



Digging for the offspring, or how to bury an ootheca underground (Insecta: Dictyoptera: Mantodea)

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Abstract

The females of several Mantodea bury their oothecae underground. Some species do so regularly, mainly those living in arid habitats, most likely to protect the eggs from heat and drought. Four morphologically distinct types of digging structures have evolved independently. Although the structures have been recognized before, their morphology is here compared in detail for the first time.

Introduction

Mantodea (praying mantids) are predatory polyneopteran insects, comprising little more than 2.300 species, currently categorized in 15 “families” (EHRMANN 2002). The internal phylogenetic relations are poorly understood, and autapomorphies for taxa within Mantodea have seldom been named. Evidence for the artificial nature of many of the major traditional groupings is based on molecular data (SVENSON & WHITING 2004).

Mantodea living in arid habitats such as deserts and savannahs face the problem of extreme heat and drought during the day and often extreme cold at night. While the nymphs and adults are adapted to such climatic conditions by morphological and behavioural traits (e.g. CHOPARD 1938), the mantodean oothecae are generally fixed to some kind of substrate (stones, wood etc.) and have to endure the climatic conditions.

Some species that usually lay their eggs above ground have been shown to bury their oothecae occasionally underground in captivity if the climatic environment is not suitable for egg development (e.g. *Humbertiella ceylonica* Saussure, 1869; MÜLLER 2001). The females of other Mantodea that bury their oothecae regularly underground (probably attached to a stone: ANDRES 1914, CHOPARD 1941) have evolved special abdominal structures that help them to do so (Figs 1-5, 7). Although the presence of such structures has been recognized before (e.g. GIGLIO-TOS 1915, 1921; CHOPARD 1941; LA GRECA 1977; DONGALAR 2007), their morphology and the resulting phylogenetic implications have not been discussed in detail before.

Results

Four different morphological types of digging devices can be distinguished, that are informally named after the taxa displaying them:

1) Eremiaphilidae-type: All Eremiaphilidae show basically the same morphological situation. In both genera, *Eremiaphila* (Figs 1, 7) and *Heteronutarsus* (Fig. 2), sternite 7 (the subgenital plate) is partly covered by the preceding sternite 6. The latter carries two sturdy, ventral spines that are elongated and pointed. While they are rather slender at their bases in all *Eremiaphila* species studied herein, they are wider and shovel-like in *Heteronutarsus* (see also CHOPARD 1941: fig. 7).

2) Rivetina-type: *Rivetina* (Fig. 3) exhibits two strong and massive ventral spines. In contrast to Eremiaphilidae, in *Rivetina* the medial sternite 7 (the subgenital plate) bears the spines.

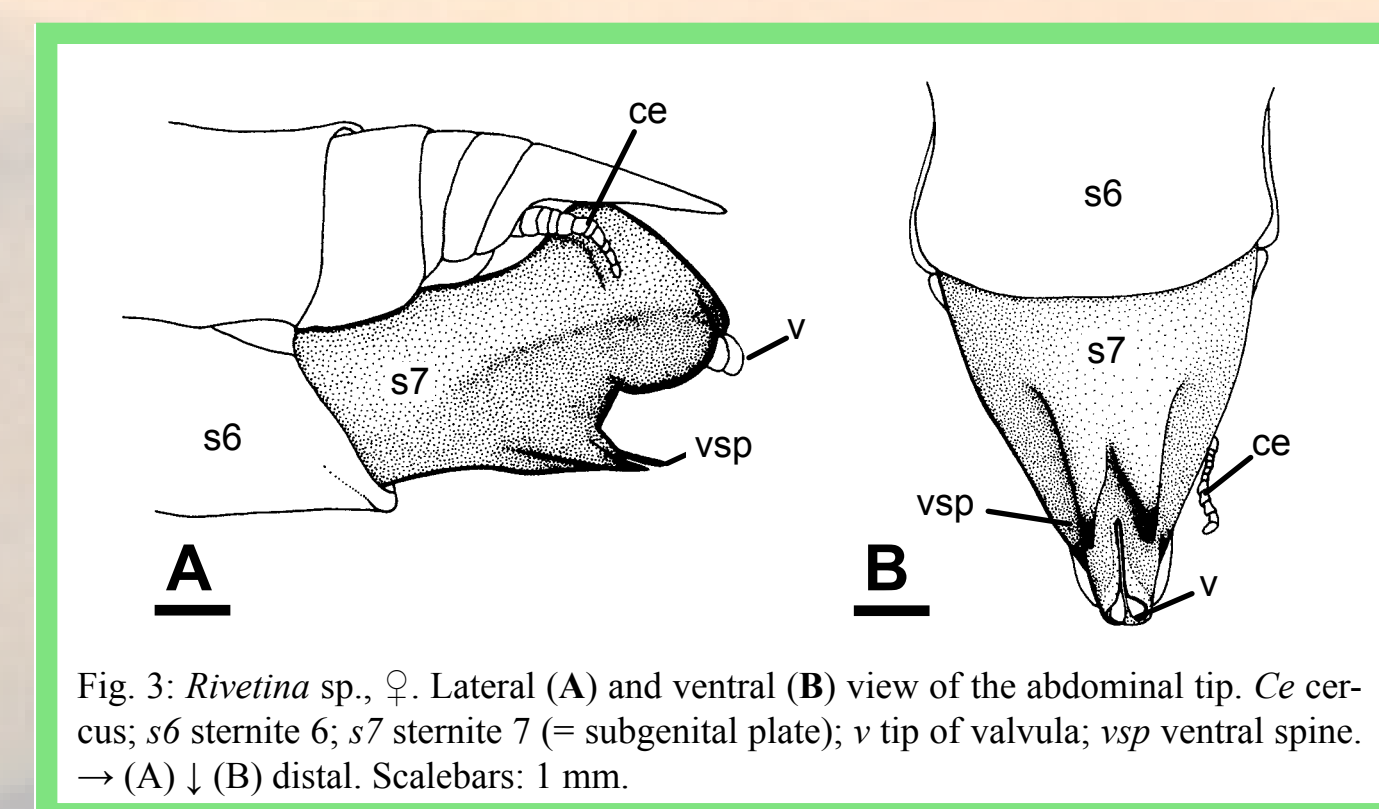


Fig. 3: *Rivetina* sp., ♀. Lateral (A) and ventral (B) view of the abdominal tip. Ce cercus; s6 sternite 6; s7 sternite 7 (= subgenital plate); v tip of valvula; vsp ventral spine. → (A) ↓ (B) distal. Scalebars: 1 mm.

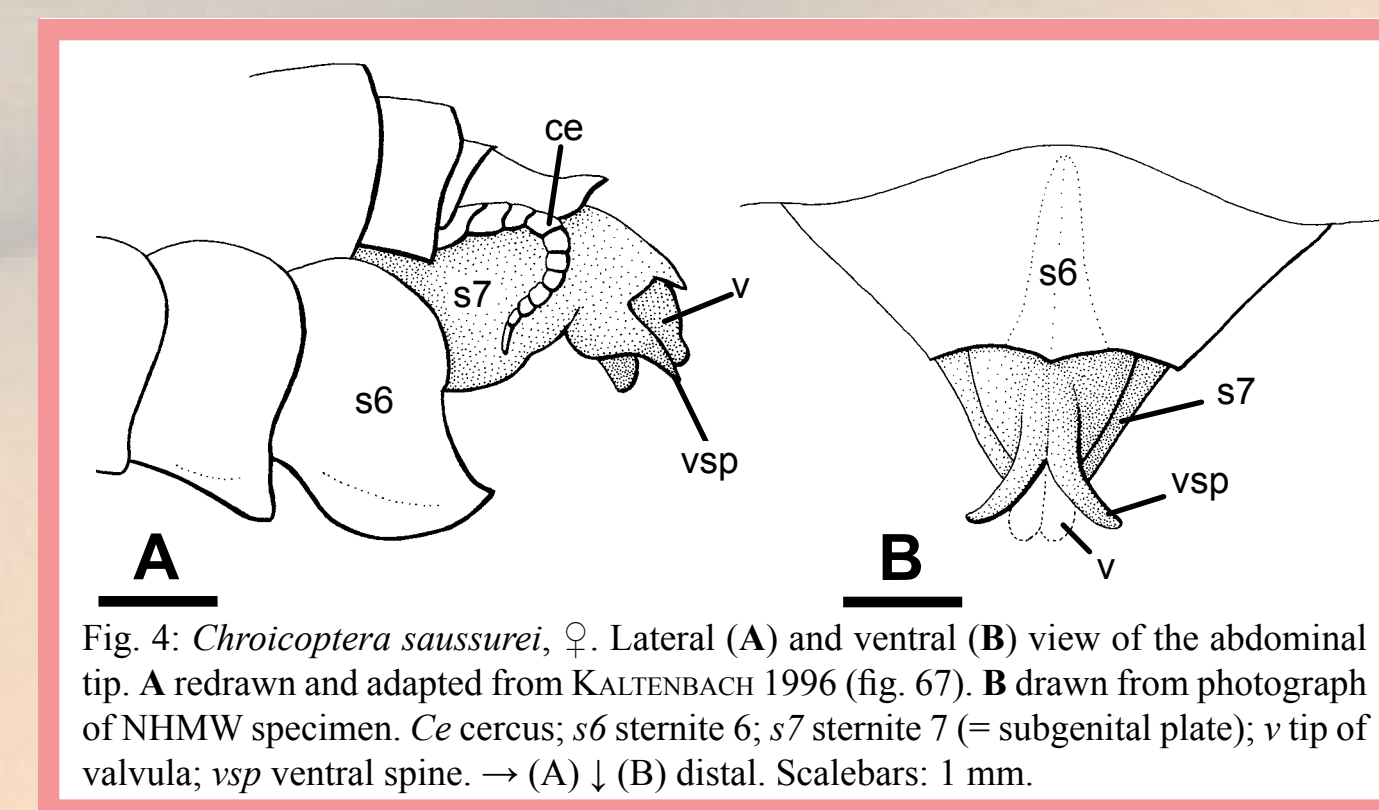


Fig. 4: *Chroicoptera saussurei*, ♀. Lateral (A) and ventral (B) view of the abdominal tip. A redrawn and adapted from KALTENBACH 1996 (fig. 67). B drawn from photograph of NHMW specimen. Ce cercus; s6 sternite 6; s7 sternite 7 (= subgenital plate); v tip of valvula; vsp ventral spine. → (A) ↓ (B) distal. Scalebars: 1 mm.

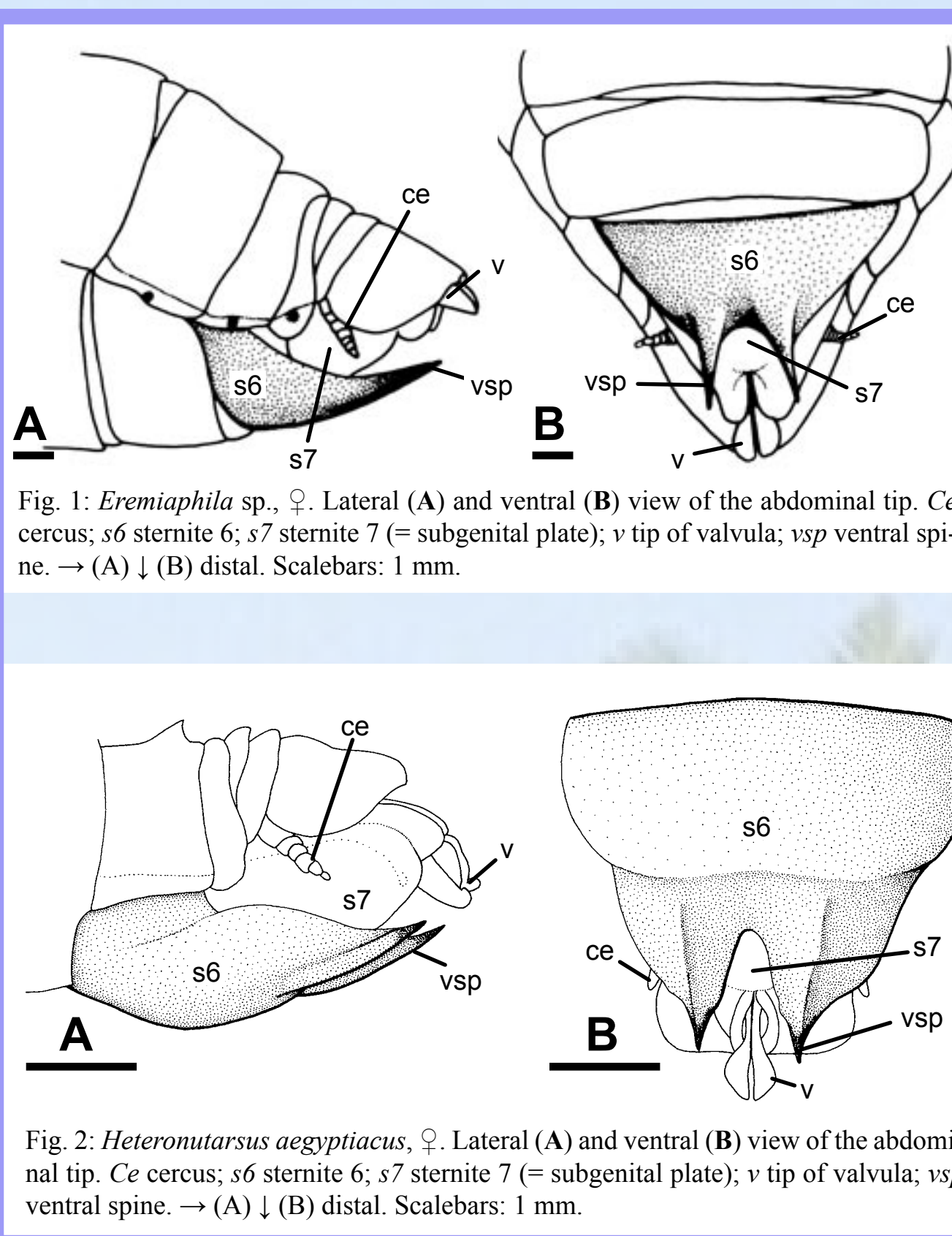
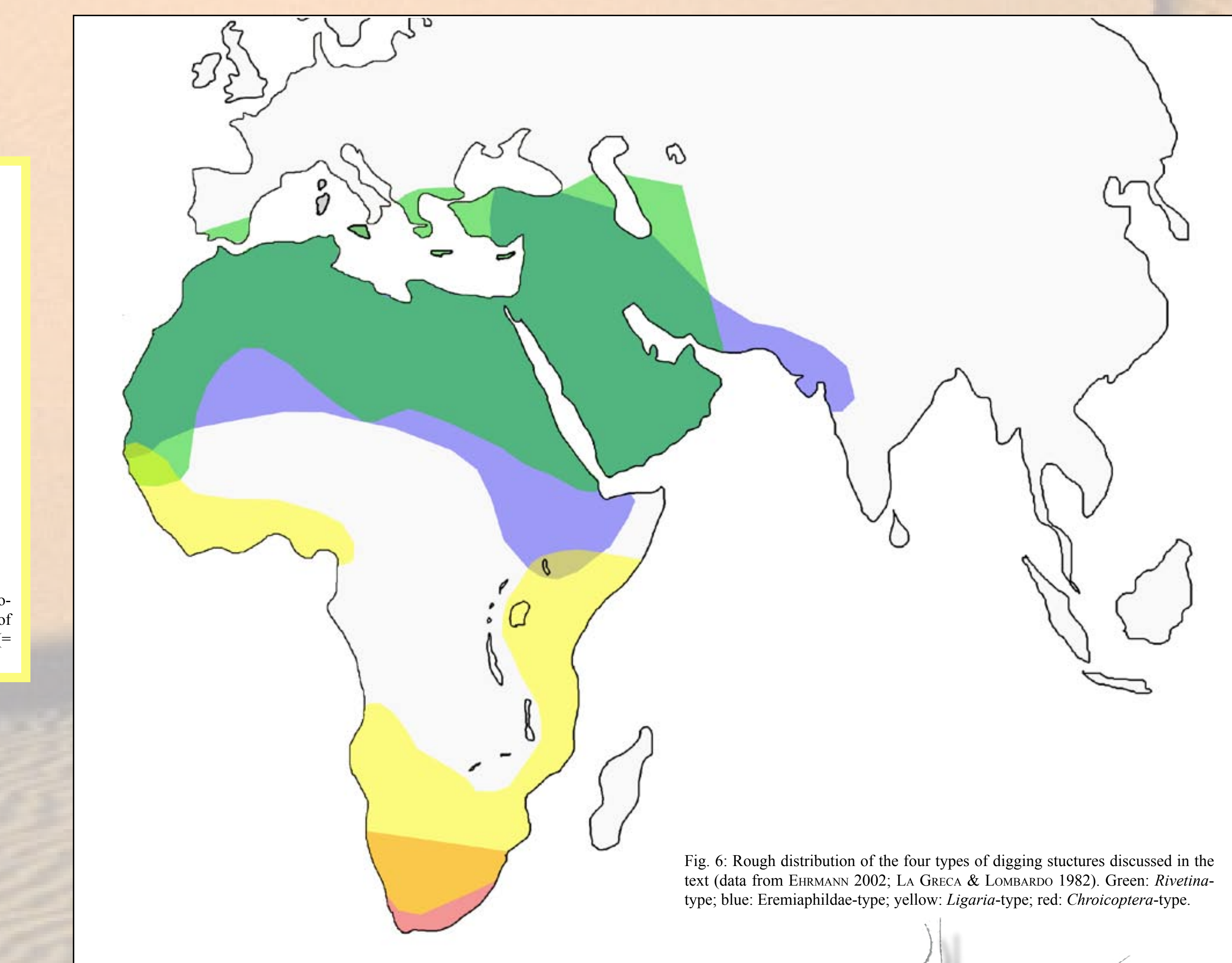


Fig. 1: *Eremiaphila* sp., ♀. Lateral (A) and ventral (B) view of the abdominal tip. Ce cercus; s6 sternite 6; s7 sternite 7 (= subgenital plate); v tip of valvula; vsp ventral spine. → (A) ↓ (B) distal. Scalebars: 1 mm.

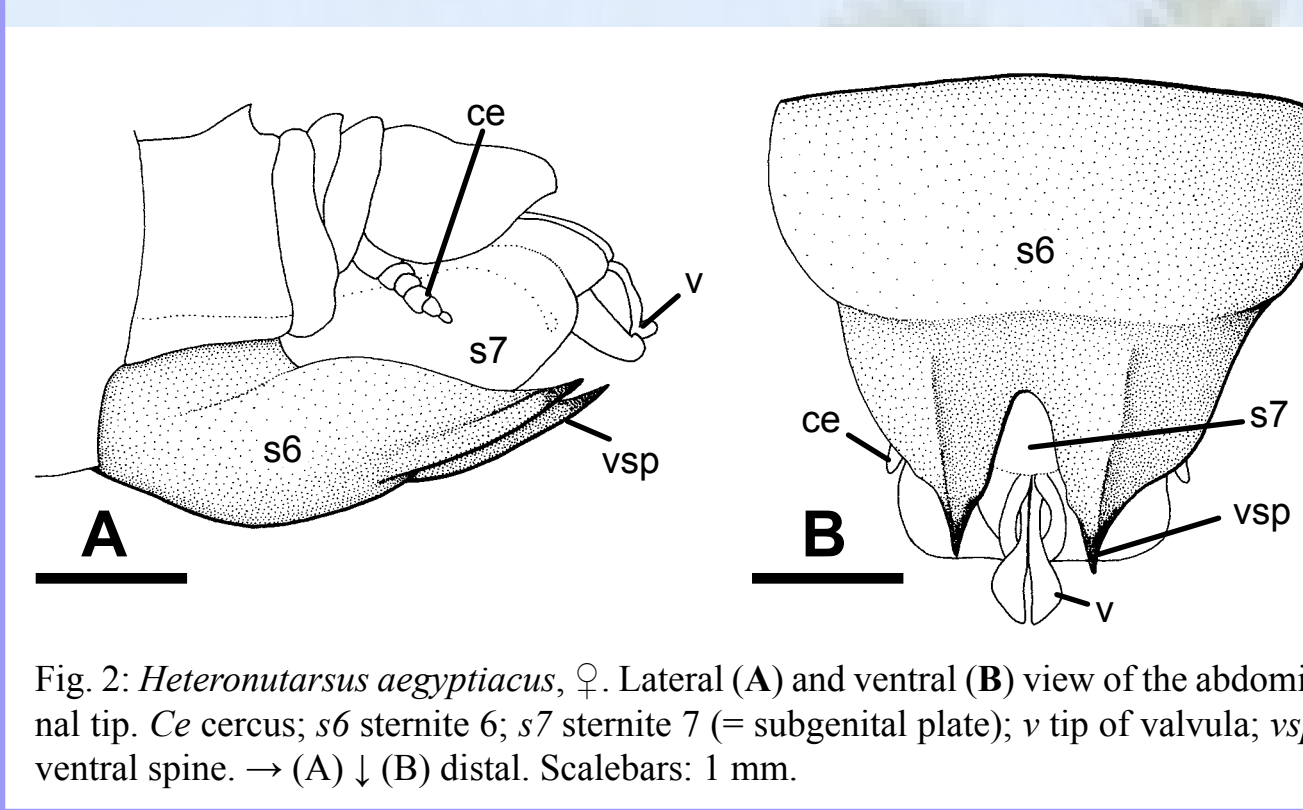


Fig. 2: *Heteronutarsus aegyptiacus*, ♀. Lateral (A) and ventral (B) view of the abdominal tip. Ce cercus; s6 sternite 6; s7 sternite 7 (= subgenital plate); v tip of valvula; vsp ventral spine. → (A) ↓ (B) distal. Scalebars: 1 mm.

3) Chroicoptera-type: *Chroicoptera* females (Fig. 4) exhibit two spines that protrude from the tip of the abdomen. These spines do not originate from the ventral valvulae but from the distal part of sternite 7 (the subgenital plate). They are slightly bent laterad, and are distinct from the type found in *Rivetina* both in shape and position.

4) Ligaria-type: In female *Ligaria*, *Ligariella*, *Parentella* (all Fig. 5) and *Entella*, the abdominal tip bears strongly sclerotized hooks originating from within the vestibulum (genital chamber). They protrude from the tip of the abdomen and point dorsad. Morphological analysis revealed that the hooks originate from the distal parts of the gonapophyses of the eighth abdominal segment (i.e. the ventral valvulae). The two-parted hooks consist of a shorter, straight dorsal part and a longer ventral part that is curved dorsad.

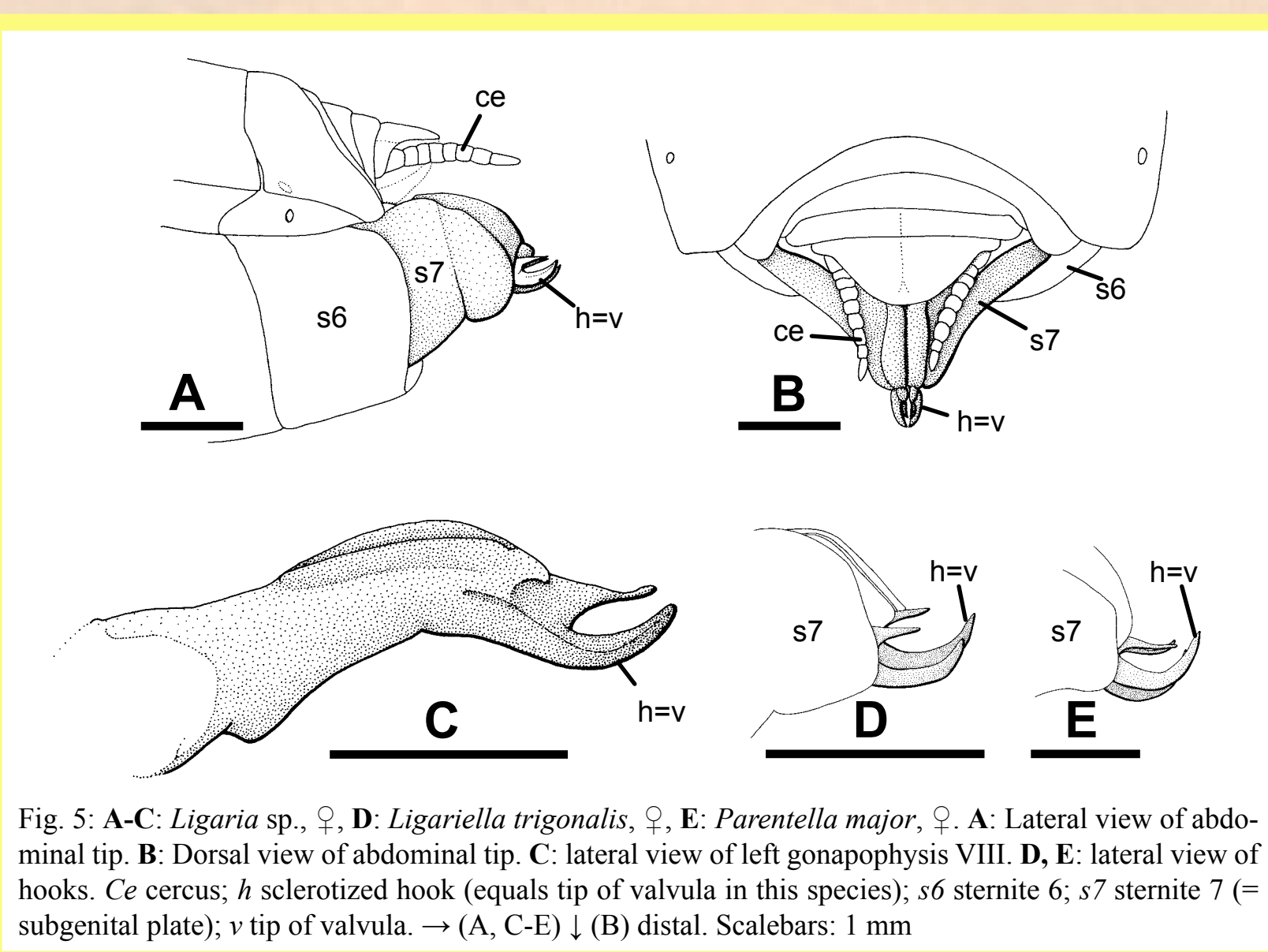


Fig. 5: A-C: *Ligaria* sp., ♀. D: *Ligariella trigonalis*, ♀. E: *Parentella major*, ♀. A: Lateral view of abdominal tip. B: Dorsal view of abdominal tip. C: lateral view of left gonapophysis VIII. D, E: lateral view of hooks. Ce cercus; h sclerotized hook (equals tip of valvula in this species); s6 sternite 6; s7 sternite 7 (= subgenital plate); v tip of valvula. → (A, C-E) ↓ (B) distal. Scalebars: 1 mm

Material & Methods

The external morphology of the following species was studied: *Chroicoptera saussurei* (Giglio-Tos, 1915) (NHMW, Vienna, drawing from photograph, and drawing from KALTENBACH 1996: fig. 67, redrawn), *Elaea machali* (Reiche & Fairmaire, 1847) (coll. Wieland), *Eremiaphila typhon* Lefebvre, 1835 (ZMB, Berlin), *Eremiaphila* sp. (2 different species; coll. Wieland), *Eremiaphila bernadstiewi* Stiewe, 2004 (picture of paratype, courtesy of T. Schulze), *Heteronutarsus aegyptiacus* Lefebvre, 1835 (NHMW, Vienna), *Humbertiella* sp. (coll. Wieland), *Ligaria* sp. (coll. Wieland, coll. K. Schütte), *Ligariella trigonalis* (Saussure, 1899) (ZMB, Berlin), *Parentella major* Giglio-Tos, 1915 (ZMB, Berlin), and *Rivetina* sp. (coll. Wieland).

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Discussion

The morphological origin of the digging devices [sternite 6, (medial) sternite 7, (distal) sternite 7, gonapophyses VIII] implicates that these structures have evolved independently at least four times.

The Eremiaphilidae-type is synapomorphic for *Eremiaphila* and *Heteronutarsus* and strongly supports the monophyly of the group. While the hooks on the gonapophyses VIII support the monophyly of *Ligaria* + *Ligariella* + *Entella* + *Parentella*, the occurrence of a distinct digging device in *Chroicoptera* puts the monophyly of the traditional Chroicopterinae (that also encompass the four former genera) in question.

The Eremiaphilidae- and the *Rivetina*-type are found mainly in the palaearctic region, whereas species exhibiting the *Chroicoptera*- and the *Ligaria*-type can be found predominantly in the Afrotropics (Fig. 6). The distributions of species exhibiting the different types of digging devices adjoin or overlap in western Africa (Eremiaphilidae-, *Rivetina*- and *Ligaria*-type in Senegal) and in eastern Africa (Eremiaphilidae- and *Ligaria*-type in Ethiopia, Kenya, Somalia). In South Africa, species of the *Ligaria*- and the *Chroicoptera*-type occur sympatrically.

Several Mantodea that have been observed in captivity while depositing their oothecae underground make wiping movements with the tip of their abdomen in order to create a depression in which the ootheca is laid and covered with sand (*Eremiaphila* sp., e.g. ANDRES 1914, and pers. obs.; *Humbertiella ceylonica*, see MÜLLER 2001; *Elaea*, *Rivetina*, see EHRMANN 2001). Observations on *Ligaria* sp. (Schütte, pers. comm. 2008) support an underground deposition of the ootheca, although the typical sweeping behaviour has not been confirmed yet. *Chroicoptera* has not been observed in captivity, but from their position and structure it can be hypothesized that the spines function as digging devices.

Some Mantodea that usually deposit their oothecae above the ground choose to bury the ootheca underground if climatic conditions do not fit the requirements for proper embryogenesis (e.g. *Humbertiella ceylonica*, see MÜLLER 2001), even though they do not exhibit any related morphological structures (pers. obs. in *Humbertiella* sp. and *Elaea marchali*). The wiping movements of the abdomen in order to dig a depression into the ground are apparently similar in species that exhibit specialized morphological digging structures (*Eremiaphila*, *Rivetina*) and in species that lack them (e.g. *Elaea*, *Humbertiella*, see EHRMANN 2001). Therefore it can be hypothesized that in species that generally dig in the ground for egg deposition, supporting structures are positively selected. It has still to be thoroughly observed if the afrotropical taxa exhibit an egg-laying behaviour similar to that of the palaearctic species.

A putative further type of digging device may be present in the monotypic *Rivetinula fraterna* (Saussure, 1871), of which the females carry two spines on the posterior edges of both sternite 6 and sternite 7 (LA GRECA 1977: 24; EHRMANN 2002: 314). This case may provide further insight in the evolution of digging structures in Mantodea, but unfortunately specimens of *Rivetinula* could not be studied yet.

To my knowledge Mantodea species from the Central Asian, North and South American, or Australian deserts, respectively, do not exhibit similar structures for burying oothecae below the surface. Future studies may reveal interesting insights into mantodean adaptations - both morphological and behavioural - to the life in arid habitats.

Acknowledgements

I am grateful to the following people (in alphabetical order):

- U. Aspöck (Naturhistorisches Museum Wien, Vienna, Austria), S. Bradler (Univ. of Göttingen, Germany), R. Ehrmann (Staatliches Museum für Naturkunde Karlsruhe, Germany), J. Goldberg (Massey Univ., Palmerston North, New Zealand), S. Matera (Erlangen, Germany), M. Ohi (Zoologisches Museum der Humboldt-Universität, Berlin, Germany), K. Schütte (Univ. of Hamburg, Germany), T. Schulze (Berlin, Germany), C. Schwarz (Univ. of Würzburg, Germany), G. Vogel (Univ. of Göttingen, Germany), R. Willmann (Univ. of Göttingen, Germany).

This study was partly funded by the German Research Foundation (DFG, project WI599/12).



Fig. 7: Mating pair of *Eremiaphila* sp. (♂ on top of ♀). Note digging spines of ♀ (arrow).