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Compound Eye Development During Caste Differentiation in the Termite *Reticulitermes speratus* (Isoptera: Rhinotermitidae)

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We morphologically examined postembryonic compound eye development in *Reticulitermes speratus* (Kolbe) to understand developmental regulation during caste differentiation. The eye primordia were shown to exist from the larval stage. The number of ommatidia and compound eye size greatly increased over the course of imaginal development. Nymphoids (second-form reproductives) possessed a developed compound eye structure on the surface of the cuticle and thick optic nerves, but individual ommatidia were not clearly discriminated. However, in the line of apterous workers and soldiers, although the outer rim of the eye was observed from second-stage workers, there were few morphological differences among instars, including ergatoids (third-form reproductives). Both nymphoids and ergatoids are slightly physogastric and have highly developed reproductive organs. These results suggest that eye development in the apterous line could be strongly arrested and that there is a weak developmental correlation between the eyes and reproductive organs in *R. speratus*.

Key words: termite, caste differentiation, compound eye, neotenic reproductive, social insect, postembryonic development

INTRODUCTION

Termites (Isoptera) are one of the major social insect groups. Since termites show hemimetabolous development, immature individuals possess the basic body pattern of adults (except that some organs are not fully developed; see below) (Weesner, 1969a). Therefore, the developmental pathways that lead to polyphenic castes in termites should result from alterations in the duration of stages in normal postembryonic developmental processes known to exist in most hemimetabolous insects. According to caste function, organs or body structures are modified in a caste-specific manner, so developmental analyses of caste-specific organs can be an effective method to understand developmental mechanisms (Koshikawa et al., 2002: Miura, 2005). Imaginal organs (e.g., external genitalia, ovary, testis, wings, and compound eyes) are fully developped in alates (primary reproductives), but absent in workers and soldiers (Weesner, 1969a, 1969b; Richard, 1969). As adults of other hemimetabolous insect possess fully developed imaginal organs, we can compare information on organ development between these other insects and polyphenic termites. Detailed observations of developmental processes of these organs during caste differentiation will provide important information on underlying developmental mechanisms.

The compound eyes of insects normally contain a number of ommatidia. A compound eye develops from the eye primordium, which is a derivative of the embryonic visual primordium. Retinal differentiation starts at the posterior margin of the eye primordium; this process is marked by formation of a morphogenetic furrow (reviewed in Friedrich, 2003). The furrow moves from its posterior starting point towards the anterior. Cells anterior to the furrow are undifferentiated, while those behind it are assembled into ommatidial clusters (Heming, 2003). Eye development in hemimetabolous insects is a process that starts in the embryo and extends through postembryogenesis. Most of the eye of the first instar is fully differentiated and functional, and ommatidia are added to the anterior, dorsal, and ventral margins of the eye during postembryonic growth (Friedrich, 2003; Nowel, 1981; Sherk, 1978; Shelton, 1983). Although knowledge of eye development in termites is fairly limited, Richard (1969) showed that the first instar of *Kalotermes flavicollis* (Fabricius) (Family Kalotermitidae) possesses the eye primordium, which assembles the undifferentiated cells, and that progressive development of compound eyes occurs. Recently, Katoh et al. (2007) closely observed compound eye development accompanying alate differentiation in *Neotermes koshunensis* (Shiraki) (Family Kalotermitidae) and found that the differentiation of cells in each ommatidium appeared to occur in young larval instars, but that the detailed structural formation of ommatidia occurred during

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the final stage of alate development. However, detailed investigations of compound eye development have not yet been conducted in other termite families.

In termites, there are two major caste developmental systems: the linear-pathway system and the dual-line system (Noirot, 1969). The family Kalotermitidae utilizes the linear caste-developmental pathway (Roisin, 2000), in which there is a pseudergate caste that has the potential to develop alate-specific organs (for terminology of termite castes, we referred to Thorne [1996] and Roisin [2000]). Other families such as Mastotermitidae, Termitidae, and Rhinotermitidae utilize the dual-line system (Roisin, 2000). In this system, caste developmental processes are divided into two lines: the 'imaginal' and 'apterous' lines. The former is the line of nymphs equipped with wing buds on the thorax, and older nymphs can molt into alates as primary reproductives. The latter is the line of apterous workers and soldiers. When the primary reproductives die after the appearance of their offspring, multiple neotenic reproductives may emerge and successfully reproduce. They can normally be differentiated from both developmental lines, i.e., nymphs and workers. Consequently, these groups with the dual-line system are very interesting examples from an evolutionary developmental perspective, because the developmental timing (e.g., from larvae to nymphs/workers, or from nymphs/workers to neotenic reproductives) of each organ in each caste may be more complicated than in groups with the linear-pathway system. It will be especially interesting to know when and how the developments of imaginal organs (e.g., ovary and compound eyes) are regulated in the different developmental lines. Differentiation should occur in the early postembryonic stages. Elucidation of morphological changes occurring during caste differentiation will facilitate an understanding of the mechanisms of developmental regulation involved.

Here, we analyzed successive stages in the development of the compound eyes of *Reticulitermes speratus* (Kolbe). In this species, differentiation into the imaginal and apterous lines occurs at the second molt (Takematsu, 1992) (Fig. 1). Moreover, nymphoids (second-form reproductives) and ergatoids (third-form reproductives) emerge from nymphs and workers, respectively. We investigated the outer and inner morphology of the compound eyes in various instars and castes, using scanning electron microscopy (SEM) and histological observations of paraffin sections. The goals of our study were to examine (1) developmental differences in compound eye formation between the two distinct caste developmental pathways, and (2) the relationship between compound eye development and reproductive organ development in several types of neotenics.

MATERIALS AND METHODS

Insects

Six mature termite colonies were collected from Kureha Hill in Toyama Prefecture, Japan, during March 2004 and 2005. Each instar (2nd stage larvae [L2], 2nd/4th/5th stage workers [W2/W4/W5], presoldiers [PS], soldiers [S], 2nd/4th/6th stage nymphs [N2/N4/N6], alates [A], nymphoids [NR], and ergatoids [ER]) (Fig. 1) was picked from each colony. Not all stages of larvae, workers, and nymphs could be found in this study; we thus selected some stages of each caste for study. Each sample was fixed in FAA solution (formaldehyde: ethanol: acetic acid, 6:16:1) for 24 hours and preserved in 70% ethanol. Worker and nymph castes were discriminated according to the length of their wing buds, number of the antennal segments, and body size (Takematsu, 1992; Tsunoda et al., 1986). We did not discriminate termites older than W5, because of the difficulties involved.

Scanning electron microscopy (SEM)

Scanning electron microscopy (SEM) was used to investigate the outer morphology of the compound eyes from the larval to alate stages. More than five samples of each instar in 70% ethanol were dehydrated by transfer into increasing concentrations of ethanol (up to 100%), then into 100% *t*-butanol. After preservation at –20°C for 2 hours, samples were dried by using a freeze dryer (Hitachi ES-2030, Tokyo, Japan), and then coated with gold by using an ion coater (Eiko IB-3, Ibaraki, Japan). Scanning electron micrographs were taken with a JSM-5510LV system (JEOL, Tokyo, Japan).

Histological observations

To describe the inner morphology of compound eyes during postembryonic development and of ovaries in neotenic reproductives, paraffin sections were made and stained with eosin and hematoxylin. The head of individual termites and the abdomen of neotenic reproductives (more than five samples of each instar) preserved in 70% ethanol were dehydrated in increasing concentrations of ethanol, then transferred into xylene and finally embedded in paraffin. Serial sections (4 μm thick; transverse for heads and parasagittal for abdomens) were made with an MRS80-074 microtome (Ikemoto, Tokyo, Japan) and stained with eosin and hematoxylin. Tissues on slides were observed with a BX-40 microscope (Olympus, Tokyo, Japan), and images were captured with a Camedia C-5050 digital camera (Olympus, Tokyo, Japan).

RESULTS

Outer morphology

The external morphology of each instar observed by SEM is shown in Fig. 2. At the larval stage, there was no obvious compound eye structure on the surface of the cuticle (n=5) (Fig. 2a). In nymphs (N2, N4, and N6), the outer structure of ommatidia was observed near the antennal socket (Fig. 2b–d). This outer structure gradually became more apparent as the number of ommatidia increased. Determined from SEM images, numbers of ommatidia were about 20 (N2), 40 (N4), and 80 (N6). For alates, the entire compound eye structure became more convex in shape, and ommatidia were seen as clearly separated units (about 110 ommatidia) (Fig. 2e). However, in the apterous line (workers and soldiers), although the outer rim of the compound eyes was observed beginning with 2nd-stage workers, compared to larvae (Fig. 2a) there were few differences among stages, including presoldiers and soldiers (Fig. 2g–k). In nymphoids, the edge of the compound eye and many separate ommatidia were clearly observed (about 65 ommatidia) (Fig. 2f). However, compound eye size was smaller and the number of ommatidia was lower than in alates. Ergatoids did not clearly possess the outer structure of the compound eyes (Fig. 2l).

Histological observations

Histological observations revealed that although external structures were not clearly observed by SEM (Fig. 2a), the primordial structures of compound eyes formed during the larval stages (Fig. 3a), when some cells of the eye primordium and a short, relatively thin optic nerve were evident. In 2nd-stage nymphs, ommatidial units consisting of several cells, probably including the retinula (sense) cell, were observed (Fig. 3b). These ommatidial units were clearly recognized at N4, showing corneagenous and retinula cells (Fig. 3c). In N6, crystalline cones were also observed (Fig. 3d), and alates possessed ommatidia of uniform size standing in a row (Fig. 3e). The optic nerve fibers in N6 were as thick as those of alates (data not shown). In the apterous line of workers and soldiers, all individuals possessed some cells of the compound eye primordium and thin optic nerve fibers (Fig. 3g–i). Throughout the developmental stages of the worker line, however, no cell differentiation in the primordium or development of the optic nerves was observed. Nymphoids possessed ommatidial structures (Fig. 3f), but no development of corneagenous or retinula cells was observed in the ommatidia. Furthermore, individual ommatidia could not be clearly discriminated, compared with those of N6 (Fig. 3d) and alates (Fig. 3e). Although ergatoids possessed the eye primordium and nerve fibers, no cell differentiation was observed in the ommatidia (Fig. 3j).

Both nymphoids and ergatoids possessed well-developed ovaries and spermathecae (Fig. 4). Each ovary was composed of several ovarioles in which long oocytes

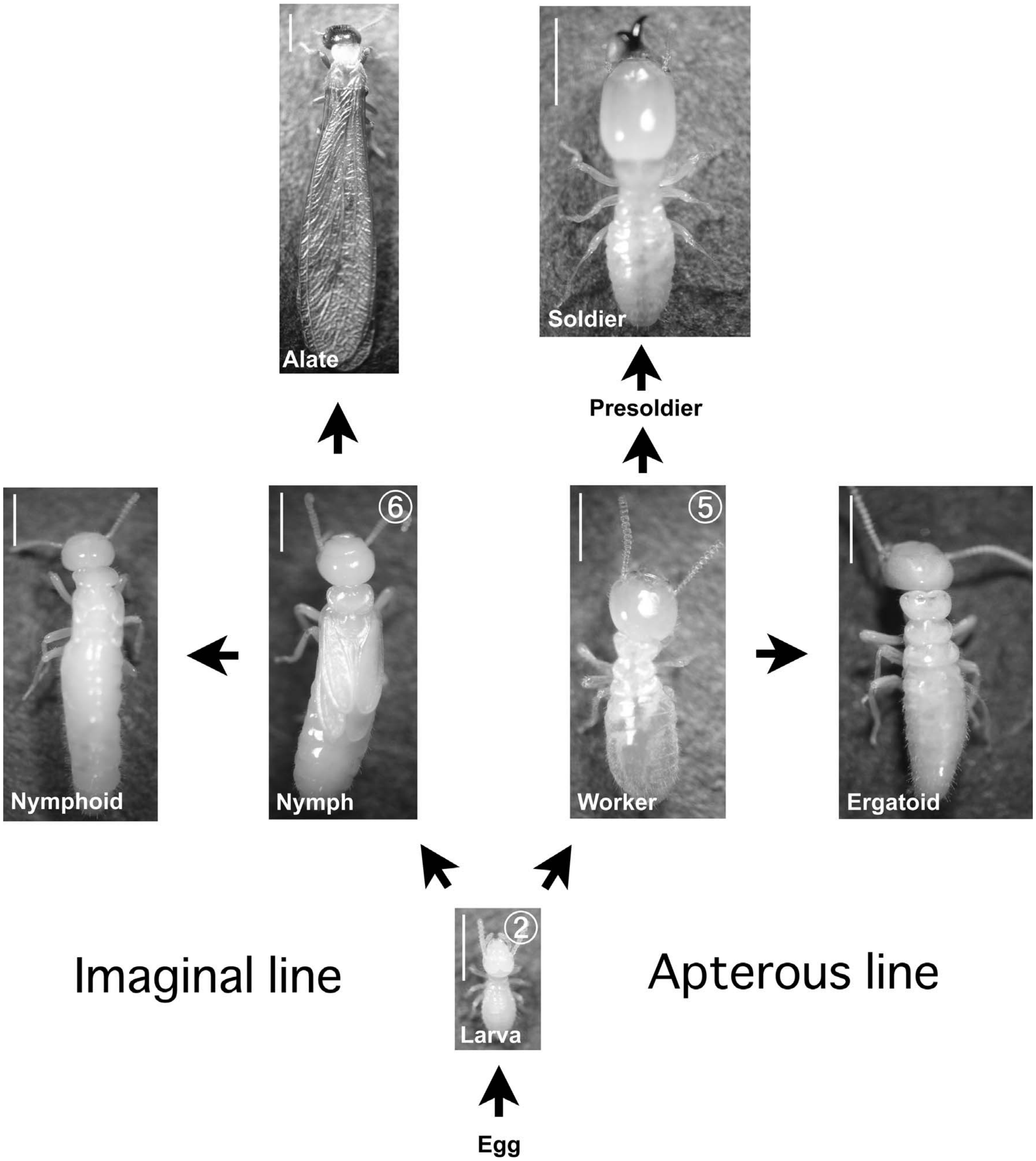

Fig. 1. Caste development in *Reticulitermes speratus*. Circled numbers indicate the instar stage of the larva, nymph, and worker shown (Takematsu, 1992). Nymphoids (second-form reproductives) differentiate from 3rd to 6th stage nymphs, and ergatoids (third-form reproductives) from workers (instars unidentified) (Shimizu, 1970; Miyata et al., 2004). Scale bars, 1 mm.

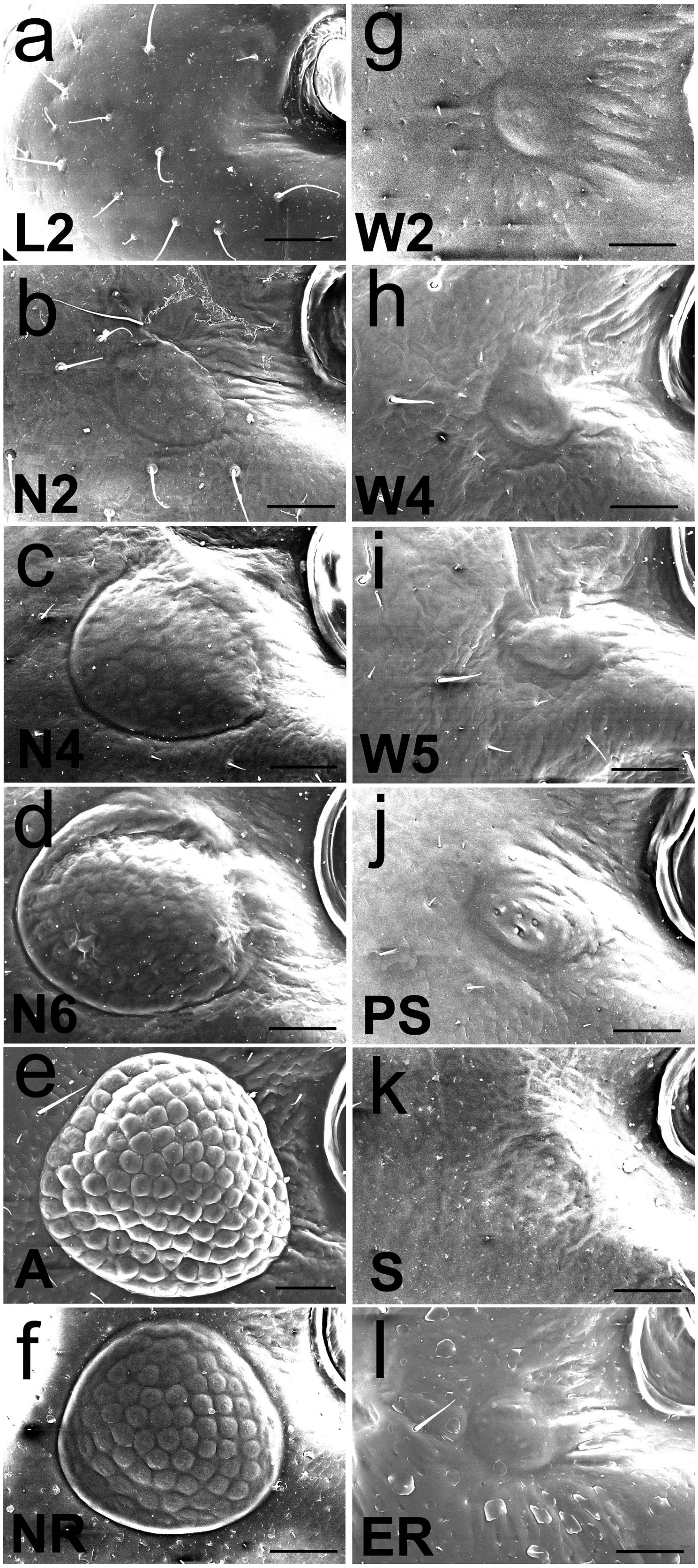

Fig. 2. Cuticle structure of the eye in each instar, observed by SEM (scanning electron microscopy): **(a)** 2nd stage larva; **(b)** 2nd stage nymph; **(c)** 4th stage nymph; **(d)** 6th stage nymph; **(e)** alate; **(f)** nymphoid; **(g)** 2nd stage worker; **(h)** 4th stage worker; **(i)** 5th stage worker; **(j)** presoldier; **(k)** soldier; **(l)** ergatoid. Scale bars, 50 μm.

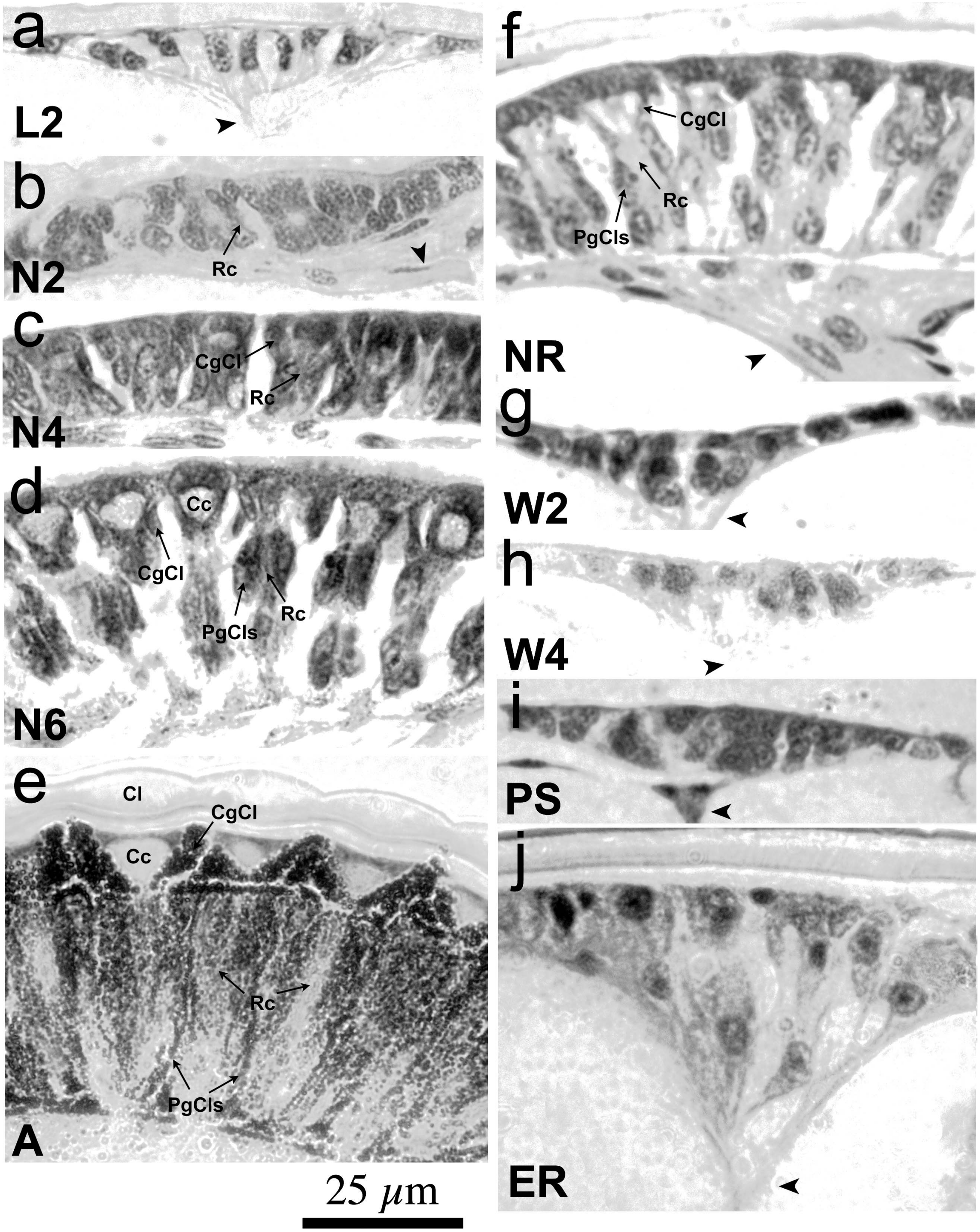

Fig. 3. Cross sections of compound eyes in each instar: **(a)** 2nd stage larvae; **(b)** 2nd stage nymph; **(c)** 4th stage nymph; **(d)** 6th stage nymph; **(e)** alate; **(f)** nymphoid; **(g)** 2nd stage worker; **(h)** 4th stage worker; **(i)** presoldier; **(j)** ergatoid. Arrowheads indicate the nerve fibers connecting the compound eye and optic lobe. CgCl, corneagenous cell; Cc, crystalline cone; Cl, corneal lens; PgCls, pigment cells; Rc, retinula cell. Scale bars, 25 µm.

containing yolk were present. Sperm was observed in the well-developed spermathecae of both neotenics (Fig. 4c, d).

DISCUSSION

Compound eye formation in each developmental pathway in *Reticulitermes speratus*

Hemimetabolous insects generally possess compound eyes with an elaborate ommatidial structure from just after hatching, and formation of the morphogenetic furrows and cell differentiation in the ommatidia begin during the embryogenesis (reviewed in Friedrich, 2003). Although the internal fine structures of the ommatidia during postembryonic growth were not clearly examined, our morphological observations on successive developmental stages of the

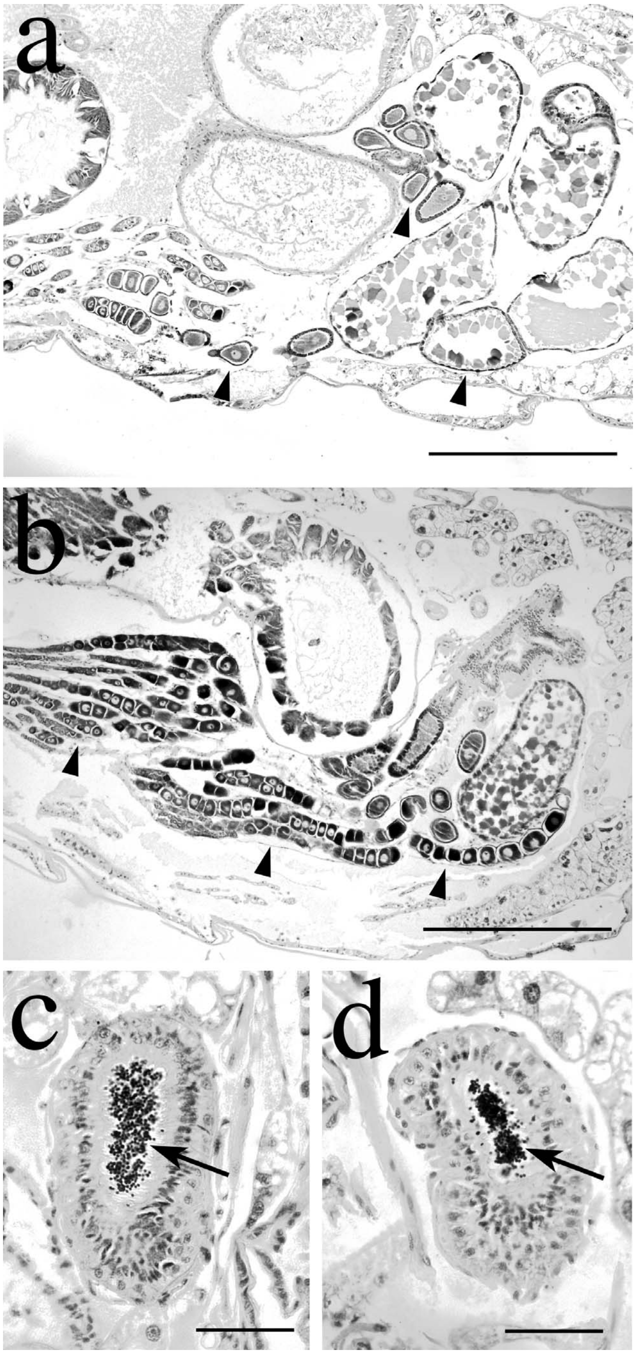

Fig. 4. **(a, b)** Cross sections of oocytes in the ovary of a nymphoid **(a)** and an ergatoid **(b)**. Arrowheads indicate the ovary. **(c, d)** Spermatheca of a nymphoid **(c)** and an ergatoid **(d)** containing numerous sperm cells (arrows). Scale bars, 500 µm (a, b), 50 µm (c, d).

compound eyes of *R. speratus* make it clear that the eye primordia existed in workers as well as in nymphs and that progressive eye development occurred throughout the course of imaginal development. The first-instar larvae of *K. flavicollis* and *N. koshunensis* possess the eye primordium, and the number of ommatidia increases with successive molts (Richard, 1969; Katoh et al., 2007). Thus, in these termite groups with the linear caste-developmental pathway (Roisin, 2000), cell proliferation occurs continuously in compound eyes between the postembryonic growth molts. In *R. speratus*, no larval individuals used in this study (n=5) possessed an obvious compound eye structure on the surface of the cuticle, but W2 showed the outer rim of the eyes (Fig. 2g) and some undifferentiated cells in the primordium (Fig. 3g). Thus, slight cell proliferation may occur from the larval stages to worker castes. However, subsequent developmental processes completely stop in apterous workers and soldiers at the beginning of ommatidium formation (Figs. 2, 3).

Katoh et al. (2007) suggested that in *N. koshunensis*, the differentiation of cells inside each ommatidium had not yet occurred in pseudergates (6th instar stage). It would be interesting to know if different suppressive or interruptive regulation exists between pseudergates of *N. koshunensis* and the apterous line of *R. speratus*. Moreover, it is possible that the suppression or interruption of eye development is determined through endocrine regulatory mechanisms, although it is still unclear if juvenile hormone, which has an essential role in termite caste differentiation (Miura, 2001; 2005), regulates the divergence between apterous and imaginal lines in *Reticulitermes*. A recent study also suggests that differentiation between these two lines is influenced by genetic factors related to each sex (Hayashi et al., 2007). Although we were not able to detect any differences in compound eye development between males and females in this study, detailed analyses of eye morphogenesis between genetically 'apterous' and 'imaginal' larvae, which can be made by using the methods of Hayashi et al. (2007), are needed to clarify this issue.

Eye formation in neotenics

In groups with the dual-line developmental system, supplementary reproductives can normally differentiate from both imaginal and apterous lines. Both nymphoids and ergatoids are slightly physogastric (Fig. 1) and have highly developed reproductive organs (Fig. 4), but the eye development is extremely different between them (Figs. 2, 3). Wingless ergatoids with compound eyes were reported in *Nasutitermes takasagoensis* (Shiraki) (Termitidae), which also has a developmental line of apterous workers and soldiers (Miura and Matsumoto, 1996). Ergatoids found in a colony of *N. corniger* (Motschulsky) likewise had a pair of reduced, poorly developed eyes (Thorne and Noirot, 1982). Moreover, Noirot and Thorne (1988) showed that the ergatoids of *N. columbicus* (Holmgren) possess compound eyes (and also variable wing buds). *Amitermes atlanticus* Fuller and *Neocapritermes opacus* (Hagen) (Family Termitidae) ergatoids also have vestigial eyes (Thorne and Noirot, 1982; Myles, 1999). Watson et al. (1975) showed that ergatoids of *Mastotermes darwiniensis* Froggatt (Family Mastotermitidae) have vestigial eyes, and traces of pigmentation appear in the eyes 1 week after the molt. These facts suggest that eye formation in termites is closely related to the development of reproductive organs. However, there are no clear developmental differences in the eyes among ergatoids, workers, and soldiers of *R. speratus* (Figs. 2 and 3), even though ergatoids (as well as nymphoids) possess well-developed ovaries and spermatheca (Fig. 4). Thus, in *R. speratus*, there seems to be no developmental link between the reproductive organs and the compound eyes in ergatoids. Interestingly, young workers (4th and 5th instars) of *R. lucifugus* Rossi and *R. santonensis* (Feytaud) develop small, pigmented eyes and variable-sized wing pads during differentiation into ergatoids, while older workers (>5th instar) do not (Buchli, 1956; Thorne and Noirot, 1982). These results suggest that there is relatively high developmental plasticity in imaginal organ morphogenesis even within the genus *Reticulitermes*. Detailed analyses of the other genera with the same caste developmental system are needed to confirm whether these results occur because of adaptive evolution in *Reticulitermes*.

Although corneagenous, pigment, and retinula cells were observed in the ommatidia of nymphoids, the eyes were greatly reduced in size compared to those of alates (Figs. 2f, 3f). Nymphoids of *R. speratus* differentiate from N3–N6 (Shimizu, 1970; Miyata et al., 2004). It is thus possible that the degree of development of the compound eyes varies among nymphoids from N3–N6. It will be necessary in future studies to analyze the developmental relationships between imago-specific organs (eye and wing) and reproductive organs during nymphoid differentiation in various nymphal instars.

Conclusions

Our histological and SEM observations showed that compound eye development in the apterous line of *R. speratus* can be strongly arrested, and that there are no clear morphological differences in the reproductive organs between supplement reproductives from apterous and imaginal lines (ergatoids and nymphoids). These results suggest that each organ normally present in the primary reproductives (alates) is regulated individually by morphogenetic factors during caste differentiation. Although further research is needed on other termite species, such different morphogenetic patterns may influence the body patterns of various castes in termites.

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