

The ootheca of *Mastotermes darwiniensis* Froggatt (Isoptera: Mastotermitidae): homology with cockroach oothecae

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The basal termite *Mastotermes darwiniensis* produces an egg mass, the nature of which is controversial. The debate centres on whether it is homologous with the oothecae of mantids and cockroaches and, if so, whether its simple structure is plesiomorphic or apomorphic within the Dictyoptera. To help resolve these issues we observed primary reproductives of *M. darwiniensis* during oviposition and examined the morphology of the reproductive product. Oviposition is cockroach-like in that the egg mass is assembled within the vestibulum and the eggs are issued externally in pairs. The reproductive product is an ootheca of the blattarian type. A distinct, tanned outer covering is stretched over the two parallel rows of eggs. No keel is present and no calcium oxalate crystals were apparent in the outer covering. We cannot rule out the possibility that the simple structure of the ootheca is plesiomorphic within Dictyoptera. However, based on (i) apomorphies shared by *Mastotermes* and Blattaria, and (ii) the life habits of Isoptera, a secondary reduction is the more plausible explanation.

Keywords: Dictyoptera; termites; oviposition; eggs; reproduction; phylogeny

1. INTRODUCTION

Despite a recent profusion of work on the subject, the relationships between the main subgroups of the Dictyoptera (Isoptera = termites, Blattaria = cockroaches and Mantodea = mantids) are still contested (reviewed by Nalepa & Bandi 2000). Some have argued that the primary dichotomy lies between the Isoptera and Blattaria plus Mantodea, while others have contended that Mantodea diverged first, with Blattaria and Isoptera either as sister groups or with Isoptera nested within the Blattaria as the sister group of Cryptocercidae.

One termite which features prominently in this debate is *Mastotermes darwiniensis* Froggatt, the sole extant member of the basal isopteran lineage Mastotermitidae. This species exhibits a curious mix of primitive and advanced characteristics. Although, cockroach-like, it has a well-developed anal lobe in the hind wing (Watson & Gay 1991) and endosymbiotic flavobacteria in the fat body (Bandi *et al.* 1995, 1997), and it also displays colony sizes, feeding and nesting habits and caste development more typical of advanced termites than of other basal groups (Hill 1942; Watson & Sewell 1985; Abe 1987).

M. darwiniensis is unique among termites in its production of an organized egg mass and the homology of this reproductive characteristic is disputed. Most references to this structure lead to a 75-year-old line drawing and description by Hill (1925) who stated that the two parallel rows of eggs are ‘... firmly cemented together by a light brown gelatinous secretion, which is sufficiently copious to completely fill the interstices between the eggs and, in some places, to extend to the exposed outer surfaces’ (p. 120). Subsequently, this description has been interpreted and reinterpreted by various authors, with the egg

mass having been described as ‘resembling’ a cockroach ootheca (Gay 1970), as a ‘highly modified’ (Marks & Lawson 1962), ‘simple’, ‘simplified’ (McKittrick 1964; Kristensen 1995) or reduced (Klass 1995) ootheca, as ‘an ootheca-like mass’ (Nichols 1989) and as ‘certainly not an ootheca’ (Boudreaux 1979; Thorne & Carpenter 1992). Boudreaux (1979) asserted that ‘The cockroach–mantid ootheca results from the tanning of protein and contains organic calcium salts. The ootheca [of *M. darwiniensis*] is more comparable to that of acridids [Orthoptera: Acrididae, short-horned grasshoppers], in that it consists of the dried secretion of the accessory glands and merely forms a thin film over the eggs’ (p. 219). Thorne & Carpenter (1992) used egg deposition as a character in their cladistic analysis of six dictyopteran taxa. They scored *M. darwiniensis* as depositing its eggs ‘in mass, two rows, with secretory envelope’ and cockroaches as ‘depositing eggs in ootheca with discrete outer case’ (p. 260). However, the distinction between a secretory envelope and a discrete outer case was not specified. Weesner (1969) and McKittrick (1964) each indicated that the egg mass of *M. darwiniensis* has no outer covering.

Because of the ambiguity in the literature and consequent long-standing disagreement, we studied reproduction in *M. darwiniensis* with the goal of clarifying egg packaging and deposition. To allow us to interpret the findings in terms of homology and character polarities, we focused on the extent to which (i) oviposition behaviour, and (ii) the structural features of the reproductive product resemble those of Blattaria, Mantodea and Acrididae.

2. METHODS

Primary reproductives of *M. darwiniensis* were collected from 17 October to 12 November 1996 at a light trap in the grounds

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of the CSIRO Tropical Ecosystems Research Centre in Darwin, Northern Territory, Australia. Pairs consisting of one male and one female dealate were placed into covered glass Petri dishes of 9 cm diameter floored with Whatman qualitative grade filter paper dampened with 2 ml distilled water. Each dish was provided with a small pad of wet cotton wool and a 2 cm × 1 cm × 3 cm block of wood (*Eucalyptus regnans* F. Muell.).

Seven females in different stages of oviposition were filmed through the glass cover of the Petri dish with a Sony CCD-TRV81 video Hi8 Handycam (Sony, Tokyo, Japan) with ×30 digital zoom; additional observations were made using a stereoscopic microscope at ×100–250 magnification. Egg masses were collected, fixed in 4% glutaraldehyde in phosphate-buffered saline, dehydrated through an alcohol series into 100% acetone, critical point dried, mounted, coated with gold and examined in a JSM-6400 scanning electron microscope. The oothecal casing was further inspected at ×400 magnification with a phase contrast microscope.

3. RESULTS

Prior to oviposition the female assumes a characteristic stance with the abdomen slightly elevated from its normal resting position (figure 1a); one (metathoracic) or more pairs of legs may be stilted. Eggs are issued from the vestibulum in pairs, although the first egg, the last egg or both may be a singlet. The dorsum of the newly emerged egg(s) adheres to the venter of the previously laid two. Eggs rest at an angle of *ca.* 45° from perpendicular, overlapped by approximately half the lateral surface of the eggs that preceded them (figure 1b). The degree of overlap between adjacent eggs was variable. The two parallel rows of eggs were neither consistently staggered nor consistently bilaterally symmetrical. The one oviposition sequence observed in its entirety, from emergence of the first egg from the vestibulum to deposition of the completed product on the substrate, required 126 min for an ootheca containing seven eggs. No further eggs were issued after 80 min; the female retained the ootheca for an additional 46 min before releasing it. The orientation of the ootheca did not change prior to deposition; there was no rotation as in some cockroaches (see Roth 1967).

Scanning electron micrographs indicate that the two rows of eggs are encased in a distinct outer covering stretched over the surface of the eggs and often prolonged into an irregular appendage of variable size at the proximal end (figure 1b). No dorsal keel or suture is evident, although the envelope appears thicker dorsally, with more of the colleterial gland secretion in the 'valleys' between adjacent eggs. A substance of different appearance is deposited over the oothecal case in some of the recesses between eggs; it is this material that probably led Hill (1925) to believe that the eggs were glued together. No material was observed in the interstices between eggs of dissected oothecae.

Oothecae are initially pale, but begin changing to their characteristic light brown colour *ca.* 10 min after emergence (also noted by Fox 1970). Tanning was essentially complete prior to oothecal deposition. No calcium oxalate crystals were evident when the oothecal wall was examined at ×400 magnification; this latter observation requires confirmation by X-ray diffraction or chemical analysis.

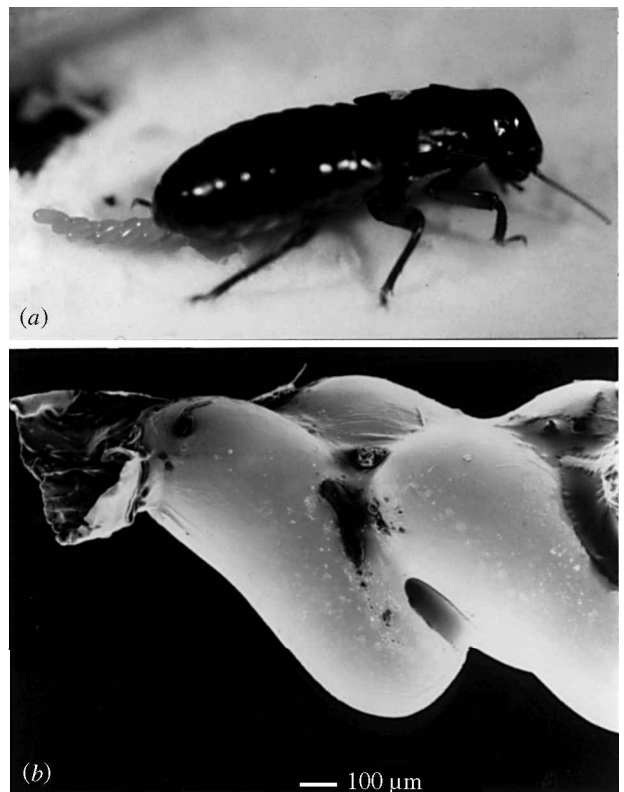


Figure 1. (a) Oviposition in a primary reproductive of *M. darwiniensis*. (b) Proximal end of an ootheca produced by a primary reproductive of *M. darwiniensis*. Eggs are enclosed by an outer covering stretched over and conforming closely to the surface of the eggs. The ootheca is rotated 180° horizontally from the ootheca in (a). Scanning electron micrograph by Mark Dominick, CSIRO.

4. DISCUSSION

It is generally accepted that the morphology of the female genitalia in *M. darwiniensis* unambiguously indicates its relationship to mantids and cockroaches (Crampton 1923; Geyer 1951; Marks & Lawson 1962; McKittrick 1964; Klass 1998). The ovipositor of this species differs little from that of other dictyopteran taxa except in its relative proportions. It consists of three pairs of valves enclosed in a vestibulum by the subgenital plate: the ventral valves (gonapophyses 8), which are the largest, the medial valves (gonapophyses 9) and the dorsal valves (gonopods), which are unsclerotized, wrinkled, membranous lobes in *M. darwiniensis*. The colleterial glands are well developed and structurally and positionally similar to those of Blattaria and Mantodea (Geyer 1951; Marks & Lawson 1962; Stay & Roth 1962; McKittrick 1964; Kenchington & Flower 1969). Membranous, longitudinal, interstitial folds occupy the floor of the vestibulum approximately halfway back in the chamber (Browman 1935; Geyer 1951); these are absent in mantids (fig. 2 in Klass 1998).

In cockroaches, the aforementioned structures function in the formation of the ootheca. Secretions from the colleterial glands are extruded into a mould formed by the interstitial folds. The valves orientate the eggs leaving the gonopore and regulate the flow and distribution of the colleterial gland secretion. The passage of the eggs between the valves stretches the pliable secretion and the

interstitial folds form a collar around the ootheca as it is extruded (McKittrick 1964; Roth 1974). When all the eggs have issued from the gonopore, the ovipositor valves are removed from the opening in the egg case and additional secretion flows out to cover the hole. Ablation experiments in cockroaches have indicated that gonopophyses 8 play the largest role in ootheca formation (Roth 1974); these are the best developed valves in *M. darwiniensis*. The gonoplares are the mould for keel formation (Roth 1974), i.e. the raised crest running along the mid-dorsal line of the ootheca (Lawson 1951; Roth 1968). The gonoplares in *M. darwiniensis* are unsclerotized and the ootheca of this species correspondingly lacks a keel. The irregular appendage on the proximal end of the ootheca of *M. darwiniensis* is probably formed by the withdrawal of the ovipositor valves at the conclusion of ootheca construction.

The ovipositor terminates within the vestibulum in Blattaria, *M. darwiniensis* and other Isoptera (McKittrick 1964). However, in Mantodea the ovipositor reaches or exceeds the posterior end of the subgenital plate (e.g. fig. 21.3B in Balderson 1991) and ootheca construction occurs external to the body. A large mass of colleterial gland secretion is expelled and whipped into a froth by the gonopophyses. The tip of the female's abdomen is inserted into this mass and performs an elaborate, repeating cycle of movements, each of which terminates in the release of a group of eggs and the formation of a corresponding part of the ootheca. There is immense variation in the morphology of the mantid ootheca; typically, the central core is divided into chambers, each of which contains a group of eggs with lateral chambers or air-filled cavities protecting them. When complete the oothecae of most mantids are pale in colour, but become tanned as they dry (Kenchington & Flower 1969; Hinton 1981).

Although a number of acridid species arrange their eggs in parallel, double rows (see fig. 158 in Uvarov 1977), the manner in which these pods are constructed differs from that in *M. darwiniensis* and cockroaches. As in mantids, the egg mass of acridids is assembled external to the body. Acridid females eject each egg individually into a hole previously excavated with the ovipositor valves and a frothy secretion is deposited after each. When the full complement of eggs has been laid, the female fills the rest of the hole with a plug of the same foam, withdraws the abdomen and covers the hole with soil or plant material (Uvarov 1966; Stauffer & Whitman 1997). Non-homology of the acridid and dictyopteran reproductive product is strongly indicated by non-homology of the glands producing the raw materials for the egg cases (Klass 1995). The colleterial glands of the Dictyoptera open into the vestibulum, posterior to the ovary (fig. 3 in Weesner 1969; Fuseini & Kumar 1973; Szopa 1981; fig. 1 in Klass 1998). The respective glands of the Acrididae ('pseudocolleterial glands') (Beier 1972) differ in that they are situated at the apex of the lateral oviducts and are mesodermal rather than ectodermal in origin. Pseudocolleterial glands are absent in some acridid taxa and, even when present, they play a relatively minor role in the formation of the egg pod. Removal of the glands only slightly reduces the volume of froth surrounding the eggs. Glandular tissues in the remaining portions of the oviducts compensate for their absence (Uvarov 1966; Hinton 1981; Szopa 1981; Stauffer & Whitman 1997).

When placed in the context of the above literature review, our results indicate that oothecae are most parsimoniously regarded as homologous in Mantodea, Blattaria and *M. darwiniensis* and, hence, are present in the ground plan of Dictyoptera. Within the Dictyoptera, the reproductive biology of *M. darwiniensis* is more characteristic of Blattaria than of Mantodea. Cockroaches and *M. darwiniensis* lack the complex behavioural sequences associated with constructing an ootheca external to the body. Like cockroaches (Roth 1970) but unlike mantids, the ootheca of *M. darwiniensis* is assembled within the vestibulum while supported by interstitial folds and issues externally from the female with the eggs in parallel, double rows. Tanning of the discrete outer covering is essentially complete prior to oothecal deposition (McKittrick 1964). *M. darwiniensis* is also homologous with cockroaches in the detailed mechanisms used to transfer bacterial fat body endosymbionts to the oocytes; these endosymbionts are absent in mantids (Sacchi *et al.* 2000). We therefore agree with Ratcliffe *et al.* (1952), Watson & Gay (1991), Klass (1995) and Kristensen (1995) who suggested that the ootheca of *M. darwiniensis* is homologous with the oothecae of cockroaches. There is no need to qualify this homologization because of the apparent lack of calcium salts and a keel; the oothecal case of at least two oviparous cockroaches lacks calcium salts (*Cryptocercus punctulatus* and *Blattella vaga*) (Stay *et al.* 1960; Roth 1968) and the oothecal case of all ovoviviparous cockroaches lacks both these features. The eggs of ovoviviparous species are encased in a soft, thin, transparent membrane which in some taxa only partially covers the eggs (fig. 158–171 in Roth 1968, 1970). In some Geoscapheinae (Blaberidae), the oothecal case has been lost altogether and the eggs are deposited as a loosely appressed mass in the brood sac (Rugg & Rose 1984; Walker & Rose 1998). The trend in ovoviviparous cockroaches appears to be the reduction and virtual elimination of the oothecal envelope and a parallel regression of the morphological structures associated with producing it (Stay *et al.* 1960; Marks & Lawson 1962; Roth 1967, 1968, 1989). The same trend is evident in termites. All Isoptera except *M. darwiniensis* have eliminated the oothecal envelope; they deposit their eggs singly, though they may glue them together with secretions from colleterial glands (e.g. Roonwal 1975; Akhtar 1978). Correspondingly, the ovipositor valves and interstitial folds in these termites are largely or entirely missing (Walker 1919; Browman 1935; Geyer 1951; Marks & Lawson 1962) and the colleterial glands are small relative to those in *M. darwiniensis* (Geyer 1951). Notably, the right colleterial gland ('third gland') has been reduced to a short appendix in all termites examined save *M. darwiniensis* (Geyer 1951). In oviparous cockroaches, the right gland produces β -glucosidase, an enzyme that triggers a chemical cascade resulting in tanning of the oothecal case (Brunet & Kent 1955).

The simple oothecae of *M. darwiniensis* and of most ovoviviparous cockroaches probably represent parallel reductions of more complex ancestral states. Termite nests and brood sacs of ovoviviparous cockroaches are both moist, protected sites for incubating eggs, allowing for the reduction and eventual elimination of defensive structures in evolutionary time. Because the oothecal case of

oviparous cockroaches is 86–95% protein (Kramer *et al.* 1991), 'this is a saving that can be easily realized' (Lameere 1909, in Wheeler 1928, p. 160). A number of morphological and physiological reductions in Isoptera may be attributed to increased homeostasis within the colony as termites evolved behavioural buffers against the environment (Emerson 1961, 1962; Nalepa & Bandi 2000). In this case, the protection against desiccation and pathogens once afforded by the oothecal case has been replaced by the social control of humidity within the nest (Marks & Lawson 1962) and the constant grooming and attention that workers lavish on eggs (e.g. Weesner 1953).

We cannot rule out the possibility that the simple structure of the ootheca in *M. darwiniensis* may represent a plesiomorphic condition within the Dictyoptera (McKittrick 1964; Thorne & Carpenter 1992); however, secondary simplification (Klass 1995; Kristensen 1995) is supported by apomorphies in the reproductive characteristics shared by *Mastoterme* and Blattaria, but not Mantodea and life-history circumstances making reduction a plausible explanation. Apomorphies shared by *M. darwiniensis* and oviparous cockroaches include intersternal folds in the vestibulum, assembly of the ootheca within the vestibulum and extrusion of the eggs in parallel, double rows. Studies of the histology and chemistry of the colleterial glands among the three dictyopteran subgroups may provide further information on the polarity of the oothecal structure in *M. darwiniensis*. Nonetheless, assembly of the ootheca outside the body, as in mantids and acridids, is most likely to be the plesiomorphic state, since the ovipositor is relatively long in the insect ground plan (Kukalová-Peck 1991) and, until the Mesozoic, most cockroach-like insects had external ovipositors (Vishniakova 1968). Characteristics of the reproductive biology of *M. darwiniensis* then support phylogenetic scenarios indicating that Mantodea diverged first, with Blattaria and Isoptera either as sister groups or with Isoptera nested within the Blattaria.

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