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Soldier-like Intercastes in the Rotten-wood Termite

Hodotermpsis sjostedti (Isoptera: Termopsidae)

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ABSTRACT—All termite species possess a distinct sterile-soldier caste in their colonies, although reproductive soldiers, with soldier characteristics and reproductive ability, have been reported from several species of the family Termopsidae. Such intercastes have been considered the primitive-soldier caste, and based on this many researchers have discussed the evolutionary origin of termite soldiers. We investigated whether such soldier-reproductive intercastes also exist in the Japanese rotten-wood termite Hodotermpsis sjostedti. Abnormal individuals with soldier-like characteristics were found and designated as soldier-like intercastes, which appeared to have both soldier and reproductive characteristics. Based on our morphometric analyses and histological examinations, we suggest that the developmental origin of this intercaste is a pseudergate, nymph or sixth-instar larva. In addition, the intercaste was found to have relatively well-developed gonads, although mature oocytes and spermatozoa were not found in female ovaries and male seminal vesicles, respectively. We conclude that the soldier-like intercaste of H. sjostedti does not have reproductive ability, which is different from all other known soldier-like intercastes in Termopsidae.

Key words: caste differentiation, gonad, morphometry, reproductive soldier, soldier neotenic

INTRODUCTION

In termites, intercaste individuals that have intermediate morphology of two or more castes have been occasionally found in a colony (e.g. Lefeuve and Thorne, 1984; Roisin and Pasteels, 1986), and are considered the by-product of plastic post-embryonic development. Among others, the ‘reproductive soldier’ (or ‘soldier neotenic’), found in three species of the genus Zootermopsis, is a notable example of an intercaste, because it provides us with insights into the evolutionary origin of termite soldiers (Heath, 1928; Myles, 1986; Roisin, 2000; Thorne et al., 2003). In Archotermopsis wroughtoni and Stolotermes brunneicornis, soldiers with functional gonads have been reported (Imms, 1919; Gay and Calaby, 1970). Myles (1986) pointed out that ‘reproductive soldiers’ or ‘soldiers with functional gonads’ are found in socially-primitive termites, and that soldiers might have originally evolved by individual-level selection under intracolonal conflict among replacement reproductives. Thorne (1997) mentioned that soldiers in the primitive termites might have retained reproductive capability, although it was unclear whether the primitive soldier functioned as a defensive caste or a replacement reproductive. Roisin (1994, 1999) criticized Myles’s hypothesis, based on two reasons: there was no evidence for an actual role of soldier weapons in intracolonal fight; and it was improbable for soldiers to become sterile if soldiers were originally reproductives. Recently, Thorne et al. (2003) revealed that reproductive soldiers are adaptive for intercolonial conflicts among incipient colonies, which is conceptually similar to Myles’s (1986) hypothesis of intracolonal conflict.

In Termopsidae, Hodotermpsis is the only genus where the presence of reproductive soldiers remains to be determined (Myles, 1986). Based on the normal caste developmental pathways of Hodotermpsis sjostedti (Miura et al., 2000, 2004), we here investigate whether reproductive soldiers exist in this species. Soldier-like intercastes were found from several colonies; therefore, we examined their morphology and fecundity. Based on these results, the developmental and evolutionary origin, and functions of the soldier-reproductive intercastes, are discussed.

MATERIALS AND METHODS

Termite sampling

Recently, seven described species of the genus Hodotermpsis were revised into the single species, H. sjostedti Holmgren (Takematsu, 1996; Huang et al., 2000). The species is distributed...
Morphometric study
To evaluate the allometric features of the soldier-like intercaste, we carried out morphometric analysis based on the measurements of body parts. We used the following 17 measurements: 1) head length; 2) maximum head width; 3) head width at base of mandibles; 4) labrum width; 5) postmentum length; 6) postmentum width; 7) left mandible length; 8) maximum head height; 9) head height at base of mandible; 10) eye diameter; 11) pronotum length; 12) pronotum width; 13) mesonotum width; 14) metanotum width; 15) femur width; 16) femur length; and 17) tibia length. The measurements were performed using an image analysis system with a CCD camera, HIM-1N (HOGA, Osaka, Japan). The data set of measurements were performed using an image analysis system with a CCD camera, HIM-1N (HOGA, Osaka, Japan). Other colony individuals were kept in the laboratory as stock at approximately 25°C under constant darkness. Soldier-like intercastes differentiated in the laboratory were also fixed in FAA fixative. After fixation, all samples were transferred to 70% ethanol for preservation.

Table 1. Summary of intercastes and their sampling conditions.

<table>
<thead>
<tr>
<th>Intercaste</th>
<th>Colony No.</th>
<th>Approx No. of Nest Mates</th>
<th>Caste in Colony</th>
<th>Date of Colony Sampling</th>
<th>Intercaste No.</th>
<th>Sex of Intercaste</th>
<th>Collection Place</th>
<th>Date of Finding Intercaste</th>
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<td>2</td>
<td>M</td>
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<td>23. May. 2000</td>
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<td></td>
<td>4</td>
<td>M</td>
<td>Lab.</td>
<td>9. Apr. 2001</td>
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<td></td>
<td></td>
<td>8</td>
<td>F</td>
<td>Field</td>
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<td></td>
<td>11</td>
<td>M</td>
<td>Field</td>
<td>16. May. 2002</td>
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<td>12</td>
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<td>18. May. 2002</td>
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<td></td>
<td>IX</td>
<td>1000 – 10000</td>
<td>Neo, Pe, L</td>
<td>18. May. 2002</td>
<td>18</td>
<td>F</td>
<td>Field</td>
<td>18. May. 2002</td>
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<td></td>
<td>19</td>
<td>F</td>
<td>Field</td>
<td>18. May. 2002</td>
</tr>
</tbody>
</table>

M: Male; F: Female; K: Primary king; Q: Primary queen; Neo: Neotenic; Nym: Nymph; Pe: Pseudergate; L: Larva. Colony II’ was experimentally made in the laboratory of nymphs from Colony II. The individual marked with an asterisk (*) was a presoldier-like intercaste, while others were soldier-like intercastes.

RESULTS
Soldier-like intercastes in H. sjostedti
Of the 28 examined colonies, a total of 20 intercaste individuals (10 males and 10 females), which had soldier-like characteristics, were found from nine colonies (Table 1). Among them, a male intercaste was found from an experi...
Intercaste in the Rotten-wood Termite

mental colony composed only of nymphs for the examination of regressive molts (Koshikawa et al., 2001). There seemed to be no correlation between the appearance of intercastes and colony size or the presence/absence of reproductives. As for head morphology, the intercastes superficially showed the intermediate characters between a pseudergate and soldier (Fig. 1). Although the inter caste mandibles were apparently longer than those of a pseudergate, only the anterior parts of the head were sclerotized, suggesting that they were different from normal soldiers (Fig. 1D and E). Most of the soldier-like intercastes had such morphological characteristics, although there was one exceptional male (Table 1, No.15, and Fig. 1F), with a morphology intermediate to that of a pseudergate and presoldier, with bag-like anterior tips on its mandibles. Most intercastes showed aggressive behavior, suggesting that the intercastes are engaged in colony defense, at least to some extent.

Morphometric study

As shown in our previous study (Koshikawa et al., 2002), the PCA well explained the allometric changes during soldier differentiation (Fig. 2A). The first principal component accounted for 87.1% of the total variance (eigenvalue: 14.81), and positively correlated with all measurements, showing the general size of insects. The second principal component, which accounted for 7.0% of the total variance (eigenvalue: 1.19), showed allometric differences. The second principal component positively correlated with 1) head length, 2) maximum head width, 3) head width at base of mandibles, 5) postmentum length, 6) postmentum width, 7) left mandible length, 8) maximum head height, 9) head height at base of mandible, 12) pronotum width and 15) femur width, but negatively correlated with 4) labrum width, 10) eye diameter, 11) pronotum length, 13) mesonotum width, 14) metanotum width, 16) femur length and 17) tibia length. Altogether, the first and second principal components expressed 94.1% of the variation among the allometric data. As seen in Fig. 2A, the soldier-like intercaste data grouped separately, indicating that intercastes have apparently different allometry from the other castes.

A scattergram of head width against left-mandible length indicates distinct morphological changes during soldier differentiation, in addition to the morphological differences of intercastes (Fig. 2B). The graph shows that these
characters of the intercastes are intermediate to those of the pseudergates and presoldiers.

Observation of reproductive organs

Among the observed castes (soldier, neotenic and intercaste), the female neotenics (supplementary reproductives) had the largest ovaries with developing oocytes (Fig. 3A). The ovaries of soldier-like intercastes and soldiers were not well developed (Fig. 3D and G), and similar to other non-reproductive castes, such as pseudergates and presoldiers (data not shown). Therefore, we concluded that the female intercastes did not have reproductive capability.

In the male neotenics, testes were well developed and produced spermatozoa (Fig. 3B), and the seminal vesicles also contained spermatozoa (Fig. 3C). However, in most soldiers, testes were degenerated and spermatozoa were not observed (Fig. 3H), and the seminal vesicles also lacked spermatozoa (Fig. 3I). In the male soldier-like intercastes, testes were less developed than those of neotenics, but greater than those of soldiers and other non-reproductive castes, and all the observed intercastes produced spermatozoa (Fig. 3E). However, no spermatozoa were observed in the seminal vesicles (Fig. 3F), suggesting that the male intercastes did not have ability to inseminate, even though they had more developed reproductive traits than the soldiers.

DISCUSSION

Morphological observations and morphometric analysis are the standard methods to infer developmental pathways in termites (e.g. Roisin and Pasteels, 1986). Therefore, we thought these methods might be useful for the characterization of the soldier-like intercaste in *H. sjostedti*. The morphometrics of the intercastes were intermediate to those of the pseudergates and presoldiers (Fig. 2B). There was one direct observation in which an intercaste was derived from an experimental colony exclusively composed of nymphs, although it remains unknown whether the intercaste was derived through one or two molts from the nymphal stage. We consider that the differentiation through two molts seems more probable, because the meso- and metanotum shapes were not trapezoidal, which is the typical evidence for an individual directly derived from a nymph through a single molt (Koshikawa et al., 2001). This species has only a single nymphal stage (brachypterous nymph) (Miura et al., 2004), and normal soldiers also differentiate from nymphs (Miura et al., 2000; Koshikawa et al., 2001). From these findings, together with the morphometric data, it seems reasonable that the intercastes differentiated from pseudergates, nymphs or sixth-instar larvae. The intercaste differentiation from neotenics, presoldiers and soldiers is thought to be improbable, because neotenics and soldiers are at the developmental end point in the differentiation pathways (Miura et al., 2000), and the regressive molt from presoldier has never been reported.

The fact that the proportion of soldier-like intercastes in a colony was considerably lower (Table 1), suggests that the intercastes are not adaptive in termite colonies, but just developmental abnormalities. We speculate that the semi-developed gonads and incomplete soldier traits in the intercastes were caused by some unusual physiological conditions. Actually, high juvenile hormone (JH) titer causes intercaste differentiations in many termites, including artificial applications of juvenile hormone analogue (JHA) (e.g. Howard and Haverty, 1979; Miura et al., 2003). In some ter-
Intercaste in the Rotten-wood Termite species, intercaste differentiation is caused by endoparasitic dipteran larvae parasitizing the head capsule (Grassé, 1986). In *H. sjostedti*, however, intercaste differentiation does not seem to be the result of such parasitism, because we did not find any larvae in the head capsule of intercastes.

The intercastes in *H. sjostedti* resembled the reproductive soldiers of *Zootermopsis* in head morphology (e.g. Fig. 3. Paraffin sections of reproductive organs. A–C: neotenics, D–F: intercastes, G–I: soldiers. A, D, G: female ovaries, B, E, H: male testes, C, F, I: male seminal vesicles. Sp: spermatozoa. In the female intercaste, the ovary was not fully developed (D). In the male intercaste, the undeveloped seminal vesicle did not contain spermatozoa (F), although the testis produced them (E). The ovoid structures in the seminal vesicles of the male neotenic (C) were considered as vacant space of seminal-vesicle secretion, which appeared at fixation. Bar indicates 200 µm.)
Myles 1986), although the fertility of soldier-like intercastes was not observed in the present study. In Archotermopsis wroughtoni and Stotermes brunneicornis, normal soldiers also possess well-developed gonads (Imms, 1919; Gay and Calaby, 1970). However, the situation in H. sjostedti is different from those of Zootermopsis, Archotermopsis and Stotermes; soldiers have degenerated gonads and there is a soldier-like intercaste that does not have reproductive ability. Thus, this intercaste cannot be considered a reproductive-soldier caste, although we cannot entirely exclude the possibility that both intercastes and reproductive soldiers exist, as our limited sampling methods mean that we might not have found them.

Recently, Thorne et al. (2003) pointed out that the reproductive soldiers in Zootermopsis play an important role in intercolonial conflicts among incipient colonies. However, the adaptive function of the soldier-like intercaste in H. sjostedti is obscure. The low proportion of intercastes in a colony suggests that they are not important, at least in a large colony. Although intercastes have not been found from incipient colonies so far, further detailed investigations are required to conclude their adaptive significance. Considering that Hodotermopsis and Zootermopsis are thought to be closely related (Krishna, 1970), reproductive soldiers in Zootermopsis might be derived from such abnormal intercastes through adaptation for defense in incipient colonies.

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