FORMICIDAE: A GLOSSARY OF MORPHOLOGICAL TERMS

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The morphological terms are listed and described here in alphabetical order. Within each definition, cross references to other defined terms are in *italics*. The sclerites of the *sting apparatus* and *male genitalia* are described because, although mostly or entirely internal in ants, they are ultimately derived from external appendages. The structure of the formicid *endoskeleton* is also outlined, as is the nomenclature of the wing *venation* and the *cells of the wings*. The names of various forms of sculpture and minor superficial features of the cuticle are omitted. These terms are of use in species-rank taxonomy, but in higher taxa they tend to be sporadic and not of universal application.

Abdomen

The classical third *tagma* of the insect body. The abdomen in ants consists of ten segments, of which the first seven (A1–A7, from front to back) are visible in the female castes (workers and queens), while A8 is also exposed in males. Each of the *tergites* of segments A1–A8 bears a *spiracle* which may be exposed or concealed. In the female castes, segments A8 and A9 are desclerotised, internal, and form parts of the *sting apparatus*, so that A7, because it is always the last visible segment, is usually referred to as being apical. In males, A8 is exposed but A9 is usually retracted and is the gonosomite, having the *male genitalia* attached to its posterior margin. Segment A10 is reduced in both sexes, at most a simple tergal arc of cuticle. In males, tergite 10 is sometimes fused to tergite 9 (= syntergite), and in many groups the sclerite bears a pair of pygostyles (= cerci) apically.

The terminology used to describe the ant abdomen may at first seem confusing. This is because two different terminology systems are in use and tend to be superimposed, but are not strictly compatible.

> The first system, based strictly on morphology, simply numbers the visible abdominal segments from front to back. This system has the advantage of indicating homologous segments between different ant taxa, regardless of the specialisations of individual segments or groups of segments in different groups of ants.

The second system employs a more casual terminology based on observed subdivisions of the abdominal segments. This system names various specialised segments or groups of segments. The advantage of this system is that the subdivisions are generally easily visible.

The first abdominal segment (A1) is the *propodeum*, represented only by its tergite (the sternite has been lost). The propodeum is immovably fused to the *thorax*. The body unit formed by the fusion of thorax and propodeum is termed the *mesosoma* (in some publications called the alitrunk or truncus, or uncommonly and inaccurately just the thorax).

The second abdominal segment (A2) is termed the *petiole*, and is always specialised. It is usually reduced in size, always separated from the preceding propodeum by a complex narrow articulation, and is usually separated from subsequent abdominal segments by at least a constriction. In the vast majority of ants the petiole is distinctly isolated both anteriorly and posteriorly.

Abdominal segments 2 (petiole) to the apical are sometimes collectively called the *metasoma* (to contrast with the *mesosoma* = thorax + propodeum). Thus the petiole (A2) may also be referred to as the first metasomal segment, A3 the second metasomal, and so on.

Abdominal segment 3 (A3) is termed the first gastral segment when it is full-sized and broadly articulated to the following segment (A4), but when reduced and distinctly isolated it is commonly called the *postpetiole*. Abdominal segment 3 articulates with the preceding petiole by means of the *helcium*, which itself is formed from the reduced and specialised *presclerites* of A3, which fit within the posterior foramen of A2 (petiole). The anterior surface of the sternite of A3 may bear a cuticular *prora*, below the helcium.

The one or two isolated segments that follow the mesosoma may be called the *waist*. An older term, *pedicel*, should be abandoned, as it is used universally elsewhere in the Hymenoptera for the first funicular (= second antennal) segment.

Abdominal segment 4 (A4) is the first gastral segment when the waist consists of petiole plus postpetiole, but A4 is the second gastral segment when the waist consists of the petiole alone. Abdominal segments 3 to the apex (when petiole (A2) alone is separated), or A4 to the apex (when petiole and postpetiole (A2 and A3) are separated), are collectively called the *gaster*, the apparent enlarged "abdomen" that comprises the terminal part of the body.

Each abdominal segment behind the first (*propodeum*) consists of a pair of *sclerites* (plates), a dorsal *tergite* (or *tergum*) and a ventral *sternite* (or *sternum*). These may all be similar, or some may be specialised by reduction, fusion, or subdivision into anterior (*presclerite*) and posterior (*postsclerite*) portions that are separated by a constriction (*cinctus*). Tergites and sternites may be referred to as abdominal or gastral, depending on whether an absolute count, or a count relative to the number of separated waist segments, is used. In workers and queens, the last visible tergite, that of A7, is named the *pygidium*, and its corresponding sternite is the *hypopygium*. They have individual names because in some groups of ants the pygidium, the hypopygidium, or both may exhibit a specialised morphology. In males the sternite of A9 is called the subgenital plate (= hypandrium, = hypopygium) as it shields the genital capsule ventrobasally.

Acidopore

The orifice of the formic acid projecting system peculiar to, and diagnostic of, the female castes of subfamily Formicinae. The acidopore is formed entirely from the apex of the *hypopygium* (sternite of A7). Often it is plainly visible as a short nozzle, generally with a fringe of short setae (*coronula*) at its apex. However, in some genera there is no nozzle or setae and the acidopore takes the form of a semicircular to circular emargination or excavation in the apical hypopygial margin. In these taxa the posterior margin of the pygidium may overlap and conceal the acidopore when it is not in use, but the structure is revealed if the pygidium and hypopygium are separated.

Aculeus: see **Sting apparatus**.

Aedeagus: see **Male genitalia**.

Ala (pl. alae): see **Wings**.

Alitrunk: see **Mesosoma**.

Anapleural sulcus: see **Pleurite/pleuron**.

Anepisternum: see **Pleurite/pleuron**.

Annulus (pl. annuli)
A simple, unsegmented ring of cuticle. For example, one of the funicular segments of the antenna, or the *torulus* (= annulus antennalis) around the antennal foramen.

Antenna (pl. antennae)
The antenna in ants is made up of a number of discrete segments, the antennomeres (sing. *antennomere*). The antennomeres consist of an elongated basal segment, the *scape* (= scapus), that is followed distally by 3–11 shorter segments in workers and queens, and 8–12 in males, which together constitute the *funiculus* (= flagellum), giving a total antennal segment count (= antennomere count) of 4–12 in females and 9–13 in males. The scape and funiculus meet at an angle so that in life the entire antenna appears bent (*geniculate*) between the two sections. The basal (first) funicular segment, the one that articulates with the apex of the scape, is sometimes called the *pedicel*. The scape articulates with the head in the *antennal foramen* (= antennal socket), a *foramen* located dorsally on the head, posterior to the *clypeus*. The funicular segments may all be simple (= *filiform*), or the segments may gradually enlarge towards the apex (= gradually incrassate), or a number towards the apex may be expanded into a distinctly differentiated *clava* (= club) that is usually of 2–3 segments but sometimes may be more. When a club is present the antenna is said to be *clavate* or *claviform*.

The antennal foramen itself is encircled by a narrow annular sclerite, the *torulus* (= antennal sclerite, = annulus antennalis), and the socket may be overhung and concealed by the *frontal lobe*. At the base of the scape is a roughly ball-like *condylar bulb* (= articulatory bulb, = bulbus), which is the part of the scape that actually articulates within the socket. Just distal of the condylar bulb is a short constriction or neck, which may be straight or curved, distal of which the scape shaft proper commences.

Antennal fossa (pl. antennal fossae)
The antennal fossa is a depressed area in the cuticle of the dorsum of the head, present in some ant taxa, that surrounds and contains the *torulus* and *antennal foramen*, which consequently appear to be somewhat sunk into the surface of the head.

Antennal scrobe (= scrobe, = scrobis)
A longitudinal groove, impression, or excavation in the side of the head, which may extend above, below, or in front of the eye, which can accommodate at least the antennal scape but sometimes may accommodate the entire antenna when scape and funiculus are folded together. Scrobes vary in development from simple, broad, shallow grooves to extensive, deep trenches, but are absent from the majority of ant genera.

Antennal socket/foramen/insertion: see **Antenna**.

Antennomere: see **Antenna**.

Anterior tentorial pits
A pair of *endophragmal pits* or impressions located anteriorly on the dorsal surface of the head capsule, at or very close to the posterior clypeal margin (*epistomal suture*) and usually close to the antennal sockets. The pits are small invaginations of the exoskeleton that indicate the points of attachment of the anterior arms of the internal skeleton (*tentorium*) of the head to the head capsule. The termination of the posterior arms of the tentorium are marked by a pair of *posterior tentorial pits*, which are located close to the *occipital foramen*.

Apophyseal lines
Externally visible lines that mark the internal track of cuticular processes for muscle attachment.

Arolium (pl. arolia)
A median, terminal lobe on the *pretarsus* (apical tarsomere) of any leg, between the pair of *pretarsal claws*. Arolia are uncommon in worker ants.

Axilla (pl. axillae): see **Mesothorax**.

Basal ring, basimere, basivolsella: see **Male genitalia**.

Basitarsus (pl. basitarsi): see **Tarsus**.

Buccal cavity (= oral fossa)
The anteroventral cavity in the head capsule, which contains the *labium* and *maxillae*. It is bounded anteriorly by the *labrum*, posteriorly and laterally by the ventral cuticle of the head (the *hypostoma* or the *genal bridge*). Within the buccal cavity the median appendage is the *labium*, which is flanked by a *maxilla* on each side of it.

Bulbus: see **Antenna**.

Bulla (pl. bullae): see **Pleurite/pleuron**.

Calcar (= spur): see **Tibal spur**.

Calyx: see **Proventriculus**.

Canthellus: see **Trulleum**.

Cardo: see **Maxilla**.

Cells of the wings
Sections of the *venation* of the wings surround areas of wing membrane that are called cells. The cells are purely a function of the veins that form their boundaries, and the shape and number of cells diminishes with the contraction or loss of various veins or parts of veins. Cells that are entirely surrounded by vein sections are termed *closed cells*, those in which one or more boundaries are missing are termed *open cells*. In ants that show the most complete venation there

are nine closed cells in the forewing (10 if the pterostigma is included), and three in the hindwing, together with a number of cells in each wing that are always open, as defined below.

Unfortunately, there is no single agreed system for naming the cells, and several nomenclatures, some of them widely recognised but some idiosyncratic, are in use. The definitions outlined here indicate which sections of the *venation* form the boundaries of each cell, proximally, anteriorly, distally and posteriorly, so that the identities of individual cells can be correlated across the various systems. The names given to the cells here are in quite common use, but are by no means universal.

Cells of the forewing, named in alphabetical order:

Basal cell [BC]. Bounded proximally by the wing base, anteriorly by Sc+R+Rs, distally by Rs·f1 and M·f1, posteriorly by M+Cu.

Costal cell [CC]. Bounded proximally by the wing base, anteriorly by C, distally by Sc or the *pterostigma*, posteriorly by Sc+R+Rs and Sc+R.

First Discal cell [DC1]. Bounded proximally by M·f1, anteriorly by Rs+M, distally by M·f2 and 1m-cu, posteriorly by Cu·f1 and Cu·f2.

First Subdiscal cell [SDC1]. Bounded proximally by cu-a, anteriorly by Cu·f2, distally by Cu·f3 and Cu2, posteriorly by A·f2.

First Submarginal cell [SMC1]. Bounded proximally by Rs·f1, anteriorly by Sc+R and R·f1, distally by 2r-rs, posteriorly by Rs+M and Rs·f2-3. Note that in the very few taxa where 1r-rs is present, SMC1 is divided into proximal and distal portions by this cross-vein. In this uncommon circumstance SMC1 (proximal) is bounded proximally by Rs·f1, anteriorly by Sc+R, distally by 1r-rs and posteriorly by Rs+M and Rs·f2. SMC1 (distal) is bounded proximally by 1r-rs, anteriorly by R·f1, distally by 2r-rs and posteriorly by Rs·f3.

Marginal cell [MC]. Bounded proximally by 2r-rs, anteriorly by R·f2 and R·f3, distally by the junction of R·f3 and Rs·f5, or distally open when these veins fail to meet, posteriorly by Rs·f4-5.

Second Discal cell [DC2]. Bounded proximally by 1m-cu and Cu·f3, anteriorly by M·f3-4, distally open, posteriorly by Cu1. In many aculeates there is an open third discal cell [DC3], but in ants this is never exhibited because cross-vein 2m-cu, which would form its proximal border, is universally absent.

Second Subdiscal cell [SDC2]. Bounded proximally by Cu2, anteriorly by Cu1, distally open, posteriorly by A·f3.

Second Submarginal cell [SMC2]. Bounded proximally by Rs·f2 and M·f2, anteriorly by Rs·f3-4, distally by 2rs-m, posteriorly by M·f3.

Subbasal cell [SBC]. Bounded proximally by the wing base, anteriorly by M+Cu, distally by Cu·f1 and cu-a, or by cu-a alone when that vein is retracted, posteriorly by A·f1.

Third Submarginal cell [SMC3]. Bounded proximally by 2rs-m, anteriorly by Rs·f5, distally open, posteriorly by M·f4. In many aculeates there is an open fourth submarginal cell [SMC4], but in ants this is never exhibited because cross-vein 3rs-m, which would form its proximal border, is universally absent.

Cells of the hindwing, named in alphabetical order:

Basal cell [BC]. Bounded proximally by the wing base, anteriorly by Sc+R+Rs, distally by Rs·f1, 1rs-m, M·f1 and M+Cu, posteriorly by M+Cu.

Costal cell [CC]. Bounded proximally by the wing base, anteriorly by C, distally by Sc+R, posteriorly by Sc+R+Rs.

Discal cell [DC]. Bounded proximally by M·f1, anteriorly by M·f2, distally open, posteriorly by Cu.
Marginal cell [MC]. Bounded proximally by Sc+R and Rs·f1, anteriorly by R, distally open, posteriorly by Rs·f2.
Subbasal cell [SBC]. Bounded proximally by the wing base, anteriorly by M+Cu, distally by cu-a, posteriorly by A·f1.
Subdiscal cell [SDC]. Bounded proximally by cu-a, anteriorly by M+Cu and Cu, distally open, posteriorly by A·f2.
Submarginal cell [SMC]. Bounded proximally by 1rs-m, anteriorly by Rs·f2, distally open, posteriorly by M·f2.
See also *Venation* and *Wings*.

Cephalon: see **Head**.

Cercus (pl. cerci): see **Abdomen**.

Cervix
Strictly, the flexible intersegmental region between the *head* and the *prothorax*. It is usually shielded from above by a neck-like projection of the anterior *pronotum*, and from below by fused anterior extensions of the *propleuron*. Sometimes the anterior portion of the pronotum which covers and protects the true cervix is also termed the cervix, or the cervical portion of the pronotum.

Cinctus: see **Girdling constriction**.

Clava/ clavate/claviform: see **Antenna**.

Clavus (= vannal lobe, = plical lobe)/**claval furrow** (= vannal fold): see **Wings**.

Claw: see **Tarsus**.

Clypeus
Anterior sclerite of the dorsal head, bounded posteriorly by the *epistomal suture*, which is commonly referred to as the *clypeal suture*, or posterior clypeal margin. The median section of the epistomal suture, immediately anterior to the frontal carinae and antennal sockets, is sometimes called the *frontoclypeal suture*. The anterior clypeal margin usually forms the anterior margin of the head in full-face view (but a projection of the *labrum* may be anterior to the clypeus in some taxa). The body of the clypeus consists of a pair of lateral portions, or narrow bands of cuticle, on each side of a shieldlike median portion. The median portion of the clypeus may be equipped with one or more longitudinal carinae, or may be variously specialised in shape. Posteriorly, the median portion of the clypeus may end in front of the antennal sockets/frontal carinae or lobes, or may project backwards between them. In some taxa the clypeus is extremely reduced and very narrow from front to back, bringing the antennal sockets very close to the anterior margin of the head.

Condylar bulb: see **Antenna**.

Coxa (pl. coxae)
The first, most basal, segment of any leg; the leg segment that articulates within the *coxal cavity* (= coxal foramen) in the ventral thorax. The coxa of the prothoracic (fore) leg is often termed the *procoxa*, that of the mesothoracic (middle) leg the *mesocoxa*, and that of the metathoracic (hind) leg the *metacoxa*.

Cupula: see **Male genitalia**.

Cuspis: see **Male genitalia**.

Declivity: see **Propodeum**.

Digitus: see **Male genitalia**.

Distivolsella: see **Male genitalia**.

Endophragmal pit
A pit or pit-like impression in a sclerite that is an external indication of the point of attachment of part of the *endoskeleton*. Endophragmal pits that are universal in ants include the *anterior* and *posterior tentorial pits* of the head, and the *mesosternal* and *metasternal* pits of the ventral mesosoma. Some groups of ants also have endophragmal pits in other locations. For example, workers of the dorylomorph genera usually have a pit laterally on the mesosomal pleuron, either immediately posterior to the mesometapleural suture, or even more posteriorly closer to the propodeal spiracle.

Endoskeleton
As well as the extensive exoskeleton, worker ants have a small but significant endoskeleton that consists of sclerotised internal plates that serve as muscle attachments (the endoskeleton of alate forms remains to be investigated).

The endoskeleton of the head is the *tentorium*, formed from united anterior and posterior pairs of arms. In ants the fusion is complete and the tentorium takes the form of a pair of longitudinal struts, attached to the head capsule anteriorly and posteriorly. In addition, each tentorial strut has an anterolateral side-branch that extends to the antennal socket. The only visible external indications of the tentorium are the *anterior tentorial pits* and *posterior tentorial pits*, which are endophragmal pits that mark the points at which the tentorial arms are attached to invaginations of the exoskeleton.

The *mesothorax* has a *mesendosternite*, derived from the invaginated *sternum* of the segment. At maximum development the mesendosternite is a thin, longitudinal, roughly triangular sclerite that extends the length of the segment and terminates posteriorly at the externally visible *mesosternal pit*. In most ant groups the dorsum of this endosclerite extends into a Y-shaped pair of apodemes that are inclined anteriorly and directed anterolaterally and dorsally, and there is usually a reinforcing cross-member between the apodemes near their base. The apices of the apodemes are usually attached to the pleuron. In dorylomorphs the apodemes are inclined posteriorly, extend laterally from their point of origin, and are strongly attached to an

invagination of the pleuron; the point of attachment is often visible externally as an *endophragmal pit*.

At the internal junction of the mesothorax and *metathorax*, just posterior to the *mesocoxal* cavities, is a raised ridge or low wall of transversely arched cuticle that appears to be derived from the invaginated fused margins of the two segments, right across their line of junction. Arising from the midpoint of this transverse cuticular wall, fused to its vertical midline anteriorly, and extending posteriorly, is the *metendosternite*. At maximum development this sclerite is similar in shape to the mesendosternite and terminates posteriorly at the externally visible *metasternal pit*. In most ant groups the metendosternite has a pair of dorsal apodemes, that may be very long, extending forward into the mesothoracic cavity above the mesendosternal apodemes, or they may fuse to the pleuron far in front of their point of origin. However, in the dorylomorphs the metendosternal apodemes are short and attached to the posterior surface of the mesendosternal apodemes.

Endosternite: see **Endoskeleton**.

Epimeral sclerite (= mesepimeral sclerite, = epimeral lobe)
In some groups of ant workers, and very commonly in alates, there is a small, sometimes detached, posterior lobe of the *mesopleuron* that covers or shields the orifice of the *metathoracic spiracle*, referred to as the epimeral sclerite (strictly the mesepimeral sclerite) or epimeral lobe. The name is derived from the ancestral morphology of the *mesopleuron*, where in more generalised forms the pleuron is divided by an oblique suture (the *pleural suture*) into an anterior *mesepisternum* and a posterior *mesepimeron*. No trace of this division remains in ants. However because of its position, this lobe, is assumed, perhaps incorrectly, to have been derived from the ancestral mesepimeron.

Epinotum
An archaic name for the *propodeum* used extensively in the past, but only by myrmecologists. *Propodeum* is the recommended term, because it is universally used elsewhere in hymenopteran morphology.

Epistomal suture: see **Clypeus**.

Exocrine gland
A gland with secretory cells located below the cuticle and has pores, ducts, or one or more orifices that open to the surface.

Fenestra (pl. fenestrae)
In general, a thin or translucent spot anywhere in the cuticle. In the wing *venation*, fenestra is the name applied to a translucent spot or apparent break in a vein which indicates the point at which a *flexion line* or *fold line* traverses the vein. In the most generalised ant wings, such fenestrae occur in Rs·f2, 2rs-m, cu-a, and Cu2 of the forewing, and in 1rs-m and cu-a of the hindwing.

Femur (pl. femora)
The third segment of any leg, counting from the basal coxal segment that articulates with the thorax. The femur is generally the longest leg segment and is separated from the *coxa* only by a

small intermediate segment, the *trochanter*. The femur of the prothoracic (fore) leg is often termed the *profemur*, that of the mesothoracic (middle) leg the *mesofemur*, and that of the metathoracic (hind) leg the *metafemur*.

Filiform (antenna)
With the antennal funiculus thread-like, the segments all of approximately the same width. The contrasting antennal form is *clavate* (club-like or clubbed), where the apical segments of the antenna are disproportionately enlarged.

Flagellum (= funiculus): see **Antenna**.

Flexion lines/folds: see **Wings**.

Foramen (pl. foramina)
A natural opening or perforation in a sclerite. Usually an opening in one sclerite that accommodates the insertion of another. For example, the *occipital foramen* (= foramen magnum) is the posterior hole in the head capsule within which the articulation with the *pronotum* is accommodated. Similarly, the *coxal cavities* are the ventral foramina within which the coxae articulate with the thorax, and the *propodeal foramen* is the posterior orifice in the mesosoma within which the petiole (A2) articulates.

Frons
The area of the dorsal head posterior to the *frontoclypeal suture*, above the antennal sockets and including the *median ocellus*. As ocelli are often absent in worker ants the posterior limit of the frons can be referred to only in a very vague way in these taxa. Ancestrally, the *anterior ocellus* arises on the posteriormost part of the frons, while the pair of posterior ocelli arise on the *vertex*.

Frontal carinae (sing. frontal carina)
A pair of longitudinal cuticular ridges or flanges on the head, located dorsally behind the *clypeus* and between the *antennal sockets*. They are very variable in length and strength of development in the various ant taxa, frequently being short and simple but sometimes extending back to the posterior margin of the head. In some groups the frontal carinae are vestigial or absent, but elsewhere they may be very strongly developed or form the dorsal margins of extensive *antennal scrobes*. In many groups the frontal carinae anteriorly, especially between the antennal sockets, are expanded into laterally projecting lobate extensions, the *frontal lobes*, which overhang and partially to entirely conceal the antennal sockets themselves. Frontal lobes may be the only expression of the frontal carinae in some groups. Sometimes the portion of the *torulus* closest to the cephalic midline is also raised and expanded into a small lobe that projects laterally. This may be visible below the frontal lobe, or be fused to the frontal lobe.

Frontal lobes: see **Frontal carinae.**

Frontal triangle (= supraclypeal area)
A small, usually triangular patch of cuticle located medio-dorsally on the head, immediately behind the clypeus and approximately between the antennal sockets or the anterior parts of the frontal carinae. Not apparent in many ant taxa and reduced or very narrow in some. In groups

where the *frontal lobes* are medially very closely approximated, the frontal triangle may be compressed and longitudinal, and appears posterior to the frontal lobes as a narrow median sclerite.

Frontoclypeal suture: see **Clypeus**.

Funiculus (= flagellum): see **Antenna**.

Furcula: see **Sting apparatus**.

Galea: see **Maxilla**.

Gaster
A useful convenience term for the swollen apical portion of the body that forms the apparent "abdomen". Morphologically the gaster consists of abdominal segments 3 to apex when the waist is of a single isolated segment (*petiole*, = A2), but of abdominal segments 4 to apex when the waist is of two isolated segments (petiole plus *postpetiole*, = A2 plus A3). In the second circumstance, the gaster, when of segments A4 to apex, may also be termed the *opisthogaster*.

Gena (pl. genae)
Area of the side of the head which is bounded in front by the anterior margin of the head capsule, and extends to the posterior margin of the head below the eye when eyes are present. In ants the gena is expanded ventrally and forms the extensive ventral surface of the head, the *genal bridge*.

Genal bridge
On the ventral surface of the head, the space between the *buccal cavity* and the *occipital foramen* is occupied by an extensive area of cuticle divided by a mid-ventral longitudinal line or groove. This surface is formed by the ventral expansion and mid-line fusion of the *genae* and is called the genal bridge. The extreme anterior margin of the genal bridge, which surrounds the *buccal cavity*, is the *hypostoma*.

Geniculate
Bent like a knee joint. The term is usually used to describe the shape of the ant's antenna in life, where the funiculus is carried at a marked angle to the scape.

Girdling constriction (= cinctus)
A constriction or sudden and marked narrowing of an abdominal segment, which usually extends around the entire circumference. For convenience it is usually stated in keys that girdling constrictions are present between two segments. This is not strictly correct as the constriction morphologically represents the separation between the *presclerites* and *postsclerites* of the more posterior segment. The greater part of the presclerites are usually inserted in the posterior end of the preceding segment and are concealed, leaving only the constriction and postsclerites visible externally.

Glossa: see **Labium**.

Gonangulum, gonapophysis, gonocoxa, gonoplac, gonostylus: see **Sting apparatus**.

Gonobase, gonocardo, gonocoxite, gonoforceps, gonolacinia, gonosomite, gonostipes, gonosquama, gonostylus: see **Male genitalia**.

Guard setae (= guard hairs)
A row or tuft of specialised setae that traverse and protect the orifice of the *metapleural gland*. These setae usually arise below the orifice of the gland and are directed upward across the orifice.

Gula
Use of this term when referring to the ventral surface of the head capsule in ants is incorrect. Morphologically, the gula is a separated medioventral sclerite of the head, which is bounded anteriorly by the *posterior tentorial pits*. In consequence the posterior tentorial pits are distant from, and considerably anterior to, the *occipital foramen*. In ants the posterior tentorial pits are located adjacent to the occipital foramen; no gula sclerite is present.

Hamuli (sing. hamulus): see **Wings**.

Harpago: see **Male genitalia**.

Head (= cephalon, = cranium, = prosoma)
The classical first *tagma* of the insect body. The head capsule is the result of the fusion of six (or perhaps seven) embryonic segments. In adult ants these segments are completely fused and indistinguishable, but most retain appendages that are conspicuous. The appendages of cephalic segment 1 are fused and form the *labrum*; the appendages of segment 2 are the *antennae*; the appendages of segment 3 are embryonic only, unrepresented in adults; the appendages of segment 4 are the *mandibles*, of segment 5 the *maxillae*, and of segment 6 the *labium*. Some morphologists argue for the presence of a seventh embryonic segment which would occur between 1 and 3 in the preceding list and bear the eyes as its appendages.

Helcium
The very reduced and specialised *presclerites* of abdominal segment 3, which form a complex articulation within the posterior foramen of the *petiole* (A2). In general the helcium is mostly or entirely concealed within the posterior foramen of the petiole, but in some groups it is partially visible.

Humerus (pl. humeri)
The anterolateral dorsal angle (shoulder) of the *pronotum*; frequently referred to as humeral angles.

Hypopygium
The sternite of abdominal segment 7 in workers and queens; the terminal visible gastral sternite in the female castes. In males the sternite of abdominal segment 9 is sometimes also referred to as the hypopygium, but *subgenital plate* (or hypandrium) is a better alternative term as it avoids the confusion caused by two non-homologous sclerites having the same name.

Hypostoma
The narrow U-shaped strip of cuticle immediately behind the *buccal cavity* with posterior and lateral margins on the anteroventral surface of the head. In ants the hypostoma is often indistinct, sometimes indiscernible, and usually merely forms the anterior margin of the *genal bridge*, to which it is entirely fused. However, in some taxa a narrow suture remains detectable between the hypostoma and the genal bridge.

Hypostomal teeth
One or more pairs of triangular or rounded teeth that project forward from the *hypostoma*, towards or slightly into the buccal cavity.

Jugum (= jugal lobe, = anal lobe): see **Wings**.

Katepisternum: see **Pleurite/pleuron**.

Labial palp (= labial palpus; pl. labial palpi).
A sensory palp, with a maximum of four segments, that arises anterolaterally on each side of the *prementum* sclerite of the *labium*. A count of the number of segments in a *maxillary palp* and a labial palp, in that order, is called the *palp formula*.

Labium
With the head in ventral view the labium is a longitudinal appendage, situated medially within the *buccal cavity*; it is flanked on each side by a *maxilla*. The labium is formed from an ancestral pair of appendages, now indistinguishably fused together along the midline to form a single structure. The main sclerite of the labium is the *prementum*. Basal to the prementum, and attaching it to the head capsule, may be a small sclerite, the *postmentum*, but this area is frequently entirely membranous. The prementum bears a pair of *labial palps*, one at each side. At the distal end of the prementum is a lobe, the *glossa*, which may be simple or bilobed apically. The base of the glossa is sometimes flanked by a much smaller lobe on each side, the *paraglossa*, but in ants these are usually extremely reduced or absent. The glossae and paraglossae together are sometimes termed the *ligula*.

Labrum
Mouthpart sclerite that hinges on the anterior margin of the *clypeus* and usually folds back and down over the apices of the *maxillae* and *labium*, shielding them when the mouthparts are not in use. In most ants the labrum is a bilobed plate that is not visible in dorsal view, but in some taxa part of it projects forward beyond the anterior clypeal margin even when the mouthparts are retracted. Occasionally it is modified into one or more long, prominent *labral lobes*.

Lacinia: see **Maxilla**.

Lancet: see **Sting apparatus**.

Laterotergite: see **Tergite/tergum**.

Leg segments (= podites)

Each leg consists of a basal *coxa* that articulates with the thorax, followed in order by a small *trochanter*, a long and generally stout *femur*, a *tibia*, and a *tarsus*. The last consists of five small subsegments (= tarsal segments, = tarsomeres) and terminates apically in a pair of claws on the apical (*pretarsal*) segment; sometimes there is also a membranous lobe, the *arolium*, between the claws. The prefixes *pro-*, *meso-*, and *meta-*, applied to any of these terms, indicates that segment on the leg of a particular thoracic segment. For example, *mesofemur* = the femur of the middle (second) leg; *metatibia* = the tibia of the hind (third) leg.

Ligula: see **Labium**.

Malar area (= malar space)
The area of the head capsule between the base of the mandible and the anterior margin of the eye. Strictly a part of the *gena* but sometimes its relative length is a useful concept in the taxonomy of some groups.

Male genitalia.
The genitalia of male ants consist of three pairs of valves at the apex of the abdomen that are bounded basally by a ring-sclerite and shielded ventrobasally by the small sternite of A9, the *subgenital plate* (= hypopygium, = hypandrium). In some groups the genitalia may be completely retracted within the body, but in others they are permanently extruded, partially to almost entirely. Most sclerites of the male genitalia, and their subdivisions, have amassed a number of synonymous names. In the following discussion, the name given first is the one preferred here; alternative names follow in parentheses.

The basalmost sections of the stout outer pair of valves (the parameres, see below) are encircled by a cuticular *basal ring* (= gonobase, = gonocardo, = cupula, = lamina annularis). This genitalic complex of basal ring + parameres, sometimes called the phallobase, is attached to the apex of the ninth abdominal segment (= gonosomite).

Of the three pairs of valves, the outermost valve on each side is the *paramere* (= gonosquama, = gonoforceps), which is usually large and conspicuously sclerotised. In ants the paramere is often a single unit, not subdivided into proximal and distal portions, although in some groups the apical section may be narrowed, elongated, or otherwise modified. In some groups, however, the paramere is subdivided into proximal and distal portions by a transverse sulcus. In this instance the proximal section, closest to the basal ring, is the *basimere* (= gonostipes, = gonocoxite, = basiparamere), and the distal portion is the *telomere* (= gonostylus, = harpago). The median valve on each side is the *volsella*, which arises basally from the inner surface of the paramere. The volsella may be a simple lobe, or may be split into a curved or hooklike dorsal lobe, the *digitus* (= gonolacinia), and a rounded lobe below it, the *cuspis* (= distivolsella), which together serve to clasp the female genitalia during copulation. Any part of the volsella that is proximal to its division into digitus and cuspis may be termed the *basivolsella* (= lamina volsellaris). The innermost pair of valves together constitute the *aedeagus* (= penis), the intromittent organ. Occasionally, each aedeagal valve has been called a *sagitta* (pl. sagittae) but this is not recommended for ants as the term sagitta is extensively used among the apoids, where it always refers to a proximal lateral process on each aedeagal valve.

Mandalus: see **Trulleum**.

Mandibles

The appendages with which ants manipulate their environment. They are extremely variable in shape, size, and dentition, and have great importance in ant taxonomy. Sometimes, but not always, the mandibles in the female castes are more strongly, or somewhat differently, developed than in conspecific males.

Margins. In full-face view, with the mandibles closed, the longitudinal margin or border of each mandibular blade that is closest to an anterior extension of the midline of the head is the *masticatory margin* (= apical margin), and is usually armed with teeth. The base of this margin, close to the anterior margin of the clypeus, usually passes through a *basal angle* into a transverse or oblique *basal margin*. The two margins may meet through a broad or narrow curve, or meet in an angle or tooth. When the mandibles are narrow or linear, the distinction between masticatory and basal margins may be lost by obliteration of the basal angle. The *external margin* (= lateral or outer margin) of each mandible forms its outer border in full-face view and may be straight, sinuate, or convex.

In many groups the dorsal base of the body of the mandible bears a number of specialised structures just distal to the mandibular articulation and proximal of the basal margin of the mandible, termed the *mandalus*, *canthellus* and *trulleum*; see under the last named for a discussion of these.

Shape. In the vast majority of ants the mandibular margins form a *triangular* or *subtriangular* shape in full-face view, but may be drawn out anteriorly while retaining the basic triangular shape and become *elongate-triangular*. In several discrete lineages the mandible has become *linear*; the blade is long and narrow and the external and masticatory margins are approximately parallel or taper gradually to the apex; the whole blade may be straight or curved. Linear mandibles may evolve in one of three ways.

(1) The base of the mandible narrows and the basal angle is obliterated, so that the basal and masticatory margins form a single margin.
(2) The masticatory margin becomes elongated and the basal margin contracted.
(3) The basal margin becomes elongated and the masticatory margin contracted.

Extremely curved mandibles, usually quite short and slender, and with few or no teeth on the masticatory margin, are termed *falcate*.

Dentition. The masticatory margin of each mandible is usually armed with a series of *teeth* or *denticles* (short or very reduced teeth), or a mixture of both, which generally extend the length of the masticatory margin. If teeth alone are present, or a combination of teeth and denticles, the mandible is *dentate*. If only tiny denticles occur on the margin the mandible is *denticulate*, and if the margin lacks any form of armament it is *edentate*. A natural gap in a row of teeth (as opposed to a site where teeth have been broken off or completely worn down) is a *diastema* (pl. diastemata) and an elongate mandible with an uninterrupted series of teeth may be described as *serially dentate*. Individual teeth are usually sharp and triangular in shape but may be rounded (*crenulate*), long, narrow, and spine-like (*spiniform*), or peg-like (*paxilliform*). Reduced teeth or denticles that occur between full-sized teeth are termed *intercalary*.

In general the first, distalmost, or *apical tooth*, the one farthest away from the anterior clypeal margin, is the largest on the masticatory margin, although in some taxa median or even basal teeth may be the largest. The tooth immediately preceding the apical is usually called the *preapical tooth* (= subapical tooth). Sometimes the term preapical teeth may be loosely applied to all the teeth that precede the apical. The tooth immediately distal of the *basal tooth* may be termed the *prebasal* (= subbasal) tooth.

In some genera teeth may also be present on the basal margin of the mandible, but in most this margin is unarmed. Some taxa also have a *basal lamella* on the mandible. This is a thin cuticular outgrowth from the margin, proximal to any teeth that may be present.

Maxilla (pl. maxillae)
With the head in ventral view the maxillae are situated within the *buccal cavity*, one on each side of the central *labium*. The basal segment of the maxilla, which attaches the structure to the head capsule, is the *cardo*. Attached distally to the cardo is the main sclerite of the maxilla, the *stipes*, which towards its apex bears a *maxillary palp*. The inner surface of the stipes bears a lobe towards its distal end, the *lacinia*, the free margin of which is usually irregular, minutely dentiform, or even pectinate. At the distal apex of the stipes is a terminal hood or lobe, the *galea*, which often folds over the lacinia.

Maxillary palp (= maxillary palpus; pl. maxillary palpi)
The segmented sensory palp on the *maxilla*, articulated to the stipes. The palp may have at most 6 segments but these are variously reduced in number in different ant groups; only very rarely are the maxillary palps absent. A count of the number of segments in a maxillary palp and a *labial palp*, in that order, is called the *palp formula*.

Mayrian furrow: see **Mesothorax**.

Mesendosternite: see **Endoskeleton**.

Mesepimeron/mesepisternum: see **Epimeral sclerite**.

Mesonotum: see **Tergite/tergum**.

Mesopleuron: see **Pleurite/pleuron**.

Mesoscutum/mesoscutellum: see **Mesothorax**.

Mesosoma (= alitrunk, = truncus, = apparent "thorax")
A convenience term for the second visible main section of an ant's body, following the head. Morphologically the mesosoma consists of the three segments of the true thorax (*prothorax*, *mesothorax*, *metathorax*), to which is fused the *propodeum* (the tergite of A1), forming a single unit.

Mesosternal pit/Mesosternal process: see **Metasternal pit/Metasternal process**.

Mesothoracic spiracle: see **Spiracle**.

Mesothorax
The second segment of the *thorax*, attached anteriorly to the *prothorax*, posteriorly to the *metathorax*, and bearing the mesothoracic (second, median) pair of legs and the first *spiracle*. In alate (winged) forms it also bears the *tegulae* and the anterior pair of *wings* (forewings).

The tergite of the mesothorax is the *mesonotum*. Anteriorly this is attached to the *pronotum*, either by a mobile suture (*promesonotal suture*), or frequently in the worker caste by fusion, in which instance the fused *nota* are termed the *promesonotum*. In alates the mesonotum is extensive and is usually divided into a larger anterior *mesoscutum* (= scutum) and a smaller posterior *mesoscutellum* (= scutellum) by a transverse *scutoscutellar* suture. In alate queens and males the mesoscutum usually has a pair of narrow, incised lines, the *parapsidal grooves* (= parapsidal lines) which extend anteriorly from the scutoscutellar suture. In males the mesoscutum also frequently exhibits a pair of *notauli* (sing. notaulus), which in older publications are often called the Mayrian furrows or prescutal sutures. When present, each notaulus arises anterolaterally, near the anterior margin of the mesoscutum, and converges on its opposite number towards the midline posteriorly. In many groups the two notauli meet medially to form a V-shape, and in some the tail of the V-shape then extends posteriorly, so that the notauli are Y-shaped. On each side of the mesoscutum, covering the extreme base of the wing, is a small sclerite, the *tegula*. In alates, immediately posterior to the scutoscutellar suture, is the mesoscutellum. On each side, between mesoscutum and mesoscutellum, is a small, usually roughly triangular area, the *axilla* (pl. axillae), that extends down toward the base of the forewing. There is often a transverse depression, immediately posterior to the scutoscutellar suture, that links the axillae across the dorsum.

Posteriorly the mesonotum is ancestrally attached to the *metanotum* (tergite of the *metathorax*), by the *mesometanotal suture*, but in workers of some ant groups the mesonotum and metanotum are entirely fused. In many workers the metanotum is reduced to a transverse groove (*metanotal groove*), and in some the metanotum is entirely absent. In the last condition the posterior of the mesonotum is attached directly to the *propodeum*, and if a suture remains between them it is the *notopropodeal suture*. The fused sclerite thus produced may be called the *notopropodeum*. In workers, the mesonotum abuts the lateral *mesopleuron*, a long sclerite which extends down to the *mesocoxa*. Mesonotum and mesopleuron may be separated by a transverse *notopleural suture*, or the two sclerites may be fused together. In alates the articulation of the forewing occurs between the mesoscutum and the mesopleuron.

Immediately behind the posterodorsal corner of the mesopleuron there may be a small lobe, or small detached sclerite, the *epimeral sclerite* (or *epimeral lobe*), which is probably a detached section of the pleurite. When present it conceals the orifice of the *metathoracic spiracle*, but this sclerite is absent in many groups (see *spiracle*).

The mesopleuron may be traversed by a horizontal *anapleural sulcus*, in which case the portion above the sulcus is the *anepisternum* (or *mesanepisternum*), that below the sulcus is the *katepisternum* (or *mesokatepisternum*).

The upper portion of the anterior margin of the mesopleuron abuts the side of the pronotum; below this is a long, free mesopleural margin against which the *procoxa* rests. Posteriorly, the mesopleuron is fused to the *metapleuron* by the oblique *mesometapleural suture*, though in workers of some groups these two sclerites are completely fused and the suture is obliterated.

The ventral surface of the mesothorax consists entirely of the pleurites, which have expanded across to the ventral midline and fused. The ancestral hymenopterous sternite of the mesothorax is internal and represented by the *mesendosternite*. The anterior margin of the ventral mesothorax often has a projecting median process that extends forward between the bases of the *procoxal cavities*, and overlaps the posterior margin of the *prosternum*. On the ventral midline of the mesothorax, anterior to the *mesocoxal cavities*, is the *mesosternal pit*, an *endophragmal pit* that marks the attachment of the mesendosternite to the exoskeleton. This pit is sometimes

accompanied by a paired, cuticular, *mesosternal process*. Immediately posterior to the mesocoxal cavities and the mesosternal pit is the arched suture that marks the junction of the mesothorax and the *metathorax*.

Metacoxal cavities
The pair of foramina located posterolaterally in the ventral surface of the *metathorax*, within which the *coxae* (basal leg segments) of the metathoracic (hind, third) legs articulate. The metacoxal cavities are located on each side of the usually U-shaped or V-shaped *propodeal foramen* in which the base of the *petiole* (A2) articulates. The propodeal foramen may be confluent with the metacoxal cavities on each side, or separated from them by a narrow bar, or a broad annulus, of cuticle.

Metanotal groove/metanotum: see **Tergite/tergum**.

Metapleural gland
An *exocrine gland*, common in female castes but very rare in males, whose orifice is on the *metapleuron*, usually situated at or near the posteroventral corner, above the level of the *metacoxa* and below the level of the *propodeal spiracle*. The swollen *bulla* of the metapleural gland is often more conspicuous than the gland's orifice, and takes the form of a shallow blister or convex swelling on the metapleuron; the bulla sometimes extends almost to the propodeal spiracle. The orifice of the metapleural gland may be a simple pore or hole, or may be protected by cuticular flanges or other outgrowths, or by *guard setae* that arise below the orifice and extend across it. In a few groups of ants the metapleural gland has been lost in all female castes.

Metapleural lobe: see **Propodeum**.

Metapleuron (pl. metapleura): see **Pleurite/pleuron**.

Metasoma
A collective term for abdominal segments 2 to apex, regardless of the absence or presence of abdominal constrictions that may occur between any of these segments.

Metasternal pit/ Metasternal process
The ventral surfaces of the *mesothorax* and *metathorax* each have an *endophragmal pit*, located on the midline anterior to the level of the *coxal cavities*. These pits mark the sites of attachment of the endoskeletal *mesendosternite* and *metendosternite* to the exoskeleton. In many groups of ants the pits are associated with a pair of cuticular projections, the mesosternal and metasternal processes. In most groups of ants the metasternal pit is distinctly anterior to the apex of the *propodeal foramen*, but in taxa where the foramen is extensive the pit may be extremely close to its apex.

Metathorax
The third segment of the *thorax*, attached anteriorly to the *mesothorax* and dorsally and posteriorly to the *propodeum*, and bearing the metathoracic (third, hind) pair of legs and usually the second *spiracle*, though this may be lost in some groups. In alate (winged) forms it also bears the posterior (hind) pair of *wings*.

The tergite of the metathorax is the *metanotum*. This sclerite is usually distinct in alates but is extremely variably developed among workers of the various groups of ants. At its fullest development in workers the metanotum is a distinct transverse sclerite between the *mesonotum* and *propodeum*, separated from each by a transverse suture, the *mesometanotal suture* anteriorly and the *notopropodeal suture* posteriorly. In workers there is a very common morphoclinal reduction from this condition, where the metanotum becomes gradually shorter until it is represented only by a narrow transverse groove (*metanotal groove*) in which the true metanotum is represented only by the extreme base of the groove. In some groups even this groove is obliterated, so that the posterior margin of the mesonotum meets the anterior margin of the propodeum. This junction may be indicated by a feeble transverse impression (*notopropodeal suture*), or the sclerites may become fully fused, forming a *notopropodeum*. Conversely, the metanotum may remain present on the dorsum but become indistinguishably fused to the mesonotum while retaining a strong suture between itself and the propodeum.

Laterally, the *metapleuron* in workers forms an oblique sclerite that is usually roughly triangular. This is often separated from the *mesopleuron* by the *mesometapleural suture*, though in some the two sclerites are completely fused and no trace of a suture remains. Similarly, the dorsal junction of the metapleuron with the propodeum may be indicated by a suture, but again the two may be entirely fused to form a single sclerite, with no trace of a suture between them. In alates the metapleuron is usually more extensive. It is commonly divided by a short transverse sulcus into an upper *metanepisternum*, below the articulation of the hindwing, and a lower *metakatepisternum*. Close to the dorsal apex of the metapleuron is the *metathoracic spiracle*, which in alates is located between the mesopleuron and metapleuron and often shielded or concealed by the *epimeral sclerite*. Among workers, in groups where the metanotum forms a discrete dorsal sclerite, the spiracle is usually located dorsally or laterodorsally, on the side adjacent to the metanotum. Elsewhere, in workers where the metanotum is greatly reduced or absent, the spiracle is lower down on the side. It is sometimes open, sometimes concealed beneath the *epimeral sclerite*, and in some groups the spiracle has been lost. The posteroventral corner of the metapleuron, above the *metacoxa*, has the bulla and orifice of the *metapleural gland*.

The ventral surface of the metathorax consists entirely of the pleurites, which have expanded across to the ventral midline and fused. The ancestral hymenopterous sternite of the metathorax is internal and represented by the *metendosternite*. The ventral metathorax commences anteriorly in a curved suture immediately posterior to the *mesocoxal cavities* and *mesosternal pit*. On the ventral midline of the metathorax, anterior to the *metacoxal cavities*, is a *metasternal pit*, an *endophragmal pit* that marks the attachment of the metendosternite to the exoskeleton. This pit is sometimes accompanied by a paired, cuticular, *metasternal process*. The *metacoxal cavities* are located close to the posterior corners of the ventral surface, and the often extensive *propodeal foramen*, within which the *petiole* (A2) articulates, extends forward between them.

Metathoracic spiracle: see **Spiracle**.

Metatibial gland
A presumably *exocrine gland* that is located on the ventral surface, or more rarely the posterior surface, of the *metatibia*, usually just proximal of the metatibial spur.

Metendosternite: see **Endoskeleton**.

Mouthparts
The feeding appendages, located anteriorly and anteroventrally on the *prognathous* head capsule. The mouthparts consist of the *mandibles*, *maxillae* and *labium*, of which the last two are located within the *buccal cavity*, on the underside of the head capsule.

Notaulus (pl. notauli): see **Mesothorax**.

Notopropodeal groove: see **Tergite/tergum**.

Notum (pl. nota)
The name applied to any one of the three ancestral thoracic tergites. Hence, *pronotum* is the notum of the *prothorax*, *mesonotum* of the *mesothorax*, and *metanotum* of the *metathorax*. In all worker ants each notum is a single sclerite, but in alate forms the mesonotum is usually subdivided. As the worker caste is derived ultimately from an alate female caste, the simple nota of the workers represent a secondary reversal to a more generalised condition.

Nuchal carina
A ridge situated posteriorly on the head capsule that separates the dorsal and lateral surfaces (*vertex* and *genae*) from the occipital surface.

Oblong plate: see **Sting apparatus**.

Occipital corners/ margin (of head): see **Posterior corners/margin**.

Occipital foramen (= foramen magnum)
The *foramen* located posteromedially in the head capsule, within which the membranous *cervix* articulates the head to the *prothorax*.

Occiput (= occipital surface)
The posterior surface of the head capsule, immediately above the *occipital foramen*. The occiput is usually vertical or nearly so above the foramen, and is separated from the *vertex* of the cephalic dorsum by the transverse posterior margin of the head capsule.

Ocellus (pl. ocelli)
A maximum of three simple, single-faceted eyes, which when present (absent in many worker ant taxa) are located in a triangle on the cephalic dorsum. Morphologically the anterior (median) ocellus marks the posterior limit of the *frons*, and the posterior (lateral) pair are on the *vertex*.

Ommatidium (pl. ommatidia)
A single optical component (facet) of the compound eye.

Opisthogaster: see **Gaster**.

Palp Formula (PF)

A standardised way of indicating the number of segments in the maxillary and labial palps. The number of maxillary palp segments is given first, the number of labial palp segments second. Thus PF 6,4 indicates that the maxillary palp has six segments, the labial palp four.

Paraglossa: see **Labium**.

Paramere: see **Male genitalia**.

Parapsidal groove: see **Mesothorax**.

Pedicel
An archaic term used in ants for the isolated body segments between *mesosoma* and *gaster*, namely the *petiole* (A2), or petiole plus *postpetiole* (A2 plus A3). Use of the term pedicel is no longer recommended in this sense, as it is used elsewhere throughout the Hymenoptera as the name for the first *funicular* segment of the *antenna*.

Peduncle (of petiole, = A2)
The relatively slender anterior section of the petiole which begins immediately posterior to the propodeal-petiolar articulation and extends back to the petiolar node or scale. It is very variable in length and thickness, but when present in any form the petiole is termed *pedunculate*. When a peduncle is absent, so that the node or scale of the petiole immediately follows the articulation with the propodeum, the petiole is termed *sessile*. If an extremely short or poorly defined peduncle occurs, the petiole is termed *subsessile*.

Penis: see **Male genitalia**.

Petiole (= abdominal segment 2 (A2), = first metasomal segment)
Morphologically the second abdominal segment (A2), the segment that immediately follows the *mesosoma*. Anteriorly, it is always articulated within the *propodeal foramen* of the mesosoma. Generally the petiole takes the form of a node (*nodiform*) or of a scale (*squamiform*) of varying shape and size, but in some taxa it may be very reduced, represented only by a narrow subcylindrical segment that may be overhung from behind by the *gaster*. The petiole bears the second abdominal spiracle and usually consists of a distinct tergite and much smaller sternite. The tergite may have a differentiated *laterotergite* low on each side and abutting the sternite. The sternite often has a specialised, depressed area anteroventrally, close behind the articulation, that is equipped with numerous short, sensory hairs: the *proprioceptor zone*. In some groups the tergite and sternite of the petiole are immovably fused together (*tergosternal fusion*).

Phallobase: see **Male genitalia**.

Plectrum: see **Stridulatory system**.

Pleurite/pleuron (pl. pleura)
The lateral sclerites of the *thorax* proper, excluding the *propodeum* which is morphologically the tergite of the first abdominal segment.

The *propleuron* (pleuron of the *prothorax*) is relatively small in ants and is mostly or entirely overlapped and concealed by the extensive lateral part of the *pronotum* when viewed in profile, but can always be seen clearly in ventral view (see *prothorax*). The *mesopleuron* (pleuron of the *mesothorax*) is the largest pleurite. It may consist of a single sclerite that extends almost the entire height of the lateral mesothorax or may be divided by a transverse sulcus (the *anapleural sulcus*) into an upper *anepisternum* and a lower *katepisternum* (see *mesothorax*). The *metapleuron* (pleuron of the *metathorax*) is located posteriorly on the side of the *mesosoma*, mostly below the level of the *propodeum* in workers but more extensive in queens and males. The metapleuron bears, in the female castes of almost all ants, the *metapleural gland* (see *metathorax*). The ventral surfaces of the mesothorax and metathorax are formed by the ventral expansion of the pleurites and their fusion along the ventral midline; the true sternites of these segments are represented only by *endoskeletal* structures. The abdominal segments do not have pleurites and each consists only of tergite (above) and sternite (below).

Podites: see **Leg segments**.

Posterior tentorial pits: see **Anterior tentorial pits**.

Postmentum: see **Labium**.

Postpetiole (= abdominal segment 3 (A3))
A convenience term for what is morphologically the third abdominal segment when it is reduced in size and markedly separated from the petiole (A2) anterior to it and from the fourth abdominal segment (A4) posterior to it.

Posterior corners/margin (of head)
With the head in full-face view, the rounded to acute posterolateral angles, where the sides of the head curve into the posterior margin; the latter extends transversely between the corners. Earlier frequently referred to as occipital corners and occipital margin, however these terms are not strictly accurate because the true occipital surface (*occiput*) is not involved.

Postsclerite/poststernite/posttergite: see **Presclerite**.

Prescutal suture: see **Mesothorax**.

Prementum: see **Labium**.

Presclerite
A distinctly differentiated anterior section of an abdominal sclerite (tergite or sternite) that is separated from the remaining posterior portion of the sclerite by a constriction, a ridge, or both.

In abdominal segments 3–7 (8 in males) it is usual for the posterior portion of each segment to overlap the anterior portion of the following segment. The overlapped area usually lacks sculpture and pilosity, but the absence of these features alone does not constitute a presclerite: there must be a constriction or ridge that separates the two zones. Presclerites derived from tergites are termed *pretergites*; those from sternites, *presternites*. The remainder of each sclerite, posterior to the constriction or ridge, is the *postsclerite*, *posttergite* dorsally and *poststernite*

ventrally. A marked constriction that separates presclerites from postsclerites and extends around the entire circumference of a segment is a *girdling constriction* (= cinctus). The presclerites of abdominal segment 3 are reduced and form a specialised articulation within the posterior foramen of segment A2 (*petiole*), the *helcium*.

Presternite/Pretergite: see **Presclerite**.

Pretarsus/Pretarsal claws (= ungues, sing. unguis): see **Tarsus**.

Prognathous (head)
Among the ants the long axis of the head is horizontal or nearly horizontal, so that the head more or less continues the line of the long axis of the body, and the mouthparts, particularly the mandibles, are at the front of the head capsule. The ventral surface of the head has an extensive cuticular area (*genal bridge*) that widely separates the *buccal cavity* from the *occipital foramen*. This *prognathous* condition is in marked contrast to almost all the other families of Hymenoptera, where the long axis of the head is vertical or nearly vertical, the mandibles are ventral, and the buccal cavity and occipital foramen are closely approximated or even confluent, a condition termed *hypognathous*.

Because of the prognathous condition of the head, references to its orientation differ from what is usual in Hymenoptera. Apart from the mandibles being anterior, what is referred to as the frontal or anterior surface of the head elsewhere in the order, is dorsal in ants.

Promesonotal suture
The transverse suture across the dorsal mesosoma and down its sides which separates the *pronotum* from the *mesothorax*. In many groups of ants the promesonotal suture is fully developed, articulated, and flexible. The posterior margin of the pronotum slightly overlaps the anterior mesonotum and the two sclerites are linked by an intersegmental membrane so that they are capable of movement relative to each other. Elsewhere, and very commonly in workers, the suture is reduced from this condition. Initially in the sequence of reduction the suture is still present and distinct but inflexible, as the posterior pronotal margin has fused to the anterior margin of the mesonotum, and the intersegmental membrane has been lost. Beyond this fused condition the suture shows a gradual morphoclinal reduction in size and degree of definition, eventually becoming nothing more than a faint line or weak impression across the dorsum, or often disappearing altogether. When fusion and obliteration of the suture is advanced, and there is little or no sign of separation of the two original sclerites, the resultant fusion sclerite is termed the *promesonotum*.

Promesonotum: see **Promesonotal suture**.

Pronotum: see **Tergite/tergum**.

Propodeal lobe (= metapleural lobe, = inferior propodeal plate): see **Propodeum**.

Propodeal spiracle: see **Propodeum**.

Propodeum

Morphologically, the tergite of the first abdominal segment (the sternite of which is lost). It is immovably fused to the *thorax* and forms most of the posterior section of the *mesosoma* (= alitrunk). An older term for this sclerite, *epinotum,* should be abandoned.

The propodeal dorsum, which is sometimes referred to as its *basal surface* or base, is usually unspecialised but frequently terminates posteriorly in a pair of teeth or spines. The sloping posterior surface is the *propodeal declivity*, and may bear a number of specialisations. Most common of these is the development of a pair of *propodeal lobes* (= inferior propodeal plates). When present these are situated at the base of the propodeal declivity, one on each side of the *propodeal foramen*, which is the posterior foramen of the mesosoma within which the *petiole* (A2) articulates. These lobes, which when present may vary considerably in shape and size, were frequently referred to as *metapleural lobes* in earlier publications, but this name should be abandoned as the lobes are morphologically part of the propodeum, not the metapleuron.

The side of the propodeum bears the *propodeal spiracle*, morphologically the first abdominal spiracle. Its shape, size, and location are variable and of considerable taxonomic value.

Prora (pl. prorae)
A cuticular process or prominence that projects forward from the anterior surface of abdominal sternite 3, below the *helcium*. Absent in many groups; when present it takes the form of a U-shaped ridge of cuticle, a tubercle of very variable size, or a distinct prow. In some specialised taxa the prora has become inserted between the tergal apices of the helcium and forms part of the articulation.

Prosoma: see **Head**.

Prosternite: see **Sternite/sternum**.

Prothorax
The first of the three segments of the *thorax*, articulated anteriorly to the *head* by the membranous *cervix*, attached posteriorly to the *mesothorax*, and bearing the prothoracic (first, anterior) pair of legs. There is no *spiracle* on the prothorax, it has been lost in the Hymenoptera.

The tergite of the prothorax is the *pronotum*, always hypertrophied in the worker caste so that it is extensively present on the dorsal mesosoma. In alate queens and in males the dorsal pronotum may be of similar size to that seen in workers, but frequently its dorsal area is reduced, so that the pronotum may be represented only by a narrow anterior collar when seen in dorsal view, or it may be completely overhung by the anterior portion of the mesonotum. Laterally, the pronotum extends down both sides of the segment in all castes and both sexes. It also extends for some distance medially on the ventral surface, behind the *procoxal cavities*, where it overlaps or fuses with the anterior margin of the ventral mesothorax. The posterior margin of the lateral portion of the pronotum usually covers and conceals the *mesonotal spiracle*, and in alate (winged) forms it extends posteriorly until it almost touches the *tegulae*. The *pleurites* of the prothorax are only partly visible in profile as they are largely concealed by the lateral parts of the pronotum (a condition termed *cryptopleury*), but the prothoracic pleurites are always conspicuous in ventral view. They are fused along the ventral midline, but laterally are movably articulated to the pronotum, so that the two propleurites move as a single unit. Mid-ventrally, between the procoxal cavities and posterior to the pleurites, is a small, usually shield-like sternite (*prosternum*), the posterior margin of which may be overlapped by an anteriorly projecting

medioventral process of the mesothorax. The procoxal cavity is complex, being bounded anteriorly by the propleurite, medially by the prosternite, laterally by the pronotum, and posteriorly by the pronotum and anterior mesothorax. The pronotum articulates with the mesonotum at the *promesonotal suture*. This may be entirely flexible, with the two sclerites linked by intersegmental membrane, but in the worker caste of many groups the pronotum may be completely fused to the mesonotum, producing a compound sclerite, the *promesonotum*. The prothorax does not have an *endoskeletal* sclerite.

Proventriculus
A muscular pump located in the intestine between the crop and the midgut. In all ants the proventriculus has a *basal bulb*, but in some the bulb is surmounted by a ring of four sclerotised *sepals*, collectively termed the *calyx*. Although an internal abdominal structure, the form of the proventriculus featured strongly in the early classifications of some subfamilies, so is included here.

Psammophore
A basketlike series of long, and usually stout, curved setae that arise from the ventral surfaces of the head and mandibles in some deserticolous ants, used for carrying sand grains. In some publications the setae of the psammophore are called *ammochaete hairs*.

Pterostigma (= stigma)
A pigmented area that is usually present on the forewing of alate ants. When present it is located immediately behind the leading edge of the wing, about half to two-thirds of the distance from the wing base to its apex, and just distal of the hinge-like mechanism. It is bounded proximally and anteriorly by vein Sc, posteriorly and distally by vein R.

Pterothorax
A term sometimes used to describe the form of the thorax in fully winged (alate) queens and males. In these alates the *notum* of the *mesothorax* (*mesonotum*) tends to be subdivided into an anterior *mesoscutum* (= scutum) and a posterior *mesoscutellum* (= scutellum), usually with a separately demarcated triangular area, the *axilla*, between them at each side. See the discussions under *mesothorax* and *metathorax*.

Pubescence
Small to minute hairlike cuticular projections which are not socketed basally.

Pygidium
The tergite of abdominal segment 7 in workers and queens; the terminal visible tergite of the abdomen in these castes.

Pygostyles: see **Abdomen**.

Quadrate plate: see **Sting apparatus**.

Radial flexion line: see **Wings**.

Remigium: see **Wings**.

Sagitta: see **Male genitalia**.

Scape: see **Antenna**.

Sclerite
Functionally, a general term for any single plate of the exoskeleton (e.g. pronotal sclerite, abdominal sclerites); more specifically, an integumental plate in which the protein sclerotin has been deposited. In the case of ants, the latter applies to all parts of the exoskeleton.

Scrobe/scrobis: see **Antennal scrobe**.

Scutoscutellar suture: see **Mesothorax**.

Scutum/scutellum: see **Mesothorax**.

Sepals: see **Proventriculus**.

Sessile (petiole): see **Peduncle**.

Seta (pl. setae)
Any stout, hairlike cuticular process that is socketed basally. Generally, as here, the terms *seta* and *hair* are interchangeable, but care must be taken to differentiate between setae and pubescence, as the latter may also sometimes be referred to as hairs.

Spiracle
An orifice of the tracheal system by which gasses enter and leave the body. Adult ants have 9 or 10 spiracles on each side of the body.

The spiracles of the *prothorax* have been lost, so the first spiracular opening occurs on the *mesothorax*. This *mesothoracic spiracle* is situated forward and quite high on the side of the segment and is usually concealed from view by a backward-projecting lobe of the *pronotum*; only rarely is its orifice open and clearly visible. The *metathoracic spiracle* may be dorsal (especially in those workers where the *metanotum* forms part of the dorsal *mesosoma*); lateral and open; lateral but concealed by a small, sometimes detached, lobe of the *mesopleuron* (the *epimeral sclerite*); or the metathoracic spiracle may be absent. Abdominal spiracles are always on the tergite of each segment. The *propodeal* (first abdominal) spiracle is usually the largest on the body. Behind this, on the *metasoma* (A2 to apex), spiracles are always visible on abdominal segments 2–4, but those on abdominal segments 5–7 are frequently overlapped and concealed by the posterior margin of the preceding tergite. A spiracle is also present on abdominal tergite 8, but in female castes this sclerite is always concealed; it is internal and forms part of the *sting apparatus* (the *spiracular plate*).

Spiracular plate: see **Sting apparatus**.

Spur (= calcar): see **Tibial spur**.

Spur formula
A simple statement of the number of *tibial spurs* that are present on the pro-, meso-, and metathoracic legs, given in that order. Thus a spur formula of 1, 2, 2, indictaes that the tibia of the prothoracic (fore) leg has one spur, and that of the mesothoracic (middle) and metathoracic (hind) legs each have two spurs.

Sternite/sternum (pl. sterna)
The lower or ventral sclerite of a segment (the tergite is the upper sclerite on the thoracic segments and the abdomen; the pleurites are the lateral sclerites on the sides of the thorax). The sternite may be a simple, flat or curved plate, or may be specialised or subdivided on some segments. On the *prothorax* the sternite (*prosternum*) is small, but visible in ventral view (see *prothorax*). The sternites of the *mesothorax* and *metathorax* are internal (*mesendosternite* and *metendosternite*, respectively), the ventral surfaces of these two segments being composed of extensions of the pleurites to the ventral midline, where they fuse (see *mesothorax* and *metathorax*). The sternite of the *propodeum* (A1) has been lost in the course of evolution, but those of the remaining visible abdominal segments are usually distinct, although the lateral margins of some may be difficult to discern because of fusion to the tergite (*tergosternal fusion*). The sternites of A8 and A9 are membranous in the female castes, internal, and associated with the *sting apparatus*. In males the sternites of A8 and A9 are visible, and that of A9 is generally called the *subgenital plate*. Abdominal sternites are usually simple, but may be subdivided or otherwise specialised. The most common modification applies to abdominal sternites 3 and 4 (uncommonly also to A5 and A6), where distinct *presternites* (see under *presclerites*) may be differentiated.

Sting apparatus (= aculeus)
Internal in the female castes (workers and queens) of the ant subfamilies in which it occurs, concealed within the apical visible segments of the abdomen. The sting apparatus is derived from parts of the ancestral exoskeleton of abdominal segments 8 and 9, subtended by a number of pairs of sclerites that are ultimately derived from the ancestral coxal homologues of those segments; one pair from segment A8 and two pairs from segment A9. Most sclerites of the sting apparatus have accumulated a number of synonymous names, as follows.
Gonangulum (= first valvifer, = triangular plate).
Gonapophysis 8 (= first gonapophysis, = first valvula, = lancet).
Gonapophysis 9 (= second gonapophysis, = second valvula, = stylet).
Gonocoxa 9 (= second valvifer, = second gonocoxa, = oblong plate).
Gonoplac (= third valvula, = gonostylus, = sting sheath).
Tergite A8 (= spiracular plate); frequently split into a pair of *hemitergites*, one on each side.
Tergite A9 (= quadrate plate); always split into a pair of *hemitergites*, one on each side.
Sternites A8 and A9 are membranous and usually inconspicuous.

The most ventral sclerites of the apparatus are the longitudinal pair of gonapophyses 8. These are attached to the base (anterior end) of the apparatus and curve posteriorly then upward, where they meet and lock with the pair of gonapophyses 9, the next sclerites dorsally. The latter are fused along their length and form the upper portion of the channel through which venom is transmitted; the lower portion of this channel consists of the pair of gonapophyses 8. Together all these sclerites are sometimes termed the *terebra*. The bases of gonapophyses 9 arise directly

from the bases of the next sclerites dorsally, gonocoxae 9, whose length is extended by the gonoplacs, which arise directly from the apex of each gonocoxa 9 and continue its line. Gonapophyses 8 are attached basally to a pair of roughly triangular gonangula, which also articulate with the bases of gonocoxae 9. The gonangula also articulate on each side with the bases of the hemitergites of A9, which extend posterodorsally. This entire system is covered from above by the arc of tergite A8, which bears the terminal abdominal spiracle. A final small sclerite, visible in some groups, is the *furcula*. This is a small, inverted Y-shaped sclerite at the extreme base of the sting apparatus; its arms are attached to the gonapophyses from which it is probably derived.

In two large subfamilies this complex venom-injecting apparatus has been abandoned in favour of repugnatorial glands or a formic acid projection system. However, dissection of these highly modified forms reveals some remnants of the original sting apparatus, here adapted to different, usually supportive, functions.

Sting sheath: see **Sting apparatus**.

Stipes (pl. stipites): see **Maxilla**, and also **Male genitalia**.

Stridulatory system
A sound-producing system present in the female castes of a number of ant subfamilies. The system consists of a *plectrum* (= stridulatory file), located on the posterior margin of abdominal segment 3 (usually, but not always, on the tergite), and an extremely finely grooved *stridulitrum* on the anterior portion of abdominal segment 4. Rapid to-and-fro movement of the plectrum along the stridulitrum produces a range of chirping or buzzing sounds.

Stridulitrum: see **Stridulatory system**.

Strigil: see **Tibial spur**.

Stylet: see **Sting apparatus**.

Subpetiolar process
A ventral cuticular projection of the sternite of the *petiole* (A2), either below the node or on its anterior *peduncle*; sometimes absent but when present very variable in shape and size.

Subgenital plate: see **Abdomen**.

Subsessile (petiole): see **Peduncle**.

Sulcus (pl. sulci)
Strictly, an external groove or impression that corresponds to an internal ridge-like inflection of the cuticle which provides mechanical rigidity. The term is also used casually for any linear impression in the cuticle without any obvious significance, and sulcus is often used interchangeably with suture.

Suture

Strictly, a line of junction between two structural sclerites. The suture may be articulated, where the component sclerites are linked by flexible intersegmental membranes and retain the ability to move relative to each other, or may be fused together and immobile. The term suture is often used interchangeably with sulcus.

Supraclypeal area: see **Frontal triangle**.

Tagma (pl. tagmata)
A fundamental unit of the body; an ancestral section of the body that is distinct from, or separated from, other body units in both form and function. In Insecta there are three ancestral tagmata, *head*, *thorax* and *abdomen*, but in ants the second and third of these have become much modified by secondary evolutionary developments.

Tarsal claws: see **Tarsus**.

Tarsus (pl. tarsi)
Collective term for the five small apical subsegments (*tarsomeres*) of any leg. The first tarsal segment (first tarsomere, basal tarsomere) of each leg articulates with the *tibia* and is termed the *basitarsus*. The next three tarsomeres are not individually named but the fifth, apical (terminal) tarsomere is the *pretarsus* and bears a pair of *pretarsal claws* (= ungues, sing. unguis). The inner curvature of each claw may be a simple, smooth, concave surface, or may have one or more preapical teeth present, or the claw may be pectinate. Sometimes a membranous lobe, the *arolium*, is present between the claws. The tarsus of the prothoracic (fore) leg is often termed the *protarsus*, that of the mesothoracic (middle) leg the *mesotarsus*, and that of the metathoracic (hind) leg the *metatarsus*. The individually named tarsomeres may be referred to in a similar way, for instance the basitarus of the prothoracic (fore), mesothoracic (middle), and metathoracic (hind) legs may be termed *probasitarsus*, *mesobasitarsus* and *metabasitarsus*, respectively. In some groups of ants the metabasitarsus bears a longitudinal groove that is probably the orifice of an *exocrine gland*.

Tegula (pl. tegulae): see **Mesothorax**.

Telomere: see **Male genitalia**.

Tentorium: see **Endoskeleton**.

Tergite/tergum (pl. terga)
The upper sclerite of a segment (the sternite is the lower, the pleurite the lateral on the *thorax*). The tergite may be a simple flat or curved plate, or may be specialised or subdivided on some segments. In terms of comparative morphology each of the three ancestral dorsal plates of the thorax, one for each segment, is termed the *notum* (pl. nota). Thus, the tergite of the *prothorax* is composed entirely of the *pronotum*. This sclerite is hypertrophied in worker ants and extends across the dorsum and down both sides of the segment, mostly or entirely concealing the *propleuron* (see *prothorax*). The *mesonotum*, tergite of the *mesothorax*, may be separated from the pronotum by the *promesonotal suture*, or the pronotum and mesonotum may be fused by obliteration of the suture in some workers to form a single sclerite, the *promesonotum*. In alate

forms the mesonotum is subdivided (see *mesothorax*). The *metanotum*, tergite of the *metathorax*, is usually present across the dorsum as a distinct sclerite in alates, but is frequently reduced and sometimes entirely lost in workers. When the metanotum is extremely reduced, the mesonotum and *propodeum* are only separated by the *metanotal groove*, a transverse impression whose base represents the last vestige of the metanotum on the dorsum (see *metathorax*). The *propodeum* is the tergite of the first abdominal segment (A1). The remaining visible abdominal segments (A2–A7 in females, A2–A8 in males) have tergites that are usually simple, but may be subdivided or otherwise specialised. The most common modification applies to abdominal tergites 3 and 4 (uncommonly also to A5 and A6), where distinct *pretergites* and *posttergites* (see under *presclerites*) may be differentiated. In general the abdominal tergites are free and attached to their respective sternites by flexible intersegmental membranes, but in some groups there is *tergosternal fusion* in segments A2 (petiole), A3 and A4. The *petiole* (A2) in some groups has a small lower section of the tergite split off from the main part of the sclerite by a distinct suture on each side, where they flank the sternite. These are called *laterotergites*, and in some taxa these sections of the tergite are mobile with respect to both the remainder of the tergite and also the sternite.

Tergosternal fusion
A condition of the abdomen where the tergite and sternite of a single segment fuse together. This may occur in some or all of segments A2 (petiole), A3 and A4; posterior to A4 there is never tergosternal fusion. The absence or presence of tergosternal fusion varies throughout the Formicidae, but in individual subfamilies it tends to be fairly consistent for most of the segments. For example, in workers tergosternal fusion is distributed as follows through the various subfamilies (u = unfused, p = partially fused, f = fused).

	A2	A3	A4
Myrmeciinae	u	u	u
Pseudomyrmecinae	u	u	u
Aneuretinae	f	u	u
Dolichoderinae	f	u/p	u
Formicinae	f	u/p	u
Myrmicinae	f	u/f	u
Amblyoponinae	u/p	u/p/f	u/f
Dorylinae	u/f	f	u
Leptanillinae	f	f	u
Ponerinae	u	f	f
Heteroponerinae	u	f	f
Ectatomminae	u/f	f	f
Proceratiinae	u/f	f	f
Agroecomyrmecinae	f	u/f	f
Paraponerinae	f	f	f

Thorax
The classical second *tagma* of the insect body. In ants and other Hymenoptera the apparent thorax consists of the usual three leg-bearing body segments of the true thorax (*prothorax,*

mesothorax, metathorax), to which the tergite of the first abdominal segment (the *propodeum*) is immovably fused. This modification means that the combined "true thorax + propodeum" cannot strictly be called the thorax, as it is not homologous with the term as used otherwise throughout the Insecta. Several names have been applied in the recent past for "true thorax + propodeum", of which three, *mesosoma*, alitrunk, and truncus have seen frequent usage. All three names are somewhat misleading as far as the ants are concerned, but all are improvements over "thorax", which is morphologically inaccurate. Currently the term *mesosoma* has gained ascendency, and is the name recommended here.

Tibia (pl. tibiae)
The fourth segment of any leg, counting from the basal segment (*coxa*) that articulates with the *thorax*. At its apex the tibia frequently bears one or two *tibial spurs*. The tibia of the prothoracic (fore) leg is often termed the *protibia*, that of the mesothoracic (middle) leg the *mesotibia*, and that of the metathoracic (hind) leg the *metatibia*.

Tibial spur (= calcar)
One or two basally socketed spurs, located at the apex of each *tibia*. The forelegs (prothoracic legs) have a single pectinate tibial spur that is modified as part of a specialised antennal cleaning device, the *strigil*. The mesothoracic (middle) and metathoracic (hind) tibia, also referred to as *mesotibia* and *metatibia*, may each have two, one, or no spurs present. When present the mesotibial and metatibial spurs may be pectinate, barbed, or simple cuticular spikes. If two spurs are present on a tibia it is usual for one to be larger then the other, and in such instances the larger spur is often pectinate, while the smaller spur is simple. A simple count of the number of tibial spurs on each of the three legs, from front to back, is the *spur formula*.

Torulus (pl. toruli) (= antennal sclerite, = annulus antennalis)
The small annular sclerite that surrounds the *antennal socket* (antennal foramen). The torulus may be horizontal, or the part closest to the midline of the head may be elevated in some taxa to such an extent that the antennal socket is almost vertical. The upper arc of the torulus may be indistinguishably fused to the inner wall of the *frontal carina*, may remain discrete, or may even project laterally as a small *torular lobe* below the frontal carina. In some groups where the frontal carina is very slender, the torulus projects laterally beyond the outer margin of the frontal carina, and becomes visible in full-face view.

Triangular plate: see **Sting apparatus**.

Trochanter
The second segment, counting from the base, of any leg; the small segment between the *coxa* and *femur*. In all recent ants the trochanter is a single segment, but represents the result of fusion of an ancestral pair of small segments. The trochanter of the prothoracic (fore) leg is often termed the *protrochanter*, that of the mesothoracic (middle) leg the *mesotrochanter*, and that of the metathoracic (hind) leg the *metatrochanter*.

Trulleum
A basin-shaped depression near the dorsal base of the *mandible*, close to its articulation. It is bounded distally by the *basal margin* of the mandibular blade and, in those groups where it

occurs, is visible just in front of the anterior clypeal margin when the mandibles are open. The trulleum in many groups is closed along its inner (medial) border by a raised ridge of cuticle, the *canthellus*. The canthellus may extend to, and even fuse with, the basal margin of the mandible (canthellus closed), or may fail to reach the basal margin (canthellus open). Proximal to both these structures, in the cuticle of the extreme dorsal base of the mandible, is a small, unsclerotised impression of variable shape, the *mandalus*. It contrasts strongly with the fully sclerotised surrounding cuticle of the mandibular base.

Unguis: see **Tarsus**.

Valvifer, valvula: see **Sting apparatus**.

Venation (= neuration)

The configuration of the veins in the wings of ants and other aculeates is very much modified from the ancestral insect pattern. Within the Formicidae the venation is complex and extremely variable. There is a finely stepped series of reductions from a formicid ancestral common pattern still represented in many subfamilies in which the venation is most complete. In general, the venation of ants is very similar to that seen elsewhere in the vespoids, and also in the apoid lineages, but in ants the cross-veins 3rs-m and 2m-cu are always absent, and there is never a *fenestra* in M·f3.

There are a number of conventions useful in understanding venation and vein nomenclature.

1 The leading edge of a wing when fully open, as if in flight, is its anterior margin; the trailing edge, in the same circumstances, is the posterior margin.

2 The abbreviations of the names of the main, longitudinal, veins that run from the wing base (proximal) towards the apex (distal), are written with an initial capital letter, for example M (= media), Cu (= cubitus). These abbreviations of the names are usually reduced from their forms as expressed in the ancestral insect wing. This is purely for convenience and brevity; the main vein homologues, as they appear in the ancestral insect wing, are noted below.

3 The abbreviations of names of the secondary veins (cross-veins), that extend between the main veins, are written in lower case throughout, for example 2r-rs, cu-a, always with the most anterior vein noted first.

4 The plus sign (+) is used to indicate sections of veins that are indistinguishably fused together longitudinally, for example Rs+M. In fused veins the one that was ancestrally anterior, closest to the leading edge, is named first.

5 The ampersand (&) can be used to indicate sections of separate veins that are fused end to end so that they appear as a single continuous vein. For example, the so-called stigmal vein, a hook-shaped vein that arises from the pterostigma in some groups, is actually composed of the second radial-radial sector cross-vein (2r-rs) fused to the fourth and fifth free abscissae of the radial sector vein (Rs); thus the stigmal vein is properly 2r-rs&Rs·f4-5. 2r-rs is written first because it is nearest to the anterior margin of the wing.

6 Sections of main veins that occur between cross-veins, or between fused sections of main veins, are termed *free abscissae* and are represented ·f after the abbreviation of a main vein, then followed by a number; for example, M·f3 is the third free abscissa of the median vein (M). This convention is useful to indicate where sections of veins have been lost or are free from fusion with other veins.

The veins, taken in order of occurrence commencing with the anterior margin (leading edge), are listed in the most complete venation pattern seen in ants.

Forewing longitudinal veins:

Costal vein (= Costa) [C]. Undivided, never fused with any other vein and sometimes absent.

Subcostal vein (= Subcosta) [Sc]. In the proximal part of its length Sc is fused with R and Rs (Sc+R+Rs), which is almost always the thickest vein section in the wing. Beyond the point of divergence of Rs, Sc remains fused to R (Sc+R) until close to the base of the *pterostigma* where they divide, after which the apical portion of Sc extends along the anterior margin of the pterostigma and R along its posterior margin. In ancestral homology, the vein called Sc here is correctly Sc2, because in some Hymenoptera a more proximal Sc1 occurs that is absent in ants.

Radial vein (= Radius) [R]. In its basal section fused to Sc and Rs (Sc+R+Rs), then continuing as Sc+R after the divergence of Rs. At the pterostigma Sc separates from R, which thereafter shows three free abscissae, R·f1–R·f3, of which R·f1 and R·f2 form the posterior margin of the *pterostigma*, and R·f3 extends along the leading edge of the wing distal of the pterostigma and termination of Sc. In ancestral homology, the vein called R here is correctly R1, because in many insect groups R branches into several veins towards its apex, R1, R2, R3, *etc*., of which R1 is the only remnant in Hymenoptera.

Radial sector [Rs]. Proximally fused with Sc and R (Sc+R+Rs). Beyond its point of divergence Rs has a maximum of five free abscissae (Rs·f1–Rs·f5), and always has a section fused with M (Rs+M), which is present between Rs·f1 and Rs·f2. The latter, in more generalised forms, has a distinct *fenestra* through which the *radial flexion line* passes. Rs·f5 may curve anteriorly to the leading edge where it meets R·f3, but often ends before reaching the margin. In its distant ancestry, Rs probably originated as a vein independent of R, but in all Hymenoptera, and almost all insects, R and Rs are fused basally. In ancestral homology, the vein called Rs here is correctly Rs1. In a very few Hymenoptera Rs branches in its distal half into Rs1 and a more posterior Rs2.

Median vein (= Media) [M]. Basally fused with Cu (M+Cu), then with a free abscissa (M·f1) before its fused section with Rs (Rs+M). Distal of this, M has a maximum of three further free abscissae (M·f2-4). In ancestral homology the vein called M here is correctly MP (media posterior), the posterior member of two original median veins. The anterior median vein (MA, media anterior) has been lost in Hymenoptera and most other insects.

Cubital vein (= Cubitus) [Cu]. Basally fused with M (M+Cu), then with a maximum of three free abscissae (Cu·f1-3) before branching, near the posterior wing margin, into Cu1 and Cu2. Cu2 sometimes anastomoses with the anal vein, but when free it has a fenestra, through which the *claval furrow* passes. In ancestral homology the vein called Cu here is correctly CuA (cubitus anterior), and its terminal branches are CuA1 and CuA2. This is because it is the anterior member of two original cubital veins, the posterior of which (CuP, cubitus posterior) has been lost in Hymenoptera.

Anal vein [A]. A single unbranched, unfused vein that is closest to the posterior margin of the wing, with three free abscissae (A·f1-3) at maximum. In ancestral homology the vein called A here is most probably 1A. In some groups of Hymenoptera two, three, or rarely four anal veins may be present (A1, A2, *etc*.).

Forewing cross-veins (a maximum of five):

First radial-radial sector cross-vein [1r-rs]. Extremely rare in ants; when present it extends from R, close to the proximal end of the *pterostigma*, to Rs, where it marks the junction of Rs·f2 and Rs·f3. Because 1r-rs is only rarely present, this section of Rs is most often seen as Rs·f2-3.

Second radial-radial sector cross-vein [2r-rs]. Extends from R at the base of the pterostigma (where it marks the junction of R·f1 and R·f2) to Rs, where it marks the junction of Rs·f3 and Rs·f4. In the most generalised ant venations 2r-rs is proximal of 2rs-m.
Second radial sector-median cross-vein [2rs-m]. Extends from the junction of Rs·f4 and Rs·f5 to the junction of M·f3 and M·f4. In more generalised forms 2rs-m has a distinct *fenestra*, through which the *radial flexion line* passes. In the most generalised ant venations 2rs-m is distal of 2r-rs. The cross-vein 1rs-m is not present in any Hymenoptera, having been obliterated by the proximal end of the fusion of Rs with M (Rs+M). A third radial sector-median cross-vein, 3rs-m, is never developed in Formicidae but is very common in other aculeates..
First median-cubital cross-vein [1m-cu]. Extends from the junction of M·f2 and M·f3 to the junction of Cu·f2 and Cu·f3. A second median-cubital cross-vein, 2m-cu, is always absent in Formicidae, though common in apoids and other vespoids.
Cubital-anal cross-vein [cu-a]. In forms with most generalised venation cu-a extends from the junction of Cu·f1 and Cu·f2 to the junction of A·f1 and A·f2. Extremely commonly, cu-a is retracted towards the wing base and arises from M+Cu. There is usually a *fenestra* in cu-a through which the *claval furrow* passes.
Hindwing veins:
These are basically the same as in the forwing, but somewhat simplified. For instance, the hindwing has no pterostigma and no section Rs+M, the main veins have fewer abscissae, the apical abscissa of Cu is simple, and there are no r-rs or m-cu cross-veins. As in the forewing, 1rs-m and cu-a have fenestrae. In a considerable number of ant taxa M·f2 has disappeared from the hindwing, so the apparently single vein that extends between Rs·f2 and Cu is actually 1rs-m&M·f1. See also *Wings* and *Cells of wings*.

The minimal forewing venation observed in ants consists merely of a very faint remnant of Sc+R+Rs.

Vertex
The portion of the cephalic dorsum that lies immediately in front of the occiput. In those groups where ocelli are absent the area can be only vaguely defined, but in those which possess ocelli the vertex is the area from immediately behind the anterior ocellus to the occiput that contains the posterior pair of ocelli. Ancestrally, the anterior ocellus is on, and marks the posterior limit of, the *frons*.

Volsella: see **Male genitalia**.

Waist
An informal collective term for the one or two isolated and reduced abdominal segments that occur between the *mesosoma* and *gaster*. When only the petiole (A2) is isolated the waist is said to be one-segmented, but in those taxa where the postpetiole (A3) is also separated the waist is said to be two-segmented.

Wings (alae, sing. ala)
Alate ants, winged queens and males, have two pairs of wings, as do all winged Hymenoptera. The forewings are largest and articulate with the *mesothorax*, where their extreme base is shielded by a *tegula* on each side. The hindwings are smaller and articulate with the *metathorax*. The forewing and hindwing on each side are held together by a series of small hooks, the *hamuli*

(sing. hamulus), that arise from the leading edge of the hindwing and engage folds on the posterior margin of the forewing. This ensures that fore- and hindwing on each side beat as a single unit in flight. In ants the hamuli usually arise only from the hindwing vein R, but in a very few groups another patch of hamuli is present more basally, on vein C.

About two-thirds of the way along the anterior forewing there is usually a pigmented patch, surrounded by veins, the *pterostigma* (= stigma), that is only very rarely absent. The main membranous area of each wing is the *remigium*, which contains the entire area between the leading edge and the *claval furrow* (= vannal fold) immediately anterior to vein A. Posterior to the claval furrow, on both forewing and hindwing, is a membranous area termed the *clavus* (= claval lobe, = vannal lobe, = plical lobe), which usually terminates in a slight *claval notch* (= preaxillary excision, = vannal notch) in the posterior wing margin. In some taxa, proximal of the clavus on the hindwing, is a separate lobe of membrane, the *jugal lobe* (= jugum, = anal lobe).

Within the membrane of the wings there are usually also two flexion lines or fold lines that allow the wing to flex during active flight. In the forewing the *radial flexion line* runs parallel and immediately posterior to veins Sc+R+Rs and Sc+R. Towards its distal end the flexion line curves anteriorly towards the base of the *pterostigma*, where it is contiguous with the hinge-like mechanism, a weakened area at the pterostigmal base that allows the outer part of the forewing to deform during flight. From there the radial flexion line extends for a short distance posteriorly, then curves distally and extends outward towards the wing margin. In many groups the track of the radial flexion line is marked by a distinct *fenestra* in vein section Rs·f2 and in cross-vein 2rs-m. Just anterior to vein A, the most posterior longitudinal vein, is the *claval furrow* (= vannal fold). This passes through a fenestra in cross-vein cu-a and usually also a fenestra in vein Cu2.

The same flexion lines occur in the hindwing, but the radial flexion line is simpler. It runs longitudinally, posterior to Sc+R+Rs, often through a fenestra in cross-vein 1rs-m, then out toward the wing margin posterior to Rs·f2. The claval furrow runs just anterior to A, with a fenestra in cross-vein cu-a. In those taxa where the hindwing retains a *jugal lobe*, the lobe is separated from the clavus by the *jugal fold*, which in ants is often represented by a cleft in the membrane.

As well as these features, each wing usually bears a conspicuous series of longitudinal and transverse *veins*, collectively termed the *venation*, together with a series of *cells*, which are areas of membrane enclosed by particular veins or sections of veins. Both of these are discussed under *Venation* and *Cells of the wings*.