Biology of Termites: A Modern Synthesis

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Editors

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Foreword by Bernard J. Crespi

Springer

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Cover illustration: imagoes, soldiers, workers and larvae of *Syntermes territus* Emerson. Photo: Yves Roisin

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While preparing the final proofs of this volume, we learned with great sadness of the death of Professor Charles Noirot on 23 September 2010, at the age of 88. Noirot was the greatest termite biologist of his generation and arguably the greatest of any generation, past or present. No part of the field escaped his influence, not least since his publications at one time or another covered every conceivable facet of the subject, though most notably that of post-embryonic development and its regulation (Pasteels 2001), but principally because he refined the lexicon and set standards for the observation, documentation and analysis of termite societies and associations which we all follow today. Our world of termitology is the less for his passing, but hugely the greater for his life and work. We dedicate this book to his memory.

London, UK — David Bignell
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Foreword

A greater and longer childhood: the comparative biology of termites.

When I was a young graduate student, Richard Alexander instilled in me the importance of cutting one's teeth on a taxonomic group – be it crickets, thrips, poison-dart frogs, barnacles or prairie dogs – and letting the deep, unresolved biological questions well up from the vast diversity within even the most humble clade. Especially among insects, a fascination emerges from systematic-through-genomic familiarity, and even a love of small, idiosyncratic creatures can develop as they lead us through convoluted pathways and tunnels of discovery.

Social insects hold a special place in the pantheons of biophilia, given the close parallels of their lives with ours. Who among us does not admit the abiding centrality of family life – the mutualistic peace entwined with strife and conflicts, first when we are children and later with bairns of our own? Of all social insects, termites may fit most closely with the human condition, as parents, alloparents, builders, soldiers, and biochemical-genomic engineers, ensconced in extended nuclear families that expand and heroically defend their homes. But perhaps most of all, as children.

Benjamin Franklin penned the phrase, "our whole life is but a greater and longer childhood", referring to ourselves, but equally applicable to termite evolution since the first cockroach helped its mother and father rear a younger sibling. A greatly-extended childhood has indeed been seen as key to modern human evolution (Hrdy 2009; Konner 2010), and it was certainly crucial to unlocking the potential of termites to dominate the globe. For both humans and isopterans, early development in a relatively-safe, nourishing niche potentiated such a heterochronic yet plastic shift, and led ultimately to a broad swath of ecological, morphological and behavioral specializations, as well as expansion of family conflicts and confluences of interest beyond those of almost all other creatures.

This book draws the vast diversity of termite adaptations together in the framework of a range of greater unresolved biological questions, from genetics through ecology and social behavior to macroevolution, that termites, as such-special insects, can help us answer. As such, the book brings into sharp focus the tremendous usefulness of termites as research systems, and the close interplay between systematics, evolutionary biology, ecology, and other, more-proximate and mechanistic disciplines. Each chapter celebrates in rigorous up to date detail, some vital facet of termite biology: their taxonomy, phylogeny, genetics, symbioses, physiology, morphology, pheromones, ecology, behavior, and status as pests, all linked by the unique characteristics, and the extended or lifelong childhoods, that define the group. As such, this book is indispensible to any serious student of Isoptera, as a source of facts, ideas, and syntheses upon which to build our future understanding. Indeed, the advances in termite biology since the last comprehensive compendium in 2000 are spectacular – from endogenous cellulases, facultatively-asexual queens, to establishment of firm links between ecology, life history and social structure that permit robust comparisons with other taxa.

And with humans, of course. The origin and form of human childhood can be seen as an evolutionary battleground of parent versus beloved-offspring strategies and countering moves: children selected to delay the age of puberty and accrue marginally-more investment, mothers selected to shorten age at weaning, reduce inter-birth intervals, and become more queen-like than any other primate (Haig 2010). Among termites, analysing evolutionary trajectories of life-history timing and inter-family interactions awaits fine-scale, dovetailed phylogenetic and behavioral-ecological studies, that are likely to further astonish and please human termitophiles – in part due to their implications for all areas of isopteran biology. This book provides the scaffold for building, conceptually and empirically, across all such disciplines and questions.

For many students of termites, the book comes at a special time, after we have lost intellectual parents of social-insect biology, Ross Crozier and William Hamilton, and must ourselves build on their ideas. *Biology of Termites: a Modern Synthesis* should serve as inspiration and foundation for new discoveries that would make them proud – and fascinated by the ongoing complexities of children and social life under soil and bark.

Vancouver, Canada Bernard J. Crespi

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Preface

The initiative for this new volume was made in 2007 by Springer and came a few years after their merger (in 2003) with the Kluwer organisation, which had published the successful preceding compilation *Termites: evolution, sociality, symbioses, ecology* (Abe T, Bignell DE, Higashi M (eds) (2000) Kluwer Academic Publishers, Dordrecht, 466p). The Kluwer book had been the first attempt to draw together the many different threads of academic termite science since the three monumental volumes of P-P Grassé's *Termitologia* (Masson, Paris, 1983, 1984, 1985), and the first academic research compendium in English since the two classic volumes of *Biology of Termites* edited by Krishna K and Weesner FM (Academic Press, New York, NY, 1969, 1970).

The purposes of the present book are (1) to provide extended coverage to areas of termite science which have advanced spectacularly since 2000, these being largely fields in which extensive molecular data have now become available (phylogeny and biogeography, immune defence, population genetics, caste determination, digestive biochemistry and intestinal microbiology) (2) to reflect new concepts of eusociality in termites and to present the emerging views of social evolution within the Isoptera, now that this group has been confirmed as a monophyletic lineage (3) to provide points of comparison with ants and some other social Hymenoptera, on social organisation and co-evolution with symbionts (4) to provide consolidating reviews in selected areas where the literature has continued to grow (cladistic taxonomy, mound architecture and function, intestinal morphology and function, community ecology and pest status for wood in service) and (5) to present reviews that were notably absent from the 2000 Kluwer book (chemical ecology and termites as pests of agriculture). Our expectation is that the new book will be regarded as the standard reference work for about a decade, and will help termites to be seen as good models for fundamental research in developmental biology, microbial ecology and social evolution, as well as major players in the ecology of the biosphere, with impact in many areas of the human economy.

We made a deliberate decision not to commission updates in certain areas that were covered in 2000. These were palaeontology, foraging, intracellular symbiosis, symbiosis with protists (sensu stricto), energy metabolism, population ecology, termites and soils, and greenhouse gas production. In some cases these topics are now subsumed under other headings, so that new material will still be reported, and in other cases our feeling is that the existing literature (including reviews published elsewhere in the last 10 years) is sufficient. We remind readers that termite biology still rests on the large body of older descriptive material of an essentially timeless nature (for example covering morphology, anatomy, behaviour, nest architecture and economic damages) and that in these respects the volumes by Krishna and Weesner and by Grassé are in no sense outdated. As before, we debated whether applied termite biology (termite control) should have a place in an academic book: the outcome is two pleasingly complementary chapters (18 and 19) dealing, respectively, with termites in agriculture and with invasive species which defy the high endemicity otherwise shown by isopterans. Both chapters explore contemporary concepts and contain extensive bibliographies.

Although we have now passed the 10th anniversary of their untimely deaths, we still need to acknowledge that the main modern initiative to draw leading termite biologists together to identify the major advances and issues in the field was that of Takuya Abe and Masahiko Higashi, so in that sense the new book is still very much their legacy. We can also acknowledge the influence of the late Ross Crozier in advancing the science of social insect genetics, the fruit of which is much in evidence in this volume. In commissioning authors for the book, the editors have tried to balance contributions between the major countries where termite research is supported and carried out: thus the UK, USA, France, Germany, Belgium, The Netherlands, Portugal, Japan and Australia are all represented. Authors from developing countries where termites are important organisms are still missing, but this absence will surely not persist for another decade. A taxonomic index, with authorities and information on synonymy, will be published separately at a future date.

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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 "superorganism"). 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 wellbeing 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

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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 Apicotermitinae. 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): Macrotermitinae, Sphaerotermitinae, Foraminitermitinae, Apicotermitinae, Syntermitinae, Termitinae, and Nasutitermitinae. 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 termites species have one or the other, however, and so all termite species are eusocial, because they have atleast 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*[1]) 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)

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[1] 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

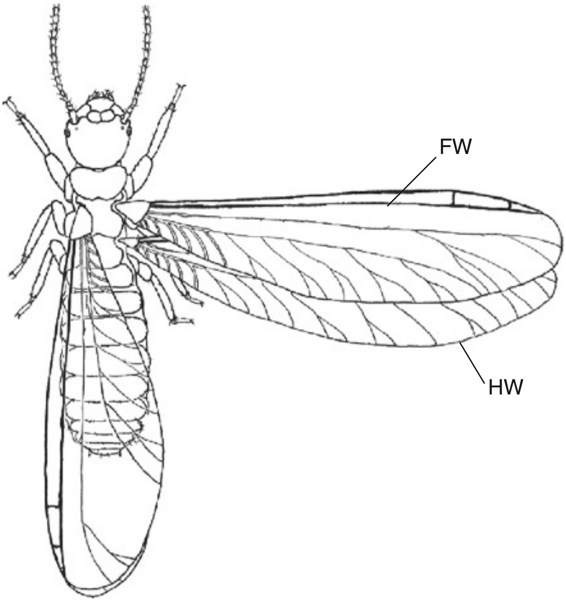

Fig. 1.1 Alate structure (illustrated by *Tenuirostritermes*), FW = forewing, HW = hindwing from Weesner (1970)

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
Postclypeus	Undivided	Undivided	Undivided	Undivided	Divided, keeled	Divided
Fontanelle	Absent	Absent	Absent	Absent	Present	Present
Pronotum	Flat	Flat	Flat	Flat	Flat	Saddle-shaped
Wing venation	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
Wing scale	F>>H	F>>H	F>>H	F>>H	F>>H[a]	F~H
Tarsal segments	5	5/4	5/4	4	4/3	4/3
Malpighian tubules	12–15	8	8	8	8	4 (2)[b]
Flagellates present in gut	Yes	Yes	Yes	Yes	Yes	No
Feeding groups	I	I	I	I	I	II, III, IV
Workers	Yes[c]	No	Yes	No	Yes[d]	Yes

[a] F ~ H in *Psammotermes*.

[b] Two Malpighian tubules in *Labiotermes*.

[c] Development pathway simpler than in other groups.

[d] No true workers in *Glossotermes* and *Prorhinotermes*.

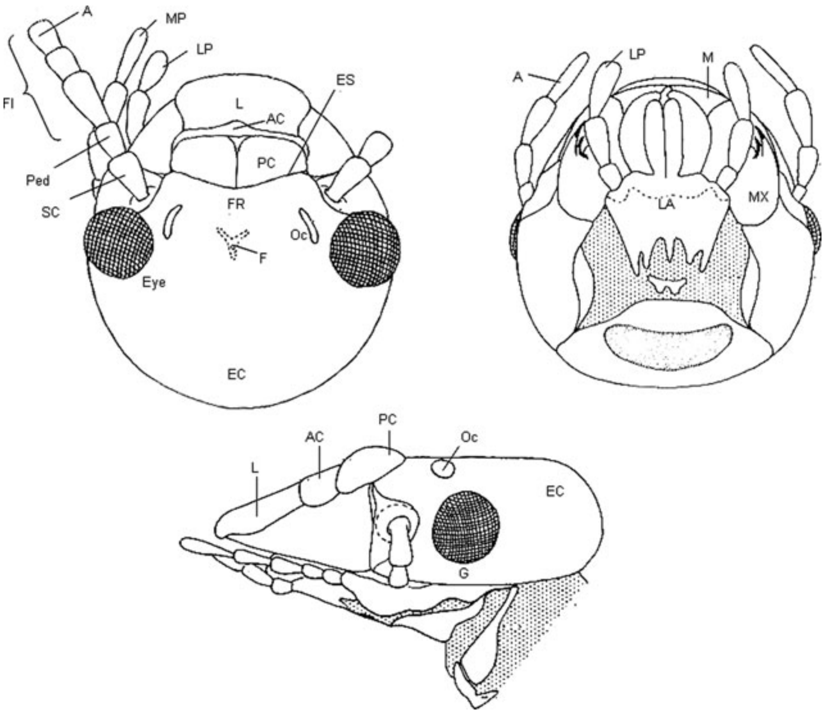

Fig. 1.2 Head of *Tenuirostritermes* (labels incomplete), from Weesner (1970). Head structures: A, antenna; SC, scape; Ped, pedicel; Fl, flagellun; MP, maxillary palps; LP, labial palps; AC, anteclypeus; PC, postclypeus; ES, epistomal suture; FR, frons; Oc, ocellus; EP, epicranium; M, mandible; MX, maxilla;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

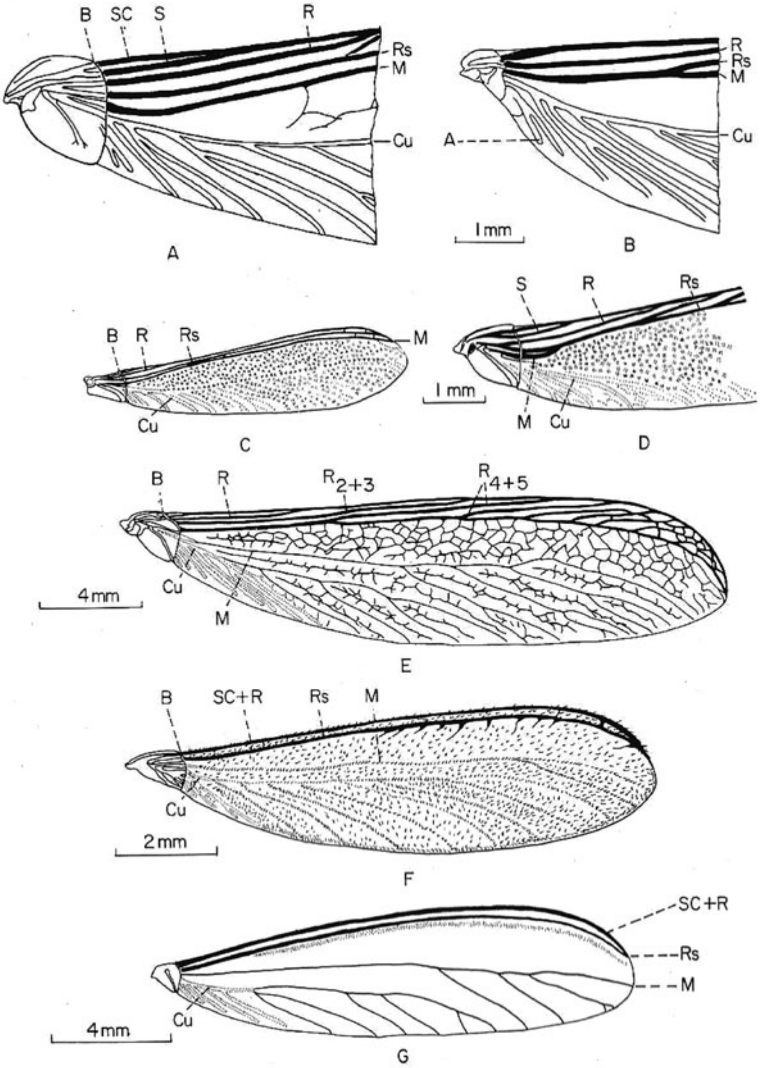

Fig. 1.3 Wing structure in different groups of termites. Wing venation. **a** Forewing of *Neotermes malatensis*; **b** hind wing of same; **c** forewing of *Glyptotermes chapmani*; **d** forewing of *Rugitermes athertoni*; **e** forewing of *Zootermopsis angusti*collis; **f** forewing of *Coptotermes 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 phylogentically 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 temite, 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

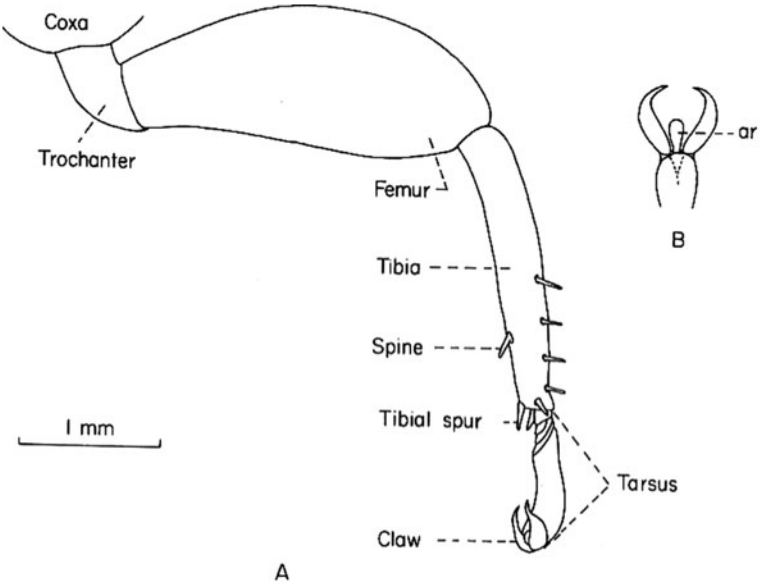

Fig. 1.4 Leg structure in *Zootermopsis angusticollis*, from Weesner (1970)

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 polar plate is convex in the left mandible and concave in the right mandible and both mandibles have no ridges. These two structures act

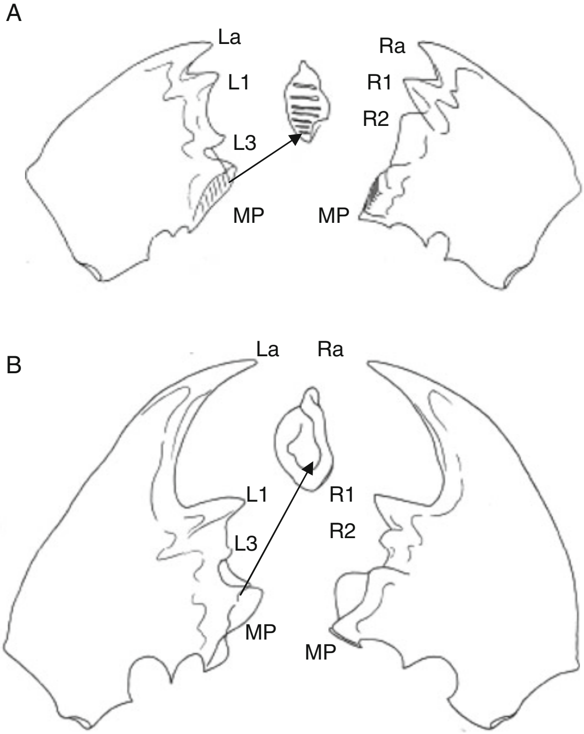

Fig. 1.5 Worker mandibles of **a** *Microcerotermes strunckii* and **b** *Megagnathotermes notandus*. La, L1, L3, left marginal teeth; Ra, R1, R2, right marginal teeth; MP, Molar plate, from Sands (1998)

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 detrivore 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 *procotodeal 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 detrivore-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

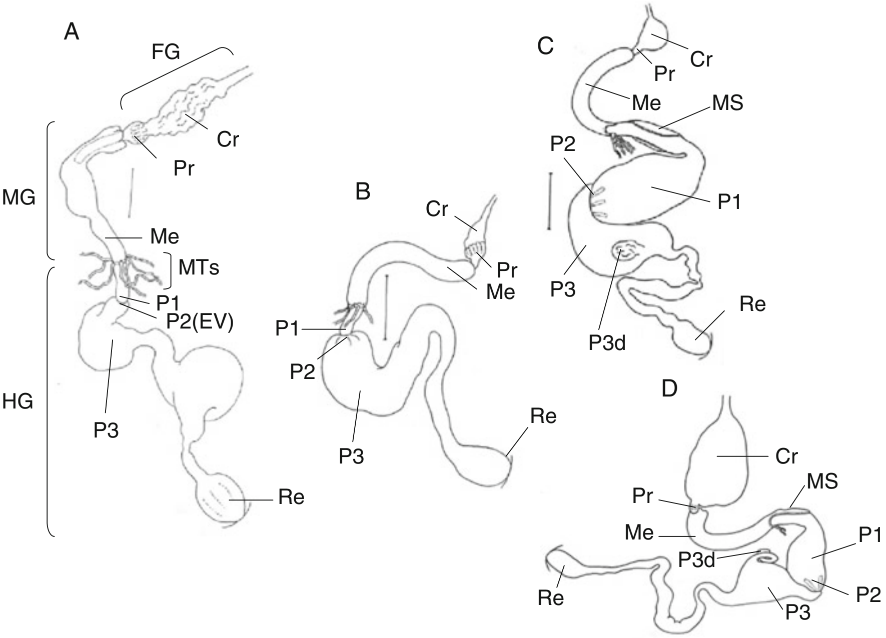

Fig. 1.6 Gut figures from Sands (1998), showing the variable elaborations of the hindgut, unravelled for illustration. Cr, crop; EV, enteric valve; FG, foregut; HG, hindgut; MG, midgut; Me, mesenteron; MS, mixed segment; MTs, Malpighian tubules; P1, P2, P3, proctodaeal segments; P3d, diverticulum; Re, 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 familes, 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).

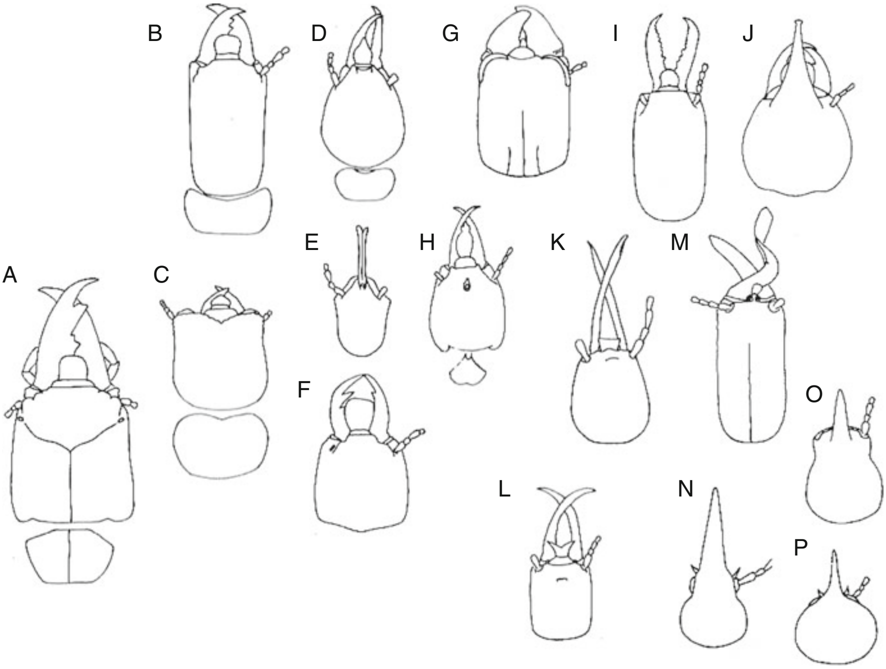

Fig. 1.7 Plan view of soldier head capsules. **a**, *Archotermopsis wroughtoni*; **b**, *Rugitermes bicolor*; **c**, *Cryptotermes verruculosus*; **d**, *Coptotermes sjostedti*; **e**, *Rhinotermes hispidus* (minor soldier); **f**, *Rhinotermes hispidus* (major soldier); **g**, *Jugositermes tuberculatus*; **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)