



**Full Length Article**

# Caste Developmental Pathways in Populations of *Microcerotermes championi* (Isoptera: Termitidae, Microcerotermitinae)

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## ABSTRACT

Caste developmental pathways in the Pakistani termite *Microcerotermes championi* (Snyder) were estimated by measuring body parts. From the size distribution of total body length, maximum width of head, Length of head from side base of mandibles and maximum width of head, indicating that, large worker is preceded by two larval instars (first instar larva & second instar large larva) followed by four successive molts, to become a large mature worker. On the other hand, small worker is also preceded by two larval stages (first instar larva & second instar small larva) followed by three successive molts to transform into a mature small worker. Sexual dimorphism is present in workers. Females are larger than males. The origin of soldier takes place from first instar worker, which after two molts changes into soldier. The first larva differentiates at the first molt either to nymphs or neuter larvae and undergoes five successive molts to become alate. Sexual dimorphism is present in alates. The males are smaller than females. © 2011 Friends Science Publishers

**Key Words:** Developmental Pathways; *Microcerotermes championi*; Worker; Soldier; Alate; Sexual dimorphism

## INTRODUCTION

Caste differentiation is deeply linked to the postembryonic development of insects. However, Hymenoptera and Isoptera have different caste systems, based on different developmental modes (Nijhout & Wheeler, 1982). Morphologically different types of individuals, or castes, are produced by means of ontogenetic regulation, which is affected by extrinsic factors such as interactions among colony members (Noirot, 1991; Miura, 2001). Termites are hemimetabolous insects and the neuter castes may be derived from various developmental stages (Miller, 1969; Noirot, 1969; Watson & Sewell, 1981).

The order Isoptera comprises lower and higher termites (Krishna, 1969). The lower termites comprise six families with symbiotic flagellate protozoans in their hindguts: while majority of the higher termites (Termitidae) lack symbiotic protozoans with tremendous variety of social specializations. In few species of lower termites, there are reversible or totipotent worker castes, able to differentiate into any caste, including reproductives, and have been termed pseudergates, which means 'false workers' (Grassé & Noirot, 1947). In contrast, terminal worker castes lose the capacity to differentiate into reproductives, although they sometimes differentiate into replacement reproductive's

(ergatoid reproductives), and are therefore called true workers. Such true workers are seen in all species of Mastotermitidae, Termitidae and some Rhinotermitidae (Miller, 1969; Noirot, 1969; Watson & Sewell, 1985; Myles, 1999). However, in some species of higher termites, sexual polymorphism in caste differentiation is known (Noirot, 1969; Roisin, 1992, 1996; Miura *et al.*, 1998).

In primitive termites, there are no differences in the caste developmental pathways between sexes, and it is easy to discriminate between sexes using abdominal sternite morphology (Weesner, 1969; Jones & La Fage, 1980; Zimet & Stuart, 1982; Myles & Chang, 1984; Henderson & Rao, 1993). So far, the caste systems of some lower termite species, such as Mastotermitidae and Kalotermitidae, have been well studied (Watson *et al.*, 1975, 1977; Noirot, 1985; Watson & Sewell, 1985; Roisin & Pasteels, 1991). In Termopsidae, being the primitive and relatively basal families (Kambhampati *et al.*, 1996), some studies have focused on the caste developmental pathway of *Archotermopsis* (Imms, 1919), *Stolotermes* (Morgan, 1959), *Porotermes* (Mensa-Bonsu, 1976) and *Zootermopsis* (Heath, 1927; Castle, 1934; Myles, 1986; Hahn & Myles, 1994).

*M. championi* (Snyder) is a higher termite of the family Termitidae. According to (Sands, 1972) the family Termitidae is subdivided into four subfamilies:

Macrotermitinae, Nasutitermitinae, Apicotermitinae and Termitinae. But recently, (Myles, 1998) has further elaborated the status of different taxonomic categories; and according to his interpretation *M. championi* now falls in subdivision Longiprocta, super family Termitidae, family Amitermitidae and subfamily Microcerotermitinae. *M. championi* (Snyder) is widely distributed in India, Bangladesh and Pakistan (Akhtar, 1974a & b, 1975; Sen-Sarma *et al.*, 1975a & b). It attacks decaying stumps of *Shorea robusta*, *Swietenia macrophylla* and standing trees of *Acacia catechu* and *Cassia fistula*. It makes dirt carton type nests at the base of Bamboo stumps and *Saccharum munja* and is a very good research material. Since the first publication by Grassi and Sandias nearly one hundred years ago (1893–1894) on caste determining mechanism in termites, this fascinating subject has attracted the attention of a large number of workers. Among the more important publications on the subject of caste differentiation are those of Watson and Sewell (1981), Myles and Chang (1984), Noirot (1985a), Weesner (1953), Noirot (1955, 1956), Williams (1959a & b), Lüscher (1976), Okot-Kotber (1981a & b, 1985), Noirot (1985b), Roison (2002) and Kenji *et al.* (2010).

The most characteristic pattern, observed in all the species of higher termites so far studied, is the visible separation, at the first molt, of the sexual and the neuter lines (Noirot, 1969). The development of sexuals is related to a precise seasonal cycle, the young nymphs appearing during a limited period of the year, whereas the production of neuter larvae is continuous (Noirot, 1985).

In Pakistan, a detailed study on developmental pathways has been carried by (Shahid, 1991) on fungus growing termites *Odontotermes obesus* (Rambur). There is a paucity of information about developmental pathways for other termite species of Pakistan. Thus, in the present study, we examined the caste composition of natural colonies of the *M. championi* to elucidate the caste developmental pathways in worker line of *M. championi* based on field colonies.

## MATERIALS AND METHODS

**Termites:** Large samples from many nests of *M. championi* were collected from Wagha border, 30 km away from Lahore, Pakistan. These nests contained numerous young nymphs and presoldiers, soldiers, workers and imagoes. Each bulk sample was first divided in categories of individuals recognizable by simple observation under a dissecting microscope (small or large larvae, workers, presoldiers, soldiers, nymphs & alates). Then each category was randomly selected for detailed biometrical studies. taxonomic terms and measurements used in the present study are as described previously (Emerson, 1945; Ahmad, 1950; Akhtar, 1975; Noirot, 1985). To study the origin of worker developmental lines, different characters were measured.

**Measurements:** Total body length (TBL), length of head to sidebase of the mandibles (LHSBM), Maximum width of head. (MWH) and Length of hind tibia. (LHT), Width of pronotum (WP), Length of pronotum (LP), Length of brain (LB), Width of brain (WB) and Length of wing pad (LWP). In nymphs, wing bud length was defined as the distance between the anterior point of junction of the mesonotal sclerite to the intersegmental membrane and the tip of the wing bud. In alates, wing length included the stump (Noirot, 1955). The individuals of an each stage were categorized according to instar and caste, based on the above measurements. Then, the number of antennal segments of individuals in each instar was counted. Only individuals with intact antennae were selected for these measurements. The number of antennal segments was difficult to count in immature instars. If we could see a narrow region in the basal area of antennae, it can be regarded as a gap between segments. This measurement was taken on slides under a Leitz microscope at a magnification of 250×.

**Sexual difference in sternites:** In *M. championi*, it is easy to determine the sex of older instars. As described previously by some researchers (Weesner, 1969), in the female, the seventh abdominal sternite becomes wider than male.

**Statistical analysis:** Numerical data of various characters were analyzed using stat software Minitab Release (Version 15) (Mehmood *et al.*, 2011).

## RESULTS

**Larvae:** Two larval morphs were readily distinguishable by size, hereafter noted L1 and LL 2. The larval instars can be easily distinguished from the large worker instar as the larvae is fragile/inactive and white due to the absence of sclerotization (including mandibles) and the gut appears empty and colorless. Measurements of larvae are shown in Table I and II. Antennal segment. Counts are 9+ in L1 and 10+ in LL2.

**First instar larva (L1):** Head and body whitish, unpigmented, head nearly round; whitish brain mass visible through cuticle; mandibles with hardly any trace of sclerotization. No external sexual characteristics present. Mandibles with apical and first marginal teeth very weakly indicated. Antennae 10-segmented. Length of hind tibia 0.15–0.20 mm. Abdomen with a pair of styli. Measurements are indicated in (Table I).

**Second instar large larva (LL2):** Head and abdomen whitish; unpigmented; head nearly round; Brain area visible through cuticle, brain area reduced. Mandibles unpigmented; inner mandibular side dirty white; rest of the area transparent. Left mandible with apical and first marginal tooth slightly more developed than that of first instar larvae; Notch between first and second marginal tooth in initial stage of development; slightly indicated. Abdomen with pair of styli.

**Table I: Range and mean (in parentheses) of measurements in individuals of the different larvae and Worker instars from *M. championi* nest population. All values are in millimeters. N=10 for each category**

Stage	Total body length	Maximum width of head	Length of hind tibia	Length of head to sidebase of mandibles
L1	0.85–1.30 (1.10)**	0.15–0.20 (0.17)**	0.30–0.40 (0.35)**	0.15–0.20(0.17)**
LL2	1.35–1.45 (1.39)**	0.25–0.30(0.26)**	0.40–0.47(0.43)*	0.22–0.30(0.26)*
SL2	1.25–1.40 (1.30)***	0.15–0.25(0.20)*	0.35–0.45(0.40)**	0.20–0.25(0.23)*
LW1	2.45–2.65 (2.54)**	0.30–0.35(0.33)*	0.55–0.75(0.64)***	0.35–0.45(0.40)**
LW2	2.55–3.10 (2.81)**	0.35–0.40(0.36)**	0.55–0.80(0.75)**	0.42–0.50(0.47)**
LW3	2.95–3.15 (3.01)***	0.40–0.50(0.45)**	0.75–0.85(0.79)**	0.45–0.56(0.50)**
LW4	3.10–3.40 (3.31)*	0.45–0.65(0.54)*	0.85–0.95(0.90)*	0.55–0.60(0.57)***
LW	4.75–4.85 (4.81)*	0.80–1.05(0.92)*	0.90–1.05(0.98)*	0.70–0.80(0.74)*
SW1	1.95–2.40 (2.21)***	0.25–0.30(0.28)***	0.50–0.65(0.59)***	0.30–0.40(0.35)**
SW2	2.45–3.00 (2.84)**	0.30–0.35(0.32)*	0.55–0.70(0.63)*	0.35–0.42(0.40)**
SW3	2.75–3.10 (2.97)*	0.37–0.45(0.41)*	0.65–0.80(0.72)*	0.46–0.48(0.47)*
SW	3.20–3.95 (3.55)	0.40–0.58(0.46)	0.80–0.95(0.89)	0.50–0.70(0.60)

L1-LL2-SL2: larval instars; LW1-LW4: Large worker instars; LW: Large mature worker; SW1-SW3: Small worker instars: small mature worker. When results of t-tests between corresponding measurements of different instars of L1-LL2, larval instars; LW1-LW4, large worker instars; LW, Large mature worker are shown in the table: \*0.05 > P > 0.01; \*\*0.01 > P > 0.001; \*\*\*P < 0.001

**Table II: Range and mean (in parentheses) of measurements in individuals of the different soldier instars from *M. championi* nest population. All values are in millimeters. N = 10 for each category**

Parameters	Pre soldier (PS1)	Mature soldier (MS)	Level of significance
Total Body length	2.75–3.85(3.49)	5.20–5.50(5.29)	*
Length of head to sidebase of mandible	0.75–0.87(0.83)	1.20–1.25(1.22)	***
Maximum width of head	0.82–0.95(0.91)	1.0–1.02 (1.00)	***
Length of pronotum	0.27–0.32(0.30)	0.37–0.40(0.38)	***
Width of pronotum	0.52–0.60(0.57)	0.37–0.48(0.36)	***
Length of brain	0.90–1.02(0.96)	1.37–1.40 (1.38)	***
Width of brain	0.77–0.95(0.89)	0.97–1.02(0.98)	*
Length of hind tibia	0.55–0.67(0.64)	0.72–0.75(0.73)	**

PS1: Pre soldier; MS: Mature soldier: When results of t-tests between corresponding measurements of different Soldier stages of PS1-MS: are shown in the table: \*0.05> P > 0.01; \*\*\*P<0.001

**Development line of large worker:** The large worker passes through 2 larval instars (first larval instar & second large larval instar) followed by four successive instars of large worker. However, the workers contain gut content and therefore appear colored due to some pigmentation. Statistical differences (P<0.05) appeared between different developmental stages, in workers (Table I) as a result of molting to older worker instars.

**First instar large worker (LW1):** The first instar large worker develops from second instar large larva. Head and body slightly brownish yellow; brain area visible and mandibles slightly pigmented. Differentiation of different teeth almost complete; styli much reduced. Length of hind tibia 0.30–0.35 mm.

**Second instar large worker (LW2):** Head slightly darker than abdomen; head with lateral side's semi parallel; mandibles more strongly pigmented; differentiation of teeth more pronounced; styli slightly indicated. Mandibles developing within old cuticle with distinct apical, first and second marginal teeth. Dirty white; length of hind tibia 0.35–0.40 mm.

**Third instar large worker (LW3):** Head round darker than abdomen; lateral sides of postclypeus dark brown; mandibles weakly sclerotized, slightly dark brownish; teeth dark brown with a blackish tinge appearance; length of hind tibia 0.40–0.50 mm.

**Fourth instar large worker (LW4):** Head round darker than abdomen; Mandibles well sclerotized. Darker brownish than third instar large worker. Teeth with blackish tinge. Length of hind tibia 0.45–0.65 mm.

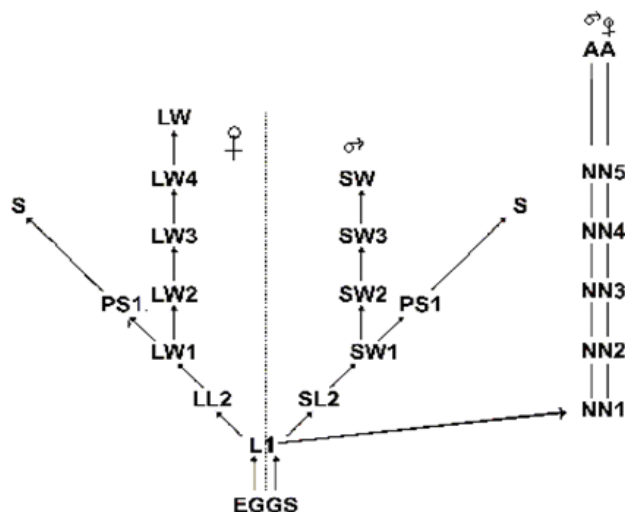
**Large worker (LW):** Head round proportionately more voluminous, yellowish brown; with lateral sides semi-parallel, slightly narrowing posterior, Mandibles strongly sclerotized; dark brown; teeth with blackish tinge. Styli absent, length of hind tibia 0.80–1.05 mm; Tarsi 4-jointed, Antennae 13 articles.

**Developmental line of small worker:** Like the large worker, the small worker passes through two larval and three successive small worker instars before becoming adult (Fig. 1). The first larval stage of large and small worker is common, but second small larval instar differs in size from the corresponding stage in the development of large worker.

**Second instar small larva (SL2):** Head and body whitish, unpigmented. Head nearly round; brain area visible through cuticle, large occupying 3/4 of the whole head capsule. Mandibles unpigmented. Tarsi 4-segmented abdomen with a pair of styli present. Length of hind tibia 0.15–0.25 mm.

**First instar small worker (SW1):** The first instar small worker develops from second instar small larva. Head slightly darker than abdomen; head round; mandibular teeth well developed, yet weakly sclerotized. Abdomen with a pair of styli slightly reduced. Length of hind tibia 0.25–0.30

**Fig. 1: Proposed schema of the caste developmental pathways of *M. championi*. Each arrow indicates a molt. L1-LL2, SL2: Larvae; PS1: Pre-soldier; MS: Mature soldier; LW1-LW4: Large worker instars; LW: Mature large worker; SW1-SW3: Small worker instars; SW: Mature small worker; NN1-NN5: Nymphal instars; AA: Alate**



mm; Tarsi 4-segmented.

**Second instar small worker (SW2):** Head and abdomen slightly darker; more sclerotized; head with lateral sides slightly semi parallel, brain area visible through cuticle reduced, mandibles more differentiated than the first instar small worker; teeth within cuticle more pigmented; tips of mandibles slightly pigmented. Length of hind tibia 0.30–0.35 mm. Styli much reduced. Tarsi 4-segmented.

**Third instar small worker (SW3):** Head and thorax darker than second instar small worker; weakly sclerotized. Mandibles more darkly pigmented than the second instar small worker; teeth completely differentiated. Antenna with 13 articles. Brain area not clearly visible through cutin. Tarsi 4-segmented. Length of hind tibia 0.37–0.45 mm.

**Small worker (SW):** Head yellowish brown; much darker than third instar small worker. Brain invisible. Mandibles much sclerotized with well differentiated notches and fully developed teeth. Antennae with 13 articles. First antennal

segment is much larger than others. Antennal articles with brownish tinge. Styli absent tarsi 4-segment. Length of hind tibia 0.40–0.58 mm.

**Developmental line of soldier:** Recognition of different stages was based both on the qualitative (degree of body pigmentation, shape of head, mandibles etc.) and quantitative differences. The origin of soldier takes place from first instar worker, which after two molts changes into soldier. The various stages of development of soldier are shown in Fig. 1. The statistical difference ( $P < 0.05$ ) appeared in soldier line (average head width of PS1 ranged 0.82–0.95 mm, 1.0–1.02 mm for mature soldier. Similarly, average length of pronotum of PS1: 0.27–0.32 mm, 0.37–0.40 mm for mature soldier; average length of hind tibia for PS1: 0.55–0.67 mm, 0.72–0.75 mm for mature soldier (Table II).

**First instar pre-soldier:** Head and abdomen whitish; head nearly round. Mandibles elongated, with a minute denticle below apical portion. Other serration not visible. Tips of mandible slightly pigmented. Abdomen with a pair of styli, antennae 12 segmented. Length of brain 0.90–1.02 mm, width of brain 0.77–0.95, length of hind tibia 0.55–0.67 mm. Tarsi, 4-segmented (Table II).

**Mature soldier:** Head elongated, parallel sided; fully sclerotized. Mandibles darkly pigmented reddish brown. Antennae yellow with brownish tinge; head sparsely hairy; mandibles well built, coarsely serrated; outer margin convex; tips moderately incurved. Antennae with 13-articles; second twice as long as third, latter shortest. Pronotum saddle shaped; anterior margin slightly notched, posterior margin almost straight. Length of hind tibia 0.72–0.75 mm. Tarsi-4-segmented.

**Developmental line of alate:** The differentiation of alate line begins from the first instar larvae which after five molts transformed into alate. The statistical difference ( $P < 0.05$ ) appeared in alate line (average head width of N1 ranged: 0.80–0.85 mm, 0.87–0.90 mm for N2, 0.92–0.94 mm for N3, 0.97–0.98 mm for N4, 0.99–1.00 mm for N5, 1.02–1.10 mm for alate. Similarly, average length of wing pad of N1 ranged: 0.80–1.05 mm, 1.12–1.34 mm for N2, 1.38–1.96 mm for N3, 2.04–2.07 mm for N4, 2.16–2.85 mm for N5, 3.18–3.45 mm for alate. Average length of pronotum of N1 ranged: 2.28–2.36 mm, 2.40–2.48 mm for N2, 2.52–2.58

**Table III: Range and mean (in parentheses) of measurements in individuals of the different nymphal instars from *M. championi* nest population. All values are in millimeters.  $N = 10$  for each category**

Parameters	N1	N2	N3	N4	N5	A
Total Body length	3.35–4.10 (3.62)	4.25–4.75 (4.50)	4.80–5.20 (5.00)	5.30–5.45 (5.37)	5.50–5.75 (5.62)	5.80–5.85 (5.82)
Length of head to sidebase of mandibles	0.40–0.45 (0.42)	0.48–0.50 (0.49)	0.52–0.54 (0.53)	0.57–0.60 (0.58)	0.62–0.64 (0.63)	0.68–0.75 (0.71)
Maximum width of head	0.80–0.85 (0.82)	0.87–0.90 (0.88)	0.92–0.94 (0.93)	0.97–0.98 (0.97)	0.99–1.00 (0.99)	1.02–1.10 (1.06)
Length of wing pad	0.80–1.05 (0.38)	1.12–1.34 (1.23)	1.38–1.96 (1.67)	2.04–2.07 (2.04)	2.16–2.85 (2.50)	3.18–3.45 (3.31)
Length of pronotum	2.28–2.36 (2.32)	2.40–2.48 (2.44)	2.52–2.58 (2.55)	2.61–2.66 (2.63)	2.68–2.74 (2.71)	2.76–2.81 (2.78)
Width of pronotum	0.62–0.67 (0.64)	0.71–0.76 (0.73)	0.94–0.99 (0.96)	1.04–1.16 (1.10)	1.28–1.39 (1.33)	1.27–1.42 (1.34)
Length of hind tibia	0.65–0.70 (0.67)	0.74–0.79 (0.76)	0.82–0.85 (0.83)	0.91–0.94 (0.92)	0.99–1.06 (1.02)	1.05–1.15 (1.10)

N1-N5: nymphal instars; A: Alate; When results of t-tests between corresponding measurements of different nymphal instars are shown in the table: \* $0.05 > P > 0.01$ ; \*\*\* $P < 0.001$  (0.88)

mm for N3, 2.61–2.66 mm for N4, 2.68–2.74 mm for N5, 2.76–2.81 mm for alate. The various stages of development of alate line are represented in (Table III).

**First instar nymph:** Head and abdomen whitish; brain area much reduced; mandibles with apical and first marginal teeth slightly indicated. Meso and metathorax with minute wing pads. Tarsi-4-jointed.

**Second instar nymph:** Head and abdomen whitish; brain area much reduced; Mandibles with apical and first marginal teeth more distinct. Meso and metathorax with distinct wing pads. Tarsi-4-jointed.

**Third instar nymph:** Head and abdomen whitish; brain area broader than first instar; teeth of mandibles pigmented; Meso and metathorax with distinct wing pads. Tarsi-4-jointed.

**Fourth instar nymph:** Brain area much larger than third instar nymphs. Differentiation of teeth more pronounced, more darkly pigmented. Wing pads longer than third instar nymphs. Tarsi-4-jointed.

**Fifth instar nymph:** Brain area large, almost occupying the whole area between antennae; wing pads whitish, extending up to ¼ of abdomen; eyes weakly indicated. Tarsi-4-jointed.

**Alate:** Head dark brown; postclypeus slightly lighter than head; anteclypeus whitish; labrum light brown; antennae brown with smoky tinge. Pronotum almost as dark as head; with whitish median streak; Legs light brown; abdominal tergites brown with reddish tinge, slightly lighter than pronotum. Head with many short hairs and few scattered long bristles; postclypeus with a few bristles and short hairs, slightly less hairy than head; pronotum slightly more hairy than head; head with lateral sides almost parallel; posterior margin slightly convex in middle. Fontanelle small circular Y-suture present. Eyes slightly bulging sub-circular. ocelli broadly oval. Separated from eyes by their long diameter. Postclypeus swollen, slightly more than twice as wide as long. Anteclypeus trapezoid. Antennae with 14 articles; second twice as long as third, latter shortest. Pronotum narrower than head; anterior margin slightly convex in middle; posterior margin shallowly depressed in middle. Tibial spurs 3:2:2; mid tibia with two thin extra spines. Tarsi-4-jointed.

## DISCUSSION

In the large family termitidae, the separation of various castes is much more pronounced than in the lower termites. Workers, which are very distinct from larvae and nymphs are always present (Noirot, 1955). Polymorphism occurs in both workers and soldiers. Caste system has been most extensively studied in two families, the Kalotermitidae and termitidae (Roisin, 2000). According to (Hadorn, 1967) caste differentiation is the programming of developmental potential by activation of specific genes. Juvenile Hormone (JH) is at the base of this control in caste polymorphism. Extrinsic control of caste determination is mediated through the environmental impact of juvenile hormone. In case of

higher termites, the most characteristic pattern observed in all the species so far studied, is the visible separation, at the first molt, of the sexual and neuter lines (Noirot, 1955 & 1969). In the following section we will discuss the developmental patterns of worker castes of *M. championi*.

The generalized developmental schema of the termitidae differs from that of Kalotermitidae in some major respects. The most noteworthy of these is the presence of an irreversible decision point separating two developmental lines at the first molt. These lines have been called sexual and neuter (Noirot & Pasteel, 1987). In the Macrotermitinae the workers are preceded by three larval stages, in all of the other subfamilies there are only two. When the males and females differ in size and this difference is apparent in the second stage (Noirot, 1955). Workers are preceded by two larval stages in all the Termitidae except, the fungus growing Macrotermitinae, in which workers are preceded by three larval instars (Noirot, 1985b). In termitinae the larvae and workers do not possess any sexual dimorphism (or else it is very slight, as in *Thoracotermes*). There is a tendency toward a reduction of number of stages of workers. In *Termes hospes* the workers can pass through three successive stages, but there is only one stage in the genera, *cubitermes*, *Noditermes*, *Pericapritermes*, *Orthotermes*, *Euchilotermes*, *Ophiotermes* and *Neocapritermes*. (In Apicotermitinae the workers are of single stage & their sexual dimorphism is not very marked) (Roisin, 2000) also studied diversity and evolution of caste patterns and reported that workers of either sex in genus *Microcerotermes* can go through at least four instars which differ slightly by size and pigmentation. Females are larger than males.

Present studies on developmental line of worker caste of *M. championi* also exhibit sexual dimorphism in workers. Females are larger than males. The large worker passes through two larval instars (First larval instar & second large larval instar) followed by four successive instars of large worker. On the other hand, the small worker comprises two larval instars (First larval instar & second small larval instar) followed by three successive instars of small worker. Our present findings are in agreement with the (Noirot, 1955 & 1969; Roisin, 2000).

Almost all of the termite species possess a soldier caste, which is believed to have evolved only once in the whole termite clade and the ancestor of Isoptera should already have had soldiers (Roisin, 1999 & 2000). Therefore, there must be some ubiquitous mechanisms of soldier differentiation throughout isopteran species. In comparison with the other social insects, moreover, there is no equivalence with soldier castes in termites. Soldiers of most termite species possess enlarged mandibles and attack against predators with biting (Weesner, 1969). However, soldiers in the subfamily Nasutitermitinae (Termitidae) have a frontal projection, called a “nasus”, from which a defensive terpenic substance is secreted (Prestwich, 1983). In either case, there must be the developmental mechanisms

making the soldier-specific morphology through only two molting events: from previous larval or worker stage to presoldier, and from presoldier to soldier. However, the previous stage from which presoldiers molt is diverse according to the termite taxa. For example, soldiers differentiate from pseudergates in many lower termite species (Miller, 1969; Noirot & Pasteels, 1987; Miura *et al.*, 2000). While in higher termites and parts of lower termites, soldiers differentiate from sterile larval individuals or from functional worker stages (Noirot, 1969).

In the termitidae, the origin of soldier is generally fixed and the stage at which they appear is very precise for each species. As is true in all termites, the differentiation of soldier occurs in two steps. The soldier is preceded by a stage, which is larval in form (lacking pigment & unsclerotized), but with the morphological trait of the soldiers. This is the "white soldier". The duration of this stage is very short generally about 2 weeks and one week in *Nasutitermes ephratae* (Holmgren), at least in the young colonies (Becker, 1961 & 1963). Very frequently the white soldier arises from a worker (Emerson, 1926; Bathellier, 1927; Light & Weesner, 1947; Noirot, 1955; Kaiser, 1956; Knowler, 1894), but in other cases it develops from larva (Bathellier, 1927; Weesner, 1953; Noirot, 1955; Becker, 1961a & 1963). These two origins may coexist in a single species. Some examples indicate that, in the majority of species there does not appear to be a special line, giving rise to the soldiers. The workers that become soldiers are true worker in morphology and behaviour and when the soldier arises from larva, these are identical with the larvae of the workers. However, this is not the case in some species, in which after the first larval molt, there is a distinct group of stage II larvae, which give rise to the white soldier at the subsequent molt [*Anacanthotermes acanthothorax* (Sjostedt), Noirot, 1955] or after an additional larval stage [*Tenuirostritermes tenuirostris* (Desneux), Weesner, 1953; *Ternervitermes* spp.; & Noirot, 1955).

In termitinae, the soldiers arise from workers. The soldiers are almost always females, although they are males in *orthotermes depressifrons* silvestri. (In Apicotermitinae, the soldiers are monomorphic and develop from female workers. In Macrotermitinae, two categories of soldier frequently occur; large one, derived from small workers, and small ones, derived from stage three larvae (*Macrotermes*, *Bellicositermes*, *Ancistotermes*, *Pseudacanthotermes*). Roisin (2000) reported that soldiers in termitidae derive in two molts from worker of either sex or sometimes from apterous larvae. Most soliders come from first instar worker, although later instars are probably able to produce soldiers as well as reported by Noirot (1955).

Present studies on *M. championi* (Isoptera: Termitidae) the soldier developmental line is an off-shoot from first instar worker of either sex, which after two molt transforms into a soldier. Other species of genus *Microcerotermes* studied so far show unique developmental

pathways in solidier caste. The current results are in agreement with that of Noirot (1955) and Roisin (2000) findings on developmental pathways.

As in lower termites, the colony of higher termites (family Termitidae) is normally headed by a pair of dealated imagines (the king & the queen), which have founded the society after swarming. The replacement of the imaginal (or primary pair) is so frequently observed in most of the lower termites, seems much less easy in higher termites, and very variable according to species (Noirot, 1955).

The alates of higher termites develop through five nymphal instars (defined as such by the presence of wing buds) and this "Imaginal line" is morphologically individualized at the molt of first instar (undifferentiated) larva. In other words, the separation of the "imaginal line" is the molt of first instar larva (presence or absence of wing buds) (Noirot, 1969).

In higher termites, the post embryonic development of the imagoes appears to be very uniform. Most authors agree that six stages preceded the imaginal molt, and the alates are of the seventh stage (Bathellier, 1927; Noirot, 1952a; Weesner, 1953; Bouillon & Mathot, 1964; Hecker, 1966). In *M. bellicosus* five nymphal instars have been recorded by Luscher (1976). Noirot (1955) and Roisin (2000) also reported that alates in genus *Microcerotermes* also develop after five nymphal instars molt. Present studies on *M. championi* revealed that the first larva differentiate at the first molt either to nymphs or neuter larvae and undergoes five successive molts to become alate. Sexual dimorphism is present in alates. The males are smaller than females.

It is concluded that large worker is preceded by two larval instars (first instar larva & second instar large larva) followed by four successive molts, to become a large mature worker. Where as, small worker is preceded by two larval stages (first instar larva & second instar small larva) followed by three successive molts to transform into a mature small worker. Sexual dimorphism is present in workers. Females are larger than males. The origin of soldier takes place from first instar worker, which after two molts changes into soldier. The first larva differentiates at the first molt either to nymphs or neuter larvae and undergoes five successive molts to become alate. Sexual dimorphism is present in alates.

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