Explosive Backpacks in Old Termite Workers

J. Šobotník,[1]* T. Bourguignon,[2,3]* R. Hanus,[1,2]† Z. Demianová,[1] J. Pytelková,[1] M. Mareš,[1] P. Foltynová,[4] J. Preisler,[4] J. Cvačka,[1] J. Krasulová,[1,5] Y. Roisin[2]

We send our young men to war; ants send their old ladies (*1*). This metaphor illustrates a long-known feature of insect societies: Older workers generally assume a larger share of defense, which may involve self-sacrifice (*2*, *3*). In some termites, suicidal defense by bursting is performed by soldiers (*4*), but, because defense is their sole function, there is little potential for age dependence. However, in a few species, workers are known to rupture and release a sticky fluid (*4*). Because workers perform a variety of tasks, this readiness for suicidal defense would be expected to increase as their aptitude for other tasks declines.

Neocapritermes taracua is a neotropical termite commonly found in decayed wood on which it feeds (*5*). Close examination of workers reveals in many (hereafter blue workers) a pair of dark blue, elongated dorsal spots at the thorax-abdomen junction (Fig. 1A). These spots are variously developed among workers and are lacking in some individuals (white workers). During aggressive encounters with other termites, blue workers actively bite and, when hampered, burst and emit a drop of fluid, which in a few seconds becomes sticky as the blue color fades out (Fig. 1B and movie S1).

The blue spots are a pair of crystal-like structures (Fig. 1C) enclosed within pouches formed by posterior outgrowths of the metanotum over the first abdominal segment. The crystals are produced by a pair of glands (crystal glands) located below the epidermal cell layer at the anterior part of each pouch (Fig. 1D). The dorsal apparatus also comprises the salivary glands, producing secretion granules stored below the dorsal wall (Fig. 1D).

Mandibles of *Neocapritermes* workers wear out with time and usage because they cannot be renewed by molting (*6*) (fig. S1A). Mature workers showed a positive correlation between fresh weight and mandible sharpness index and a negative relationship between crystal weight and mandible sharpness index, indicating that, as the feeding efficiency of workers decreases, they build up their backpacks for suicidal fighting (fig. S1, B and C).

Blue workers were more aggressive than white workers toward other soil-feeding termites, such as *Labiotermes labralis*, and they burst sooner after being seized by their opponent (fig. S2). Bursting liquid from blue workers was more effective than liquid from white workers against *L. labralis* (table S1). Removing the blue crystals reduced the toxicity of blue workers to the level of white workers. Reciprocally, the toxicity of white worker bursting fluid was enhanced by the addition of blue crystals but remained lower than that of blue workers (table S1). This pinpoints the importance of the reaction between blue crystals and salivary secretion to achieve toxicity.

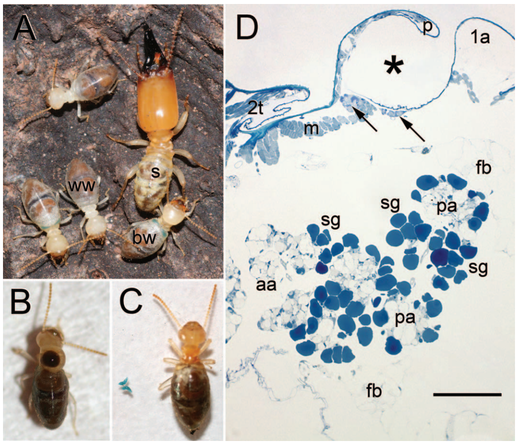

Fig. 1. Anatomy of the defensive apparatus of *N. taracua*. (**A**) Soldier (s) with two blue (bw) and two white workers (ww). (**B**) Blue worker after autothysis triggered by grasping it with tweezers. (**C**) Blue worker after removal of the blue crystals (placed next to it). (**D**) Section of anterior abdomen of a blue worker. Asterisk marks crystal-bearing pouch (crystal dissolved); arrows mark crystal gland cells. Scale bar, 200 μm. 1a, first abdominal segment; 2t, mesothorax; aa, anterior acini (clumps of secretory cells); fb, fat body; m, muscles; p, dorsal part of the crystal-bearing pouch; pa, posterior acini; sg, aggregates of secretion granules budding off posterior acini.

An important component of the blue crystal is a 76-kD protein (hereafter called BP76) as judged from the protein pattern on a 15% SDS–polyacrylamide gel electrophoresis (PAGE), and by a single blue band on the 10% native PAGE gel (fig. S3A). By using mass spectrometric methods, we confirmed the molecular weight of BP76 (fig. S3B) and detected the presence of 9 ± 2 ng (SD) of copper per crystal (fig. S3, C and D). Its molecular weight, color, and copper content suggest that BP76 is an oxygen-binding type III copper protein of the hemocyanin/phenoloxidase family, known to occur in arthropods (*7*).

The defensive apparatus of *N. taracua* is exceptional. First, it involves a previously unknown exocrine gland, unusual in its product (the copper-containing blue crystal protein) and its storage (the external "backpack" pouches). Second, its efficacy derives from the reaction, upon autothysis, of the labial gland secretion and the blue crystals. Consistent with theory, workers develop this weaponry and increase their proneness to use it as their feeding efficiency decreases when their mandibles become worn.

References and Notes

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Supplementary Materials
www.sciencemag.org/cgi/content/full/337/6093/436/DC1
Materials and Methods
Figs. S1 to S3
Table S1
References (*8–11*)
Movie S1

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[1]Institute of Organic Chemistry and Biochemistry, Academy of Sciences of the Czech Republic, 166 10 Prague, Czech Republic. [2]Evolutionary Biology and Ecology, Université Libre de Bruxelles, 1050 Brussels, Belgium. [3]Graduate School of Environmental Science, Hokkaido University, Sapporo 060-0810, Japan. [4]CEITEC (Central European Institute of Technology) and Department of Chemistry, Faculty of Science, Masaryk University, 625 00 Brno, Czech Republic. [5]Department of Analytical Chemistry, Faculty of Science, Charles University in Prague, Albertov 6, 128 43 Prague, Czech Republic.

*These authors contributed equally to this work.
†To whom correspondence should be addressed. E-mail: robert@uochb.cas.cz