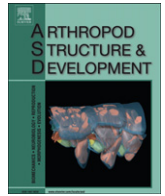




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Postembryonic development of the unique antenna of Mantophasmatodea (Insecta)

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ABSTRACT

The postembryonic antennal development and life cycle of a member of the insect order Mantophasmatodea (*Lobatophasma redelinguysense*) was investigated using a series of annulus counts and a time sequence of head capsule measurements. The life cycle comprised six instars. Females achieved significantly larger head capsules from instar 2 onwards, resulting in adult females having a larger mean head capsule diameter (2.58 mm) than males (2.27 mm). Antennae of first instar larvae comprised a smooth four-segmented basiflagellum and a seven-segmented, sensilla-rich distiflagellum. Lengthening of the basiflagellum was achieved by the addition of two annuli per moult, generated by division of the basal annulus (meriston). Annulus number and the unique annulation pattern of the distiflagellum remained constant until adulthood. The segmentation pattern of adult antennae (comprising a basiflagellum and a distiflagellum of 14 and seven annuli respectively) and mode of antennal elongation was consistent for all 11 species examined. Subdivisions in basiflagellar annuli were observed in adults of all species examined, although they are not considered to be true annular divisions. The structure of the mantophasmatodean antenna appears to be autapomorphic within Insecta, bearing little resemblance to that of Grylloblattodea, Dictyoptera or Phasmatodea, all putative sister groups of the Mantophasmatodea. However, the mode of flagellar elongation most closely resembles that of Isoptera, Blattaria and Dermaptera.

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1. Introduction

The insect order Mantophasmatodea (Heelwalkers, Gladiators) was first described by Klass et al. (2002) nearly a century after the description of the last insect order, Grylloblattodea. To date eight described and four undescribed species have been recorded from South Africa (Picker et al., 2002; Klass et al., 2003a, b; Damgaard et al., 2008), seven species have been described from Namibia (Klass et al., 2002, 2003a; Zompro et al., 2002, 2003; Zompro, 2005; Zompro and Adis, 2006), and one from Tanzania (Klass et al., 2002). In addition, four fossil species from Baltic amber and one from the Jurassic belong to the order (Zompro, 2001; Engel and Grimaldi, 2004; Arillo and Engel, 2006; Zompro, 2008a; Huang et al., 2008).

The Mantophasmatodea clearly belong to the clade Neoptera (Klass et al., 2002). They are distinguished from other neopteran orders by a number of apomorphies (Klass et al., 2003a; Klass and Eulitz, 2007; Baum et al., 2007), of which a dorsal projection of the tarsi, an upcurved course of the subgenal sulcus, a projecting

drumming organ on the male subgenital plate, and a highly specialised antennal structure are most striking. A number of morphological and molecular studies have attempted to identify the phylogenetic position of Mantophasmatodea within Neoptera (summary in Damgaard et al., 2008). However, this must be viewed in the context that the relationships among the principal lineages of Neoptera are generally widely unresolved, with many conflicting hypotheses proposed in recent years (summary and discussion in Klass, 2007a, b).

On the morphological side, the presence of “connecting bands” in the flagellum of the spermatozoa supports a clade comprising Mantophasmatodea, Grylloblattodea, Dictyoptera and Orthoptera (Dallai et al., 2003, 2005). A sister group relationship between Mantophasmatodea and Grylloblattodea is vaguely indicated by a few characters most of which, however, show a high degree of homoplasy across the Insecta: various embryonic features (Machida et al., 2004), ovariole morphology and ultrastructure (Tsutsumi et al., 2005), similarities in the mandibles (Baum et al., 2007) and proventricle (Klass et al., 2002), and absence of wings and ocelli (Beutel and Gorb, 2006). A special inner transport epithelium in the basal part of the antennal vessel wall (Pass et al., 2006) and the structural pattern of the right part of the

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(asymmetrical) male genitalia (Klass et al., 2003a) could be synapomorphies of Mantophasmatodea and Dictyoptera. On the other hand, Phasmatodea and Mantophasmatodea share a projecting sclerite above the male genitalia (Klass et al., 2003a). Zompro (2005) concluded that Orthoptera are sister to Mantophasmatodea, but the study avoids cladistic theory and detailed character evaluation (see Zompro, 2008b: p. 24 for a far-reaching rejection of phylogenetic methodology by this author). Among the relevant molecular studies, Terry and Whiting (2005) as well as Kjer et al. (2006) (both also including a morphological character matrix) obtained a sister group relationship between Mantophasmatodea and Grylloblattodea. Cameron et al. (2006), using a smaller taxon sample and entire mitochondrial genomes, obtained a sister group relationship between Mantophasmatodea and Phasmatodea. Thus the Grylloblattodea, Dictyoptera and Phasmatodea presently appear as the best candidates to be the sister group of Mantophasmatodea, but the evidence is highly conflicting (Damgaard et al., 2008; Klass, 2007a, b).

The life history stages and postembryonic development of Mantophasmatodea are virtually unknown. Such information could contribute to an understanding of the interordinal relationships of Mantophasmatodea. In particular, the antennae are complex structures, which undergo considerable postembryonic morphogenesis. The mode of morphogenesis of these organs might provide useful autapomorphies for Mantophasmatodea (as their final structure already did: Klass et al., 2003a) and characters for future phylogenetic studies of neopteran relationships.

In the 'polyneopteran' taxa, the simplest (and most likely plesiomorphic) of the three modes of antennal development involves exclusively the division of the first annulus of the flagellum (meriston) into two or three annuli at each moult, which do not undergo any further division; the antenna is thus lengthened from near its base. Non-dividing annuli known as singletons are present from the first instar. This mode of antennal growth has been documented in the Isoptera (Fuller, 1920), some Blattaria (Blattidae), Zygentoma, Ephemeroptera and Plecoptera (Qadri, 1938) and in the Dermaptera (Davies, 1966). In the second and more complex mode of antennal development, three distinct annular zones (meriston, meristal annuli and singletons) can be defined within the antennal flagellum. The meriston divides at each moult to produce a varying number of meristal annuli (doublets), which each undergo one further subdivision at the subsequent moult. The remaining annuli (singletons) are present from the first instar, and never divide (Campbell and Priestley, 1970). This mode of antennal growth is found in some Blattaria (Blattidae – Schafer and Sanchez, 1973; Blaberidae – Schafer, 1973) and Mantodea (Bugnion). In the third mode of antennal growth (Orthoptera – Burnett, 1951) the meristal annuli are not only derived from the division of the most basal annulus (meriston) but instead from several basal or even all annuli in the flagellum of the first instar. This is recorded in Phasmatodea (Roth, 1917), where all annuli of the flagellum divide at least once and singletons are thus absent.

Mantophasmatodea have a unique antennal structure (Klass et al., 2003a; Drilling, 2005). The flagellum is divided into a basal and a distal region (basi- and distiflagellum respectively). In the species studied by Klass et al. (2003a), the basiflagellum was found to consistently comprise 14 annuli separated by "strong articulations". In addition, however, the distal annuli of the basiflagellum show a further subdivision into a basal and a distal 'sub-annulus' by a "weak articulation". The distiflagellum consistently comprises seven annuli, the first of which is long and the second very short. The following five annuli are shorter than the first and decrease in size successively towards the distal end of the flagellum. In the counting of annuli in Klass et al. (2003a), both the basal and distal sub-annulus of a subdivided annulus were included as separate units in order to document differences between specimens.

Here we provide the first detailed description of the life cycle of the Mantophasmatodea, and track the development of the pronounced adult size dimorphism characteristic of all Mantophasmatodea. In addition we describe in detail the ontogenetic development and structural changes of the mantophasmatodean antenna.

2. Materials and methods

2.1. Collection and rearing

Putative first instar nymphs of *L. redelinghuysense* were collected from two separate populations in the winter rainfall region of the Western Cape Province, South Africa. Nine females and six males were collected on 11 June 2002, 13 days after the first heavy autumn rains 4 km north of Redelinghuys (32.46°S, 18.55°E) from Sandveld vegetation in the fynbos biome. A further 12 females and 21 males of the same species were collected on 31 May 2005, approximately 20 days after the first winter rains in mountain fynbos in the same biome near Citrusdal (32.66°S, 19.22°E). Both sites had been visited at intervals before the first autumn rains, when no nymphs were found to be present. All insects were captured by beating or sweeping vegetation. In the laboratory nymphs were reared individually in small plastic containers, and supplied with water-soaked paper towelling and a daily provision of small leafhoppers, termites and fruit flies. Nymphs were maintained at a constant temperature of 22 °C, with a natural light:dark cycle. Nymphs were sexed by the presence or absence of ovipositor lobes on the post-abdominal segments.

The following additional preserved material was used for comparative purposes. Nymphs of the Namibian species *Praedatophasma maraisi* (Brandberg Massif, Erongo District, Namibia, 21.15°S, 14.58°E, 15 May 2003) and *Sclerophasma pesisense* (Paresisberge, Otjiwarongo District, Namibia 20.36°S, 16.28°E, May 2002) were reared from egg pods. Diapause was broken using a cold period followed by increased moisture and rising temperatures, resulting in staggered emergence over a period of 6 weeks. Additional South African species examined included *Namaquaphasma ookiepense* (Garies, Northern Cape Province, South Africa, 30.56°S, 17.99°E, 2 September 2004), *Karoophasma biedouwense* (Biedouw Valley, Western Cape Province, South Africa, 32.08°S, 19.25°E, 7 October 2006), *Hemilobophasma montaguense* (Montagu, Western Cape Province, South Africa, 33.77°S, 20.13°E, 25 August 2006), *Austrophasma rawsonvillense* (Montagu, Western Cape Province, South Africa, 33.77°S, 20.13°E, 25 August 2006), *Austrophasma gansbaaiense* (Grootbos, Western Cape Province, South Africa, 34.54°S, 19.41°E, 4 October 2006), an undescribed species ('Austrophasmatidae sp.n. 1' in Damgaard et al., 2008; Hillandale, Beaufort West district, South Africa, 31.95°S, 22.76°E, 22 August 2003) and a further undescribed species ('Austrophasmatidae sp.n. 3' in Damgaard et al., 2008; Clanwilliam Dam, Western Cape Province, South Africa, 32.22°S, 18.85°E, 18 September 2006). Specimens of *Tanzaniophasma* sp. were kindly provided by C. Martin (Cape MacClear, Malawi, 13.97°S, 34.82°E, 20 January 2007).

2.2. Measurements and statistics

For the laboratory-reared *L. redelinghuysense* nymphs collected from Redelinghuys, individual head-width measurements (taken transversely across the broadest point of the head to the outer edge of the eyes) were taken irregularly at 2–5 day intervals. Number of antennal annuli and similar head-width measurements were recorded every second day for all *L. redelinghuysense* Citrusdal specimens. When taking measurements, nymphs were immobilised in a folded plastic film. In both instances, measurements were made using micrometer eyepiece readings on a Wild L8 (Leica)

stereomicroscope at 120 and 250-x magnification, and converted to millimetres. For the antennal count, the number of annuli in both the basiflagellum (excluding the scape and the pedicel) and the distiflagellum was recorded. The smooth basiflagellar annuli were easily distinguished from the densely setose distiflagellar annuli (Klass et al., 2003a; Drilling, 2005). The presence of an exuvium in the rearing container or a sudden increase in head-width or basal annulus number was indicative of a change of instar (exuviae were frequently eaten).

A *t*-test was performed to compare male and female head-width measurements at each stage of development and to determine if males and females experienced different degrees of growth one instar to the next. The growth of each specimen from one instar to the next was determined by subtracting the average head-width measurement for one instar (individual readings taken at 2-day intervals) from the average value for the following instar. To determine the overall growth rate each measurement was plotted against time in a linear plot, and the slope of the line interpreted as rate of growth. A *t*-test comparing slopes of two lines (Zar, 1999) was used to evaluate between-sex growth rates.

2.3. Light and scanning electron microscopy

The antennae of selected, alcohol-preserved specimens were examined under a Wild m400 photomicroscope and photographed with an Axiocam digital camera, to record the presence of developing annuli within the meriston. A few specimens of both sexes and representing each instar were killed by freezing and prepared for Scanning Electron Microscopy (SEM) of the antennae by fixation in a 2.5% glutaraldehyde phosphate buffered fixative for 5–6 h. Fixed specimens were washed in phosphate buffer solution, serially dehydrated and stored in pure ethanol. Dehydrated specimens were critical point dried, mounted, carbon coated and observed under a Stereoscan S440i (Leica) scanning electron microscope.

3. Results

3.1. Establishing morphological markers for the various instars

First instar *S. pesisense* and *P. maraisi* nymphs reared from egg pods in the laboratory had four annuli in the basiflagellum of their antennae. In addition, the smallest *L. redelinguysense* and *K. biedouwense* nymphs collected in the field had the same number of annuli in the basiflagellum. No nymphs were ever noted to have less than four annuli in the basiflagellum. Thus, the presence of four annuli in the basiflagellum was used to indicate first instar nymphs for all species. Further observations in laboratory-reared *L. redelinguysense* specimens (below) indicated that two annuli are added to the basiflagellum at each moult. Thus second instar nymphs were identified by the presence of six annuli in the basiflagellum, third instar by the presence of eight annuli and so on.

3.2. Number of instars and size dimorphism

Using the above criteria, first instar nymphs were identified among the *L. redelinguysense* specimens collected from Redelinguys, while all the *L. redelinguysense* specimens from Citrusdal were identified as second instar nymphs. The growth of the Redelinguys specimens was monitored for approximately 48 days. During this period six females and one male reached the fifth instar, but no specimens reached adulthood. The growth of the Citrusdal specimens was monitored for approximately 55 days. During this period five females and nine males reached adulthood, passing through five instars including the adult (Fig. 1). Given that the latter trial was initiated with second instar nymphs, it is evident that the life cycle consists of six instars. During each instar head-width

measurements remained constant, opposed to the dramatic increase occurring after a moult (Fig. 1).

Female *L. redelinguysense* from the Citrusdal population were significantly larger than the males at each stage of development (Table 1; but first instar unknown). The females from Redelinguys were only significantly larger than the males in the second instar (Table 1). In addition, for certain instar transitions, female *L. redelinguysense* specimens grew more (i.e. experienced a significantly greater increase in headwidth diameter) than males (Redelinguys specimens: instar 1–2: *t*-test, $P = 0.032$; Citrusdal specimens: instar 3–4: *t*-test, $P < 0.001$; instar 4–5: *t*-test, $P < 0.001$).

For the entire period of observation, females from Citrusdal and Redelinguys had a faster growth rate than the males, however this difference was not significant (Citrusdal: slope of female growth curve = 0.0059, slope of male growth curve = 0.0052, $P > 0.05$; Redelinguys: slope of female growth curve = 0.0226, slope of male growth curve = 0.0137, $P > 0.05$).

3.3. Antennal development

The antennae of first instar *L. redelinguysense* comprised four annuli in the basiflagellum and seven annuli in the distiflagellum (Fig. 2, Table 2). Throughout development the seven annuli of the distiflagellum remained constant in number, while the basiflagellum increased in length by the addition of two annuli at each moult (Fig. 2, Table 2). In addition to the laboratory-reared *L. redelinguysense* specimens, all other mantophasmatodean nymphs examined always had an even number of annuli (4–12) in the basiflagellum and seven annuli in the distiflagellum (Table 2). The adult antennae of all the species examined had 14 annuli in the basiflagellum and 7 annuli in the distiflagellum. A different number of basiflagellomeres (13) occurred only in three cases and then only on one side of the body, and was due to some deformation (see below for distiflagellomeres).

In *L. redelinguysense* it was possible to determine that the two new annuli were derived from the division of the most basal annulus of the basiflagellum, which thus constitutes a meriston. In the fifth instar antenna two light zones were visible within the meriston dividing this first annulus into three new annuli (Fig. 3). The lengthening of the antennae at each moult was due to both the lengthening of the individual annuli that were present from the first instar in both the basi- and distiflagellum (Fig. 2, stepped lines 1 and 2) and the growth of the new annuli derived from the meriston during the previous moult (Fig. 2, stepped lines 2 and 3). The annuli of the distiflagellum retained their original relative sizes as they lengthened throughout development. The meriston was found to decrease in length from the first instar to adulthood, though this first annulus was always larger than the next, second annulus of the basiflagellum (Fig. 2).

Only during the final moult from the fifth instar to adulthood in *L. redelinguysense*, were secondary subdivisions formed in the distal annuli of the basiflagellum. Under transmitted light it was possible to see these developing subdivisions as light zones within the annuli of a fifth instar specimen (Fig. 3), indicating a significant change in the structure of the annulus in the area of the subdivision. SEM observation of the antennae revealed that the secondary subdivisions were very different in external appearance to the primary divisions that separated successive annuli. While the divisions between the most distal annuli of the basiflagellum appear as clear constrictions involving a membrane, secondary subdivisions were only visible as a change in the texture of the exoskeleton (Fig. 4). The position of the most basal secondary subdivision within the adult basiflagellum varied within individuals (left versus right antenna), and between individuals of the same species. This variation was also noted in the ten additional species examined (Table 2).

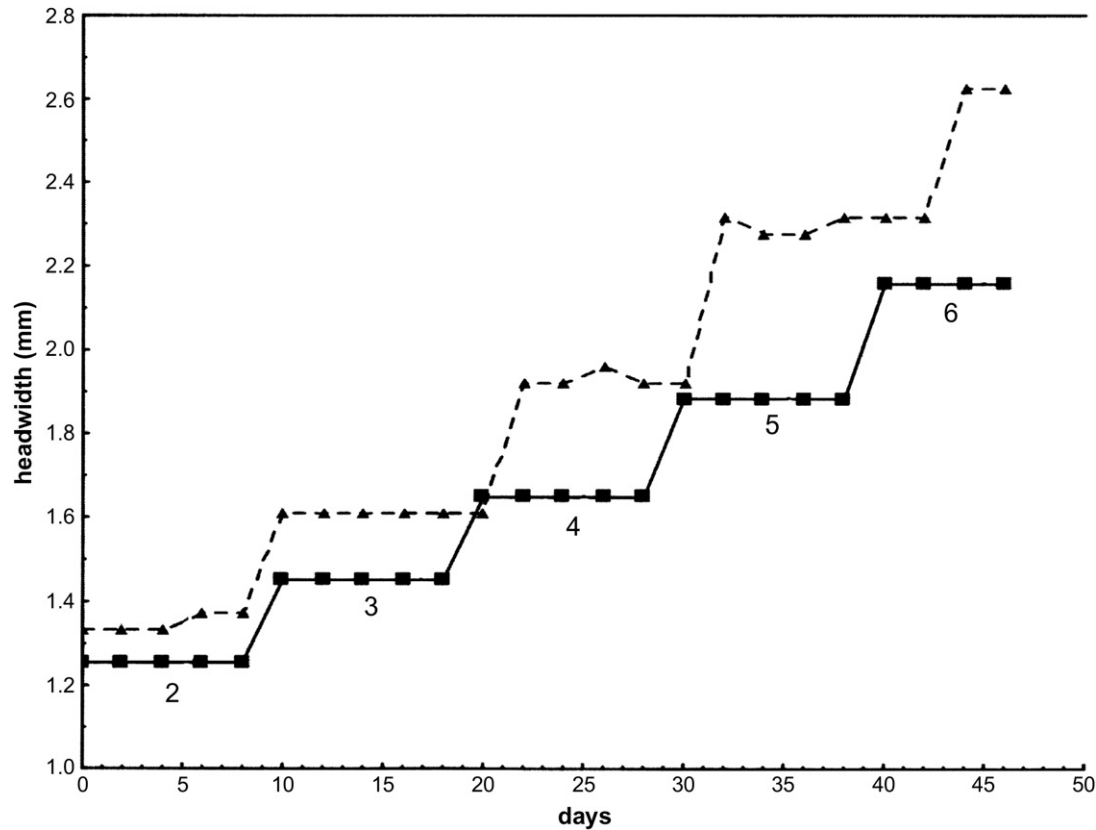


Fig. 1. Progression of development from instar 2 to instar 6 (=adult) for a representative laboratory-reared female (▲) and male (■) *L. redelinghuysense* specimen from Citrusdal. Each triangle or square represents a single measurement. The plateaus indicate within-instar measurements, while the ascending lines indicate rapid growth following a moult from one instar to the next. The numbers indicate instars 2–6. The females had a larger head-width than the males at every stage of development.

4. Discussion

4.1. Life cycle and growth

Hatching of Mantophasmatodea is initiated by the first rains of the season. In the South African species emergence from the resistant egg pod is triggered by the first autumn rains and the life cycle is completed in early spring, when the rains subside. Tojo et al. (2004) reported that *K. biedouwense* (from the semi-arid succulent karoo biome) reached adulthood after four moults, over a period of about 3 weeks. In this study, *L. redelinghuysense* from the more mesic fynbos biome reached maturity after five moults (five nymphal instars), with the postembryonic development extending over almost 2 months. Tojo et al. (2004) suggested that life cycle duration of Mantophasmatodea might be influenced by climate. However, it is unlikely that the minor differences in climate between the succulent karoo and the fynbos biomes would result in such a drastic difference between the life cycles of the two species.

It is more likely that Tojo et al. (2004) initiated rearing with second rather than first instar nymphs (no counts of antennal annuli reported). Our data for mantophasmatodean antennal structure strongly supports a consistent life history pattern of six instars for all eleven species examined (including *K. biedouwense*), where the smallest nymphs had four and the adults 14 basiflagellar annuli. As demonstrated for *L. redelinghuysense*, basiflagellar annulus number is a good indicator of instar, with four annuli indicating a first instar nymph, six annuli indicating a second instar nymph and so on. Five moults are thus required to accumulate the observed number of 14 basiflagellar annuli in adults.

By instar 6 (adult), females were considerably larger than the males, a trend also noted by Klass et al. (2003a). This size dimorphism was evident in all species examined in this study, and is likely associated with fecundity selection in female insects. This study showed that sexual size dimorphism was already evident in the very early stages of postembryonic development. While size dimorphism was not evident in the first instar, females grew faster

Table 1

The average head-width (mm \pm SD) of each instar of female and male *L. redelinghuysense* from Redelinghuys and Citrusdal

Population		Stage of development					
		Instar 1	Instar 2	Instar 3	Instar 4	Instar 5	Adult
Redelinghuys	Female	1.07 \pm 0.12 (7)	1.24 \pm 0.03 (9)*	1.45 \pm 0.05 (9)	1.76 \pm 0.06 (9)	2.09 \pm 0.04 (6)	–
	Male	1.04 \pm 0.00 (5)	1.18 \pm 0.04 (6)	1.48 \pm 0.17 (2)	1.76 (1)	1.84 (1)	–
Citrusdal	Female	–	1.35 \pm 0.03 (12)*	1.59 \pm 0.03 (12)*	1.90 \pm 0.04 (8)*	2.27 \pm 0.06 (6)*	2.58 \pm 0.13 (5)*
	Male	–	1.32 \pm 0.04 (20)	1.53 \pm 0.05 (19)	1.73 \pm 0.07 (13)	2.01 \pm 0.09 (12)	2.27 \pm 0.11 (9)

Numbers in parentheses indicate the number of individuals measured. Citrusdal specimens were collected in instar 2, while none of the specimens from Redelinghuys reached adulthood. *Denotes significant differences between the female and male head-width measurements for each population at the indicated stage of development (*t*-test, $P < 0.05$ for all comparisons).

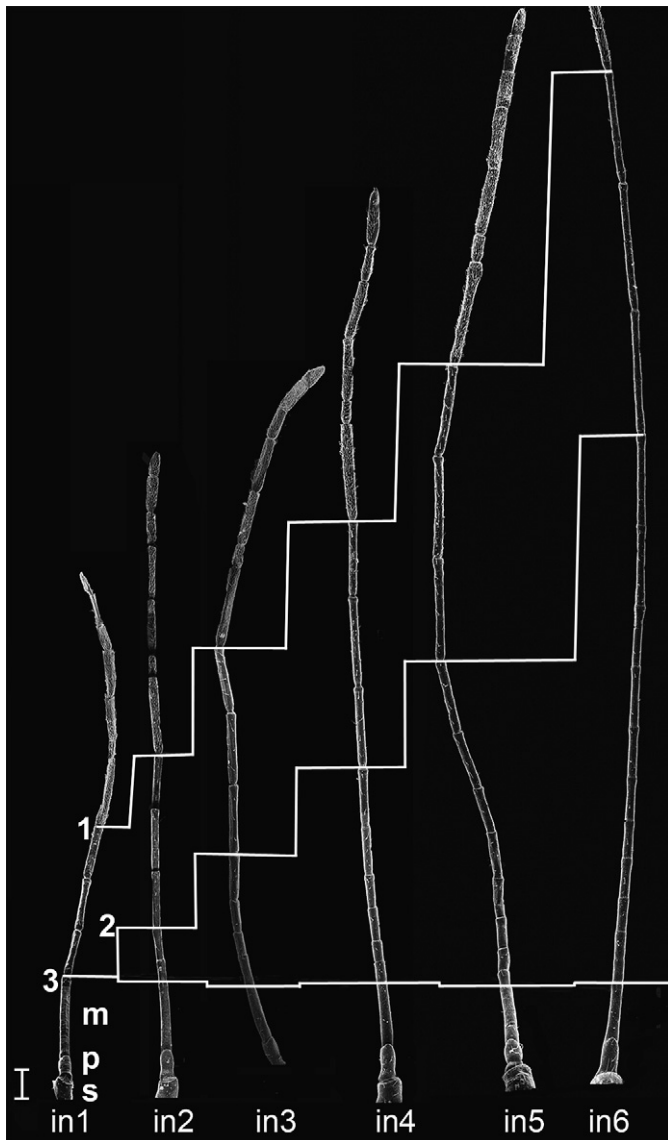


Fig. 2. Antennae from *Citrusdal L. redelinghuysense* at each instar of development (1–5), and at adulthood. All antennae reproduced to same scale. The antennae for instars 1, 3 and the adult are from female specimens, while the antennae for instars 2, 4 and 5 are from males. The number of annuli in the basiflagellum at each instar is as follows: first instar: 4, second instar: 6, third instar: 8, fourth instar: 10, fifth instar: 12 and adult: 14. Line 1 divides the distiflagellum from the basiflagellum. Line 2 depicts the progressive movement of the three annuli of the first instar basiflagellum to the end of the adult basiflagellum, due to the successive addition of new annuli by the division of the meriston. Line 3 marks the distal border of the meriston (first annulus of the basiflagellum). m, meriston; p, pedicel; s, scape, Scale bar = 200 μ m.

than the males in all subsequent moults, achieving far larger adult size. However, this was achieved neither by adding additional instars to the female life cycle, nor by an increased nymphal duration of females (Esperk et al., 2007).

4.2. Adult antennal structure, development and phylogenetic implications

Both the structure (Klass et al., 2003a) and the mode of development of the mantophasmatodean antenna are unique, and provide several potential autapomorphies for the order. The separation of the adult antennal flagellum into a basiflagellum of 14 annuli, the distal ones displaying secondary divisions, and a distiflagellum of seven annuli with dense sensillae and annuli showing

specific length ratios is constant within all species examined and has no parallel amongst the Insecta (see also Klass et al., 2003a; Drilling, 2005). This combined with the consistent pattern of antennal development within Mantophasmatodea supports the molecular and morphological evidence for the monophyly of the order (Klass et al., 2003a; Damgaard et al., 2008) and may provide additional morphological characters that could be employed in future studies on the placement of the order within Neoptera. Importantly, our study confirms that the typical structure of the antenna also occurs in *Tanzaniophasma* (see also Klass et al., 2003a). This taxon, which has not yet been included in molecular studies, has male genitalia very different from other Mantophasmatodea (Klass et al., 2002, 2003a) and is a good candidate to be the sister group of all other extant Mantophasmatodea (Klass et al., 2003a). On the other hand, none of the potential sister taxa of Mantophasmatodea – Dictyoptera, Phasmatodea, and Grylloblattodea – share any of the peculiar mantophasmatodean antennal features, thus no hint to a relationship of Mantophasmatodea to any of these taxa can be inferred from adult antennal structure.

In Baltic amber mantophasmatodean fossils, antenna structure has not been considered in detail so far. Yet, based on the results on antennal structure in Klass et al. (2003a) and the present paper, some interesting points can be noted. For the holotype nymph of †*Raptophasma groehni*, Zompro (2008a) indicates an annulus number of 14. This is surprising, as in all extant nymphs (and adults) there is an even number of annuli in the basiflagellum plus seven in the distiflagellum, hence an odd total number. Fig. 2 in Zompro (2008a) appears to show the differentiation between basi- and distiflagella, and there seems to be eight annuli in the distiflagellum. The shortest annulus of the distiflagellum is not the second (as in extant specimens), but the third and it is comparatively less short. The two annuli basal to it are not as extremely long, as is the first in extant specimens. It thus appears likely that the distiflagellum was less modified in these fossils as compared to the extant Mantophasmatodea, where the second annulus has become further shortened and perhaps the first has originated by a fusion of the former first and second annuli. Engel and Grimaldi (2004, Fig. 3) and Arillo and Engel (2006, Figs. 1 and 2) show the antenna of *Adicophasma spinosa* and *Adicophasma grylloblattoides* respectively and count 16 annuli in total in *A. grylloblattoides*. It is possible to discern only five basiflagellar annuli (excluding pedicel and scape) and 10 more setose distiflagellar annuli. The annuli of the distiflagellum do not show the strong differences in length, as in extant taxa. This all may support the monophyly of a clade comprising all extant Mantophasmatodea (to the exclusion of at least *Raptophasma* and *Adicophasma*), which are characterised by a specific structural pattern of the distiflagellum.

In the adult mantophasmatodean antennae, the few observed deviations from a total of 14 basiflagellar annuli were the result of aberrant divisions of the meriston resulting from developmental stress and antennal damage during development (Table 2). Fuller (1920) indicated that in termites odd-jointed antennae arise as a result of the fusion of the two new annuli before dividing from the meriston, or through the fusion of the more proximal annulus of the pair with the meriston. A similar anomaly was seen in adult male *L. redelinghuysense* and *A. gansbaaiense* specimens, explaining the presence of an odd number of annuli (13) in the basiflagellum of these specimens. The odd number of annuli (13) in the basiflagellum of one female adult *L. redelinghuysense* was due to the absence of a division between the last annulus of the basiflagellum and the first annulus of the distiflagellum. In a few instances, abnormally slow rates of development resulted in aberrant patterns of secondary division of basiflagellar annuli in *L. redelinghuysense* (Table 2). In addition, accidental loss of the distiflagellum was accompanied by a lack of secondary division in the most distal basiflagellar annuli of this species and *P. maraisi*.

Table 2
The antennal structure of eleven species of Mantophasmatodea examined during postembryonic development and at adulthood

Species	Instar	Sex	# individuals examined	Annulus count (left antenna, right antenna)		Annulus bearing first of secondary divisions (left antenna, right antenna)
				Basiflagellum	Distiflagellum	
<i>Lobatophasma redelinghuysense</i>	1	Female	1	4, 4	7, 7	n/a
<i>Lobatophasma redelinghuysense</i>	2	Female	20	6, 6	7, 7	n/a
<i>Lobatophasma redelinghuysense</i>	2	Male	12	6, 6	7, 7	n/a
<i>Lobatophasma redelinghuysense</i>	3	Female	12	8, 8	7, 7	n/a
<i>Lobatophasma redelinghuysense</i>	3	Male	19	8, 8	7, 7	n/a
<i>Lobatophasma redelinghuysense</i>	4	Female	8	10, 10	7, 7	n/a
<i>Lobatophasma redelinghuysense</i>	4	Male	13	10, 10	7, 7	n/a
<i>Lobatophasma redelinghuysense</i>	5	Female	6	12, 12	7, 7	n/a
<i>Lobatophasma redelinghuysense</i>	5	Male	11	12, 12	7, 7	n/a
<i>Lobatophasma redelinghuysense</i>	Adult	Female	2	14,14	7, 7	10, 10
<i>Lobatophasma redelinghuysense</i>	Adult	Female	1	14,14	7, 7	12, 11
<i>Lobatophasma redelinghuysense</i>	Adult	Female	1	14,14	7, 7	8, 9
<i>Lobatophasma redelinghuysense</i>	Adult	Female	1	13,14	7, 7	7, 10
<i>Lobatophasma redelinghuysense</i>	Adult	Male	2	14,14	7, 7	10, 10
<i>Lobatophasma redelinghuysense</i>	Adult	Male	1	14,13	7, missing	10, 9
<i>Lobatophasma redelinghuysense</i>	Adult	Male	1	14,14	7, 7	8, 9
<i>Lobatophasma redelinghuysense</i>	Adult	Male	1	14,14	7, 7	8, 8
<i>Lobatophasma redelinghuysense</i>	Adult	Male	2	14,14	7, 7	8, 8; absent from 9
<i>Lobatophasma redelinghuysense</i>	Adult	Male	1	14,14	7, missing	8, 8; absent from 13 and 14
<i>Lobatophasma redelinghuysense</i>	Adult	Male	1	14,14	7, 7	8, 10; absent from 9 on left
<i>Karoophasma biedouwense</i>	1	Female	1	4,4	7, 7	n/a
<i>Karoophasma biedouwense</i>	2	Female	1	4,4	7, 7	n/a
<i>Karoophasma biedouwense</i>	Adult	Female	1	14, 14	7, 7	8, 8
<i>Karoophasma biedouwense</i>	Adult	Female	1	14, 14	7, 7	9, 9
<i>Karoophasma biedouwense</i>	Adult	Male	1	14, 14	7, 7	9, 8
<i>Hemilobophasma montaguense</i>	Adult	Male	1	14, 14	7, 7	8, 8
<i>Hemilobophasma montaguense</i>	Adult	Male	1	14, 14	7, 7	9, 8
<i>Austrophasma rawsonvillense</i>	2	?	1	6, 6	7, 7	n/a
<i>Austrophasma rawsonvillense</i>	5	?	1	12, 12	7, 7	n/a
<i>Austrophasma rawsonvillense</i>	Adult	Female	1	14, 14	7, 7	9, 9
<i>Austrophasmatidae</i> sp.n. 1*	Adult	Female	1	14, 14	7, 7	10, 10
<i>Austrophasma gansbaaiense</i>	Adult	Female	1	14, 13	7, 7	11, 11
<i>Austrophasma gansbaaiense</i>	Adult	Female	1	14, 14	7, 7	10, 10
<i>Austrophasmatidae</i> sp.n. 3*	Adult	Male	3	14, 14	7, 7	8, 8
<i>Austrophasmatidae</i> sp.n. 3*	Adult	Female	1	14, 14	7, 7	8, 8
<i>Namaquaphasma ookiepense</i>	Adult	Female	3	14, 14	7, 7	8,8
<i>Praedatophasma maraisi</i>	1	?	1	4, 4	7, 7	n/a
<i>Praedatophasma maraisi</i>	2	?	1	6, 6	7, 7	n/a
<i>Praedatophasma maraisi</i>	4	?	2	10, 10	7, 7	n/a
<i>Praedatophasma maraisi</i>	5	Female	1	12, 12	7, 7	n/a
<i>Praedatophasma maraisi</i>	Adult	Female	1	14, 14	missing	6, 6; absent from 13 and 14
<i>Praedatophasma maraisi</i>	Adult	Female	1	14, 14	missing	5, 6; absent from 13 and 14
<i>Praedatophasma maraisi</i>	Adult	Male	1	14, 14	7, 7	6, 6; absent from 13 and 14
<i>Sclerophasma pesisense</i>	1	?	3	4, 4	7, 7	n/a
<i>Sclerophasma pesisense</i>	2	?	1	6, 6	7, 7	n/a
<i>Sclerophasma pesisense</i>	Adult	Male	1	14, 14	7, 7	6, 6
<i>Sclerophasma pesisense</i>	Adult	Male	2	14, 14	7, 7	5, 5
<i>Sclerophasma pesisense</i>	Adult	Female	3	14, 14	7, 7	6, 6
<i>Sclerophasma pesisense</i>	Adult	Female	1	14, 14	7, 7	8, 8
<i>Tanzaniophasma</i> sp	2	?	2	6, 6	7, 7	n/a
<i>Tanzaniophasma</i> sp	3	?	3	8, 8	7, 7	n/a
<i>Tanzaniophasma</i> sp	4	?	1	10, 10	7, 7	n/a
<i>Tanzaniophasma</i> sp	5	?	2	12, 12	7, 7	n/a
<i>Tanzaniophasma</i> sp	Adult	Male	1	14, 14	7, 7	6, 6

The number of annuli in both the basi- and distiflagellum of the left and right antennae is given for nymphs and adults. In the case of adults, the position of the first secondary division within the basiflagellum is indicated. *Undescribed new species in Damgaard et al. (2008).

In all the species examined, secondary divisions were always present in the more distal basiflagellar annuli of the adult antennae; Klass et al. (2003a) described these divisions as weak articulations, with low flexibility, and considered them as a putative autapomorphy of the order. As explained above, these divisions are always much less distinct than, and structurally different from neighbouring primary divisions. While in all Mantophasmatodea the basiflagellum is consistently divided into 14 annuli by the series of primary divisions, the secondary subdivisions show variation in number as the position of the basalmost of these divisions varies. Although this character showed much intraspecific variation, it is informative for the intraordinal

phylogeny of Mantophasmatodea. In the taxon-dense COI and 16S phylogeny of Damgaard et al. (2008) the Namibian clades Mantophasmatidae (here represented by *Sclerophasma*) and *Praedatophasma* + *Tyrannophasma* (here represented by *Praedatophasma*) are in a position basal to the purely South African Austrophasmatidae (including the remaining taxa here examined) (Klass et al., 2003a). Considering the data in Klass et al. (2003a, Table 1) and herein, in the Namibian taxa the basalmost secondary division is in basiflagellomere 5, 6, or 7 (rarely 8), while in all Austrophasmatidae it is further distally, in basiflagellomere 8, 9, 10, 11, or 12. *Tanzaniophasma* corresponds with the Namibian taxa in this respect.

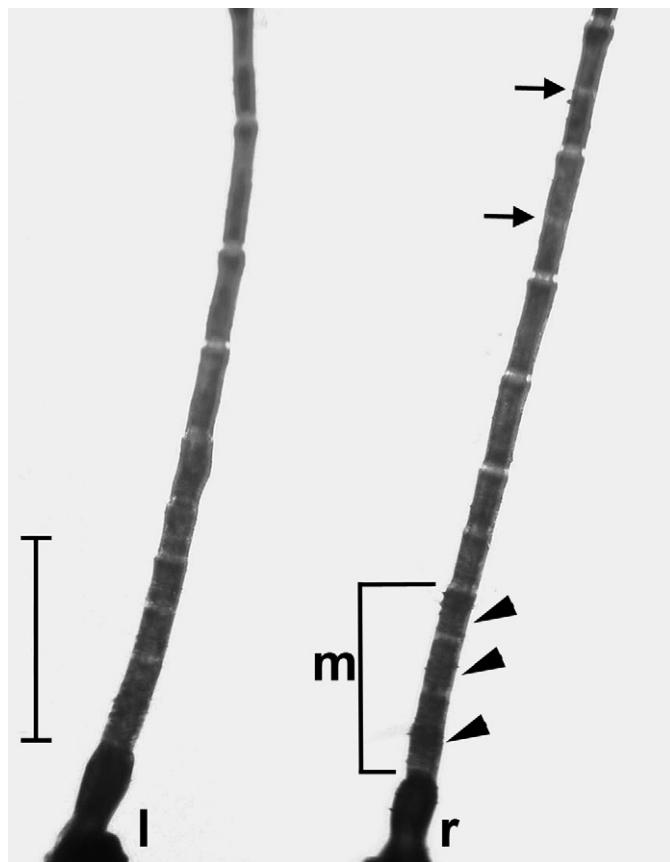


Fig. 3. Antennae from a fifth instar Citrusdal *L. redelinghuysense* viewed with transmitted light, showing the presence of developing annuli (arrow heads) within the meriston (bracketed) and developing secondary subdivisions (arrows) in the future eighth and ninth annuli. m, meriston; l, left antenna; r, right antenna. Scale bar = 500 μ m.

The ontogenetic development of the mantophasmatodean antenna may represent the simplest mode of antennal growth in which new annuli are added to the antennae by the division of the first annulus of the antennal flagellum (the meriston) alone. In *L. redelinghuysense* antennal growth involved the division of the meriston into three new annuli at each moult. This mode of growth was confirmed by the observation of three new annuli within the

capsule formed by the meriston prior to moulting. Although in this study this phenomenon was only observed in the fifth instar, it is very likely that it also occurs in the previous instars. This mode of antennal growth also occurs in Isoptera (Fuller, 1920), Blattaria (*Blatta orientalis*: Qadri, 1938) and Dermoptera (*Forficula auricularia*: Henson, 1947; *Hemimerus vicinus*: Davies, 1966). However, subtle differences in antennal development are evident between these taxa. While the meriston in *L. redelinghuysense* divides consistently into three new annuli at each moult, the meriston of both soldier and worker termites does not divide after the fourth (penultimate) moult (Fuller, 1920). In both female and male *Blatta* no new annuli are produced in the fourth instar, however, two new annuli are added to the male antenna during the sixth instar, the final instar before adulthood (Qadri, 1938). In *H. vicinus* (Davies, 1966) annular number remains constant from the first instar to the second. However, during the second moult the meriston divides into three annuli, while in the third and final moult one additional annulus is added. Thus, the ontogenetic flexibility of antennal growth patterns even within one order (e.g. Blattodea) may limit the phylogenetic value of this character.

Nonetheless, it is interesting to note that the mode of antennal growth in Mantophasmatodea is distinct from that described for most of the proposed sister groups. In Mantodea (*Empusa agena*: Bugnion, 1921), a putative sister group proposed by Dallai et al. (2003; but see Klass and Eulitz, 2007) and Phasmatodea (Roth, 1917), a proposed sister group in Klass et al. (2003a) and Cameron et al. (2006), the antennae are lengthened by the division of not only the meriston, but also a few of the following basal annuli known as meristal annuli. The mode of antennal growth in the Grylloblattodea, a proposed sister group supported by nuclear DNA-sequences (Terry and Whiting, 2005; Kjer et al., 2006), has not been clearly defined. Nagashima (1982) described the first annulus of the flagellum in *Galloisiana nipponensis* as a meriston, suggesting that it is the formative zone of the antenna. Vrsansky et al., 2001 described the first annulus of the flagellum of *Galloisiana olgae* as three times longer than the second, once again indicating the likely presence of a meriston, as one long annulus could divide into a series of shorter annuli. Yamasaki (1982) illustrated the antenna of a first instar *G. nipponense* with dotted lines dividing the meriston into five annuli, possibly indicating immature annuli within this extremely long first annulus. Slight constrictions depicted in the contours of a few successive annuli following the meriston may indicate that they also divide during the subsequent moult, i.e., represent meristal annuli. Yamasaki (1982) however, does not

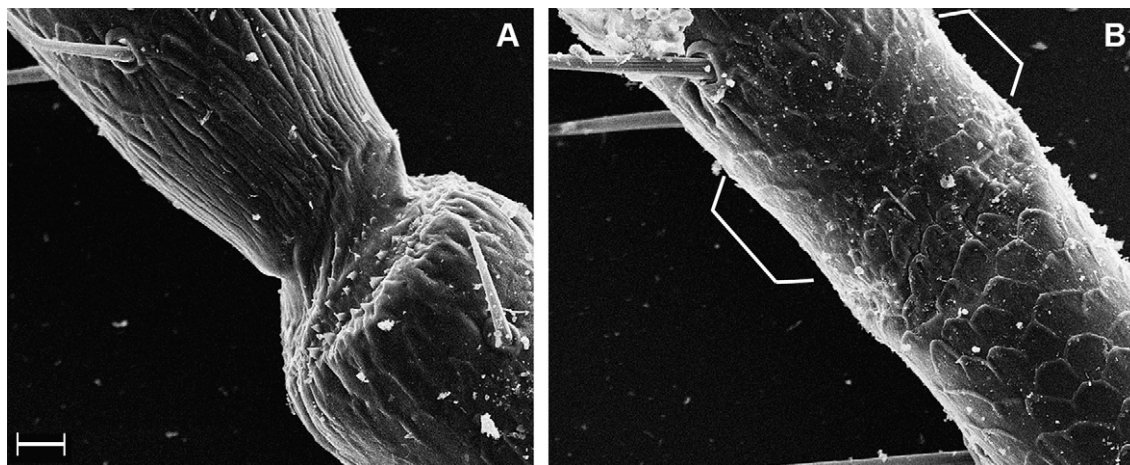


Fig. 4. The structure of the divisions in the basiflagellum of the adult antenna of *L. redelinghuysense*. A, The primary division between the 13th and 14th annuli of the adult antenna is visible as a clear constriction between the successive annuli. B, The secondary subdivision within annulus 14th of the adult antennae (bracketed), which can be recognised by a change in the texture of the antenna exoskeleton. Same scale in both A and B, scale bar = 10 μ m.

discuss this feature. If the grylloblattodean meriston functions as suggested by these sparse indications, it would have little in common with that of Mantophasmatodea, where only the meriston divides into only three annuli at each moult.

However, if the secondary divisions of the distal basiflagellar annuli of the mantophasmatodean antennae are considered as formative 'true' divisions between successive annuli, these annuli may be considered as meristal annuli that undergo a delayed division to produce doublets. If this is the case, then the mode of growth of the basiflagellum does not conform to any of the described modes, but instead represents a unique pattern of antennal growth within the 'polyneopteran orders', intermediate between mode 1 and 2 as described previously (see Introduction). The delayed meristal activity may be restricted to the distal part of the basiflagellum, possibly because this area is older than the newly formed basal annuli and the latter are too young to develop this activity.

4.3. Conclusions

A time-frame series of measurements of reared nymphs of *L. redelinghuysense* showed that in this species the life cycle comprises six instars (including adulthood), and takes approximately 2 months to complete. Except for the first instar, females were always larger than males, and had a faster rate of development, resulting in appreciable sexual size dimorphism in adults. The life cycle is linked to the rainy season, which in the South African species occurs during winter.

The unique antenna consists of a sensilla-rich, seven-segmented distiflagellum, where the number of annuli remains constant throughout development, and a smooth basiflagellum. The basiflagellum has four annuli in the first instar, and increases in length by the division of a basal annulus, the meriston, into three annuli at each moult, thus increasing the number of basiflagellar annuli by two at each moult. The six instars can therefore each be identified by the annulus count, which reaches 14 in instar 6 (the adult). Secondary divisions of the annuli are formed at the final moult; they differ from the (distal) primary divisions, as they are neither membranous nor constricted. Yet they might represent incomplete divisions of an annulus, if their origin is due to a delayed subdivision of annuli having the potential to act as meristal annuli. The position of the most basal secondary division of the antenna provides some useful phylogenetic information, and correlates with the clades identified on the molecular trees of Damgaard et al. (2008), which separate the families Austrophasmatidae and Mantophasmatidae. The emergent pattern is one of a consistent antennal composition for all of the nine species examined, indicating that the observed development pattern and adult structure of the mantophasmatodean antenna are likely to provide useful autapomorphies for the order.

The described mode of antennal development reveals similarities between the Mantophasmatodea and the 'polyneopteran' groups, Dictyoptera-Blattodea (including cockroaches and termites) and Dermaptera. A sister group relationship with Dictyoptera is also supported by characters of antennal blood vessels (Pass et al., 2006) and the structure of the male genitalia (Klass et al., 2003a). The mode of antennal growth was very different to that of Phasmatodea, identified by Klass et al. (2003a) and Cameron et al. (2006) as a possible sister taxon. In addition, no support was found in antenna structure and development for a sister relationship with Grylloblattodea (Terry and Whiting, 2005; Beutel and Gorb, 2006; Kjer et al., 2006); however, the antennal development of Grylloblattodea requires more intensive examination.

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