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Mein Zeichen

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### **Review for the PhD thesis by Robert Hanus**

#### **Biology of the soldier caste in the termite genus *Prorhinotermes* (Isoptera: Rhinotermitidae)**

Robert Hanus investigated in his PhD Thesis the role of soldiers in three *Prorhinotermes* species. In his studies he showed that soldiers have a wide range of behavioral tasks and are highly adapted for defense. They reach high numbers within a colony which is unusual for a one-piece nesting species but probably related to the fact that *Prorhinotermes* can leave the nest to exploit and settle in a new piece of wood.

Robert Hanus' studies are highly relevant within the field of termites' biology and social evolution. Among termites there are two types which differ in social complexity: (i) the so-called one-piece nesting species which lack morphologically differentiated workers and which nest in a single piece of wood that serves both as food and shelter (wood-dwellers) and (ii) the so-called multiple-pieces species which have an morphologically differentiated worker caste (true workers) and which go out foraging. The transition between both types is crucial for the understanding of the evolution of social complexity in termites with the latter group presenting nowadays more than 80 % of all termite species. *Prorhinotermes* might represent such a transition life type as they nest and feed within a single piece of wood but leave it to inhabit a new piece of wood when they are running low in food resources. Thus, studying this genus can provide important insights in the evolution of social complexity.

The PhD Thesis is very well written and very carefully prepared. At the beginning Robert Hanus gives an impressive overview about the state of the art of termite research with a

special focus on soldiers. In this review he summarized the results of 533 papers showing that Robert Hanus is deeply familiar and highly engaged in his research. The results of his own work on soldiers are published in six papers of peer-reviewed international journals and an poster presented at a conference. In addition, in the Appendix Robert Hanus added five published papers on termites where he also was involved in as an co-author.

The experiments for these papers were very carefully done using were necessary highly sophisticated techniques such as electron microscopy, radioscopy or gas chromatography – mass spectrometry and detailed behavioral experiments. The data were appropriately analysed and revealed interesting results, which were discussed in relation to the currently available literature. All papers are well written and read well. One minor concern that I had with some papers was that the data derived from one termite colony that has been collected already in the 1960thies and kept in the laboratory since then. Results based on one parental colony might be colony specific and laboratory conditions might have an influence. However, besides this all studies revealed convincing results.

The PhD thesis ends with a general conclusion placing the results in a general context and showing their broader implications. One major implication concerns the phylogenetic position of *Prorhinotermes* and associated with it the question whether one-piece nesting termites which lack true workers (such as *Prorhinotermes*) present the ancestral state in termite evolution or a derived state. Robert Hanus concludes that *Prorhinotermes* might present an intermediate stages between one-piece nesting termites and foraging termite species. As it still lacks true workers but already leaves the nest the soldiers take over multiple tasks and are more numerous than in the one-piece nesting termites, both shown in his thesis work. I fullfy agree with Robert Hanus concerning his conclusion. I just want to add a few additional thoughts for consideration and discussion.

1) Leaving the nest in *Prorhinotermes* is not foraging in its common sense, as food is not brought back to the nest. It should be rather regarded as 'house hunting' like in some ant species. The termites move to a new piece of wood and settle in there without leaving the new nest thereafter. This might explain the lack of true workers in these species as there is no continues foraging and thus low selective pressure for foraging adaptations and probably also low indirect benefit gains through brood care. See for instance our recent results on the drywood termite *Cryptotermes secundus* that imply that the 'pseudergates' are not involved in brood care and mainly stay to gain direct fitness benefits by inheriting the nest (Korb 2007, *Frontiers in Biology*)

2) I think the nest stability discussion by Higashi et al. is quite misleading. The stability of one-piece nesting termites is very high, in general much higher than in most termites species with true workers (foraging termites). The nests can last for several generations of

termites (e.g. they provide a valuable resource to inherit; at least one cycle of replacement reproductives). Moreover, the conditions are also more stable than in termites with true workers where environmental influences by predators, or temperature are much more pronounced. The important difference between the one-piece nesters and the foraging species are that the nest longevity/food availability declines predictably whereas in foraging species conditions vary less predictably. From a life history perspective this difference is important because only the former conditions select for a flexible development as shown by the one-piece nesters (see also discussion in Korb & Katrantzis 2004, *Evo & Dev*).

3) I think, the sister taxon relationship of the termites with the Cryptocercidae (wood roaches) also strongly suggests that the one-piece nesting life type with a lack of true workers presents the ancestral state in termite's evolution.

To conclude, I support Robert Hanus' studies, I consider the thesis suitable for the defense as its quality fully fulfils the criteria necessary for obtaining a PhD degree. Thus, I highly recommend the acceptance of Robert Hanus application for a PhD degree.

Osnabrück, den 30.05.08



Prof. Dr. Judith Korb