

# Chapter 1

## An Introduction to Termites: Biology, Taxonomy and Functional Morphology

Paul Eggleton

**Abstract** Termites are fully social insects, with an extraordinary range of morphological forms. It is now clearly established that they are a very specialised form of cockroach, with far more complex social systems than other cockroaches, and with a far wider range of diets. Termites all live in colonies, with reproductives (kings, queens, and nymphs), soldiers and “helpers” (true workers and also immature stages that assist within the colony to some extent). Termite morphological and anatomical adaptations are caste-specific, with structures evolving independently in reproductives (to allow dispersal, pair bonding and fecundity), workers (foraging and feeding, tending and feeding of immatures, nest construction) and soldiers (only defence). The modifications seen in termite societies are similar to those found in the somatic parts of multicellular organisms, leading to the idea that a termite colony is best thought of as a single organism (or, more controversially, a “super-organism”). The structures that termites build, the mounds and nests, might also be defined as part of this organism. Mounds and nests contribute greatly to the well-being of termite colonies by providing shelter, fortifications and climate control. Overall, termites have amongst the most complex social, anatomical and structural adaptations of any animal.

### 1.1 Introduction

Most people are aware of termites, either directly or indirectly. Throughout the tropics everyone knows that termites are voracious eaters of houses and crops, while a smaller number understand that they also have a role in improving soil quality. In the US they cause more economic damage than fire and flood combined, predominantly by feeding on structural timbers. In contrast, here in the UK, where there are no termites, they are mostly known by anecdote and through an iconic sequence in David

---

P. Eggleton (✉)

Termite Research Group and Soil Biodiversity Programme, Entomology Department, Natural History Museum, London, SW7 5BD, UK

e-mail: P.eggleton@nhm.ac.uk

Attenborough's *Life on Earth* when he crawled inside a termite mound. In this chapter I will introduce termites, by briefly discussing their biology, classification and functional morphology. I set the scene for later chapters by presenting background information and placing termites in a wider context. Termites are eusocial cockroaches. They live in complex societies that can be modelled as "superorganisms" – where the individuals form part of a larger self-regulating entity (Wilson 1992). They feed on dead plant material at different stages of decomposition (Donovan et al. 2001). They live predominantly in tropical regions, where they are by far the most important decomposer animals (Davies et al. 2003).

## 1.2 Diversity, Taxonomy, Classification

Termites are easy to distinguish from all other insect groups, as they have very distinctive morphologies in all their castes. However, the phylogenetic position of termites has been long debated. The majority view is that termites form part of the order Dictyoptera (along with cockroaches and mantids), and that within that order they are phylogenetically nested within the cockroaches (Inward et al. 2007a; Legendre et al. 2008; Ware et al. 2008). They are close to the Blattidae, and their sister group is the woodroach, *Cryptocercus*. The details of these relationships are discussed in Chapter 2. Some researchers have argued that this means that an order-level classification for termites is unwarranted (Eggleton et al. 2007; Inward et al. 2007a), but others (Lo et al. 2007; Engel et al. 2009) have rejected this idea, predominantly for reasons of nomenclatural stability. In this chapter I simply use the word "termite" as it unambiguously describes the same set of species. A related problem is the use of the term "cockroach-like" as it is tautological if used to describe features of a group that is actually within the cockroaches. Here I will use it to describe a similarity to the common ancestor of termites and *Cryptocercus*, or more simply, as similarity to "non-termite cockroaches". There is a direct analogy between this problem and that concerning the group left when dinosaurs are defined without the birds, leaving the "non-avian dinosaurs".

There are approximately 2,600 described species of termites (Kambhampati and Eggleton 2000) with perhaps 500–1,000 species still left to describe. The most recent higher classification (Engel et al. 2009) splits those species into nine extant families and proposes two fossil ones, with one "family" of uncertain status. Generally, the basal families are more cockroach-like and the apical ones more specialised: this can be particularly seen in the Mastotermitidae and the "Termopsidae". All groups are fully eusocial, although some dry-wood-nesting termites (Kalotermitidae) may not have functionally active workers.

The Mastotermitidae, with just a single extant species restricted to northern Australia, are acknowledged to be the oldest family, with many cockroach-like features (e.g. wing venation, retention of an ootheca, presence of the endosymbiont *Blattabacterium*). However, they have true workers and nest away from their food. Two slightly more recent groups, the 'Termopsidae' and the Kalotermitidae both nest and feed in single pieces of dead wood: the termopsids in wet logs in temperate

rain forests, and the kalotermitids in dry wood in tropical rainforest tree canopies, isolated islands and semi-deserts. These groups do not have true workers, although they always have soldiers. A specialised group within or close to the termopsids, the Hodotermitidae, are grass-feeders across semi-arid regions of the Old World, and have well developed nests built away from their food. The Rhinotermitidae are widespread, being the only family that extends significantly into subtropical and warm temperate regions, for example in North America and Europe (Weesner 1965). They have true workers and mostly build their nests away from their food. The Termitidae make up the bulk of extant species and are dominant in tropical regions, particularly rain forests and savannas.

Other families have been proposed in the past – in particular the Indotermitidae, which are clearly specialised Apicotermittinae. The Serritermitidae, still recognised in the most recent classification (Engel et al. 2009), is probably better placed as a subfamily of the Rhinotermitidae. The present family-level classification is still likely to change in the future as two families, the Rhinotermitidae and the “Termopsidae” (split up by Engel into a number of families), are probably not natural groupings.

The ranks between family and generic levels are generally poorly worked out. The Mastotermitinae has only one species. The Termopsidae have three fairly disparate subfamilies (Termopsinae, Stolotermitinae, Porotermitinae). The Kalotermitidae have no accepted subfamily classification. The Rhinotermitidae have subfamilies that mostly contain a single or two genera, with the exception of the Rhinotermitinae. Within the Termitidae seven subfamilies were most recently recognised by Engel et al. (2009): Macrotermittinae, Sphaerotermitinae, Foraminitermitinae, Apicotermittinae, Syntermitinae, Termitinae, and Nasutermitinae. However, this subfamily-level classification still remains somewhat unsatisfactory and, despite recent improvements, needs a complete revision. This has been known for some time (e.g. see Kambhampati and Eggleton 2000; Inward et al. 2007b), particularly with respect to the Termitinae, which are clearly a paraphyletic group, and the Syntermitinae, which are probably recognised at too high a taxonomic rank. The most important barrier to a reclassification within the Termitidae is the difficulty of resolving relationships between taxa at the most apical part of the termite tree (Inward et al. 2007b).

### 1.3 The Colony

A termite colony is a family of termite individuals all living together. It generally has an inanimate and an animate part. The animate part is the individuals living within the colony; the inanimate part is the structures built by individuals within which they live. Sometimes the inanimate part of the colony is just a few tunnels, but often it is a very extensive and sophisticated structure.

The animate part of a colony has immatures and typically three main adult castes: reproductives (queens, kings, and alates), workers, and soldiers. The queen is generally the only egg-laying individual in the colony. The king is her consort and his only

task appears to be to mate with her regularly (Korb 2008). The alates are winged reproductives preparing to leave the nest in order to swarm, to pair and to start new colonies. Workers, on the other hand, never leave the nest except to forage for food. They are the mainstay of the colony, and their roles are numerous. They forage for food and water, build and repair colony structures, and tend the immatures, alates, the king and the queen. Soldiers have only one job: to defend the colony, and particularly the queen and the king. This simple description of caste structure is complicated by some species that have no soldiers and others that have no workers. All termite species have one or the other, however, and so all termite species are eusocial, because they have at least one sterile caste that is pre-determined during the immature stages (Boomsma 2009).

The life cycle is similar in all termites. Colonies produce winged reproductives (“alates”), often at the start of the rainy season in drier or seasonal habitats, but all the year round in wetter, aseasonal habitats (Martius et al. 1996). These reproductives land on the ground or on a piece of dead wood and pair up: one male with one female. The pair then found a colony, either in the soil or in dead wood. They mate and produce workers (or pseudergates) that begin to tend young, to build colony structures and to forage for food. Slightly later in the colony’s development soldiers are produced. When the colony has reached maturity alates are produced again, and the cycle continues.

## 1.4 The Colony as (Super)organism

An individual in a termite colony is not really like a standard solitary insect. If you separate it from the colony it will die. Even the alates, which can survive for some time apart from the nest, need to pair and form a new colony to survive. The main reason for this obligate association with the colony is that each caste lacks some element that is present in a solitary insect. Workers and soldiers have no reproductive tract; soldiers and reproductives cannot feed themselves; workers and reproductives generally cannot defend themselves effectively; soldiers and workers cannot disperse. These functions, reproduction, feeding, defence and dispersal, are all, by necessity, combined in a solitary insect. The question then arises – to what degree is an individual termite a real biological individual? Using an analogy with a human body, we generally do not think of our organs as individual organisms, so why should we think the same of individual termites? This reasoning by analogy leads to the idea that a termite colony is the individual, and so to the concept of the superorganism.

A superorganism is defined as a collection of agents that can act in concert to produce phenomena governed by the collective (Holldobler and Wilson 2009), although, as we will see, this definition fits the concept of an organism equally well. The superorganism concept is, of course, not restricted to termites: all other fully eusocial insects have colonies that can be defined in the same way. The key evolutionary point in superorganisms is that it is the breeding entity, the colony, that is selected. This leads to some interesting conceptual possibilities, because the way that termites interact with the environment looks very different if we deal with the

colony as the “individual” rather than dealing with a single termite as the “individual”. It seems eminently sensible to treat the colony as the individual organism, as the parts of the colony do not have all the necessary properties of an organism. Organisms must persist and they must reproduce (in fact, they must persist long enough *to* reproduce). The elements that make up the colony do not individually have these two properties. None can persist and reproduce on their own without the resources of the colony. Alates, which seem closest in overall form and function to solitary cockroaches, will die rapidly without the assistance of the first workers produced at the inception of the colony. This way of thinking of a colony tells against the term “superorganism” as, in fact, the colony is simply an organism constructed at a higher level of organisation.

One of the first naturalists to realise how similar a termite mound is to a much larger single animal was Eugene Marais, an Afrikaner who wrote a fascinating book (*The Soul of the White Ant*<sup>1</sup>) emphasising the similarity between termite colonies and humans. He likened the roles of individual parts of a colony to the functions of the human body, and although the idea was a little contrived and fanciful, it points the way, I believe, to a generally valid way of understanding the functional biology of termites – by considering the functions of the colony and how they are achieved.

When discussing caste structure and function it seems useful to define some generally accepted terms. Individuals in a colony are either *immature* or *mature*, depending on whether they can develop further. *Castes* are the morphologically distinct, task-specific groups of individuals within a colony. In a termite colony these comprise *reproductives* (winged reproductives: alates, queens, kings), *workers*, *soldiers* and immatures. Immatures are known as either *larvae* (if they have no wing buds) or *nymphs* (if they have wing buds). Soldier may have up to five worker *morphs* (e.g. in *Psammotermes*). More commonly there may be major and minor soldiers (in many fungus-growing termites) and occasionally a third morph (e.g. *Acanthotermes*, *Velocitermes*). Major and minor workers are very common throughout the group, particularly in the Macrotermitinae and Nasutitermitinae. In all termites, nymphs, larvae, workers and soldiers are all juveniles, as they retain their prothoracic glands (Noirot and Pasteels 1987).

The colony organism divides its functions through its inanimate and animate parts, as follows:

1. Reproduction and dispersal (alates, queens, king)
2. Construction, feeding and tending (workers):
3. Active defence (soldiers)
4. Protection, homeostasis, fortification (nest, mound)

---

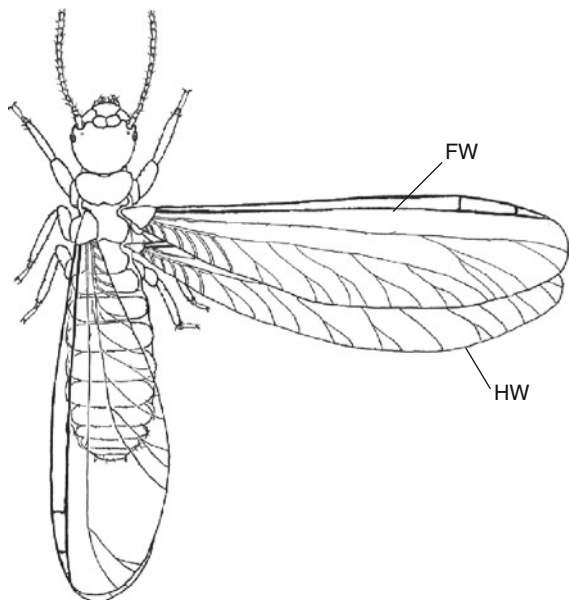
<sup>1</sup>Marais’s work first appeared in a series of magazine articles in the early 1920s, and was published as a book (*Die Siel van die Mier*) in 1937, a year after his death. Modern editions in English have been published by Penguin Books, and most recently by New York University Press and by Osiran Books. The text is widely available. A similar work (*The Life of the White Ant*) produced in 1927 by Maurice Maeterlinck (George Allen and Unwin Ltd) is now considered to plagiarise Marais’s ideas.

## 1.5 Reproduction and Dispersal: Alates

As with all animals, termites need to disperse, mate and establish new homes. The alates do all these tasks. They are produced within the colony either continuously or periodically. Generally if they are produced seasonally they develop to maturity just before the rainy season and they all fly off at the same time in great swarms. The large number of alates produced is probably an anti-predator herd-like defence (Jeschke and Tollrian 2007). These flying termites provide food for many other animals; in one study 200 vertebrate predators in 31 species attacked alates from a *Macrotermes subhyalinus* colony, during four separate nuptial flights (Dial and Vaughan 1987).

The alates fly for a variable time and then land on the ground to search for a mate. The flight presumably ensures that there is a greater probability of finding a mate from another, less closely related, nest (but see Chapter 12 by Vargo and Husseneder, this volume). Once a mate has been found most termites run around as a pair looking for a suitable nesting site (Mitchell 2007). One individual (usually the male) grabs on the end of the abdomen of an individual of the opposite sex and they run together (*tandem running*). In a few species individuals of one sex shed their wings and then the pair takes off again and flies on briefly. In many ecosystems the ground is only soft enough to dig into during the rainy season, which partially explains the flight timing. Once the pair has dug a small chamber they mate and the queen (as she is now) lays eggs that give rise to workers. Soldiers are only produced later.

Alates, are, in sense, closest to solitary insects. They generally look like long, thin cockroaches, with slender wings in which generally the two pairs of wings look essentially the same (Fig. 1.1). Alates interact with the outside environment



**Fig. 1.1** Alate structure (illustrated by *Tenuirostritermes*), FW = forewing, HW = hindwing from Weesner (1970)

much more than the other castes and we can use them to set out the basic body plan of termites because they look more similar to other closely related insect groups. Like most insects a termite alate is split into three body regions – a head, a thorax and an abdomen. There is, however, considerable variation in key structures across the termite families (Table 1.1). The following functional morphology descriptions generally follow the far more detailed descriptions of Weesner (1970), and employ his terminology. I have used forward/front for anterior and behind/back for posterior. I have concentrated on describing only the major features of termite morphology and anatomy, focusing on the structures that are most important functionally.

### 1.5.1 Head (Figs. 1.1 and 1.2)

All termite alates have *eyes* and one pair of *lateral ocelli* on the dorsal (top) surface: eyes are obviously necessary for dispersal and mate recognition (Fig. 1.2). Termites do not have a median ocellus and in some species the lateral ocelli are also absent. The rest of the dorsal part of the head is arranged as in most orthopteroid insects with a *labrum* at the front end, followed by a *clypeus*, subdivided into a *postclypeus* and *anteclypeus*. The labrum is generally small and tongue-shaped in all alates. Behind the clypeus, and separated from the clypeus by the *epistomal suture* is the main part of the head capsule, with the *frons* at the front and the *epicranium* behind. The boundary between the frons and the epicranium is not well defined. In some termites (Table 1.1) there is a pit in the middle-front of the frons, called the *fontanelle*. The fontanelle is apparently non functional in alates, but has a defensive function in soldiers, as it is the end of a gland that produces anti-predator chemicals (Santos and Costa-Leonard 2006). On either side and to the front of the frons are the paired *antennae*. These are long thin, unbranched and unclubbed, structures in termites, with 11–33 segments. As in all insects they have a number of sensory functions. The segment closest to the head is known as the *scape*, the segment next to it is the *pedicel*, which is nearly always shorter than the scape. All the segments beyond the scape are known collectively as the *flagellum*. From the side the eyes are below the frons on both sides. Below the eyes is the *gena* or “cheek”. The mandibles can be clearly seen in front of the antennae.

The structures on the underside of the head are rather complex (Fig. 1.2). The mouthparts have three components: the *maxillae*, the *labium*, and the *mandibles*. The maxillae and labium both carry palps for food sensing and handling. They are generally very similar in all termites and do not merit further discussion here. Alate mandibles are generally simplified versions of those found in the workers (see below). Alates do not appear to have any mandibular defences against predators.

### 1.5.2 Thorax (Fig. 1.1)

As with all insects, the thorax is divided into three segments: *prothorax*, *mesothorax*, and *metathorax*. Each segment has a pair of legs. The mesothorax and metathorax also have a pair of wings. The legs and wings are anchored to plates along the thorax. I will not describe these in detail as they have a broadly similar function in most insects. The mesothorax and metathorax have these plates well developed,

**Table 1.1** Main morphological characters of termites families. Wing venation: SC, subcosta; R, radius; RS, radial sector; M, media; Cu, cubitus; A, anal; F, forewing; H, hindwing. In the first four families a short subcostal vein is sometimes present between the costal margin and the radial sector. The anal vein is sometimes present as a stub in the same families. Does not include fossil groups (see Engel et al. 2009)

Family	Mastotermitidae		Termopsidae		Hodotermitidae		Kalotermitidae		Rhinotermitidae, Serritermitidae		Termitidae	
	Undivided	Absent	Undivided	Absent	Undivided	Absent	Undivided	Absent	Undivided, keeled	Present	Divided	Present
Postclypeus	Undivided	Absent	Undivided	Absent	Undivided	Absent	Undivided	Absent	Divided, keeled	Present	Divided	Present
Fontanelle	Flat	Flat	Flat	Flat	Flat	Flat	Flat	Flat	Flat	Flat	Saddle-shaped	Saddle-shaped
Pronotum	SC, R, RS, M, Cu, A	SC, R, RS, M, Cu	SC, R, RS, M, Cu	SC, R, RS, M, Cu	SC, R, RS, M, Cu	SC, R, RS, M, Cu	SC, R, RS, M, Cu	SC, R, RS, M, Cu	[SC+R], RS, M, Cu	[SC+R], RS, M, Cu	[SC+R], RS, M, Cu	[SC+R], RS, M, Cu
Wing venation	F>>H	F>>H	F>>H	F>>H	F>>H	F>>H	F>>H	F>>H <sup>a</sup>	F>>H <sup>a</sup>	F~H	F~H	F~H
Wing scale	5	5/4	5/4	5/4	5/4	5/4	4	4/3	4/3	4/3	4/3	4/3
Tarsal segments	12–15	8	8	8	8	8	8	8	8	4 (2) <sup>b</sup>	4 (2) <sup>b</sup>	4 (2) <sup>b</sup>
Malpighian tubules	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	No	No	No
Flagellates present in gut	I	I	I	I	I	I	I	I	I	I	II, III, IV	II, III, IV
Feeding groups	Yes <sup>c</sup>	No	No	Yes	Yes	Yes	No	No	Yes <sup>d</sup>	Yes <sup>d</sup>	Yes	Yes

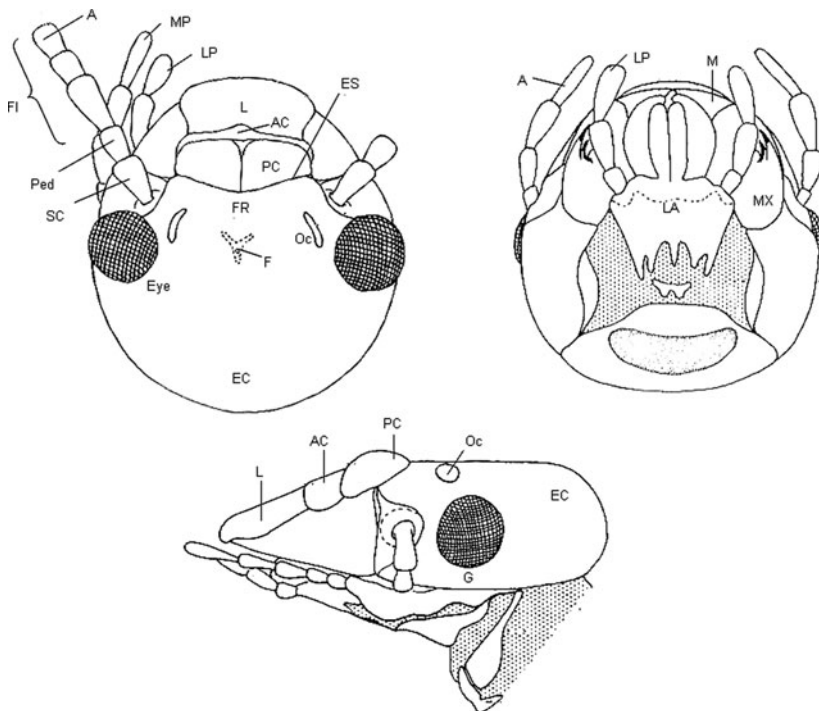
<sup>a</sup>F ~ H in *Psanmotermes*.

<sup>b</sup>Two Malpighian tubules in *Labiotermes*.

<sup>c</sup>Development pathway simpler than in other groups.

<sup>d</sup>No true workers in *Glossotermes* and *Prorhinotermes*.



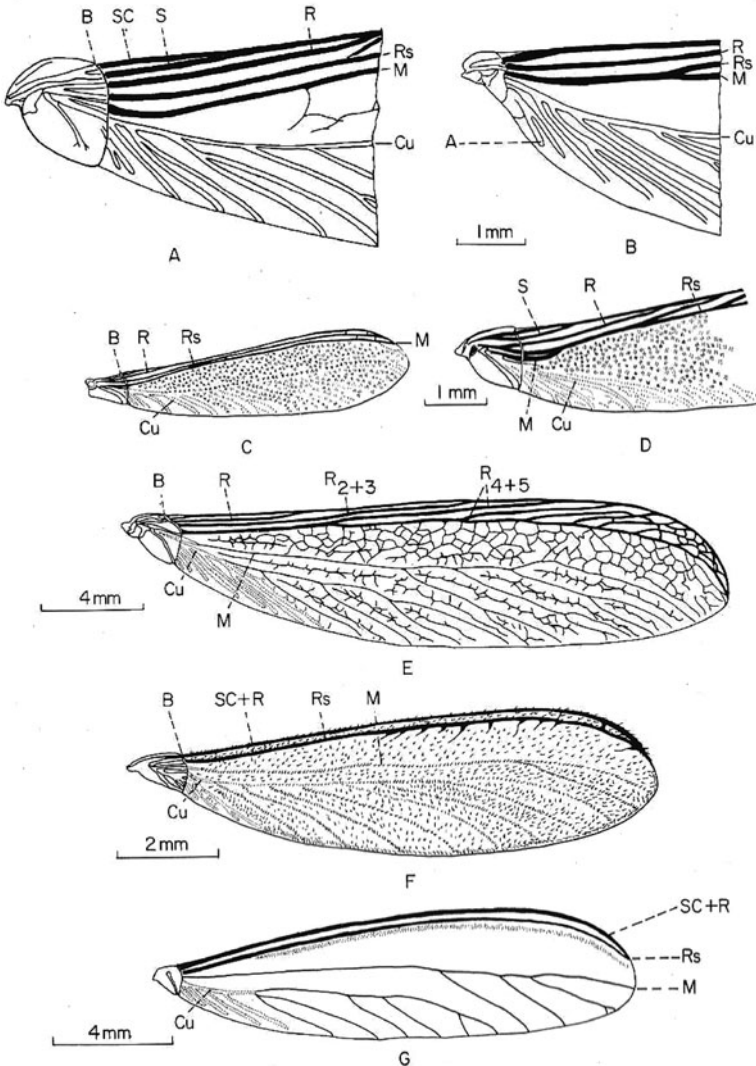


**Fig. 1.2** Head of *Tenuirostritermes* (labels incomplete), from Weesner (1970). Head structures: A, antenna; SC, scape; Ped, pedicel; Fl, flagellum; MP, maxillary palps; LP, labial palps; AC, anteclypeus; PC, postclypeus; ES, epistomal suture; FR, frons; Oc, ocellus; EP, epicranium; M, mandible; MX, maxilla; LA, labium; G, gena

but the prothorax, which has no wings, has much smaller plates. The plates on the top (dorsal) surface of the thorax are well developed and vary somewhat across the termites. These are the *pronotum*, *mesonotum* and *metanotum*. The *pronotum* is usually simple and shield-like, but can be variable. The pronotum is saddle-shaped in all Termitidae, but flat in all the other families (Table 1.1).

### 1.5.3 Wings (Figs. 1.1 and 1.3)

Termite alates are generally poor flyers: their technique is to launch themselves into the air and fly in a random direction. Their main anti-predator defence seems to be the very large numbers of alates that are released from the colony simultaneously. Larger termites generally fly further than smaller ones, with very large alates being strong but poorly directed fliers (Weesner 1965). Alates fly to get clear of the parental colony, to find places with a suitable mate, and to find a suitable place to found a colony. Here there is a clear difference between those termites that are one-piece nesters, who must find a suitable nest site within their feeding substrate, and separate-piece nesters, where the colony can be founded in the soil at some distance from the feeding substrate.



**Fig. 1.3** Wing structure in different groups of termites. Wing venation. **a** Forewing of *Neotermes malatensis*; **b** hind wing of same; **c** forewing of *Glyptotermes chapmani*; **d** forewing of *Rugitermes athertoni*; **e** forewing of *Zootermopsis angusticollis*; **f** forewing of *Coptotermes pacificus*; **g** forewing of *Nasutitermes pictus*. A, anal vein; B, basal or humeral suture; Cu, cubitus vein; M, media vein; R,  $R_{2+3}$ , radius veins; Rs,  $R_{4+5}$ , radial sector; SC, costal margin; S, subcosta, from Weesner (1970)

Termite fore wings and hind wings are very similar, hence the traditional scientific name for the termite order, the Isoptera (Greek: iso = same, ptera = wing). The wings are held parallel with the body at rest and at right angles when flying. The basal part of the wing is covered by a wing scale. The end of this scale is where the wings are shed after landing, there is a suture (the *humeral suture*)

here, which allows the wings to be shed automatically, in all families except the Mastotermitidae, where the wing is chewed off above the scale. Wings are clearly useless underground. The fore wing scale is always larger than the hind wing scale, but the relative sizes differ between families (Table 1.1).

Termite families differ most profoundly in the venation in the wings. There has been a progressive simplifying of the venation in more phylogenetically apical groups (Table 1.1), so that the Termitidae have the simplest wings, and the Mastotermitidae have the most complex (Fig. 1.3). The Mastotermitidae also have a unique cockroach-like structure, the anal lobe, a part of the wing lost in all other termites. Historically, wing venation has been hard to describe, with many different systems proposed. In termites, Emerson's (1965) system is usually used. The following notes are for a termite, like *Mastotermes darwinensis*, which has the full complement of veins. The front of the wing has a heavily sclerotised false vein (false because it does not develop from a tracheal tube), the *costal margin*. The precosta and costa veins found in some other insects are absent. The next vein inwards is the short *subcosta*. Following that are three *radius* veins,  $R_1$ ,  $R_2$  and  $R_3$ , which may be separate or fused in any combination. The next vein is the *radial sector*, which reaches to the wing, or close to it, and may split into several sub-veins. Next to this vein, in the middle of the wing, is the *cubitus*, which branches as it goes down the wing, ending on the wing margin. The final set of veins, the *anal veins*, is only well developed in the Mastotermitidae. The functional significance of all these structures is unclear, as all termites seem to be about as bad as each other at flying. The loss of individual veins may represent a general body size reduction across the termite phylogenetic tree.

#### 1.5.4 Legs (Fig. 1.4)

Termites are reliant on their legs for most of their movement – termite alates fly only briefly. The legs are fairly constant across castes, although soldier legs can be heavier and more conspicuously armed. Termite legs follow the standard pattern for insects. Starting closest to the body these are the *coxa*, *trochanter*, *femur*, *tibia* and *tarsus*. In termites the coxa of the second and third pair of legs is divided by a deep suture into the *meron* and the coxa proper. The trochanter is short, the femur relatively large, and the tibia relatively long and thin. The tarsus has a variable number of short joints (Table 1.1) followed by a long terminal joint with a large claw. The tibia also has a variable number of *tibial spurs* at its far end. In some termites there is an *arolium*, between the claws. This sticky pad-like structure is absent in most termites, probably because they do not generally have to climb up smooth surfaces (Crosland et al. 2005).

#### 1.5.5 Abdomen

The abdomen has ten segments, consisting of upper and lower plates: the *tergites* and the *sternites* respectively. Nine of the ten tergites are wide and substantial, while

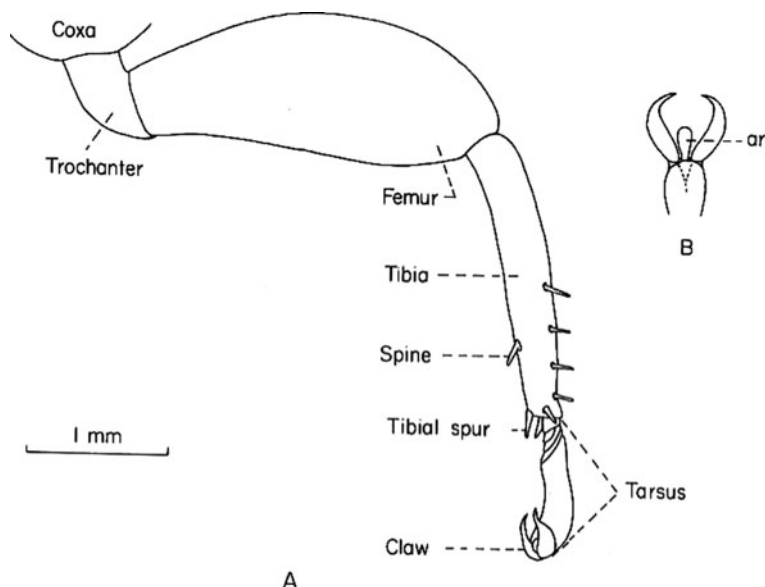


Fig. 1.4 Leg structure in *Zootermopsis angusticollis*, from Weesner (1970)

the tenth (the *epiproct*) is elongated and tapering. The tergites are identical in males and females. The first sternite is small or absent. The second through to sixth sternite are broader than long and similar in males and females. The seventh sternite of the female alate (the *hypogynium*) is large, often completely covering sternites eight and nine, which are modified. These modifications of the sternites do not occur in males and this is one of the most reliable ways to sex alates. Mature males generally have *styli* (unjointed processes) at the ends of the ninth sternite, but these vary widely across species. Mature females lack these structures. The tenth sternite (the *paraproct*) is similar in both sexes. It is divided in the middle, forming a pair of plates, one on each side of the body. The sides of the paraprocts have segmented *cerci*, usually with two joints. Both the cerci and styli are sensory structures, their gradual loss in termite evolutionary history suggest that they may not be very useful inside a colony or when foraging.

The internal reproductive system of termites is greatly simplified when compared with other cockroaches. The male has no intromittent organ, and in most species the sperm are immotile and aflagellate. The striking exception to this is in the Mastotermitidae, where the sperm are multiflagellate but appear to have limited motility (Riparbelli et al. 2009). This pattern is repeated in the females, where the genital structures are again simple, except in the Mastotermitidae, which have a clearly defined ovipositor, homologous with those found in cockroaches (Nalepa and Lenz 2000). The mechanism of mating is very poorly studied, but it is known that the ovarioles are very well developed in the Termitidae, where some queens become extraordinarily distended (*physogastric*) and lay many thousands of eggs during a lifetime. The lack of motile sperm, intromittent organs, and the general

lack of sexual dimorphism is unsurprising in a group where monogamous lifetime pair bonds are the norm and where, therefore, sperm competition does not occur (Morrow 2004).

Termite eggs are unadorned, with smooth surfaces. They are laid singly in all species except *Mastotermes*, which lays eggs in an ootheca-like structure, similar to that found in other cockroaches, but simplified (Nalepa and Lenz 2000). The eggs are always laid within the colony, so the protective role of the ootheca is unnecessary.

## 1.6 Worker Morphology

The head, thorax and abdomen of workers is essentially similar to those in the alates, except for the absence of wings and any genital structures. Workers, however, have much more strongly developed mandibles, reinforced with generally small amounts of zinc and manganese (Cribb et al. 2008). In the Kalotermitidae, the mandibles are strongly reinforced with zinc to allow them to break into the very strong dry dead wood on which they feed. Almost all worker termites are blind, as they lack compound eyes. The few exceptions are all early branching groups, some of which, but not all, forage above ground. However, there are also many blind surface foragers so the connection between above ground foraging and eyes may be mostly a phylogenetic signal.

## 1.7 Construction, Feeding and Tending

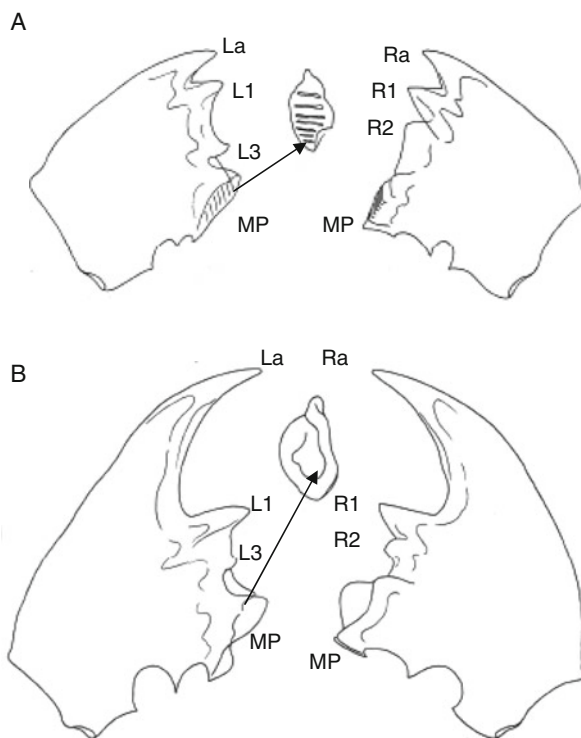
Workers do almost all the work within the colony, and they live and work predominantly within the colony. Even when foraging, most workers are protected under sheeting or runways. Only a relatively few grass, microepiphyte and litter-feeders forage unprotected on the surface. In those cases the foraging morphs are conspicuously more sclerotised than the non-foraging morphs. Workers are sterile, they never reproduce. However, in many species workers can develop into supplementary reproductives if the primary reproductives die (Roisin 2001, see also Chapter 9 by Miura and Scharf and Chapter 10 by Matsuura, this volume). Not all termite species have true workers. In the Kalotermitidae and the Termopsidae there are no true workers, and the immatures may not help very much (Korb 2008). In all these cases the termites nest and feed in dead wood and there is no requirement for nest building or foraging. It is not clear how much tending these groups do, possibly, in some cases none. However, even in this case all the species are eusocial, as they have soldiers that never reproduce.

### 1.7.1 Feeding

Only workers forage. Termites feed on dead plant material at all stages of decomposition (“humification”, see Donovan et al. 2000; Hyodo et al. 2008). This includes, in order of humification: microepiphytes, living stems and roots, dry grass, dead

leaves, dead wood, very decayed dead wood plastered with soil, humus and (apparently mineral) soil. Feeding preferences vary between species and higher taxa and can be classified according to their position on the humification gradient leading to four feeding groups (Donovan et al. 2001; see Chapter 14 by Bignell, this volume). Group I feeds on dead wood and grass and have relatively simple guts. Group II feeds on wood, grass, leaf litter and microepiphytes and have more complex guts. Group III feeds on humus (i.e. soil-like material with recognisable plant material in it). Group IV feeds on soil (i.e. soil-like material with a high proportion of silica and no recognisable plant material).

Termite worker-imago mandibles are very variable in the number of their marginal teeth, but functionally they seem to fit into two groups: (a) grinding (milling), and (b) pounding (pestle and mortar) (Donovan et al. 2001; Fig. 1.5). The molar plates are heavily ridged in the grinding type, with the left molar plate concave and the right convex. As the mandibles rub against each other, the molar plates grind up the plant material, often dead wood, which is a very fibrous material. In the pounding type the molar plate is convex in the left mandible and concave in the right mandible and both mandibles have no ridges. These two structures act



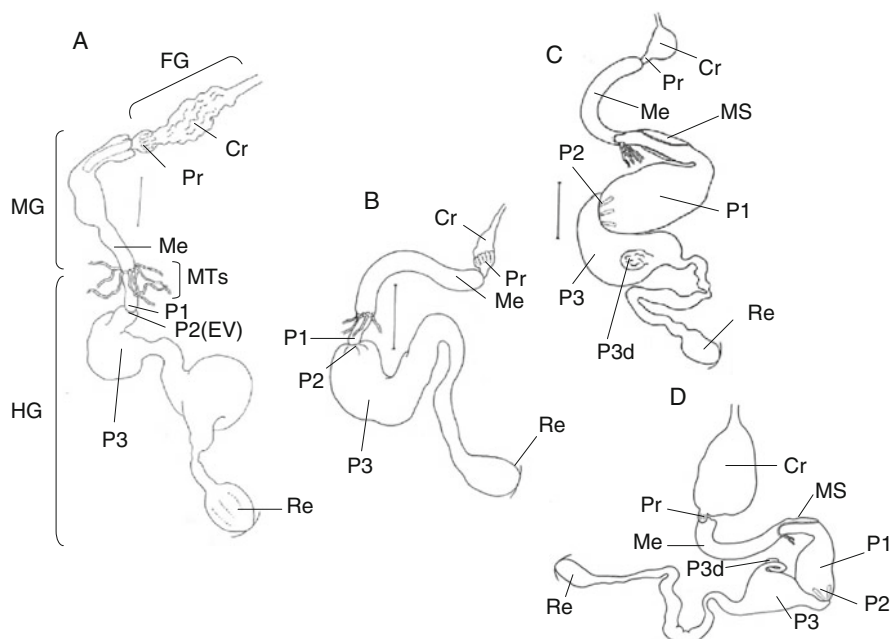
**Fig. 1.5** Worker mandibles of **a** *Microcerotermes strunckii* and **b** *Megagnathotermes notandus*. La, L1, L3, left marginal teeth; Ra, R1, R2, right marginal teeth; MP, Molar plate, from Sands (1998)

like a pestle and mortar, pounding the feeding substrate, which is usually soil or humus. Correlated with this molar plate structure is the size of the first apical tooth. In the grinding type, the tooth is short, and the distance between the apical and first marginal teeth is also short. The apical and first marginal teeth seem to be used to tear off fibres of wood. In the pounding type the first apical tooth is long and the distance between the apical and first marginal teeth is also long. In this case the apical and first marginal teeth seem to be used to cut out a relatively large volume of soil. These mandible adaptations are associated not only with diet but also with gut structure.

Termite guts are very complicated structures. Early branching families are very like closely related cockroaches but later branching families are strongly modified. The general pattern is for the cockroach-like guts to have a generalist detritivore type structure, while the more derived guts switch to a more complex hindgut fermentation structure. Insect guts are split into three distinct parts: *foregut* (stomatodeum), *midgut* (mesenteron) and *hindgut* (proctodeum). The food is ingested and passes into the foregut, which contains the *crop* (stomach) and then the *proventriculus* (gizzard), a grinding organ. From the proventriculus the food enters the midgut, which is the primary source of enzymes in most insects. The midgut has *midgut caeca* which are enzyme production and enzyme-product absorption sites. At the junction between the midgut and the hindgut are the *Malpighian tubules*, which have an excretory function. This junction also has a *proctodeal valve* in many insects. The partly digested food then passes into the hindgut, which is of variable length and structure, but usually contains a rectum and an anus. The hindgut is often short in insects that have no significant microbial symbioses.

In the least derived termite guts (and in the closely related wood-feeding cockroach, *Cryptocercus*), all of which feed on wood or grass, the structure is essentially as described above (Fig. 1.6a). The proventriculus is well developed and assists in fragmenting the food. The midgut is relatively extensive, and often has mid-gut caeca, which are points of absorption for fluid resulting from enzymatic breakdown. The hindgut is relatively small, with proctodeal segment 3 (or paunch: an enlarged sac at the beginning of the hindgut) the best developed part. In all of the termite families except the Termitidae, the paunch is packed with flagellates. This form of gut represents a combination of a generalist detritivore-type (as in cockroaches, e.g. *Periplaneta*) and a hindgut fermentation system, where the flagellates ferment the partly-digested food under anaerobic conditions. Most textbooks have generally attributed the digestion of dead wood to the hindgut flagellates. However, we now know that all studied wood- and grass-feeding termites produce their own cellulases, and in addition that many wood-feeding termites in the Termitidae digest wood efficiently without any flagellates (see Chapter 3 by Lo et al., Chapter 14 by Bignell, and Chapter 16 by Brune and Ohkuma, this volume). Overall digestion is therefore divided between mid-gut enzyme production and hindgut microbial fermentation.

Nearly all the important variations from this basic intestinal model are found in the Termitidae. In that family alone the hindgut flagellates have been lost and this appears to have accelerated the evolution of physiological and anatomical



**Fig. 1.6** Gut figures from Sands (1998), showing the variable elaborations of the hindgut, unravelled for illustration. Cr, crop; EV, enteric valve; FG, foregut; HG, hindgut; MG, midgut; Me, mesenteron; MS, mixed segment; MTs, Malpighian tubules; P1, P2, P3, proctodaeal segments; P3d, diverticulum; Re, rectum. **a**, *Hodotermes* (Hodotermitidae), feeding-group I, grass-feeder; **b**, *Coptotermes* (Rhinotermitidae), feeding-group I, wood-feeder; **c**, *Cubitermes* (*Cubitermes*-group Termitidae), Feeding-group IV, soil-feeder; **d**, *Ophiotermes* (*Cubitermes*-group Termitidae), Feeding-group IV, mound-feeder

innovations. The main changes are the simplification of the proventriculus, the loss of the midgut caeca, the development of a *mixed segment*, a reduction in the number of Malpighian tubules, the development of a sclerotised *enteric valve* between the first and third parts of the hindgut, and the extensive (and very variable) development and compartmentalisation of the hindgut (Fig. 1.6c, d). All of these changes represent feeding either more efficiently on an existing food (wood, grass) or on entirely new substrates (humus, soil). In both cases selection seems to have produced hindgut fermentation systems of greater sophistication. A system of numbering hindgut sections in the Termitidae (which are commonly also separated compartments) was devised by Holmgren (1909) and was most recently reviewed by Noirot (2001). It provides, with just a few variations in the published literature, a consistent scheme of homology by allocating the enteric valve to its own section (P2); the section anterior to the valve is thus the P1, and those posterior to it are therefore P3, P4 and P5 (the last being the rectum).

The most elaborated guts in termites are those of the *Cubitermes*-group termitids that feed on soil with no discernible plant materia in it. They show all of the above innovations (Fig. 1.6d, e). In *Cubitermes*, a typical member of the group, the mandibles are of the pounding type, and the homogenised soil passes through the



mouth to a small proventriculus, which is poorly sclerotised and seemingly does not alter the ingested soil. The midgut is short and tubular and overlaps with the (embryologically proctodaeal) P1 for about half its length, to produce the mixed segment. This structure is unique to termites and appears to be a fluid exchange site associated with excretion and a preliminary microbial processing of the food (see [Chapter 14](#) by Bignell and [Chapter 16](#) by Brune and Ohkuma, this volume). The Malpighian tubules attach at the junction between the midgut and the hindgut and are clustered over the mixed segment to form a *Malpighian knot*. Beyond the mixed segment the P1 expands greatly to form a large sac. At the posterior end of this sac are the heavily sclerotised ridges of the enteric valve (Fig. 1.6). This structure is highly variable across the Termitidae and its function is somewhat obscure. In soil-feeders it probably helps to separate clay particles, which have abundant soil organic matter (SOM) associated with them, from silica (sand) particles, which are inert. The enteric valve may ensure that clay particles stay in the hindgut longer than silica particles (Donovan 2002). Peristaltic contractions may assist this process. Beyond the P1 is another very large sac, the P3, which in the *Cubitermes*-group has a distinctive *P3 diverticulum* (which expands and contracts as coarse fractions of soil flux in and out of it). The mixed segment, P3 and P4 are packed with prokaryotic microbes (see [Chapter 14](#) by Bignell, [Chapter 15](#) by Ohkuma and Brune, and [Chapter 16](#) by Brune and Ohkuma, this volume). The whole gut allows highly refractory organic material in soils to be digested, probably, in part, by releasing proteins, peptides and amino acids immobilised as SOM (Ji and Brune 2005, 2006). The most extreme guts are those of the *Cubitermes*-group mound feeders (the *Ophiotermes*-group), that feed on the already digested faeces of other *Cubitermes*-group species in the mound matrix. These have enormously enlarged crops and salivary glands, and curiously twisted P3 diverticula (Fig. 1.6). The large crop is probably developed to cope with the very large amount of mound material that they must ingest in order to extract anything digestible from the mounds.

Between the two extremes of gut structure there are numerous forms, which generally fall in an intermediate position on the termite phylogenetic tree (see [Chapter 2](#) by Lo and Eggleton, this volume). The fungus-growing termites (Macrotermitinae) have retained the a rather phylogenetically-basal gut structure, probably because much of their forage is digested by the mutualistic fungus.

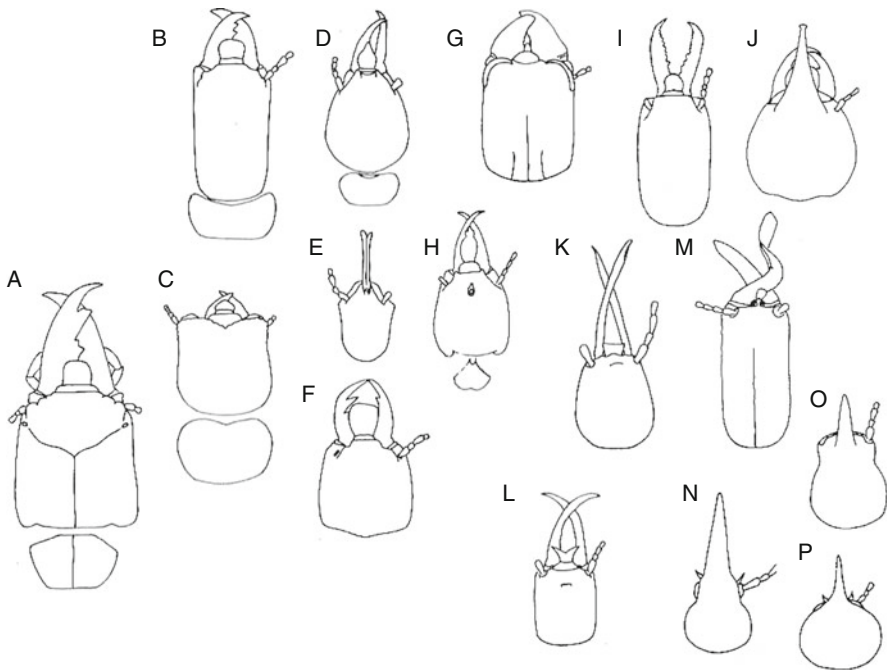
### 1.7.2 Nursing

The immatures of termites are small white, unsclerotised and essentially helpless. They have to be fed by the workers/helpers. The workers assimilate the food that they eat and re-secrete nutrients in a form palatable to the immatures. In the non-termitid families, which all have gut flagellates, this is closely connected with passing the flagellates from workers to larvae, and occurs by *proctodeal trophallaxis*. The immatures are fed by secretions from the anus, which contain the symbionts and woody particles. This method of feeding does not occur in the termitids, where the flagellates have been lost. *Stomodeal trophallaxis*, where immatures are fed from glands in the head through the mouth is found in all termites.

Grooming is important in all groups, particularly in order to remove potentially parasitic microbial populations. The relative amount of time that workers spent grooming is probably related to parasite load in the nesting and feeding substrates (e.g. termopsids in wet wood probably have a higher fungal load than kalotermitids in dry wood).

## 1.8 Active Defence: Soldiers

The soldiers in a colony have only one function – to defend the colony. They generally have large, highly sclerotised heads and powerful, highly modified, mandibles. They also often have chemical defences (Prestwich 1984). Soldiers were the first sterile caste to evolve (Thorne et al. 2003). It seems probable that the most important termite predators are ants, and much of the variation in soldier morphology is in response to ant predation pressure. Vertebrate predation may also be very important, but there is little evidence that these predators generally kill entire colonies. Generally vertebrate termitophages can wound a colony, but only ants can destroy it (Leal and Oliveira 1995).



**Fig. 1.7** Plan view of soldier head capsules. **a**, *Archotermopsis wroughtoni*; **b**, *Rugitermes bicolor*; **c**, *Cryptotermes verruculosus*; **d**, *Coptotermes sjostedti*; **e**, *Rhinotermes hispidus* (minor soldier); **f**, *Rhinotermes hispidus* (major soldier); **g**, *Jugositermes tuberculatus*; **h**, *Acanthotermes acanthothorax* (minor soldier); **i**, *Microcerotermes fuscotibialis*; **j**, *Armitermes grandidens*; **k**, *Promirotermes orthocopes*; **l**, *Procubitermes niapuensis*; **m**, *Pericapritermes urgens*; **n**, *Angularitermes nasutissimus*; **o**, *Coarctotermes suffuscus*; **p**, *Nasutitermes octopilis*, from Weesner (1970)

Soldiers show the greatest of variation of any caste, not only between species but also within species. Many species have several morphs and sometimes the morphs have very divergent structures, due to very different methods of defence. At the generic and species level soldier morphology is the most important source of taxonomic characters. These variations can be seen almost entirely in the head capsules of soldiers (Fig. 1.7). The labrum, for example, is highly variable: it can be: tongue shaped (basal condition, Figs. 1.7a–d, g, i), bilobed (Termitinae, Fig. 1.7 l), asymmetrical (Termitinae, Fig. 1.7m), and guttered (Rhinotermitinae, Fig. 1.7e–f). The postmentum is usually enlarged, often with process or node. Soldier mandibles are also highly variable – sometimes reduced or vestigial (Rhinotermitinae, Termitidae: Nasutitermitinae, Figs. 1.7e–f, n–p). The fontanelle can be absent (basal condition, Fig. 1.7a–c), highly enlarged (Coptotermitinae, Fig. 1.7d), or at the end of a variable length process (Syntermitinae, Nasutitermitinae, Figs. 1.7j, n–p). All these variations clearly relate to the way the soldiers repel predators. For example, in those cases where soldiers block tunnels (*phragmosis*) the soldier head width has been shown to be under stabilising succession (Matsuura 2002; Roux et al. 2009).

Soldier morphology, however, cannot be separated from the colony structure, the nature of the feeding substrate, and the energetic cost of producing soldiers for the colony. These all interact to produce four main defence strategies: *strong-point*, *counter-attack*, *labyrinth*, and *trail-guarding*.

- a. Strong-point defence is where soldiers retreat to defensible points within the nest (e.g. soldier heads as in Fig. 1.7a, c, l).
- b. Counter-attack defence is where soldiers come out of the nest to swamp the enemy (e.g. soldier heads as in Fig. 1.7e–f, j).
- c. Labyrinth defence is where the workers build a complex set of tunnels, most of which are not occupied (as in *Cephalotermes*, where soldiers are very rare). This means that any ant predators entering the nest will have very long search times before they encounter any prey.
- d. Trail-guarding is where a trail of foraging workers are defended by actively guarding soldiers (e.g. soldier heads as in Fig. 1.7o). The most striking example of this is found in *Hospitalitermes*, where workers scrape micro-epiphytes from the bark of standing trees and nasutes soldiers stand at the edge of the foraging parties and are highly effective at deterring ants from attacking (Miura and Matsumoto 1998).

Both the type and number of soldiers depends on the defence strategy used. Strong-point defenders have large heads, and in some species they have ridges or crests on the head to secure the head within the tunnels. As strong points are necessarily limited, and such soldiers are presumably expensive to construct, there tends to be low soldier:worker ratios in such colonies. In contrast, counter-attack relies on having very large numbers of soldiers, and so the soldiers must be relatively cheap to produce. In a labyrinth nest the onus is on the workers to produce the complex nest structures and there is obviously a cost involved in producing such extensive structures.

**Table 1.2** Morphological characters of termitid clades. Inner and outer refer to the position of the posterior mesenteric extension forming the mixed segment, and are with respect to the edge of the intestinal coil in situ (see Sands 1998). Feeding groups are those of Donovan et al. (2001). Iif refers to feeding-group II fungus-growing termites

	Macrotermitinae	Foraminitermitinae, Sphaerotermitinae	Apicotermitinae	Termitinae, nasutitermitinae
Mixed segment	No	No	Inner	Outer
Feeding groups	Iif	II, III	III, IV	II, III, IV
Malpighian tubule attachment	At midgut-hindgut junction	At midgut-hindgut junction	To posterior midgut	At midgut-hindgut junction
Malpighian knot	No	Pseudo-	True	True

Prestwich (1984) classified termite soldiers according to their physical and chemical defences. Recent attempts to improve on the classification using more sophisticated methods of analysing shapes have only been partially successful (e.g. Scholtz et al. 2008), although they do support the general value of the scheme. All non-termitids have fully functional soldiers. However, within the termitids there are two clades (possibly even three) where soldiers have been lost – the *Anoplotermes*-group, and the *Protohamitermes*-group (Inward et al. 2007b). A number, but not all, of these are autothysic. *Autothysis* is the self-destructive rupturing of the abdomen when in contact with a predator ant to extrude the sticky, and possibly poisonous, guts (Sands 1982). The mechanism, presumably designed to work in tunnels causes the predator to stick to the autothysic worker, and with repeated encounters the accumulated bodies will eventually block the tunnel and repel the attack (Table 1.2).

## 1.9 Protection, Stability, Fortification: Nests and Mounds

Termite colonies live inside a *nest*, and if the nest is covered with or made from earth to create a structure protruding above the soil surface then it becomes a *mound*. Mounds and nests protect against the environment, keep the internal climate stable, and fortify against predators (a range of nest types is shown in Fig. 1.8). However, not all termite colony structures fulfil all these functions. In fact, there are probably more termites that produce amorphous underground nests than those that produce complex multi-function nests or mounds (e.g. see Eggleton et al. 1996).

Abe and co-workers developed a nesting classification for termites dependent on the position of the nesting and feeding substrates (e.g. see Higashi et al. 1992). *One-piece nesters* nest and feed in the same substrate (usually wood). *Intermediate-nesters* nest and feed in the same substrate but can forage into that substrate nearby. *Separate-piece nesters* nest in one substrate and forage out into another. It is only the separate-piece nesters that habitually need material from outside the colony area to construct their nests.

The most complex colony constructions are found in the Termitidae, Rhinotermitidae and Hodotermitidae – groups which all have true workers and most of which are separate-piece nesters. Where there are no true workers (e.g. in Termopsidae, Kalotermitidae, *Prorhinotermes*) colony constructions tend to be simpler. The most complex nest building of all is found in the Macrotermitinae (the fungus-growing termites), exemplified by the huge soil mounds built by species in the genus *Macrotermes*. Mounds of equal size but lower internal complexity are built by the Australian termitid *Nasutitermes triodiae*. A mature living *Macrotermes* mound is arguably the most complex colonial organism known in nature. A case can be made for all the castes, the mound, and the fungus, all being part of a single organism. If so it is also probably the only organism that can completely decompose dead plant material, including all its lignocellulose, leaving virtually no residue (Ohkuma 2003).

Termites build their nests with faeces. This makes perfect sense as their substrates are relatively inert to pathogens, are cheap to produce, and are generally good structural materials. There are two sorts of building material: partly digested plant matter, which produces *carton nests*, and soil, which produces *soil nests and mounds*. Not all of these nests are conspicuous, as many colony centres are found underground, particularly in tropical rain forests (Eggleton et al. 1996). The soldierless Apicotermitinae, for example, generally build no obvious nest structures and appear to live in a set of amorphous tunnels. In non-termitid mound builders, the carton nest is built inside a soil mound (e.g. in many Australian *Coptotermes*) but in the termitids soil mounds usually have no carton material inside. The fungus comb of the Macrotermitinae may well be homologous with the carton nests of *Coptotermes*, with the carton material being used as food for the mutualistic fungus (Donovan et al. 2001). A substantial minority of termites, particularly the single-piece nesting kalotermitids and termopsids, nest in dead wood and live within the tunnels created by their feeding. Although these groups do produce faecal structures, they do not make carton nests.

### **1.9.1 Protection and Stability**

The main environmental challenges for colonies are rainfall, heat and gas exchange. These problems tend to become greater with colony size and complexity. Within rain forests temperatures are buffered, but rainfall can be torrential and continuous. The erosion of mounds then becomes a very serious problem. However, carton mounds in tropical rain forests rarely have anti-rain protection, probably because carton is a more rain-resistant material than soil. Mounds in the soil, however, often have “drip tip”-like structures that allow the efficient flow of water over and around them.

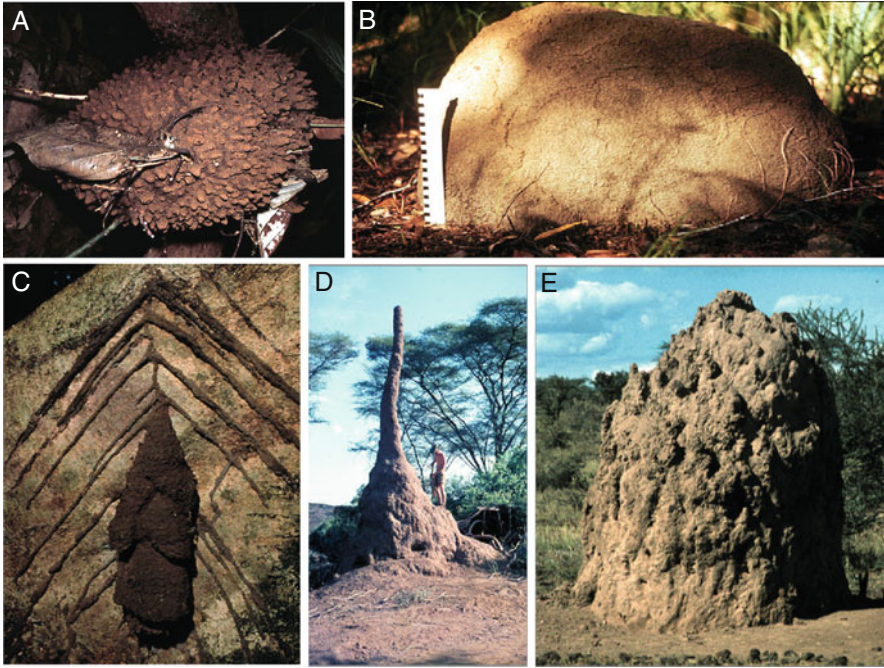
Temperature fluctuations outside rain forests are a much bigger problem: isolated termites can survive only in a very narrow range of temperatures. Most termites use the thermal properties of their nesting substrate to aid temperature control. In hot dry areas this means nesting in the soil, which is an extremely thermally buffered environment (Turner and Soar 2008). Termite nesting within logs may also

be reasonably well temperature-buffered. Large colonies in dry, hot areas have significant temperature control problems, and this is where architecturally-complex mounds have a role. This is particularly true in Australia, Africa and, to a lesser extent, South America in the genera *Coptotermes*, *Nasutitermes*, *Macrotermes*, *Cornitermes* and *Syntermes*. *Macrotermes* on the African plains build the most complex known non-human architectural structures. In such habitats, mound structure may often be a trade off between thermoregulation and gas exchange (Korb 2003). For example, Turner and Soar (2008) have shown that, in at least some species, big mounds in savannas act like lungs. The old model of mound ventilation (the “thermosiphon”) proposed by (Luscher 1951) now seems not to fit the available data (Korb and Linsenmair 2000)

### 1.9.2 Fortification

The need for fortification from predators is very clear, as many animals feed on termites (Das and Coe 1994; De Visser et al. 2008). The nest/mound structure is just as important in defence as the soldier morphology and behaviour. Many termite nests are made of carton and are not particularly strong. Carton nests are usually defended using counter-attack strategies. Many mounds, however, are made up of faecal soil, and these are usually defended as strong-points. In *Cubitermes*, for example, the cells within the soil mound are connected by short tunnels or apertures that are just the right diameter for soldiers to block them (Perna et al. 2008). In the most sophisticated nests (e.g. within the Macrotermitinae), the colony has a “queen cell”, a highly fortified central chamber in which the queen and king are defended as a last resort.

There seems to have been a long history of predation of termite mounds and nests. The earliest plausible termite-feeding animal was the Jurassic mammal *Fruitafossor*, which had very similar adaptations to extant termite-eating mammals, such as aardvarks and anteaters (Luo and Wible 2005). At least one group of dinosaurs, the alvarezsuarids, seem to have been specialised termitophages, with fore limbs adapted to break into termite colonies in dead wood (Longrich and Currie 2009). Modern termite-eating mammals are very common, particularly in the tropics. Those that break directly into mounds include aardvarks, anteaters, pangolins, many species of bears, apes (particularly chimpanzees), numbats, many lizards, amphibians etc. The Aardwolf appears to feed only on grass-harvesting termites of the genus *Trinervitermes* (Koepli et al. 2006), which are common in African savannahs. Chimpanzees that feed on termite mounds use a range of tools (Suzuki et al. 1995) to extract termites, and *Australopithecus* appears to have used bone tools in a similar way (Backwell and d’Errico 2001). However, the primary predators of termites are undoubtedly ants (see above), although in some cases this predator-prey relationship is complicated by ants that are *inquilines* (i.e. live inside termite colonies). These may provide some protection from other raiding ants, although overall, completely ant-free nests seem to be the healthiest. Many other species live inside termite nests, as commensals, predators, parasites, or mutualists (Jaffe



**Fig. 1.8** Epigeal termite mounds, illustrated by **a**, *Laccositermes* sp. (SE Asia); **b**, *Cubitermes severus* (West Africa); **c**, *Procupitermes arboricola* (West/Central Africa); **d**, *Macrotermes bellicosus* (East Africa); **e**, *Amitermes laurensis* (Australia). All photos from the Termite Research Group photo collection, NHM

et al. 1995). In addition, mounds can be important refugia to protect animals from fire (Yarnell et al. 2008) or just to give protection and shelter in otherwise hostile environments. Mounds are not just ecologically important when they are occupied. Abandoned termite mounds can be a source of important nutrients for large mammals, particularly in nutrient poor areas (Ruggiero and Fay 1994), and their eventual erosion is a normal part of longer-term local nutrient cycling (Holt and Lepage 2000) (Fig. 1.8).

## 1.10 Conclusions

Termite colonies are organism-like entities with strong division of labour between different subcomponents. This leads to a wide range of anatomical and morphological adaptations within each species, and therefore, within each individual termite mound. Comparable variation between is only seen in other colonial organisms, particularly other social insects (ants, corbiculate bees, vespids). However, none can match the complexity of anatomical specialisation, body form and colony structure of termites.

## References

- Backwell LR, d'Errico F (2001) Evidence of termite foraging by Swartkrans early hominids. *Proc Natl Acad Sci U S A* 98:1358–1363
- Boomsma JJ (2009) Lifetime monogamy and the evolution of eusociality. *Philos Trans R Soc Lond B Biol Sci* 364:3191–3207
- Cribb BW, Stewart A, Huang H, et al (2008) Unique zinc mass in mandibles separates drywood termites from other groups of termites. *Naturwissenschaften* 95:433–441
- Crosland, MWJ, Su, N-Y, Scheffrahn, RH (2005) Arolia in termites (Isoptera): functional significance and evolutionary loss. *Insectes Soc*, 52:63–66
- Das I, Coe M (1994) Dental morphology and diet in anuran amphibians from South India. *J Zool* 233:417–427
- Davies RG, Eggleton P, Jones DT, et al (2003) Evolution of termite functional diversity: analysis and synthesis of local ecological and regional influences on local species richness. *J Biogeogr* 30:847–877
- De Visser SN, Freymann BP, Schnyder H (2008) Trophic interactions among invertebrates in termitaria in the African savanna: a stable isotope approach. *Ecol Entomol* 33:758–764
- Dial KP, Vaughan TA (1987) Opportunistic predation on alate termites in Kenya. *Biotropica* 19:185–187
- Donovan SE (2002) A morphological study of the enteric valves of the Afrotropical Apicotermitinae (Isoptera: Termitidae). *J Nat Hist* 36:1823–1840
- Donovan SE, Eggleton P, Bignell DE (2001) Gut content analysis and a new feeding group classification of termites. *Ecol Entomol* 26:356–366
- Donovan SE, Jones DT, Sands WA, Eggleton P (2000) The morphological phylogenetics of termites (Isoptera). *Biol J Linn Soc* 70:467–513
- Eggleton P, Beccaloni G, Inward D (2007) Save Isoptera: a comment on Inward et al. – response to Lo et al. *Biol Lett* 3:564–565
- Eggleton P, Bignell DE, Sands WA, et al (1996) The diversity, abundance and biomass of termites under differing levels of disturbance in the Mbalmayo Forest Reserve, southern Cameroon. *Philos Trans R Soc Lond B Biol Sci* 351:51–68
- Emerson AE (1965) A review of the Mastotermitidae (Isoptera), including a new fossil genus from Brazil. *Am Mus Novit* 2236:1–46
- Engel MS, Grimaldi DA, Krishna K (2009) Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. *Am Mus Novit* 3650:1–27
- Higashi M, Abe T, Burns TP (1992) Carbon-nitrogen balance and termite ecology. *Proc R Soc Lond B Biol Sci* 249:303–308
- Holldobler B, Wilson EO (2009) *The superorganism: the beauty, elegance, and strangeness of insect societies*. W. W. Norton, New York, NY and London, 522 pp
- Holmgren N (1909) Termitenstudien I. Anatomische Untersuchungen. *Klg Svenska Vetenskapsakad Handl* 44:1–215
- Holt JA, Lepage M (2000) Termites and soil properties. In: Abe T, Bignell DE, Higashi M (eds) *Termites: evolution, sociality, symbioses, ecology*. Kluwer Academic Publisher, Dordrecht, pp 389–407
- Hyodo F, Tayasu L, Konaté S, et al (2008) Gradual enrichment of <sup>15</sup>N with humification in a below-ground food web: relationship between <sup>15</sup>N and diet age determined using <sup>14</sup>C. *Funct Ecol* 22:516–522
- Inward D, Beccaloni G, Eggleton P (2007a) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biol Lett* 3:331–335
- Inward DJG, Vogler P, Eggleton P (2007b) A comprehensive phylogenetic analysis of termites (Isoptera) illuminates key aspects of their evolutionary biology. *Mol Phylogenet Evol* 44: 953–967
- Jaffe K, Ramos C, Issa S (1995) Trophic interactions between ants and termites that share common cests. *Ann Entomol Soc Am* 88:328–333



- Jeschke JM, Tollrian R (2007) Prey swarming: which predators become confused and why? *Anim Behav* 74:387–393
- Ji R, Brune A (2005) Digestion of peptidic residues in humic substances by an alkali-stable and humic-acid tolerant proteolytic activity in the gut of soil-feeding termites. *Soil Biol Biochem* 37:1648–1655
- Ji R, Brune A (2006) Nitrogen mineralization, ammonia accumulation, and emission of gaseous NH<sub>3</sub> by soil-feeding termites. *Biogeochemistry* 78:267–283
- Kambhampati S, Eggleton P (2000) Taxonomy and phylogeny of termites. In: Abe T, Bignell DE, Higashi M (eds) *Termites: evolution, sociality, symbioses, ecology*. Kluwer Academic Publishers, Dordrecht, pp 1–23
- Koepfli KP, Jenks SM, Eizirik E, et al (2006) Molecular systematics of the Hyaenidae: relationships of a relictual lineage resolved by a molecular supermatrix. *Mol Phylogenet Evol* 38:603–620
- Korb J (2003) Thermoregulation and ventilation of termite mounds. *Naturwissenschaften* 90: 212–219
- Korb J (2008) Termites, hemimetabolous diploid white ants? *Front Zool* 5:15
- Korb J, Linsenmair KE (2000) Ventilation of termite mounds: new results require a new model. *Behav Ecol* 11:486–494
- Leal IR, Oliveira PS (1995) Behavioral ecology of the neotropical termite hunting ant *Pachycondyla* (= *Termitopone*) *marginata* – colony founding, group-raiding and migratory patterns. *Behav Ecol Sociobiol* 37:373–383
- Legendre F, Whiting MF, Bordereau C, et al (2008) The phylogeny of termites (Dictyoptera: Isoptera) based on mitochondrial and nuclear markers: implications for the evolution of the worker and pseudergate castes, and foraging behaviors. *Mol Phylogenet Evol* 48:615–627
- Lo N, Engel MS, Cameron S, et al (2007) Save Isoptera: a comment on Inward et al. *Biol Lett* 3:562–563
- Longrich NR, Currie PJ (2009) *Albertonykus borealis*, a new alvarezsaur (Dinosauria: Theropoda) from the Early Mastrichtian of Alberta, Canada: implications for the systematics and ecology of the Alvarezsauridae. *Cretaceous Res* 30:239–252
- Luo ZX, Wible JR (2005) A late Jurassic digging mammal and early mammalian diversification. *Science* 308:103–107
- Luscher M (1951) Air-conditioned nests. *Sci Am* 205:138–145
- Martius C, Bandeira AG, da Silva Medeiros LG (1996) Variation in termite alate swarming in rain forests of central Amazonia. *Ecotropica* 2:1–11
- Matsuura K (2002) Colony-level stabilization of soldier head width for head-plug defense in the termite *Reticulitermes speratus* (Isoptera: Rhinotermitidae). *Behav Ecol Sociobiol* 51:172–179
- Mitchell JD (2007) Swarming and pairing in the fungus-growing termite, *Macrotermes natalensis* (Haviland) (Isoptera: Macrotermitinae). *Afr Entomol* 15:153–160
- Miura T, Matsumoto T (1998) Foraging organization of the open-air processional lichen-feeding termite *Hospitalitermes* (Isoptera, termitidae) in Borneo. *Insectes Soc* 45:17–32
- Morrow EH (2004) How the sperm lost its tail: the evolution of aflagellate sperm. *Biol Rev* 79: 795–814
- Nalepa CA, Lenz M (2000) The ootheca of *Mastotermes darwiniensis* Froggatt (Isoptera: Mastotermitidae): homology with cockroach oothecae. *Proc R Soc Lond B Biol Sci* 267: 1809–1813
- Noirot C (2001) The gut of termites (Isoptera). Comparative anatomy, systematics, phylogeny. II. Higher termites (Termitidae). *Ann Soc Entomol Fr* 37:431–471
- Noirot C, Pasteels JM (1987) Ontogenetic development and evolution of the worker caste in termites. *Experientia* 43:851–860
- Ohkuma M (2003) Termite symbiotic systems: efficient biorecycling of lignocellulose. *Appl Microbiol Biotechnol* 61:1–9
- Perna A, Jost C, Couturier E (2008) The structure of gallery networks in the nests of termite *Cubitermes* spp. revealed by X-ray tomography. *Naturwissenschaften* 95:877–884
- Prestwich GD (1984) Defense-mechanisms of termites. *Annu Rev Entomol* 29:201–232

- Riparbelli MG, Callaini G, Mercati D, et al (2009) Centrioles to basal bodies in the spermiogenesis of *Mastotermes darwiniensis* (Insecta, Isoptera). *Cell Motil Cytoskeleton* 66:248–259
- Roisin Y (2001) Caste sex ratios, sex linkage, and reproductive strategies in termites. *Insectes Soc* 48:224–230
- Roux EA, Roux M, Korb J (2009) Selection on defensive traits in a sterile caste – caste evolution: a mechanism to overcome life-history trade-offs? *Evol Dev* 11:80–87
- Ruggiero RG, Fay FM (1994) Utilization of termitarium soils by elephants and its ecological implications. *Afri J Ecol* 32:222–232
- Sands WA (1982) Agonistic behavior of African soldierless Apicotermitinae (Isoptera, Termitidae). *Sociobiology* 7:61–72
- Sands WA (1998) The identification of worker castes of termite genera from soil of African and the Middle East. CAB International, Wallingford, CT
- Santos CA, Costa-Leonard AM (2006) Anatomy of the frontal gland and ultramorphology of the frontal tube in the soldier caste of species of Nasutitermitinae (Isoptera, Termitidae). *Microsc Res Tech* 69:913–918
- Scholtz OI, Macleod N, Eggleton P (2008) Termite soldier defence strategies: a reassessment of Prestwich's classification and an examination of the evolution of defence morphology using extended eigenshape analyses of head morphology. *Zool J Linn Soc Lond* 153:631–650
- Suzuki S, Kuroda S, Nishihara T (1995) Tool-set for termite-fishing by chimpanzees in the Ndoki Forest, Congo. *Behaviour* 132:219–235
- Thorne BL, Breisch NL, Muscedere ML (2003) Evolution of eusociality and the soldier caste in termites: influence of intraspecific competition and accelerated inheritance. *Proc Natl Acad Sci U S A* 100:12808–12813
- Turner JS, Soar RM (2008) Beyond biomimicry. What termites can tell us about realizing the living building. *Proceedings of the First International Conference on Industrialized, Intelligent Construction (I3CON)* 1: 1–18
- Ware JL, Litman J, Klass KD, Spearman LA (2008) Relationships among the major lineages of Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. *Syst Entomol* 33:429–450
- Weesner F (1965) The termites of the United States. The National Pest Control Association, Elizabeth, NJ, 70 pp
- Weesner F (1970) External anatomy. In: Krishna K, Weesner F (eds) *Biology of termites*, vol I. Academic Press, New York, NY, pp 1–23
- Wilson EO (1992) The effects of complex social-life on evolution and biodiversity. *Oikos* 63:13–18
- Yarnell RW, Metcalfe DJ, Dunstone N, et al (2008) The impact of fire on habitat use by the short-snouted elephant shrew (*Elephantulus brachyrhynchus*) in North West Province, South Africa. *Afr Zool* 43:45–52