

Developmental Stages and Castes of Two Sympatric Subterranean Termites *Macrotermes gilvus* and *Macrotermes carbonarius* (Blattodea: Termitidae)

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ABSTRACT The developmental stages and castes of two sympatric subterranean termites, *Macrotermes gilvus* (Hagen) and *Macrotermes carbonarius* (Hagen) (Blattodea: Termitidae) were studied and biometric descriptors of each caste were developed for the identification of both species. Biometric descriptors revealed five well-defined groups of larval castes. After sex determination, three larval instars were detected in the development of minor and major worker castes. The first larval instars consist of both males and females which are homogenous in size. Size sexual dimorphism, in which females are smaller than males, occurs in the second larval instars, third larval instars, and worker castes. Minor and major soldiers are female sterile castes. Pictorial evidence of the fourth larval instar of *M. carbonarius* is presented herein; the individuals closely resemble minor workers but are poorly pigmented and have a distended abdomen, future presoldier-like mandibles, and a meso- and metanotum. In reproductive caste development, nymphs (derived from the first larval instars) undergo five moults from first to fifth instars before becoming winged termites.

KEY WORDS development, caste, *Macrotermes gilvus*, *Macrotermes carbonarius*, sexual dimorphism

A biometric approach commonly is used for determining caste developmental pathways and for the allometric study of termites (Okot-Kotber 1981, Roisin and Pasteels 1991, Miura et al. 1998, Roisin and Lenz 1999, Miura et al. 2000). The postembryonic development of higher termites is highly variable compared with that of lower termites. Caste systems have been extensively studied in two families, Termitidae and Kalotermitidae, that exhibit forked and linear developmental pathways, respectively. The Macrotermiinae, a subfamily of the Termitidae, is characterized by having 1) three larval stages in the development of the worker caste, 2) a single stage worker caste, and 3) nonsex-linked dimorphic soldiers that arise from female larval instars. The workers show remarkable sexual dimorphism with major workers (male) and minor workers (female) (with the exception of the genus *Syntermes*) (Noirot 1969).

The genus *Macrotermes* is abundant in Afrotropical and Asia regions. *Macrotermes gilvus* (Hagen) and *Macrotermes carbonarius* (Hagen) (Blattodea: Termitidae) are serious pests of wooden structures and of agricultural crops such as sugar cane, which are planted on land formerly covered by rain forest (Roonwal 1970, Cowie et al. 1989). *M. gilvus* is a secondary structural pest that can occur once the dominant *Coptotermes* species are suppressed or elim-

inated via termite baiting (Lee 2002, Lee et al. 2007). To date, *M. gilvus* infestation can be controlled only by chemical spraying; paper-based baits are ineffective against this species, possibly due to lack of palatability and biological variation (e.g., caste developmental pathway) of the species (Ngee et al. 2004, Lee et al. 2007).

Studies of termite developmental pathways may provide insight about termite evolution and caste developmental plasticity within a colony. Several studies of caste developmental pathways of *Macrotermes* have been reported previously [Noirot 1969, *Macrotermes bellicosus* (Smeathman); Okot-Kotber 1981, *Macrotermes michaelsoni* (Sjöstedt)], but biological data are scarce for *Macrotermes* spp. from Southeast Asia (e.g., *M. gilvus* and *M. carbonarius*). Evidence for the presence of fourth larval instars in *Macrotermes* is particularly fragmentary. Hence, the goal of this study was to elucidate the caste developmental pathways of both species. We also provide detailed biometric descriptors of both species.

Materials and Methods

Study Site and Specimen Collection. We collected a total of eight colonies of *M. gilvus* and three colonies of *M. carbonarius* from Universiti Sains Malaysia, Minden Campus, Penang, Malaysia (5° 21' N, 100° 18' E). Termites were collected during the relatively short seasonal interval during which production of nymphs

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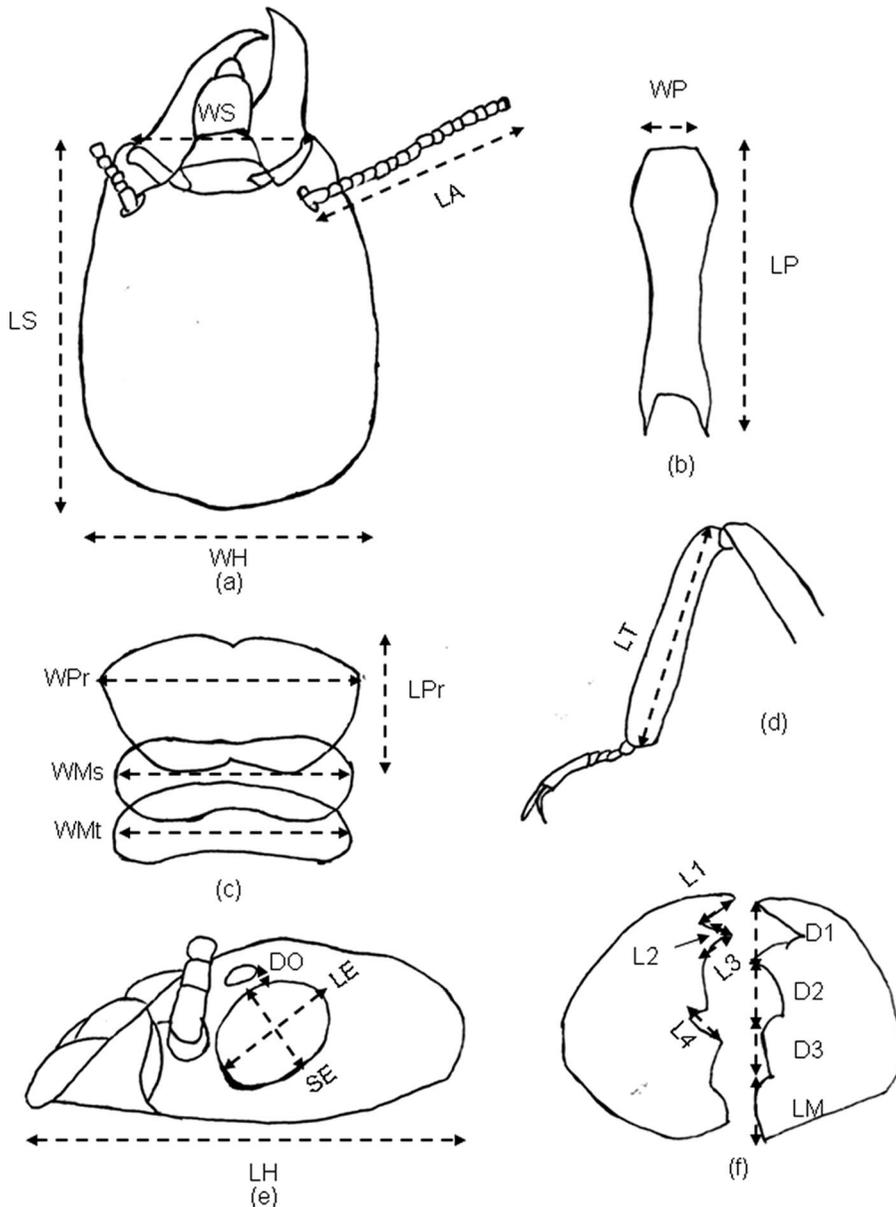


Fig. 1. Diagram of measured parts of a termite. (a) WH, width of head; WS, width of head to side base of mandibles; LS, length of head to side base of mandibles; LA, length of antenna. (b) WP, width of postmentum; LP, length of the postmentum. (c) WPr, width of pronotum; WMs, width of mesonotum; WMt, width of metanotum; LPr, length of pronotum. (d) LT, length of third hind tibia. (e) LH, length of head to tip of labrum; LE, long diameter of eye; SE, short diameter of eye; DO, distance between eye and ocellus. (f) D1, distance between apical tooth and first marginal tooth; D2, distance between first marginal tooth and second marginal tooth; D3, distance between second marginal tooth and molar prominence; LM, length of molar plate; L1, posterior cutting edge of apical tooth; L2, anterior cutting edge of first marginal tooth; L3, posterior cutting edge of first marginal tooth; L4, anterior cutting edge of second marginal tooth.

and alates occurred. The mature epigeous nests (height, 0.10–0.56 m) were selected for this study to enhance the chances of obtaining sexual castes. Termite mounds were excavated carefully to minimize injuries to the termites. To remove the outer layer casing, we dug a trench around the base of the nest and applied sideways force. The entire cover of the mound was removed to maintain the integrity of the nest. Random

samples were taken from the population of each colony. The samples were placed into plastic storage boxes (320 by 250 by 130 mm) and transported to the laboratory. The termites were collected by tapping detached nest materials onto trays, and samples were preserved in 70% ethanol before morphometric analysis.

Measurements of Termite Castes. Various parts of termite were observed using an SZ61 stereomicro-



Fig. 2. Ventral abdomen of the larval instars after removal of fat tissue, gut, and ventral cord and hematoxylin staining for sex determination: female (A) and male (B). The rudiment of the spermatheca is only found in sternite 8 of the female. Scale bar = 0.5 mm. (Online figure in color.)

scope (Olympus, Tokyo, Japan) with IC Imaging Standard, version 2.1 (The Imaging Source Europe GmbH, Bremen, Germany) and measured using Analysis Image Processing software (Soft Imaging System GmbH, Münster, Germany). Figure 1 shows the characters that were measured.

Principle component analysis (PCA) (using SPSS, version 11.0, SPSS Inc., Chicago, IL) was performed on the measured parts based on Okot-Kotber (1981), e.g., width of the head (WH) and the pronotum (WP) and the length of the antenna (LA) and the third hind tibia (LT) to evaluate correlations among these parameters. Discriminant analysis (using SPSS, version 11.0) was carried out to classify individuals into groups.

We also recorded the number of fully developed antennal segments and noted the segments that were incompletely formed (especially in the active growth region) by using a plus sign (Miura et al. 1998, Roisin and Lenz 1999). For example, 12 segments with an incomplete segment were indicated by 12⁺.

Sex Determination. To distinguish the sexes of five distinct-sized larvae, 30 termites of each size were

preserved in formalin-alcohol-acetic acid. Sex determinations were conducted as described by Miura et al. (1998) and Roisin and Lenz (1999). The abdomen was cut in the frontal plane and the dorsal half of the abdomen, the gut, and the fat body that obscured the rudimentary sex organs were removed. The specimen was stained with alcoholic hematoxylin for 45–60 min and then rinsed in hydrochloric alcohol (0.5% HCl in 80% ethanol) for a few minutes until the genital apparatus was visible. The position of the rudimentary sex organs made it possible to distinguish between male and female individuals. Females are characterized by rudimentary oviducts that lie at the posterior margin of sternite 7, by spermatheca on sternite 8, and by colleterial glands on sternite 9 (Fig. 2A). Rudimentary seminal vesicles of male lie at the end of sternite 9 (Fig. 2B).

Results

Tables 1 and 2 present the number of antennal segments and measurements for individuals of the

Table 1. Range and mean (in parentheses) of measurements of larval instars, workers, presoldiers, and nymphs from *M. gilvus* (in millimeters)

	No. antennal segment	Antennal length	Max. head width	Third hind tibial length	Pronotum width
L1 ♀♂ (n = 170)	12, 12 ⁺	0.57–0.78 (0.67)	0.43–0.57 (0.51)	0.20–0.35 (0.28)	0.28–0.38 (0.31)
L2 ♀ (n = 160)	14 ⁺ , 15	0.94–1.16 (1.06)	0.61–0.73 (0.67)	0.45–0.55 (0.51)	0.39–0.49 (0.43)
L2 ♂ (n = 185)	14 ⁺ , 15	1.15–1.45 (1.26)	0.75–0.89 (0.81)	0.56–0.76 (0.60)	0.50–0.57 (0.52)
L3 ♀ (n = 125)	16 ⁺ , 17	1.47–1.96 (1.72)	0.91–1.08 (0.99)	0.89–1.10 (1.01)	0.60–0.69 (0.64)
L3 ♂ (n = 140)	17	1.98–2.55 (2.27)	1.24–1.63 (1.40)	1.11–1.75 (1.21)	0.70–0.90 (0.79)
W1 ♀ (n = 50)	17	1.85–2.32 (2.06)	1.20–1.40 (1.28)	1.21–1.60 (1.41)	0.75–0.93 (0.81)
W2 ♂ (n = 15)	17	2.55–3.11 (2.82)	1.82–2.05 (1.94)	1.72–1.88 (1.79)	1.01–1.09 (1.06)
PS1 ♀ (n = 10)	17	2.30–2.45 (2.38)	1.21–1.31 (1.25)	1.35–1.50 (1.43)	0.86–0.97 (0.92)
PS2 ♀ (n = 6)	17	2.73–2.92 (2.83)	2.00–2.29 (2.09)	1.92–2.24 (2.03)	1.70–1.92 (1.76)
N1 (n = 17)	13, 13 ⁺	1.01–1.13 (1.09)	0.64–0.68 (0.66)	0.46–0.55 (0.50)	0.40–0.49 (0.45)
N2 (n = 56)	15, 15 ⁺	1.52–1.74 (1.62)	0.81–0.95 (0.88)	0.78–1.04 (0.92)	0.62–0.79 (0.70)
N3 (n = 26)	17, 17 ⁺	1.99–2.25 (2.14)	1.13–1.31 (1.21)	1.21–1.67 (1.49)	1.01–1.15 (1.10)
N4 (n = 11)	19	2.33–2.88 (2.66)	1.51–1.64 (1.58)	2.10–2.28 (2.17)	1.53–1.62 (1.57)
N5 (n = 9)	19	2.95–3.33 (3.13)	1.95–2.15 (2.06)	2.66–3.19 (2.86)	2.13–2.39 (2.31)

L1–L3, larval instars; W1, minor worker; W2, major worker; PS1, minor presoldier; PS2, major presoldier; N1–N5, nymphs.

Table 2. Range and mean (in parentheses) of measurements of larval instars, workers, presoldiers, and nymphs from *M. carbonarius* (in millimeters)

	No. antennal segment	Antennal length	Max. head width	Third hind tibial length	Pronotum width
L1 ♀ ♂ (n = 35)	12, 12 ⁺	0.67-0.89 (0.78)	0.45-0.61 (0.55)	0.26-0.46 (0.36)	0.30-0.40 (0.36)
L2 ♀ (n = 50)	14 ⁺ , 15	1.09-1.37 (1.24)	0.71-0.79 (0.75)	0.61-0.79 (0.73)	0.45-0.59 (0.52)
L2 ♂ (n = 48)	14 ⁺ , 15	1.54-1.83 (1.68)	0.87-1.07 (0.97)	0.83-1.05 (0.91)	0.53-0.69 (0.64)
L3 ♀ (n = 35)	16 ⁺ , 17	1.95-2.29 (2.07)	1.03-1.28 (1.13)	1.31-1.44 (1.44)	0.71-0.83 (0.76)
L3 ♂ (n = 24)	17	2.96-3.44 (3.20)	1.59-1.92 (1.76)	1.87-2.00 (1.92)	0.96-1.13 (1.04)
L4 ♀ (n = 6)	17	2.80-2.99 (2.89)	1.60-1.81 (1.68)	2.21-2.36 (2.27)	1.24-1.29 (1.27)
W1 ♀ (n = 50)	17	2.44-3.00 (2.77)	1.65-1.8 (1.72)	2.13-2.39 (2.30)	1.11-1.21 (1.16)
W2 ♂ (n = 15)	17	4.65-5.51 (4.98)	2.84-2.98 (2.92)	3.11-3.43 (3.30)	1.64-1.76 (1.70)
PS1 ♀ (n = 10)	17	3.43-3.87 (3.61)	1.75-1.88 (1.81)	2.16-2.62 (2.45)	1.43-1.53 (1.50)
PS2 ♀ (n = 10)	17	4.25-4.57 (4.47)	2.61-2.92 (2.79)	3.35-3.60 (3.46)	2.27-2.40 (2.33)
N2(?) (n = 18)	15, 15 ⁺	1.76-1.86 (1.79)	0.90-1.00 (0.95)	1.11-1.21 (1.15)	0.84-0.89 (0.87)
N3(?) (n = 46)	17, 17 ⁺	2.35-2.78 (2.60)	1.23-1.36 (1.30)	1.76-1.97 (1.85)	1.12-1.46 (1.38)

L1-L4, larval instars; W1, minor worker; W2, major worker; PS1, minor presoldier; PS2, major presoldier; N2(?) - N3(?), predicted nymphs.

larval instars, workers, presoldiers, and nymphs from *M. gilvus* and *M. carbonarius*, respectively.

Larvae. For both *M. gilvus* and *M. carbonarius*, five groups of larval castes that exhibited distinct sizes were readily recognized. The first larval instar (L1) was not sexed due to the absence of distinguishable sexual characteristics (Weesner 1969). These larvae were homogenous. Both female and male L2s and L3s were found, and the females were smaller in size. PCA revealed only one direction of variability which accounted for 94.3 and 97.2% of the total variance for *M. gilvus* and *M. carbonarius*, respectively. It is highly correlated to all variables (width of the head and the pronotum and the length of antenna and the tibia); thus, it provide a good estimation of overall size.

For *M. carbonarius*, the L4s are morphologically similar to minor workers (Fig. 3). These larvae are unpigmented and possess a distended abdomen and worker-like mandibles that enclose future presol-

dier-like mandibles and the meso- and the metanotum (Fig. 4).

Workers. The major workers are male (larger) and the minor workers are female (smaller). Workers possess 17 well-defined antennal segments. Measurements of larval individuals and sex determination indicated that smaller L3s give rise to minor workers and larger L3s give rise to major workers. Workers go through a single worker instar stage.

Nymphs. For *M. gilvus*, five nymphal instar stages were easily differentiated based on size and number of antennal segments. L1s give rise to the first nymphal instar (N1), which undergo five successive moults to become alates. The N1 and female L2 do not separate well in the discriminant graph (Fig. 5), but the former has tiny pointed wing buds on the mesonotum and metanotum. The early fourth nymphal instar appears unpigmented. The fifth nymphal instar is lightly pigmented and has well-developed eyes.

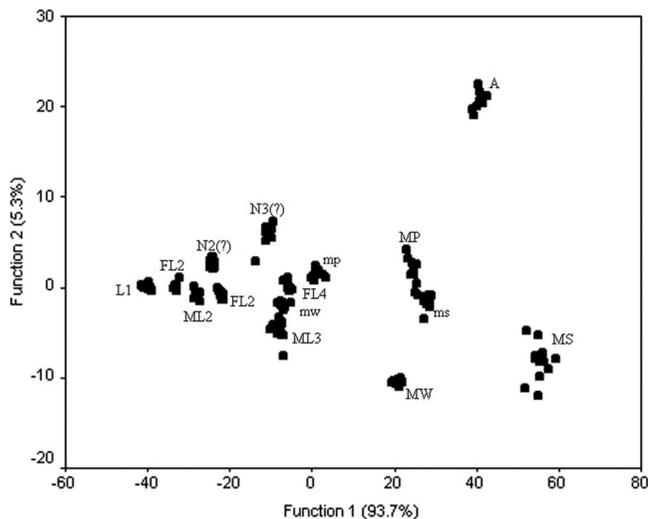


Fig. 3. Canonical discriminant functions of the caste system in *M. carbonarius*. L1, first larval instar; FL2-FL4, female second to fourth larval instars; ML2-ML3, male second and third larval instars; N2(?) - N3(?), predicted nymphal instars; W, major worker; PS, major presoldier; S, major soldier; w, minor worker; ps, minor presoldier; s, major soldier; A, alate.

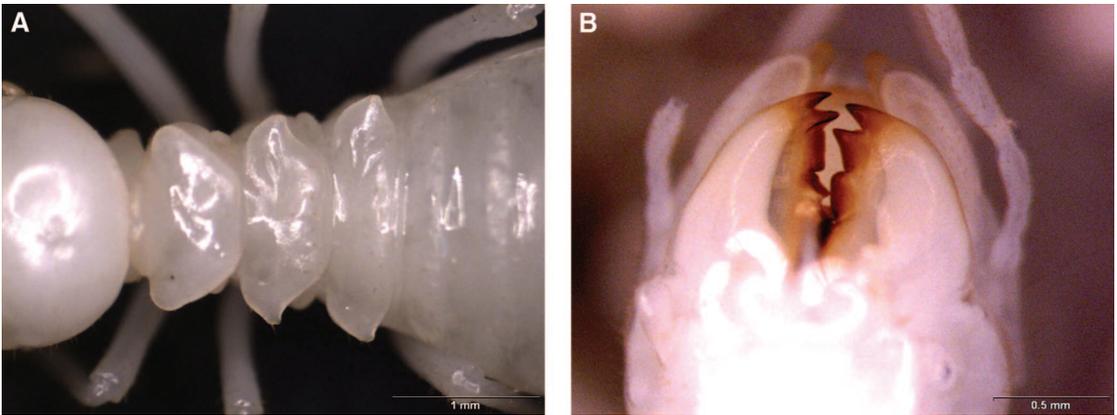


Fig. 4. Fourth larval instar of *M. carbonarius*. (A) Future presoldier-like meso/metanotum. Scale bar = 1 mm. (B) Worker-like mandibles, which enclose to future presoldier mandibles. Scale bar = 0.5 mm. (Online figure in color.)

For *M. carbonarius*, only two stages of nymphal instars were observed in this study. Based on the number of antennal segments and antennal structure, the nymphal instar with 15/15⁺ segments and a head width of 0.95 mm probably was the second instar, whereas the nymphal instar with 17/17⁺ segments and a head width of 1.30 mm probably was the third instar.

Soldiers. Presoldiers are nonsclerotized and have the morphological features of soldiers. Soldiers are females and show nonsex-linked dimorphism. The soldiers in *M. carbonarius* have slightly longer appendages compare with *M. gilvus* and their head-tibia index is 0.92 (major soldiers) and 0.80 (minor soldiers). Table 3 provides measurement data for the soldiers of both species.

Alates. Table 4 provides measurement data for the alates of *M. gilvus* and *M. carbonarius*. Alates arise from N5 and retain antennae with 19 segments. Antennal mutilation usually occurs after the colony is estab-

lished leading to the loss of five or more segments. The left mandible possesses two marginal teeth with a deep notch between them; the right mandible has two marginal teeth and a subsidiary tooth at the base of the anterior cutting edge of the first marginal tooth (Table 5).

The second segment of the antenna is subequal to the third segment in alates of *M. gilvus*. Alates of this species have a pair of brownish wings and abdominal segments. *M. gilvus* alates exhibit a significant sexual size difference in head width [Student's *t*-test, $t(18) = 3.849$, $P < 0.05$] and pronotal width [Student's *t*-test, $t(18) = 3.591$, $P < 0.05$]. However, no significant differences between sexes in antennal and tibial length were detected.

In *M. carbonarius* alates, the third antennal segment is longer than the second antennal segment and the wings and abdominal segments are black. No significant differences were detected between sexes in head

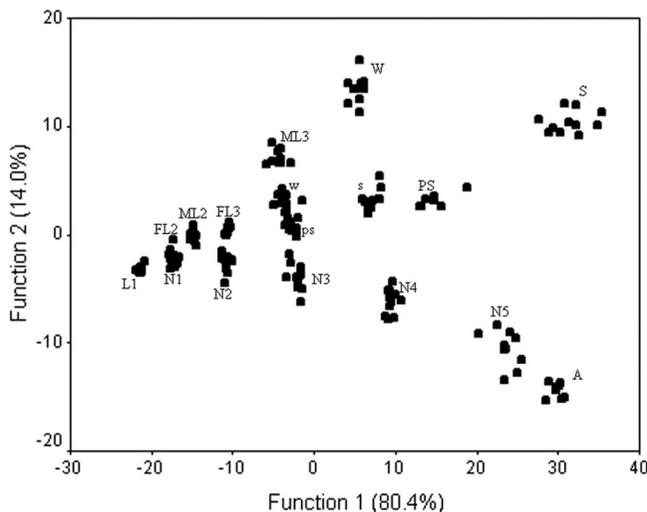


Fig. 5. Canonical discriminant functions of the caste system in *M. gilvus*. L1, first larval instar; FL2–FL3, female second and third larval instars; ML2–ML3, male second and third larval instars; N1–N5, nymphal instars; W, major worker; PS, major presoldier; S, major soldier; w, minor worker; ps, minor presoldier; s, major soldier; A, alate.

Table 3. Range and mean (in parentheses) of measurements of the soldiers of *M. gilvus* and *M. carbonarius* (in millimeters)

	<i>M. gilvus</i>		<i>M. carbonarius</i>	
	Major soldier (n = 10)	Minor soldier (n = 10)	Major soldier (n = 24)	Minor soldier (n = 20)
Length of antenna	2.68–3.18 (2.94)	2.42–2.79 (2.62)	5.54–6.09 (5.86)	4.63–5.15 (4.95)
Maximum width of head	3.05–3.34 (3.17)	1.77–1.87 (1.81)	4.06–4.58 (4.40)	2.84–3.03 (2.95)
Width of head to side of mandible	1.64–1.85 (1.74)	0.92–1.10 (0.99)	2.34–2.71 (2.57)	1.77–1.93 (1.86)
Length of head to side mandible	3.23–3.65 (3.43)	1.93–2.32 (2.19)	4.43–5.47 (4.93)	3.11–3.75 (3.47)
Length of postmentum	2.47–2.65 (2.57)	1.34–1.55 (1.44)	3.44–3.83 (3.64)	2.20–2.70 (2.52)
Width of postmentum (apical)	0.48–0.57 (0.53)	0.33–0.39 (0.36)	0.61–0.79 (0.73)	0.45–0.58 (0.55)
Maximum length of pronotum	1.08–1.31 (1.19)	0.74–0.88 (0.81)	1.33–1.73 (1.62)	1.00–1.40 (1.23)
Width of Pronotum	2.49–2.73 (2.60)	1.26–1.40 (1.33)	2.84–3.24 (3.06)	2.16–2.29 (2.23)
Width of mesonotum	2.31–2.67 (2.45)	1.07–1.22 (1.14)	2.71–3.12 (2.91)	1.77–1.91 (1.81)
Width of metanotum	2.30–2.73 (2.46)	1.14–1.28 (1.20)	2.63–3.09 (2.83)	1.84–2.00 (1.94)
Length of third tibia	2.29–2.64 (2.47)	1.68–2.00 (1.85)	4.56–5.07 (4.77)	3.00–3.97 (3.69)

width, pronotal width, and antennal length. However, male alates of *M. carbonarius* have a longer tibia than females [Student *t*-test, $t(24) = -2.889$, $P < 0.05$].

Discussion

Antennal length, head capsule width, and third hind tibial length are valuable parameters in identifying larval instars of Termitidae (Noirot 1955, Okot-Kotber 1981). In the current study, we found that pronotal length is also a useful parameter. Roisin and Lenz (1999) used the length of the pronotum and mesonotum in their study of developmental pathways in *Coptotermes lacteus* (Froggatt). In this study, we also tried to use cercal length and body length, but these parameters proved to be too variable. Antennal length has been shown to be a less reliable parameter for the differentiation of instars in *Microcerotermes turneri* (Froggatt) (Stewart and Zalucki 2006) and *Neotermes papua* (Desneux) (Roisin and Pasteels 1991). Apparently, the numbers of antennal segments increase parallel to larval development, and this relationship may be helpful in larval instar identification.

The early developmental fork separates Termitidae from more primitive group (Kalotermitidae) which the nymphal (sexual castes) line starts to split from apterous (nonsexual castes) line at the first molt. However, in most rhinotermitids, the nymphal and apter-

ous line forks at the second molt (Roisin 2000). In the current study, sex discrimination reveals three successive larval instars occur in the developmental pathway. Sexual dimorphism among the larval castes starts in second larval stage, whereas males are larger than females. It might be a general pattern in the subfamily of Macrotermitinae (Roisin 2000). The situation differs from Termitinae, Nasutermitinae, and Apicotermitinae in which only two larval instars are present in the developmental pathway and females always larger than males (Roisin and Pasteels 1987, Roisin 1996, Miura et al. 1998, Roisin 2000, Stewart and Zalucki 2006).

Nonsex-linked dimorphism occurs in soldiers, as soldiers are all females. This indicates that soldiers are derived from the minor worker line of development. Noirot (1969) noted that presoldiers arising from workers are common in the Termitidae. The unpigmented L4 of *M. carbonarius* shows a remarkable similarity to a minor worker. The L4 mentioned by Okot-Kotber (1981) varies from our observation; Okot-Kotber (1981) reported that the L4 is larger than a minor worker and has longer appendages. Noirot (1955, 1969) (*M. bellicosus*) and Darlington (1986) described the precursor of a major presoldier as identical to a normal minor worker, except that it is poorly sclerotized and has a larger body mass. In our study, neither the L4 as described above nor a weakly sclerotized minor worker was observed for *M. gilvus*. Thus, for this species we are unable describe the developmental pathway of the major presoldier. Figure 6 shows the caste developmental pathway for both species.

Both species can be readily differentiated by their color. In *M. gilvus*, the head capsule of workers and soldiers is reddish brown in color, whereas *M. carbonarius* has a heavily chitinized black colored head. In addition, the soldiers of *M. gilvus* can be distinguished from all other *Macrotermes*, by the conical shape of the anterior region of the hyaline tip in the soldiers, whereas *M. carbonarius* soldiers possess a trilobed hyaline tip (Tho 1992). Larvae of both species are morphologically identical, but differ in size. Thus, the description provided in this study might be the only feasible method to distinguish the larval stages of both species.

Table 4. Range and mean (in parentheses) of measurements of the alates of *M. gilvus* and *M. carbonarius* (in millimeters), $n = 10$ (mixed sexes) for each species

	<i>M. gilvus</i>	<i>M. carbonarius</i>
Length of antenna	3.51–4.10 (3.74)	4.78–5.34 (5.10)
Maximum width of head	2.08–2.22 (2.15)	2.63–2.72 (2.67)
Length of head to tip labrum	2.80–3.16 (3.02)	3.43–3.73 (3.64)
Long diam of eye	0.80–0.92 (0.85)	0.76–0.85 (0.81)
Short diam of eye	0.64–0.74 (0.68)	0.60–0.68 (0.65)
Long diam of ocellus	0.34–0.39 (0.37)	0.23–0.31 (0.26)
Short diam of ocellus	0.22–0.36 (0.30)	0.22–0.26 (0.23)
Distance between eye and ocellus	0.10–0.17 (0.12)	0.18–0.24 (0.20)
Width of pronotum	2.43–2.60 (2.52)	3.20–3.42 (3.33)
Length of pronotum	1.44–1.69 (1.60)	1.73–1.98 (1.86)
Length of third tibia	3.33–3.71 (3.55)	4.42–4.89 (4.67)
Length of forewing (cm)	2.30–2.50 (2.39)	2.20–2.40 (2.37)
Length of without wing (cm)	1.50–1.60 (1.56)	1.50–1.60 (1.54)

Table 5. Range and mean (in parentheses) of measurements of the mandibles of the alates from *M. gilvus* and *M. carbonarius* (in millimeters), *n* = 10 (mixed sexes) for each species

	<i>M. gilvus</i>		<i>M. carbonarius</i>	
	Right mandible	Left mandible	Right mandible	Left mandible
Distance between apical tooth and first marginal tooth	0.17–0.19 (0.18)	0.14–0.16 (0.15)	0.21–0.24 (0.23)	0.17–0.18 (0.18)
Distance between first marginal tooth and second marginal tooth	0.24–0.27 (0.25)	0.40–0.44 (0.42)	0.30–0.32 (0.31)	0.54–0.57 (0.56)
Distance between second marginal tooth and molar prominence	0.28–0.31 (0.30)	0.09–0.17 (0.12)	0.30–0.38 (0.34)	0.10–0.19 (0.14)
Length of posterior cutting edge of apical tooth	0.13–0.28 (0.18)	0.14–0.17 (0.15)	0.20–0.27 (0.24)	0.15–0.21 (0.18)
Length of anterior cutting edge of first marginal tooth	0.13–0.15 (0.14)	0.13–0.15 (0.14)	0.17–0.19 (0.18)	0.14–0.19 (0.17)
Length of posterior cutting edge of first marginal tooth	0.20–0.27 (0.23)	0.10–0.13 (0.12)	0.23–0.30 (0.27)	0.11–0.14 (0.13)
Length of anterior cutting edge of second marginal tooth	0.06–0.09 (0.07)	0.09–0.13 (0.11)	0.08–0.11 (0.09)	0.16–0.19 (0.17)
Length of molar plate	0.27–0.32 (0.30)		0.33–0.45 (0.41)	

For *M. gilvus*, head capsule width and pronotal width of the female alate were slightly larger than those of the male alate. The female alate and male alate of *M. carbonarius* showed no significant difference for any body parts measured except for tibial length, which was longer in males than in females. However, this difference was always small. It is impossible to distinguish between male and female alates. This is also true for alates of *M. michaelseni* (Darlington 1986). In many cases, females are larger than males (Noirot 1969, Roonwal 1975, Thorne 1983, Matsuura 2006) as females are under consistent selection for high fertility (Boomsma et al. 2005, Husseneder and Simms 2008).

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References Cited

Boomsma, J. J., B. Baer, and J. Heinze. 2005. The evolution of male traits in social insects. *Annu. Rev. Entomol.* 50: 395–420.

Cowie, R. H., J.W.M. Logan, and T. G. Wood. 1989. Termite (Isoptera) damage and control in tropical forestry with special reference to Africa and Indo-Malaysia. *Bull. Entomol. Res.* 79: 173–184.

Darlington, J.P.E.C. 1986. Seasonality in mature nests of the termite *Macrotermes michaelseni* in Kenya. *Insectes Soc.* 13: 168–189.

Husseneder, C., and Simms, D. M. 2008. Size and heterozygosity influence partner selection in the Formosan subterranean termite. *Behav. Ecol.* 19: 764–773.

Lee, C. Y. 2002. Subterranean termite pests and their control in the urban environment in Malaysia. *Sociobiology.* 40: 3–9.

Lee, C. Y., C. Vongkaluang, and M. Lenz. 2007. Challenges to subterranean termite management of multi-genera faunas in Southeast Asia and Australia. *Sociobiology* 50: 213–221.

Matsuura, K. 2006. A novel hypothesis for the origin of the sexual division of labor in termites: which sex should be soldiers? *Evol. Ecol.* 20: 565–574.

Miura, T., Y. Hirono, M. Machida, O. Kitade, and T. Matsumoto. 2000. Caste developmental system of the Japanese damp-wood termite *Hodotermopsis japonica* (Isoptera: Termitidae). *Ecol. Res.* 15: 83–92.

Miura, T., Y. Roisin, and T. Matsumoto. 1998. Developmental pathways and polyethism of neuter castes in the processional nasute termite *Hospitalitermes medioflavus* (Isoptera: Termitidae). *Zool. Sci.* 15: 843–848.

Ngee, P. S., T. Yoshimura, and C. Y. Lee. 2004. Foraging populations and control strategies of subterranean termite in the urban environmental, with special reference to baiting. *Jpn. J. Environ. Entomol.* 15: 197–215.

Noirot, C. 1955. Recherches sur le polymorphisme des termites superieures (Termitidae). *Ann. Sci. Nat. Zool.* 17: 399–595.

Noirot, C. 1969. Formation of castes in the higher termites, pp. 311–350. *In* K. Krishna and F. M. Weesner [eds.], *Biology of termites*, vol. 1. Academic, New York.

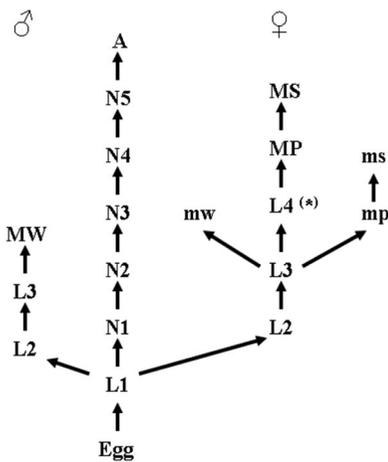


Fig. 6. Caste developmental pathways of *M. gilvus* and *M. carbonarius*. L1–L4, first larval instar to fourth larval instar; N1–N5, first larval instar to fifth larval instar; MW, major worker; MP, major presoldier; MS, major soldier; mw, minor worker; mp, minor presoldier; ms, minor soldier; A, alate; *, only found in *M. carbonarius*.

- Okot-Kotber, B. M.** 1981. Instars and polymorphism of castes in *Macrotermes michaelsoni* (Isoptera, Macrotermitinae). *Insectes Soc.* 28: 233–246.
- Roisin, Y.** 1996. Castes in humivorous and litter-dwelling Neotropical nasute termites. (Isoptera, Termitidae). *Insectes Soc.* 43: 375–389.
- Roisin, Y.** 2000. Diversity and evolution of caste patterns, pp. 95–119. In T. Abe, D. E. Bignell, and M. Higashi [eds.], *Termites: evolution, sociality, symbioses, ecology*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Roisin, Y., and M. Lenz.** 1999. Caste developmental pathways in colonies of *Coptotermes lacteus* (Froggatt) headed by primary reproductives (Isoptera, Rhinotermitidae). *Insectes Soc.* 46: 273–280.
- Roisin, Y., and J. M. Pasteels.** 1987. Caste developmental potentialities in the termite *Nasutitermes novarumhebridarum*. *Entomol. Exp. Appl.* 44: 227–287.
- Roisin, Y., and J. M. Pasteels.** 1991. Polymorphism in the giant cocoa termite, *Neotermes papua* (Desneux). *Insectes Soc.* 38: 263–272.
- Roonwal, M. L.** 1970. Termites of the Oriental Region, pp. 315–384. In K. Krishna and F. M. Weesner [eds.], *Biology of termites*, vol. 2. Academic, New York.
- Roonwal, M. L.** 1975. Sex ratios and sexual dimorphism in termites. *J. Sci. Ind. Res.* 34: 402–416.
- Stewart, A. D., and M. P. Zalucki.** 2006. Developmental pathways in *Microcerotermes turneri* (Termitidae: Termitinae): biometric descriptors of worker caste and instar. *Sociobiology* 48: 727–740.
- Tho, Y. P.** 1992. Termites of peninsular Malaysia. *Malayan For. Rec.* no. 36. Forest Research Institute of Malaysia, Kuala Lumpur.
- Thorne, B. L.** 1983. Alate production and sex ratio in colonies of the Neotropical termite *Nasutitermes corniger* (Isoptera: Termitidae). *Oecologia (Berl.)* 58: 103–109.
- Weesner, F. M.** 1969. The reproductive system, pp. 156. In K. Krishna and F. M. Weesner [eds.], *Biology of termites*, vol. 1. Academic, New York.

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