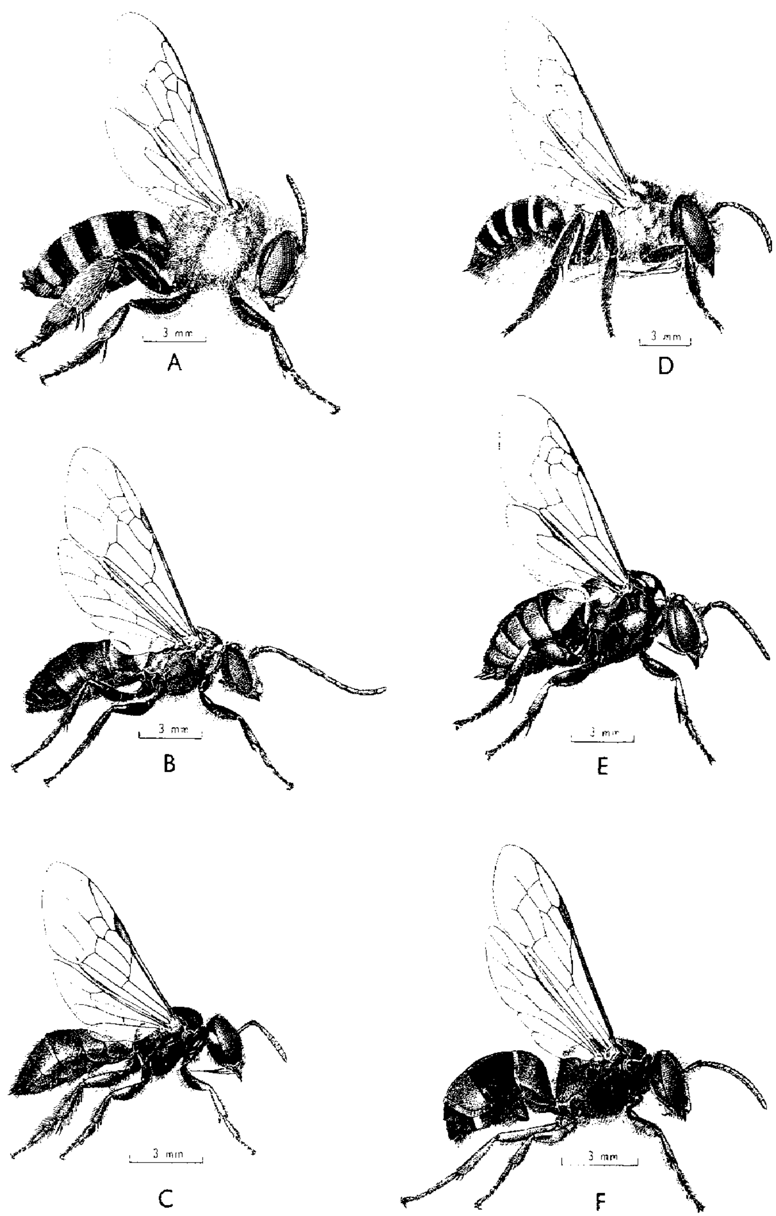


Fig. 37.36. Apoidea: A, *Amegilla cingulata*, Anthophoridae-Anthophorinae-Anthophorini; B, *Lasioglossum altichum*, Halictidae; C, *Exoneura bicolor*, Anthophoridae-Xylocopinae-Ceratinini; D, *Megachile chrysopyga*, Megachilidae; E, *Thyreus nitidulus*, Anthophoridae-Anthophorinae-Melectini; F, *Hyleoides concinna*, Colletidae-Hylaeinae. [M. Quick]



nest burrow. The larvae thus occupy an environment very different from that of most bee larvae, and are provided with head and body projections totally different from those of other species of bees. In nearly all the species there is a primitive social organization. Young adult females remain in the nests and care for their own younger brothers and sisters, and there is a weak caste system, queens and workers being anatomically alike externally, although the queens average larger than the workers. Queens mate, lay eggs, and are relatively long-lived, whereas workers usually do not mate, usually do not lay eggs, and probably are relatively short-lived. The nature of this primitive social organization is little known (Michener, 1965a).

*Inquilina* is closely related to *Exoneura*. It differs primarily by the reduction in the scopa, and lives as a social parasite in the nests of certain species of *Exoneura*. There are also species of *Allodapula* which appear to be social parasites in the nests of other species of the same genus (Michener, 1961a).

**58. Apidae.** This family contains all of the highly social bees and the tropical American Euglossini, in which pollen is carried in a corbicula. It consists of 2 subfamilies. The BOMBINAE are large, robust, usually hairy bees with the hind tibial spurs present. There are no Australian species, and efforts to introduce European species of *Bombus* (bumble bees) have been unsuccessful, although several are established in New Zealand. The APINAE are represented by the introduced *Apis mellifera* and native species of *Trigona*.

*A. mellifera* is of commercial importance as a honey producer and as a pollinator in many parts of the continent. It visits a wide range of native flowers, and has escaped from hives into hollow trees, holes in banks and cliffs, and other nesting sites. The combs of cells are made of wax, and are vertical, hanging down from some support in the nesting cavity. Honey and pollen are stored in cells similar to brood cells. The female castes are very different from one another, the queen lacking a corbicula and being unable to survive without the accompanying workers. *A. mellifera* is easily distinguished from almost all other Australian bees by the densely hairy surfaces of the eyes.

*Trigona* (Fig. 37.35C) includes the small, dark, 'native bees' of the northern half of the continent. Like honey bees, they exist in large colonies consisting of a structurally strikingly differentiated queen without corbiculae, and thousands of workers. Unlike honey bees, they are unable to sting. They place their brood cells either in clusters (Australian species of the subgenus *Plebeia*) or in horizontal combs with the cells opening upward (subgenus *Tetragona*), unlike the vertical combs of *Apis*. They store honey and pollen not in cells like brood cells but in large wax pots totally different from the brood cells. The nests are almost always in hollow trees. Establishment of new nests is not by the departure of the old queen and a swarm of workers as in *Apis*, but is a gradual process in which workers from a nest locate a new site, carry nesting materials (wax, resin) there, construct a new nest, and even carry provisions to it. Ultimately a young queen goes there and establishes herself with a group of workers, but interchange between the new and the old nest may go on for some weeks after the arrival of the young queen at the new nest. Old queens are so heavy and swollen that they cannot fly, and hence could not depart to establish new nests as in *Apis*. In *Trigona* queens are produced in special large queen cells, as in *Apis*. The nests of Australian species have been described by Michener (1961b).

## Superfamily FORMICOIDEA

*by* W. L. BROWN JR *and* R. W. TAYLOR*

**59. Formicidae.** Superfamily and family coextensive, consisting entirely of social species, each usually having a (winged) male, (deciduously winged or wingless) female, and (wingless, neuter-female) worker castes. All

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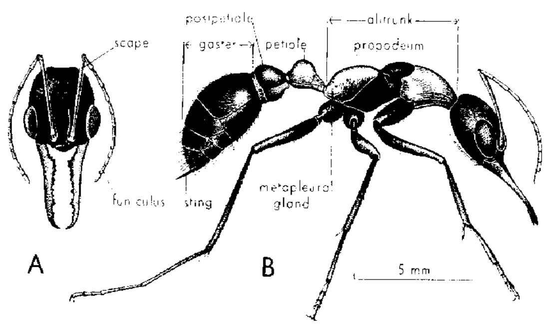


Fig. 37.37. *Myrmecia nigrocincta*, Formicidae-Myrmeciinae, worker: A, head, frontal; B, whole insect, lateral. [F. Nanninga]

forms have a nodiform, binodal, or scale-like 'waist' consisting of the modified true abdominal segment 2 or 2 + 3. With the exception of a few rare parasitic forms and the males of army ants (Dorylinae), all ants have a large metapleural gland with external bulla and a small orifice, opening on each side of the metathorax at its lower posterior corners (Fig. 37.37).

Ants have a characteristic facies, and are normally confused (among non-mimics) only with female mutillid or thynnine wasps and certain other wingless Hymenoptera, which, however, lack the peculiar waist and metapleural glands. There are perhaps 10,000 known, valid species of the world already in collections; approximately a tenth of these occur in Australia. The world tally may expand to 15,000 as collecting is improved and extended; ultimately the Australian count may exceed 1,500 species.

The female castes are the female proper, or *queen*, and the *worker*. The worker caste may be subdivided into *soldier*, *media*, *minor*, etc. phases. Female caste differences are phenotypic, and arise during ontogeny due to the interaction of an intrinsic system of physiological thresholds with variation in amount or composition of the larval food (and pheromones?), and in some cases, of the nutriment stored in the egg.

The virgin queen bears wings, has a well-developed pterothorax and flight muscles, large compound eyes and 3 ocelli, and is usually larger than workers of the same species. Her gaster is relatively bulky and contains well-developed ovaries and fat body.

The worker lacks wings, and has greatly reduced pterothoracic structure. The only flexible or semi-flexible joint lies between the pro- and mesothorax: even this is soldered solid in Myrmicinae, many Ponerinae, and some genera of other subfamilies. The metanotum may be obsolete, or represented by a narrow impressed piece with paired spiracles (*Myrmecia*, some Formicinae) or by a transverse metanotal groove. Head as in queen, but usually with smaller compound eyes (sometimes absent) and ocelli reduced or absent; mouth-parts and antennae are usually the same, and function similarly, in both worker and queen.

The soldier phase (Figs. 37.38C, D), when present, is larger than the other workers, and has a disproportionately large head, sometimes absolutely larger even than that of the queen. Worker minor and soldier are either connected by a series of intermediate forms (*Anisopheidole*, *Pheidologeton*, most *Camponotus* and *Melophorus*), or else normally lack the intermediate forms ('dimorphism' of *Pheidole* and *Oligomyrmex*). The soldiers apparently function mainly as defenders of the colony against attack, especially by other ants.

Various wingless intermediates between queens and workers occur in some species. These are the *ergatogynes* (ergatoids), which may accompany true queens in the nest, or replace them as the reproductive caste. Ergatogynes serving as functional queens are unusually frequent among Australian species,



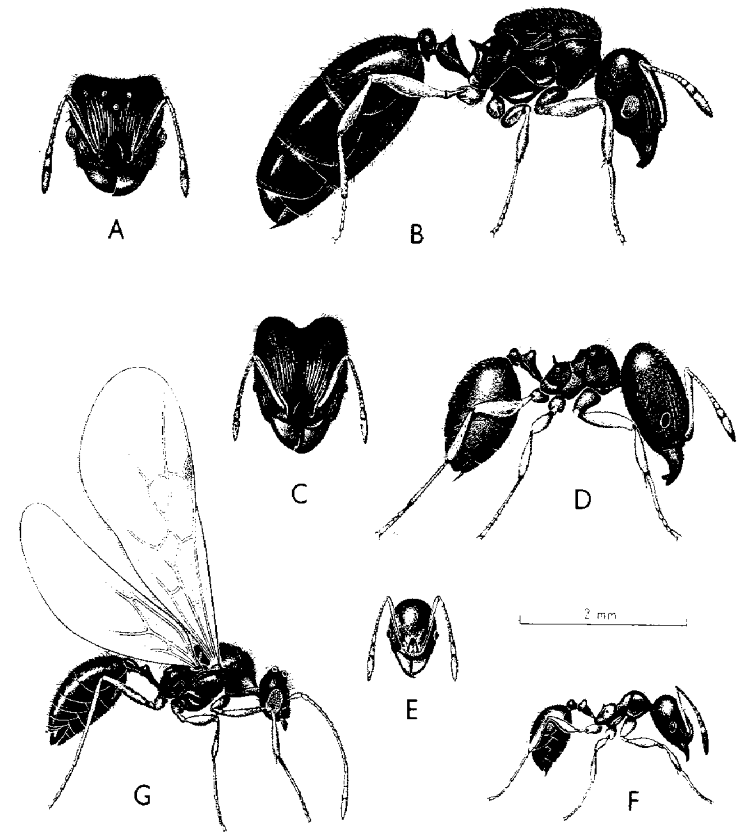


Fig. 37.38. Castes of *Pheidole* sp., Myrmicinae: A, B, queen; C, D, major worker ('soldier'); E, F, minor worker; G, male. [F. Nanninga]

and are common in *Myrmecia*, *Heteroponera*, *Leptogenys*, *Sphinctomyrmex*, *Mayriella*, and *Leptomyrmex*. In many *Rhytidoponera*, *Diacamma*, and *Leptogenys* neither queen nor differentiated ergatogyne is known, and the queen function is assumed by workers capable of egg production and normal fertilization with sperm storage. In some genera, such as *Aenictus*, *Leptanilla*, and the ponerine *Onychomyrmex*, which probably all follow a group-predatory, nomadic existence (i.e. are army ants), the reproductive female is a bizarre type of ergatogyne with enlarged, ovary-filled gaster, and is referred to as a *dichthadiigyne*.

Males are usually permanently winged, with relatively small heads and large compound eyes and ocelli; their mandibles are much modified, and often reduced and apparently functionless. In most species the males are larger than the workers and smaller than the queens. Male genitalia are unremarkable in most ants, and are easily homologized with the basic pattern in aculeate Hymenoptera (Snodgrass, 1941). The terminalia seem promising as discriminatory characters within *Myrmecia*, *Amblyopone*, *Bothroponera*, and the dolichoderine genera. In a few scattered species of *Hypoponera*, *Cardiocondyla*, and *Technomyrmex* there are ergatoid males, wingless and with more or less worker-like characteristics.

Both female and male sexes of ants share a primitive number of palpal segments (6 maxillary, 4 labial) with other old hymenopteran families, but this formula is reduced to as low as 1, 1 in some specialized ant genera. The primitive ant antennal count is 13 in the male and 12 in the female, but this number is often reduced in either or both sexes; queens and workers of some Dacetini (Myrmicinae) have as few as 4 segments, but male numbers do not fall so low. The worker-queen antennae, and sometimes those of males, are elbowed, with the scape forming the elongate basal segment. Ant wing venation has undergone convergent reduction in several advanced lines in different subfamilies (Figs. 37.8H, 38G; Brown and Nutting, 1950). In general, veins or parts of veins are lost in lineages that have undergone reduction in body size; reversal of the size trend does not lead to replacement of regular venational elements.

Internally, adult ants are remarkable chiefly for (1) the development of the crop, and especially of its sclerotic posterior valve, the proventriculus, which is elaborate in the Dolichoderinae and Formicinae, and varies widely to furnish valuable tribal or even generic characters (Eisner, 1957); and (2) the great variety and prominence of glands that open externally in various parts of the body, most of them apparently secreting pheromones—substances that are primary media of social and sexual communication (Pavan and Ronchetti, 1955; E. Wilson, 1963).

Larvae of ants (Fig. 37.39) share the white, grub-like, apodous condition of other aculeate larvae, and are dependent on the adult female castes as food providers. So radically reduced are most larval characters in even the primitive ants that the main evolutionary opportunities for morphological change clearly have lain in adding new structures or elaborating old ones. Significant trends in different lineages involve the elaboration of tubercles or specialized hairs that fasten the larvae to nest walls or ceiling, or clump them together for quick transport by the workers. The number of larval instars is not known for any ant species, but there are probably 3. Most primitive ants, and most Formicinae, spin a pupal cocoon; but the pupae are naked in Myrmicinae, Pseudomyrmecinae, and Dolichoderinae, as well as in several groups of Dorylinae and scattered species in other subfamilies.

Winged males and queens are usually produced in the colony at a time of the year that is fixed for the species. Where males and queens are both winged, a mass nuptial flight or flights may occur, during which mating takes place. After copulation the male wanders off and dies, while the queen divests herself of her wings and seeks a place to start a new colony. In the higher genera the wing muscles are converted into fat body that serves as a food supply during the lean time of nest foundation, when the queen remains enclosed in a small chamber. In some primitive genera the queen leaves the chamber to hunt from time to time. In forms having ergatogynes, and in some winged species, the nuptial flight is much modified, and may be reduced to a precopulatory promenade on the nest surface or nearby vegetation. In genera such as *Rhytidoponera* and the army ants males leave their own nests and fly to other nests, where mating takes place.

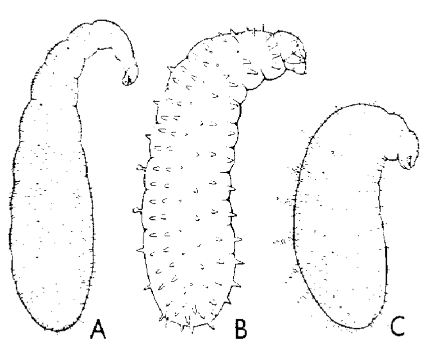


Fig. 37.39. Larvae of ants: A, *Amblyopone* sp., Ponerinae; B, *Hypoponera* sp., Ponerinae; C, *Pheidole* sp., Myrmicinae. [S. Curtis]



Established nests may contain a single dealate, egg-laying queen, or there may be several to many queens present. In the latter case colony reproduction may occur by simple fission or 'swarming', or by a kind of budding process.

A few ants in different groups found their nests by entering colonies of another species and living there as social parasites or inquilines. In the so-called temporary social parasites the host queen is killed, either by the inquiline queen or by host workers, and a mixed nest is formed of host workers with the inquilinous queen and her worker offspring; such a nest gradually loses its host workers and becomes a pure independent society of the inquilinous species. Probably a number of Australian ants are temporary parasites; *Rhoptromyrmex* and some *Bothriomyrmex* are likely examples. Permanent social parasites have specialized to the extent that the parasitic species requires the continued presence of the host species in order to survive and reproduce. Such parasites commonly lack a worker caste altogether; well-known Australian examples are *Myrmecia inquilina* (hosts *M. nigriceps* and *M. vindex*) and *Strumigenys xenos* (host *S. perplexa*). The special type of permanent parasitism known as *dulosis*, or slave-making, in which workers of the 'slave' component in the mixed colony are constantly replenished by the addition of pupae acquired through mass raids on neighbouring pure nests of the host species, is so far not known to occur in Australia.

Conclusive generalizations on orientation and communication in ants are not possible at this time. The known methods of communication are: (1) olfactory, through the medium of volatile pheromones, secreted by specific glands upon a particular stimulus and evoking a particular response, such as alarm behaviour or trail-following; (2) gustatory, particularly during food exchange by regurgitation from the crop or stomach; (3) auditory, including tapping, stridulation, and other sounds transmitted mainly through the substrate; (4) mechanical, including antennal stroking, body recoil, etc.; and (5) visual, in those forms with well-developed eyes.

Ants usually live in more or less permanent nests, excavated in the soil or in wood, or utilizing pre-existing cavities in plants or in rocks. The great majority of Australian ants inhabit the ground layers, in chambers deep in the soil or under rocks or other objects. Many species, particularly those of arid areas, construct mounds or disc nests, often with a large entrance, and a surface cover of pebbles, charcoal, etc. (e.g. Fig. 5.39). In forests, rotting logs and small fragments of rotting wood are favoured nesting sites. Although a number of Australian ants nest in twigs (in *Camponotus*, *Crematogaster*, *Myrmecorhynchus*, *Tetraponera*, and *Metapone*), this habit is best developed in the northern areas, and is not as common as in some parts of the world. Other tree-dwelling ants belong to *Polyrhachis*, which often build silken or plant-fibre nests on leaves, twigs, or bark; to *Podomyrma*, which frequently choose beetle burrows in solid wood; to *Oecophylla*, the weaver ants, which build nests of leaves joined by sheets of larval silk (Fig. 5.38); to *Myrmecia mjobergi*, a nester in epiphytic ferns, and to *Iridomyrmex cordatus* and the *Pheidole* species that live in the hollows of the tubers of the epiphytic 'ant-house plants' (*Myrmecodia* and *Hydnophytum*). Aside from these ant plants, and perhaps a few other less well understood plants also belonging to the Indo-Malayan intrusive floral element of the north, symbiotic relations between ants and plants apparently are not well developed in Australia.

Australian ants vary by taxa from highly specific predators (Cerapachyini on other ants, *Discothyrea* on spider eggs, some *Leptogenys* on slaters, *Metapone* on termites, most *Strumigenys* on entomobryoid Collembola, etc.) to scavengers and near-omnivores. Some genera of Myrmicinae, notably *Pheidole*, *Chelaner*, and *Meranoplus*, have species that depend on seed-harvesting for much of their food. Many genera attend homopteran insects for their honey-dew, and some ants, for instance the subterranean *Acropyga*, are obligatory tenders of symbiotic root-feeding plant lice. Forms such as the bulldog and jumper ants (*Myrmecia*; Frontispiece and Plate 5, S) feed largely on nectar and honey-dew as adults; the queen and youngest larvae subsist on worker-laid 'trophic' eggs, and the older larvae are fed on insect prey. Regurgitative feeding of the queen and brood is common in the higher genera.

Some formicine ants in arid areas (*Melophorus bagoti*, *Camponotus* spp.) store regurgitated honey-dew and nectar in the enormously distended crops of special large 'honeypot' workers (Figs. 5.5, 35) that remain in deep chambers of the nest. While this is obviously a mechanism of food storage, its relationship to special needs during poor seasons has never been properly studied.

Foraging in ants seems to involve two main kinds of orientation that are followed by different taxa: (1) by individuals learning restricted feeding areas, to which they return repeatedly; and (2) by trail-following, in which foraging is induced and directed by a chemical trail laid by food-laden workers returning to the nest. Foraging in many taxa is rather strictly either by day or by night, but in others it seems to be controlled more by temperature or humidity, without apparent regard for light conditions.

Many predators commonly thought to eat ants, such as *Myrmecobius fasciatus* and *Tachyglossus aculeatus*, actually feed primarily on termites and eat true ants less often. A number of Australian birds are frequent ant feeders, including the magpies (*Gymnorhina*), the coachwhip bird (*Psophodes crepitans*), and especially the thickhead (*Pachycephala pectoralis*). Various agamid lizards feed extensively on ants in the arid lands; of these *Moloch horridus* is a specialist predator of certain desert *Iridomyrmex*. Frogs (e.g. *Pseudophryne corroboree*) and spiders take many ants in Australia, as possibly also do the burrowing typhlopid snakes. Ant-lions (Neuroptera) exact their formicid toll. Many arthropods live as inquilines in ants' nests and feed on ant larvae or adults, or on the secretions, the food stores, or the cast-off wastes of ants, in such diverse orders as: Collembola, Thysanura, Hemiptera, Neuroptera, Coleoptera (Carabidae–Paussinae, Pselaphidae, Ptiliidae, Scydmaenidae, Staphylinidae, Histeridae, Scarabaeidae, Ptinidae, Limulodidae, Clambidae, Dermestidae, Silvanidae, Tenebrionidae, Aculagnathidae, Colydiidae, Brenthidae), Lepidoptera (Lycaenidae), Diptera (Phoridae, Syrphidae, Milichiidae), Hymenoptera (Diapriidae, Bethylidae), and various mites. Ants specializing in predation on other ants probably include all species of cerapachyines and at least 2 of *Melophorus*; army ants of the genus *Aenictus* also belong here.

Ants are host to various parasites, including ascomycete fungi (*Cordyceps* and *Laboulbenia*), juvenile mermithid nematodes, and the metacercarial stage of a sheep fluke, *Dicrocoelium dendriticum* (Brangham, 1959). Internal and external parasitoid insects attacking ants are certain phorid flies, Strepsiptera, and eucharitine Pteromalidae (p. 920), among others.

Ant colonies may contain as few as ten adults, or up to millions, but colony size in most Australian species is under 2,000 workers. Colonies may, however, be extremely numerous in tropical forest, savannah woodland, or semi-desert like that covering so much of Australia, and it is not uncommon to find 20 or 30 nests in a single rotten log, or even two or three colonies of different species under the same stone. Upwards of 150 species have been found in a few square km of lowland rain forest in New Guinea, and similar counts could no doubt be made in north Queensland.

Their ubiquity, their sheer abundance, and their generally high rates of activity make ants in Australia one of the most important animal groups in the environmental system of energy flow. Ants tend to be active through the seasons, and many of them are rather general feeders. As predators and scavengers of other arthropods, their operations are probably broadly beneficial, and the distributions of many other kinds of insects, including especially sawflies, predatory beetles, and termites, are strongly influenced, or determined, by the presence or absence of ants in their niches. A little appreciated influence of ants is their role in the vertical mixing and aeration of the soil. Even in temperate North America, with a much poorer complement of ants, transport by ants of particles upward from lower horizons has been found to be of importance in soil formation (see also p. 284).

Occasional harvester species may cause some damage by attacking crop seed-beds or collecting the seeds of forest trees, but the main agricultural damage done by ants is in connection with their guarding and transporting of aphids and coccids harmful to vegetable crops and orchards. Indeed, several kinds of scale insects are a serious threat only when tended by ants. Australians as a rule feel the baneful influence of ants most directly in the home, where introduced species such as the Argentine ant (*Iridomyrmex humilis*), black house ant (*Technomyrmex albipes*), and





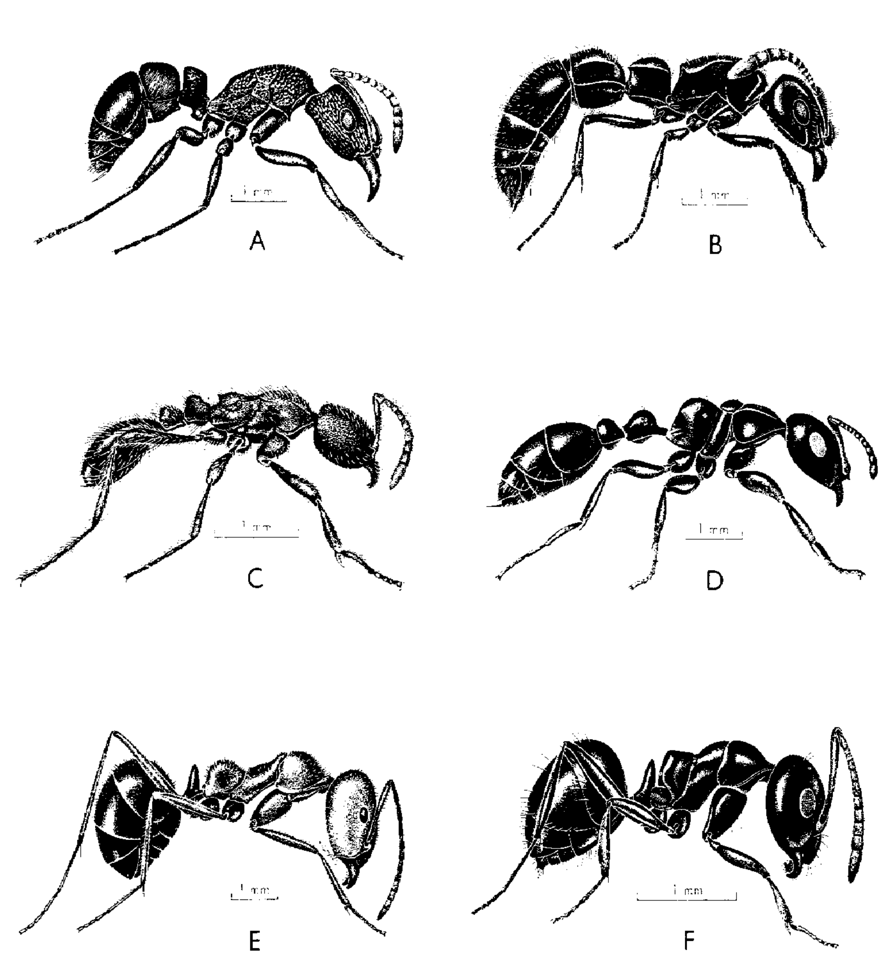


Fig. 37.40. Some representative ants, workers: A, *Rhytidoponera metallica*, Ponerinae; B, *Lioponera* sp., Ponerinae-Cerapachyini; C, *Aenictus* sp., Dorylinae; D, *Tetraponera* sp., Pseudomyrmecinae; E, *Iridomyrmex purpureus*, Dolichoderinae; F, *Prolasius* sp., Formicinae. [F. Nanninga]

hospital ant (*Monomorium pharaonis*) are the main pests in the south, while *Pheidole megacephala*, the fire ant (*Solenopsis geminata*), and the ghost ant (*Tapinoma melanocephalum*) are familiar nuisances in tropical Australia. Bush pests include the ferociously stinging bulldog ants and jumpers of the genus *Myrmecia*, the mainly nocturnal sugar ants (*Camponotus* spp.), and the meat ants (*Iridomyrmex* spp.). The last-mentioned species can be a serious pest around homes and food-processing plants.

All of the 8 ant subfamilies occur in Australia. The MYRMECIINAE (*Myrmecia* and *Nothomyrmecia*) include the most primitive living ants, and are restricted to Australia and New Caledonia. This subfamily is represented elsewhere by the extinct Oligocene genera *Prionomyrmex* (Baltic amber) and *Ameghinoa* (Argentina). *Nothomyrmecia* is the most archaic known living ant. Among the other major subfamilies, PONERINAE (including Cerapachyini) are exceptionally well developed, but DORYLINAE and PSEUDOMYRMECINAE are represented only by a few Indo-Malayan elements in the tropical north.

[W. Brown, 1953, 1955, 1958, 1960; Clark, 1930; Emery, 1910–25; Ettershank, 1966; W. Wheeler, 1918.]

*Key to the Subfamilies of Formicidae—Workers*

(Where there are two figures in the square brackets, the first is the number of genera and the second the number of species known in Australia.)

1. Gaster attached to alitrunk by a waist consisting of 2 more or less reduced and nodiform segments (Figs. 37.37,38) .................... 2
   Gaster attached to alitrunk by a waist consisting of a single reduced segment, which may be nodiform, erect or inclined scale-like, or even prostrate and more or less hidden by overhanging gaster (Figs. 37.40A,E,F) ......... 7
2. Larger species, total length usually exceeding 8 mm, with large eyes and long, slender, serially dentate mandibles. [*Myrmecia*; 65 spp.; Fig. 37.37] .......................... MYRMECIINAE (pt.)
   Smaller species, or, if largest workers or soldiers are over 8 mm, eyes very small or absent and/or mandibles not elongate ...... 3
3. Pygidium flattened at apex, the flattened part bordered with denticles arranged in rows on each side; underside of head with a strong carina on each side running forward from posterior corner. [Cerapachyini-*Lioponera* (Fig. 37.40B), *Syscia*, *Sphinctomyrmex*; 55 spp.] ............................ PONERINAE (pt.)
   Pygidium simple; no distinct carinae on underside of head extending forward from posterior corners ................................ 4
4. Eyes lacking; small to minute army ants. [Queens dichthadiiform, i.e. blind, wingless, with simple alitrunk, gaster long and bulky] ........................................................ 5
   Eyes large to minute, but normally present in Australian forms; not army ants ........... 6
5. Extremely minute (under 2·5 mm) slender yellow species, with 12-segmented antennae. [Rare and subterranean; *Leptanilla*; 1 sp.] ...................................... LEPTANILLINAE
   Small species, but usually over 2·5 mm long; antennae 10-segmented. [*Aenictus*; 3 spp.; Fig. 37.40C] .......................... DORYLINAE
6. Tarsal claws toothed; tibial spurs of mid and hind legs distinctly pectinate; Australian species very slender, black, with large eyes; inhabiting hollow twigs and similar plant cavities. [*Tetraponera*; 2 spp.; Fig. 37.40D] ................................ PSEUDOMYRMECINAE
   Tarsal claws simple; tibial spurs of mid and hind legs, when present, simple or at most very indistinctly pectinate; body form and nesting habits very diverse (Fig. 37.38). [37, 284; e.g. *Podomyrma*, *Crematogaster*, *Meranoplus*, *Strumigenys*] ....................... MYRMICINAE
7. Sting well developed and functional, usually extended and visible in dead specimens ...... 8
   Sting absent, or vestigial and not extensible ........................................................ 9
8. A large (10 mm or more), tawny yellow species with large convex eyes set at the middle of the sides of the head; long, robust mandibles with finely dentate inner margins; palpi segmented 6,4; alitrunk and petiole much as in *Myrmecia*; body with abundant stiffly erect hairs; tarsal claws toothed. [Presumably in south-western W.A.; *Nothomyrmecia*; 1 sp.] ................................ MYRMECIINAE (pt.)
   Disagreeing with some or all of the above characters. [28, 200; e.g. *Amblyopone*, *Rhytidoponera* (Fig. 37.40A), *Leptogenys*, *Odontomachus*] ....................... PONERINAE (pt.)
9. Seventh sternite rolled into a short ventro-apical cone with a round apical orifice (with or without a coronula of minute hairs) that serves as a nozzle for a defensive acid spray; not to be confused with the cloacal orifice, which is more dorsal and normally hidden (Fig. 37.40F). [21, 370; e.g. *Melophorus*, *Oecophylla*, *Camponotus*, *Polyrhachis*] ................. FORMICINAE
   Gastric apex without such an acid-spray-ejecting cone (dried specimens may sometimes have the 7th sternite distorted into a more or less conical shape, but then still without a circular orifice); defensive secretion in the form of a viscous fluid, ejected through a slit-like orifice. [10, 120; e.g. *Leptomyrmex*, *Iridomyrmex* (Fig. 37.40E), *Technomyrmex*] .................................... DOLICHODERINAE



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