 70]. Similarly, in the Dorylinae, *Dorylus* has abdominal structure like *Cheliomyrmex*, while *Aenictus* workers have a strongly constricted postpetiole.
 28. This, perhaps once major, group includes the living relict *Aneuretus simoni* (Sri Lanka) and three extinct Oligocene genera of Europe or North America [E. O. Wilson, T. Eisner, G. C. Wheeler, J. Wheeler, *Bull. Mus. Comp. Zool. Harv. Univ.* 115, 81 (1956)].
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 36. These include species of *Santalum* and *Exocarpos* (Santalaceae), *Comesperma* (Polygalaceae), *Dionella* (Liliaceae), *Amyema* (Loranthaceae), *Enchylaena* (Chenopodiaceae), *Geijera* (Rutaceae), *Callitris* (Cupressaceae), *Eucalyptus* and *Melaleuca* (Myrtaceae), as identified by R. Pullen, I. Brooker, and G. Chippendale (personal communication).
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 41. Others, in addition to A. D. Bishop, R. H. Crozier, and P. S. Ward (Australia), involved in the research on *Nothomyrmecia* discussed in this article are T. Eisner, B. Hölldobler, G. C. Wheeler, J. Wheeler, E. O. Wilson (United States); P. Duelli (Switzerland); and H. Markl (Germany).