White-gutted soldiers: simplification of the digestive tube for a non-particulate diet in higher Old World termites (Isoptera: Termitidae)

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Abstract Previous observations have noted that in some species of higher termites the soldier caste lacks pigmented particles in its gut and, instead, is fed worker saliva that imparts a whitish coloration to the abdomen. In order to investigate the occurrence of this trait more thoroughly, we surveyed a broad diversity of termite specimens and taxonomic descriptions from the Old World subfamilies Apicotermitinae, Cubitermitinae, Foraminitermitinae, Macrotermitinae, and Termitinae. We identified 38 genera that have this “white-gutted” soldier (WGS) trait. No termite soldiers from the New World were found to possess a WGS caste. Externally, the WGS is characterized by a uniformly pale abdomen, hyaline gut, and proportionally smaller body-to-head volume ratio compared with their “dark-gutted” soldier (DGS) counterparts found in most termitid genera. The WGS is a fully formed soldier that, unlike soldiers in other higher termite taxa, has a small, narrow, and decompartmentalized digestive tube that lacks particulate food contents. The presumed saliva-nourished WGS have various forms of simplified gut morphologies that have evolved at least six times within the higher termites.

Keywords Apicotermitinae · Cubitermitinae · Foraminitermitinae · Macrotermitinae · Termitinae · Enteric valve armature · Proctodeum

Introduction

Trophallaxis is the mouth-to-mouth (stomodeal) or anus-to-mouth (proctodeal) exchange of alimentary contents between members of a social insect colony (Wilson 1971). Termite soldiers lack chewing mandibles and must obtain their food as liquids or pastes offered by nestmate workers (Grasse 1949). In the lower wood-feeding termites (e.g., Kalotermitidae and Rhinotermitidae), soldiers are fed with worker gut contents which consist of mixtures of masticated wood particles and saliva (Grasse 1982; Noirot 1969). The diets of most higher termites (Termitidae) are much more varied (Donovan et al. 2001), and soldiers are nourished by stomodeal trophallaxis with particles of worker-masticated wood, leaf litter, soil, fungus, bacteria, herbaceous plants, lichens, algae, or some derivation of these (e.g., sound vs. severely decayed wood). Workers of soil-feeding termites, which constitute the majority of termitid genera, ingest masticated mixtures of humus, roots, mycelia, lignified...
tissue, silica grains, etc. (Sleaford et al. 1996; Donovan et al. 2001; Donovan 2002) which are transferred to their soldiers. These particulate suspensions impart a contrasting darker coloration to the gut tubes of both mature workers and soldiers, which are visible through their opaque or nearly transparent integument.

Grassé (1949) reported that in some higher termites (probably mostly in soil-feeding taxa), the diet of soldiers may consist wholly of the worker’s saliva in its clear or opalescent form. Noirot (1955) observed that soldiers of Procubitermes curvatus Silvestri (Cubitermitinae) have an exclusively liquid diet and their digestive tube, contrary to that of their workers, lacks particulate food content. Noirot (1955) further noted that soldiers of Pericapritermes ursgens Silvestri (Termitinae) also have an exclusively liquid diet which imparts a whitish-yellowish color to their abdomens. Noirot and Noirot-Timothée (1969) reported that soldiers of Basidentitermes, Fastigitermes, Orthotermes, Proboscitermes, Procubitermes, and Promirotermes also have a strict liquid (saliary) diet but did not mention their abdominal coloration. Finally, in her key of southern African termitine genera, Uys (2002) used abdominal coloration, an artifact of a salivary diet, in her first couplet (“creamy yellow to creamy white” for the African genera Angulitermes, Basidentitermes, Lepidotermes, Noditermes, Pericapritermes, Promirotermes, Unguitermes, and Unicornitermes; and “greyish-black” for Amitermes, Batillitermes, Crenetermes, Cubitermes, Euchilitermes, Microcerotermes, Okavangotermes, Ovambotermes, and Termes).

Despite its importance, the morphological and phylogenetic underpinnings of this bipartite soldier condition have received little or no additional attention. This led us to examine soldiers from an extensive collection of termites worldwide and to interpret soldier description literature. We show that Old World termitid soldiers can be sorted into two groups: the “white-gutted” soldier group (WGS) and the more common “dark-gutted” soldier group (DGS). Herein, we identify WGS genera, compare the external and internal morphology of WGS and DGS from selected genera of higher termites, and present information from the literature that we use to reconstruct the ancestral state of soldier gut type from a recently published termite phylogenetic tree.

Materials and methods

Photos of whole or partial termite bodies were taken as multi-layer montages using a Leica M205C stereomicroscope controlled by Leica Application Suite version 3 software. Preserved specimens were taken from 85% ethanol and suspended in a pool of Purell® Hand Sanitizer (70% ethanol) to position the specimens within a clear plastic Petri dish. Enteric valve armature (EVA) images were taken from slide mounts using a Leica CTR 5500 compound microscope with differential interference contrast optics and the same montage software. All photographed specimens and those listed in Table S1 (electronic supplementary material) are housed in the University of Florida Termite Collection in Davie, Florida, which contains 42,595 colony samples of 229 described and new genera. African termite specimens were collected in the field for primate nutrition and/or termite diversity studies between 1989 and 2016. Terminology of the worker gut follows that of Sands (1998) and Noirot (2001). We used one phylogenetic tree of Termitidae recently published by Bourguignon et al. (2017) to reconstruct the ancestral state of the soldier gut. We pruned the tree so that one representative of each genus for which we know the type of soldier gut remains. The tree was a Bayesian phylogenetic chronogram inferred from full mitochondrial genomes with third codon position excluded. Two states were considered, WGS and DGS. We used the function “ace” of the package phytools (Revell 2012) implemented in R version 3.2.0. The model implemented by ace was a maximum likelihood model with equal rate of transition between states.

Results

Our examination of termite specimens (Table S1), and the descriptive wording of taxa we lacked revealed that at least 38 Old World genera have the WGS morph (Table 1). All are soil/humus feeding species (non-flocculent and silica particles abundant in worker gut) with the exception of the plant-feeding Angulitermes (Debelo and Degaga 2014), Eremotermes (Akhtar and Sarwar 2003), Forficulitermes (Scheffrahn and Krček 2015), Promirotermes (Davies et al. 2015), Synhamitermes (Shanbhag and Sundararaj 2012), and the fungus feeding Acanthotermes, Pseudacanthotermes, and Synacanthotermes, that have abundant flocculent contents in the worker gut but lack silica particles. These eight genera all lack soldiers with asymmetrical snapping mandibles (Table 1). The WGS morph is recognizable externally by its uniformly pale abdomen and proportionally smaller body-to-head volume ratio (Figs. S1, S2) compared with the darker abdomens and larger body-to-head proportions of the DGS taxa (Fig. S3). Unlike Noirot’s 1969 “white soldier” or the equivalent term “presoldier” (Noirot and Pasteels 1987) which describe the stage before the final soldier molt (Fig. 1b inset), the WGS are fully developed and possess functional mandibles.

Internally, the digestive tubes of WGS are variously simplified, shortened, narrowed, and/or decompartmentalized, and lack particulate food contents (Figs. 1, 2, S4) present in the workers of their species (Figs. 1b, f, 2c) or in
| Genus               | Subfamily                   | Region* no. species | Mandible                  | Coloration                     | References                      |
|---------------------|-----------------------------|--------------------|---------------------------|--------------------------------|---------------------------------|
| Acanthotermes       | Macrotermitinae             | Eth, 1             | Piercing, cutting         | White                           | Current paper                   |
| Angulitermes        | Termitinae                  | Eth, Ore, Pale, 29 | Symmetrical snap          | Creamy white                    | Uys (2002), Harris (1964)       |
| Basidentitermes     | Cubitermitinae              | Eth, 8             | Piercing, cutting         | White                           | Current paper                   |
| Capritermes         | Termitinae                  | Eth, 1             | Asymmetrical snap         | White                           | Current paper                   |
| Dicuspiditermes     | Termitinae                  | Ore, 20            | Asymmetrical snap         | Yellowish white                 | Akhtar (1975)                   |
| Eremotermes         | Termitinae                  | Eth, Ore, Pale, 10 | Piercing, cutting         | Whitish                         | Chhotani (1997)                 |
| Eburnitermes        | Apicotermitinae             | Ore, 1             | Piercing, cutting         | Whitish                         | Chhotani (1966)                 |
| Euhamitermes        | Apicotermitinae             | Ore, 24            | Crushing                  | Body lighter than head          | Chhotani (1975)                 |
| Eurytermes          | Apicotermitinae             | Ore, 6             | Crushing                  | Whitish                         | Chhotani (1997)                 |
| Fastigitermes       | Cubitermitinae              | Eth, 1             | Piercing, cutting         | White                           | Current paper                   |
| Forficulitermes     | Termitinae                  | Eth, 1             | Piercing, cutting         | Abdomen paler than head         | Emerson (1960), Scheffrahn and Křeček (2015) |
| Homalotermes        | Termitinae                  | Ore, 4             | Asymmetrical snap         | Whitish                         | Chhotani (1997)                 |
| Indocapritermes     | Termitinae                  | Ore, 1             | Asymmetrical snap         | Whitish                         | Chhotani (1997)                 |
| Indotermes          | Apicotermitinae             | Ore, 10            | Piercing, cutting         | White                           | Current paper                   |
| Krishnacapritermes  | Termitinae                  | Ore, 2             | Asymmetrical snap         | Whitish                         | Chhotani (1997)                 |
| Labiocapritermes    | Termitinae                  | Ore, 1             | Asymmetrical snap         | Whitish                         | Chhotani (1997)                 |
| Labritermes         | Foraminitermitinae          | Ore, 3             | Piercing, cutting         | Yellowish white                 | Anonymous                      |
| Lepidotermes        | Cubitermitinae              | Eth, 9             | Piercing, cutting         | White                           | Uys (2002)                      |
| Mirocapritermes     | Termitinae                  | Ore, 8             | Asymmetrical snap         | Yellowish white                 | Chhotani (1997)                 |
| Macrotermes         | Cubitermitinae              | Eth, 2             | Piercing, cutting         | Abdomen paler than pronotum     | Emerson (1960)                  |
| Noditermes          | Cubitermitinae              | Eth, 7             | Piercing, cutting         | White                           | Current paper                   |
| Orthotermes         | Cubitermitinae              | Eth, 2             | Piercing, cutting         | White                           | Current paper                   |
| Pericapritermes     | Termitinae                  | Eth, Ore, Pale, 40 | Asymmetrical snap         | White                           | Current paper                   |
| Piloterms           | Cubitermitinae              | Eth, 1             | Piercing, cutting         | Abdomen whitish                 | Emerson (1960)                  |
| Probosciters        | Cubitermitinae              | Eth, 2             | Piercing, cutting         | Hyaline                         | Scheffrahn and O’Malley (2010)  |
| Procapritermes      | Termitinae                  | Ore, 13            | Asymmetrical snap         | Pale yellow                      | Thapa (1982)                    |
| Procuubitermes      | Cubitermitinae              | Eth, 9             | Piercing, cutting         | White                           | Current paper                   |
| Profastigitermes    | Cubitermitinae              | Eth, 1             | Piercing, cutting         | Abdomen paler than pronotum     | Emerson (1960)                  |
| Promiroters         | Termitinae                  | Eth, 10            | Symmetrical snap          | White                           | Current paper                   |
| Pseudacanthoterms   | Macrotermiteinae            | Eth, 6             | Piercing, cutting         | White                             | Current paper                   |
| Pseudocapritermes   | Termitinae                  | Ore, 2             | Piercing, cutting         | Creamy white                     | Chhotani (1997)                 |
| Quasitermes         | Termitinae                  | Eth, 1             | Asymmetrical snap         | Pale                             | Katie Cribbs                    |
| Sinocapritermes     | Termitinae                  | Ore, 16            | Asymmetrical snap         | Abdomen without soil content    | Chiu et al. (2015)              |
| Speculitermes       | Apicotermitinae             | Ore, 12            | Crushing                  | White                            | Chhotani (1997)                 |
soldiers and workers of DGS species (Figs. 3, S3). Several gut morphologies are represented in the WGS group. In Basidentitermes, the WGS gut segments form a very long tube with an enlarged crop (C) and rectum (P5) at either end (Fig. 1c). The midgut (mesenteron, M, and mixed segment, MS), can barely be differentiated because they differ from

Table 1 continued

| Genus             | Subfamily     | Region¹, no. species | Mandible          | Coloration        | References          |
|-------------------|---------------|----------------------|-------------------|-------------------|---------------------|
| Synacanthotermes  | Macrotermitinae| Eth, 3               | Piercing, cutting | White             | Current paper       |
| Synhamitermes     | Termitinae    | Ore, 4               | Piercing, cutting | Yellow white      | Chhotani (1997)     |
| Unguitermes       | Cubitermitinae| Eth, 7               | Piercing, cutting | Creamy white      | Uys (2002)          |
| Unicornitermes    | Cubitermitinae| Eth, 1               | Piercing, cutting | Creamy white      | Uys (2002)          |

¹ Eth Ethiopian, Ore oriental, Pale palarctic, Pap papuan
² Underlying dark cuticle
³ http://termitesandants.blogspot.com/2012/05/labritermes.html

Fig. 1  a White-gutted soldier (WGS) of Basidentitermes n. sp.; b B. malelaensis Emerson live habitus of soldiers, workers, and queen (inset presoldier (PS) and nestmates of B. n. sp.; c uncoiled gut of B. n. sp. WGS; d enteric valve armature (EVA) of B. n. sp. worker; e EVA of B. malelaensis worker; and f lateral view of B. malelaensis worker with abdominal integument removed (triangle marks location of EVA). C crop (includes gizzard), M mesenteron, MS mixed segment, P1–P5 first through fifth proctodeal segments
each other only slightly in shape and diameter. The proctodeal segments P1–P4 of the Basidentitermes WGS show no discernable junctures and the EVA is absent. In the Promirotermes WGS (Fig. S4a), the crop, mesenteron, mixed segment, and rectum are all well developed but the proctodeal segments P1–P4 form a long and serpentine tube without clear sectional delineations. The EVA is absent in the Promirotermes WGS soldier. The Pericapritermes WGS (Fig. S4b) has a rather short gut tube and all segments are recognizable but it too lacks the EVA. Unlike the previous genera, the gut segments of the Procubitermes WGS are all recognizable and it has remnants of the enteric valve armature (Fig. 2a), albeit less developed than that of the LIL (Fig. 2b) or that of the fully sclerotized EVA of the fully formed worker (Fig. 2c). In comparison, the DGS taxa have more robust hindgut morphologies similar to their workers, and, akin to workers, the entire DGS alimentary tract contains grainy particulate matter (e.g., Cubitermes schererri Rosen, Fig. 3a, b). Additionally, the DGS soldier has a fully developed EVA similar to that of its worker and LIL (Fig. 3c–e).

Our phylogenetic tree includes 83 taxa belonging to 82 genera (Fig. 4). The ancestral state reconstruction shows, with strong support, that WGS evolved at least once in Cubitermitinae, twice in Termitinae, and once in Api- cotermitinae. We also included some members of the basal Termitidae subfamilies, i.e., Foraminitermitinae, Macrotermitinae, and Sphaerotermitinae and found that WGS also evolved in these subfamilies: once in the soil-feeding Labritermes (Foraminitermitinae), and at least twice in Macrotermiteinae.

Discussion

13 WGS genera of Apicotermitinae, Cubitermitinae, Macrotermiteinae, and Termitinae are included in both Table 1 and the phylogenetic tree we used to reconstruct the ancestral state of soldier gut. Our tree shows that WGS evolved from DGS at least four times in these lineages. Because our tree did not include all the species recorded with WGS, there is a possibility that WGS evolved independently in more lineages. One of them is Forficulitermes, a genus recently transferred from Cubitermitinae to Termitinae (Scheffrahn and Křeček 2015). The absence of WGS taxa in the New World is enigmatic given the common ancestry of both New and Old World Apicotermitinae and Termitinae (Bourguignon et al. 2017).

In Noirot’s 1966 description of Eburnitermes grassei (Apicotermitidae), he reports that soldiers of this species possess a “yellowish-white abdomen due to the fact that the digestive tract does not contain solid food”. Due to lack of material, we did not examine the gut contents of the E. grassei soldier; however, other apicotermitine genera with soldiers examined including Allognathotermes sp., Coxotermes boukokoensis Grassé and Noirot, Duplidentitermes sp., Heimititermes sp., Jugositermes tuberculatus Emerson, Phoxotermes cerberus Collins, and Rostrotermes cornutus Grassé all possess the DGS form and contain solid dark particulates in their guts.

For the Termitidae, salivary secretions from workers are the sole or primary nutrients for all immature stages (Grassé 1982; Noirot 1969). The immature stages, white in color, are generally found near reproductive centers of the nest for all termite feeding groups, including soil-feeders (Fig. S5a–d).
and wood-feeders (Fig. S5e, f). Casual observations of the guts of the last instar larvae (LIL, usually the second instar, Noirot 1969) and presoldier stages sampled from about 120 termitid genera, both Old and New World, show no traces of particulate content (Scheffrahn, pers. obs.).

Although trophallaxis and salivary secretions in the WGS have not been studied, some inference from the DGS group may be useful in understanding the diet common to all dependent castes in the Termitidae. For example, using radionuclide tracing, Alibert (1963) confirmed that larvae and presoldiers of *C. fungifaber* Sjöstedt received salivary secretions from workers, while mature soldiers and workers received regurgitated foregut contents. Studies of New World Termitidae show that worker salivary (labial) gland secretions contain complex aqueous admixtures of proteins and other non-volatile compounds (Sillam-Dussés et al. 2012) which nourish dependent castes. Of New World Termitidae show that worker salivary (labial) gland secretions contain complex aqueous admixtures of proteins and other non-volatile compounds (Sillam-Dussés et al. 2012) which nourish dependent castes. Billen et al. (1989) found that the worker salivary glands of *Macrotermes bellicosus* (Smeathman) are substantial and consist of three secretory cell types, while the soldier gland has only a single type that secretes a defense fluid (Prestwich 1979). However, upon reaching maturity, the DGS guts are filled with dark particulate matter from stomodeal trophallaxis (e.g., Figure 3a). Therefore, the worker-to-larval + presoldier trophallaxis in DGS and the worker-to-larval + presoldier + soldier trophallaxis in the WGS is a special form of nutrient sharing with food originating from the salivary gland (buccal trophallaxis?) and not from the foregut (stomodeal trophallaxis).

For the first time, this study introduces the external and internal morphology of the WGS underlying the observations of Noirot (1955, 1966), Noirot and Noirot-Timothée (1969), and Grassé (1949, 1982). Although we did not analyze the WGS worker saliva or guts, the matter found in WGS soldier crops (Fig. 2a inset) has the appearance of a secretory substance. Although obvious in both live and preserved material, the coloration of the WGS is omitted in taxonomic descriptions by some renowned taxonomists such as Emerson AE, Krishna K, and Sands WA. We suspect that their focus was on the complex external morphology of the soldier head capsule, and that the internal anatomy of soldiers had been supplanted by the greater interest in worker internal anatomy.

Compared with other insects, the digestive tube of higher termite workers is morphologically complex (Noirot 2001) and provides for multifaceted nutrient metabolism (Bignell 2010). Although the soldier gut in all taxa is largely overlooked, the similarity of the DGS to its workers (e.g., Fig. 3c, d) suggests similar structure and function. The relatively well-developed midgut (M + MS) in WGS (Figs. 1c, 2a, and S4) is similar to DGS and suggests that its proteolytic function (Ji and Brune 2005) is retained as might be expected from a salivary diet. The termid worker gut has evolved to optimize microbial symbiosis (Brune 2013).

In soil-feeding termites, the gut digests particulates which are comparably nutrient poor and recalcitrant. To accomplish this, soil-feeding termites have compartmentalized physiochemical gut environments to nurture their

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Fig. 3 *Cubitermes schereri* (Rosen) a Dark-gutted soldier (DGS); B worker of with abdominal integument removed. Enteric valve armature of c DGS, d worker, and e last instar larva. See Fig. 1 for abbreviation definitions.
prokaryotic symbionts (Brune 2013), no doubt at some energy cost. One advantage of the WGS/LIL nutritional scheme over that of the particulate feeders might be to redirect the energy demands lost to soil digestion toward defensive function (WGS) and growth (LIL). For this, the mature workers must carry a greater metabolic burden to feed high-energy secretions to their white-gutted nestmates.

The EVA is well developed in soil-feeding termites. Donovan (2002) and Bignell (2010) suggest that the EVA spines and combs fractionate gut contents by size to expose...
more digestible organic particles to microbial fermentation. Alternately, Scheffrahn (2013) argues that these structures enhance microbial inoculation of ingested material before entry into the P3. In either case, the EVA probably enhances fermentation of the gut contents before entering the P3 for microbial digestion. As would be expected from a liquid diet, the WGS generally lack an EVA and their P3 is relatively small. Remnants of the EVA and enlargement of the hindgut segments in both the WGS and the LIL of Procubitermes (Fig. 2a) suggest that the conversion to a salivary diet is more recent in this genus. We hope that this paper will stimulate studies on the composition of food and dynamics of trophallaxis in all termites.

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White-gutted soldiers: simplification of the digestive tube for a non-particulate diet in…