

Biology of South African Heel-walkers, with Special Reference to Reproductive Biology (Insecta: Mantophasmatodea)

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Abstract

The biology of South African heel-walkers was described, with special reference to the reproductive, *i. e.*, pre-mating, mating and ovipositing behaviors. The heel-walkers have apparently adapted their life cycle to the short rainy season, to survive in a harsh environment. They survive the dry season as eggs underground, and the first instar nymphs hatch at the beginning of the rainy season, and grow quickly, attaining maturity in about three weeks. Mating in heel-walkers starts after an act of communication known as “drumming,” and continues for many hours at the bottom of plants (*e. g.*, about three days in *Karooophasma biedouwensis*). Mated females search carefully for a suitable site to oviposit, and then deposit a hard pod containing 10 to 12 eggs, just below the surface of the soil. Females deposit egg pods several times at intervals of three or four days. After the reproductive season at the end of the short rainy season, their life cycle ends in due course. The life cycle of South African heel-walkers is univoltine.

Introduction

In May 2002, a new insect group “order Mantophasmatodea,” named after the Mantodea (praying mantises) and Phasmatodea (walking sticks), was established by Klass *et al.* (2002), based on three old museum specimens described as three different species: 1) an ethanol preserved female described as *Mantophasma zephyra* (type species of the new genus, the new family and the new order) collected in Namibia in 1909, 2) a dried male described as *M. subsolana* collected in Tanzania in 1951 [Klass *et al.* (2003) have reclassified this species as *Tanzaniophasma subsolana* of a new family Tanzaniophasmatidae (cf. Table 1)], and 3) a 45-million-year-old Baltic amber fossil described as *Raptophasma kerneggeri*. The establishment of this new insect order comes 88 years after the last description of the order Grylloblattodea (= Notoptera) in 1914 (cf. Walker, 1914).

At around the time of publication, living mantophasmatodean populations were discovered in Namibia (*e. g.*, the highlands around Mt. Brandberg, Erongo Province; cf. Adis *et al.*, 2002; Zompro *et al.*, 2002) and South Africa (a broad area of the Western Cape Province including the Namaqualand and part of the Northern Cape Province; cf. Picker *et al.*, 2002). We have started their taxonomical and biological studies (Klass *et al.*, 2003; Picker *et al.*, 2003). Members of the

Table 1 Classification of members of the order Mantophasmatodea (after Klass *et al.*, 2003; Zompro *et al.*, 2003).

Family	Genus	Species	Type locality	Reference	Collection site*
Mantophasmatidae					
	<i>Mantophasma</i>	<i>zephyra</i>	Brandberg (Namibia)	Klass <i>et al.</i> (2002, 2003), Zompro <i>et al.</i> (2002, 2003)	1
	<i>Sclerophasma</i>	<i>paresisensis</i>	Paresisberg (Namibia)	Klass <i>et al.</i> (2003)	2
Tanzaniophasmatidae					
	<i>Tanzaniophasma</i>	<i>subsolana</i>	Ufipa Dish (Tanzania)	Klass <i>et al.</i> (2002, 2003), Zompro <i>et al.</i> (2002, 2003)	3
Austrophasmatidae					
	<i>Austrophasma</i>	<i>caledonensis</i>	Caledon (South Africa)	Klass <i>et al.</i> (2003)	4
	A.	<i>gansbaaiensis</i>	Gansbaai (South Africa)	Klass <i>et al.</i> (2003)	5
	A.	<i>rawsonvillensis</i>	Rawsonville (South Africa)	Klass <i>et al.</i> (2003)	6
	<i>Lobophasma</i>	<i>redelinghuysensis</i>	Redelinghuis (South Africa)	Klass <i>et al.</i> (2003)	7
	<i>Hemilobophasma</i>	<i>montaguensis</i>	Montagu (South Africa)	Klass <i>et al.</i> (2003)	8
	<i>Karophasma</i>	<i>biedouwensis</i>	Biedouw (South Africa)	Klass <i>et al.</i> (2003)	9
	K.	<i>botterkloofensis</i>	Botterkloof Pass (South Africa)	Klass <i>et al.</i> (2003)	10
	<i>Namaquaphasma</i>	<i>ookiepensis</i>	O'okiep (South Africa)	Klass <i>et al.</i> (2003)	11
Described mantophasmatodean taxa of uncertain placement					
	<i>Prædatophasma</i>	<i>maraisi</i>	Karasberg (Namibia)	Zompro <i>et al.</i> (2002, 2003), Klass <i>et al.</i> (2003)	12
	<i>Raptophasma</i>	<i>kerneggeri</i> **	Baltic area (Lithuania)	Klass <i>et al.</i> (2002, 2003), Zompro <i>et al.</i> (2002, 2003)	—
	<i>Tyamophasma</i>	<i>gladiator</i>	Brandberg (Namibia)	Zompro <i>et al.</i> (2003)	1

*Refer to numbers in Fig. 1.

**A 45-million-year-old fossil species collected from Baltic amber.

order Mantophasmatodea grow to a length of 2–3 cm, without wings and ocelli, and walk on their “heels”(= the fused first to third tarsomeres in each leg) whereas insects usually walk on their “toes”(= pretarsus + distal parts of tarsus). After this unique and diagnostic style of walking, we have proposed the common name “heel-walkers” (Machida and Tojo, 2003; Picker *et al.*, 2003; Tojo and Machida, 2003). So far, four living species from Namibia and eight from South Africa have been described by Zompro *et al.* (2002, 2003) and Klass *et al.* (2002, 2003). Klass *et al.* (2003) have not only described the new South African heel-walkers, but reclassified all species hitherto described (Table 1).

According to Klass *et al.* (2002, 2003), the new order Mantophasmatodea are phenotypically orthopteroid insects,

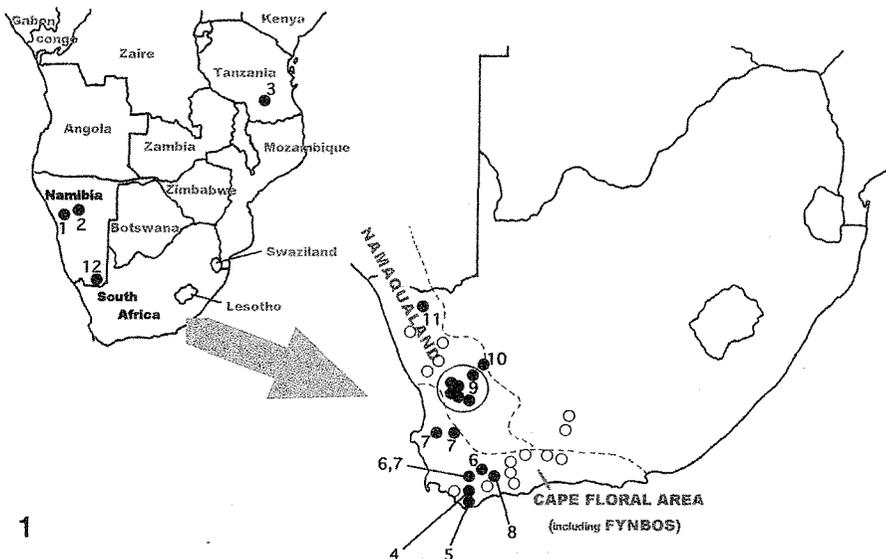


Fig. 1 Distribution of mantophasmatodean species. For the locality and mantophasmatodean names, refer to Table 1. These maps are reconstructed from previous studies (Klass *et al.*, 2002, 2003; Picker *et al.*, 2002; Zompro *et al.*, 2002, 2003) plus some new data (open circles) from our 2003 field trip.

with features which allow one to differentiate them from the dictyopteroid insect orders Mantodea, Blattodea and Isoptera, and from the other orthopteroid orders Phasmatodea, Orthoptera, Grylloblattodea, Plecoptera and Dermaptera. Twenty-one unique synapomorphic characters of the new order were discussed by Klass *et al.* (2003). On the other hand, Dallai *et al.* (2003) examined the relationships of heel-walkers with other orthopteroid taxa based on a cladistic analysis of the comparative morphology of sperm, and supported that praying mantises are the sister group of heel-walkers. However, heel-walkers also share many morphological characters with members of other orthopteroid taxa, and their phylogenetic position still remains controversial.

We have started studying the comparative embryology and reproductive biology of Mantophasmatodea, to clarify arguments pertaining to the groundplan and its evolutionary transition, and reconstructing the phylogeny of orthopteroids (cf. Machida *et al.*, 2004; Tsutsumi *et al.*, 2004). In the first part of our studies, we outline the biology, with special reference to reproduction, mainly of South African heel-walkers.

Observation and Discussion

We had been observing the heel-walkers' behavior in the field from winter in 2002 and 2003. At the same time, we had also observed their behavior, with special reference to reproduction, in the laboratory. Heel-walkers were collected in South Africa from a specific succulent desert area known as "Namaqualand" (or "karoo," "succulent karoo") or the cape floral plains including a type of plain called the "Fynbos" (cf. Table 1; Fig. 1), in winter to spring (from early August to mid September) of 2002 and 2003. Nymphs and adults were kept at room temperature in separate plastic cases to prevent cannibalism. Fruit flies as food and a little water were provided every day. A mature male and female, a pair who had displayed mutual "drumming" pre-mating behavior (see the "Mating" section), were reared together in a case, and checked for mating behavior and copulation. Copulated females were moved to a separate plastic case with soil collected from the field for oviposition.

Life cycle of South African heel-walkers

South African heel-walkers mostly live in a specific succulent desert area called the Namaqualand, and on plains known as the Fynbos. Namaqualand, where *Karoophasma biedouwensis*, *K. botterkloofensis* and *Namaquaphasma ookiepensis* are found, is a desert area spreading over southern Namibia and part of South Africa (Fig. 1). In the region, however, rains from June to late August (or till early September), the "rainy season," transform the land into a spectacular flowering garden of succulent plants in spring (late August and September). However, the land reverts to its desert state in the summer season from late September to April or May of the next year. In the dry season, the daily difference between high and low temperatures is as much as 20–30°C.

To survive in this harsh environment, heel-walkers have apparently adapted their life cycle, from hatching to breeding, to the short rainy season. They survive the dry season as eggs underground (Fig. 2). According to our field observations in 2003, the first instar nymphs hatch one or two weeks after the first rains in winter. They feed on other tiny insects, and grow quickly, to become adults after four moults during about three weeks. Spring is also the reproductive season for heel-walkers (*e. g.*, from late August to mid September in the Biedouw Valley, Namaqualand which is the type locality of *K. biedouwensis*; Fig. 2). After mating in males and after oviposition in females, their life

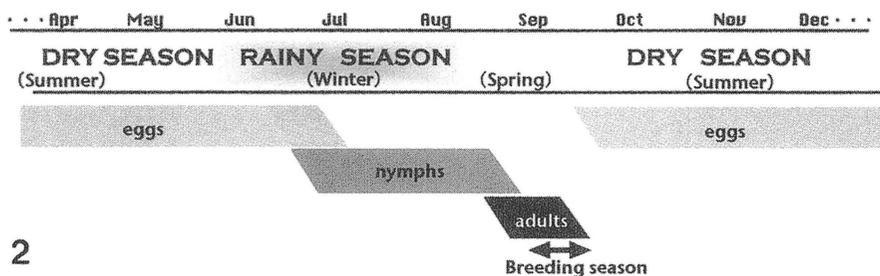


Fig. 2 The general seasonal changes at Namaqualand (Biedouw Valley, Western Cape Province) and the life cycle of the heel-walkers *Karoophasma biedouwensis*.

cycle ends in due course early in the dry summer (*e. g.*, early to mid October in the Biedouw Valley). In Namaqualand, the life cycle of heel-walkers is univoltine.

The species *Austrophasma caledonensis*, *A. gansbaaiensis*, *A. rausonvillensis*, *Lobophasma redelinghuysensis* and *Hemilobophasma montaguensis* living in the Fynbos area, on the other hand, have not been well studied. Although their life cycle may be fundamentally similar to that of heel-walkers in Namaqualand, it slightly differs in the timing of hatching, mating and ovipositing, because summer is slightly less dry in the Fynbos area than Namaqualand.

Mating

The mating behavior of heel-walkers is unique. "Drumming," an act of communicating by tapping substratum such as the ground or a plant with the abdomen, was observed prior to mating. At first, the male walks around his habitat and produces vibrations by tapping his abdomen on a plant. The female receives the call vibrations through the substratum, and responds with answering vibrations produced by her own tapping. According to our field and laboratory observations in three species, *Austrophasma gansbaaiensis*, *Hemilobophasma montaguensis* and *Karophasma biedouwensis*, and a probably undescribed species from Ladismith (Western Cape Province), the tapping frequency of one unit of the female's response is lower than that of the call made by the male. Drumming behavior for mating has been reported in the other orthopteroid insects: *e. g.*, most arctoperlarian plecopterans (*e. g.*, Hanada *et al.*, 1994; Hanada, 1996; Stewart, 1997), gryllid and tettigoniid orthopterans (*e. g.*, Morris, 1971, 1980; Bell, 1980), and blaberid blattodeans (*e. g.*, Roth and Hartman, 1967). Drumming behavior has also been reported in hodotermitid and termopsid isopterans, however, they do not use it for mating but for conveying information to other colony members (*cf.* Howse, 1964).

The mating style is similar to that typical of orthopteroid insects (*e. g.*, stoneflies, grasshoppers, ice crawlers, praying mantises and walking sticks): the male rides on the female's back, and twists his abdomen around that of the female from the left or right side. According to our field observations in two species, *K. biedouwensis* at Namaqualand (Biedouw Valley, Western Cape Province) and *H. montaguensis* at Montagu (Western Cape Province), in 2002 and 2003, copulation starts on plants with the insects hanging on to a twig, branch or leaf (Fig. 3). The female then climbs down the plant with the male on her back, and they continue mating at the bottom of the plant. The mating period is extremely long, the average for seven pairs in *K. biedouwensis* observed in the laboratory being 2.85 days \pm 0.19 (S. E.) (*cf.* Picker *et al.*, 2002; Machida and Tojo, 2003; Tojo and Machida, 2003), with the male frequently being eaten after copulation has ceased. The longest mating we observed in *K. biedouwensis* was approximately four days (about 95 h). In other species, the mating period is also extremely long (*e. g.*, over 24 h in several pairs in *H. montaguensis*, and about 26 and 64 h in two pairs of an undescribed species from Ladismith). This extraordinarily long mating is considered to be a common characteristic of heel-walkers, and it may serve to prevent other males from mating with the female, as suggested for "prolonged copulation" in many other orders, *e. g.*, Odonata (Wolf *et al.*, 1989; Cordero, 1990; Michiels, 1992; Corvet, 1999), Phasmatodea (Sivinski, 1983), Lepidoptera (Drummond, 1984), Diptera (Thornhill, 1980), Coleoptera (Snead and Alcock, 1985; Peschke, 1987), Hymenoptera (Rutowski and Alcock, 1980), and the Heteroptera (McLain, 1980; Sillén-Tullberg, 1981; Carroll and Loye, 1990; Carroll, 1991), or also as suggested for the "mate grasping" in many other orders, including the tandem flights by male dragonflies after copulation (Waage, 1984; Cordero, 1990; Thompson, 1990; Alcock, 1994; Ueda, 1996).

Egg oviposition

According to our observations in the laboratory in late spring (early to mid September) of 2002 and 2003, female heel-walkers (*e. g.*, *Karophasma biedouwensis* and *Hemilobophasma montaguensis*) start searching for the best site to oviposit by making holes in the ground (surface of the soil) with their caudal end. This searching behavior is observed mainly at night.

At night or before dawn, the female elaborately cleans her ovipositor using her mouth parts, and deposits an egg pod containing approximately 10 to 12 large eggs, just below the surface of the soil (Fig. 4). The eggs are bound together with a cementing material mixed with sand into a very hard pod (see Machida and Tojo, 2003; Tojo and Machida, 2003; Machida *et al.*, 2004). The egg pod may protect the eggs from the heat and aridity of the long and extremely dry summer season (about nine months: from late September to late May or to June). According to our observations in the laboratory, the ovipositing of one egg pod takes about 1 h. Females repeat the process several



Fig. 3 Mating of *Hemilobophasma montaguensis* observed in the field. The small and slender male on the female's back inserted his penis into the female's genitalia by twisting his abdomen around hers from the right side.

times at intervals of a few days (about 3–4 days). We calculated that one female lays 50–100 eggs in total during her lifetime. Despite the hardness of the egg pod, it softens under high humidity or immersion in water. Such a change under wet conditions may be inevitable for the hatching of the first instar nymphs. In fact, we observed in the field many first instar nymphs of *K. biedouwensis* hatch out one or two weeks after the first rains in winter (late August to early September).

We have obtained enough living mantophasmatodean specimens and eggs to start developmental and reproductive biological studies of the group. As for our ongoing studies, one can refer to Machida *et al.* (2004) and Tsutsumi *et al.* (2004).

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Fig. 4 Oviposition in *Karoophasma biedouwensis*. A mated female deposited eggs with a cementing material mixed with sand. Arrows indicate traces of her search for the best site to oviposit.

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