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Thanatosis and morphological adaptations in the mite genera *Lamnacarus* and *Pygmodispus* (Acari, Heterostigmatina, Scutacaridae)

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Abstract

In the mite family Scutacaridae, several species belonging to different genera show thanatosis or 'playing dead' behaviour. Some of them possess morphological features that are obviously connected with this behaviour. We compared the morphological adaptations to thanatosis in females of *Lamnacarus ornatus* Balogh and Mahunka, 1963 to those in *Pygmodispus* (*Allodispus*) *pavidus* Ebermann, 1997. To exhibit no point of attack to predators, the mites must retract their legs and cover them with adapted structures. Although the principles of the morphological adaptations to thanatosis are similar in *P.* (*A.*) *pavidus* and *L. ornatus*, there are differences in their completion.

Keywords: Thanatosis, morphological adaptations, Scutacaridae, *Pygmodispus pavidus*, *Lamnacarus ornatus*

1. Introduction

Thanatosis or 'playing dead' behaviour is a common reaction of mites to predator pressure. It is displayed by animals that are armoured with strongly sclerotised cuticular structures. Often, morphological adaptations are established that allow the withdrawal of the legs, which are supposed to be the most vulnerable body parts. Ebermann (1991a) described thanatosis and the corresponding morphological features in the mite family Scutacaridae, focusing on the females of *Pygmodispus* (*Allodispus*) *pavidus* Ebermann, 1997. The morphological adaptations of females of *Lamnacarus ornatus* Balogh and Mahunka, 1963 to thanatosis are described by Ebermann as being extremely similar, although the two genera are only distantly related. In our study, we investigated the reaction of *L. ornatus* to foreign-touch stimuli, analysed the morphological features of females using scanning electron micrography and compared them to those of *P.* (*A.) pavidus*.

2. Materials and Methods

Females of *L. ornatus* were extracted from decayed compost from a composting facility (Petzendorf, Styria, Austria; 46°55'29''N, 15°22'07''O) using Berlese-Tullgren funnels. Laboratory cultures were established adopting the rearing method according to Ebermann

(1991b), whereby the compost served as a source of nutritional fungi. The reaction of the mites to foreign-touch stimuli, induced by pricking them with thin insect needles, was observed under a stereomicroscope (Olympus SZ 40). Additionally, various other animals that were found in the compost (Collembola, Gamasina, adults and larvae of Staphylinidae, Coleoptera) were held together with several individuals of *L. ornatus* to study the interactions between them.

Scanning electron micrographs were made at the Institute for Electron Microscopy and Fine Structure Research Graz (FELMI) with a Quanta 600 FEG low-vacuum scanning electron microscope (SEM). The mites were placed on aluminium stubs covered with coal without any further preparation and could be observed to be still moving for several minutes through the SEM.

3. Results

Active females of *L. ornatus* usually stretched out all four legs (Fig. 1a). After touch stimuli, they retracted their legs (Fig. 1b) and remained immobile for several seconds up to one minute. They also contracted remarkably, which suggests the existence of strong dorsoventral musculature. When put into water, the mites also displayed thanatosis. Dead specimens found in the rearing boxes always had all their legs in an outstretched position. The observance of *L. ornatus* in the SEM showed that the mites can extend and retract single legs of both body sides independently.

Upon random encounters with other small arthropods, *L. ornatus* reacted by staying immobile for only a very short time or did not react at all. Sometimes, Gamasina and larvae of Staphylinidae investigated *L. ornatus* intensively with their mouthparts, which always caused the mites to perform thanatosis. After such investigations, *L. ornatus* played dead for several more seconds and then started moving again.

3.1. Morphological comparison of *L. ornatus* and *P. (A.) pavidus*

The anterior sternal plate and the gnathosoma of *L. ornatus* are tilted upwards as in *P.(A.) pavidus* (Figs 2a, 2b, 3b), so that legs I and II can be withdrawn into the recess between the sternal plate and tergite C (Figs 1b, 3a). The posterior sternal plate is enlarged and thus creates further space into which the legs can be withdrawn. No 'lateral plates' as in *P. (A.) pavidus* (Fig. 2) are developed, instead the ventral setae *3c* and *4c* (as well as, to some extent, setae *2b*) are broadened, dagger-like and are positioned at the very edge of the sternal plate (Fig. 3d). When the mite displays thanatosis, these setae adjoin the tergite C and thus cover the retracted legs I, II and III. In *P. (A.) pavidus*, the accordant ventral setae are thin and short (Fig. 2a) and the retracted legs are covered by the 'lateral plates' (Figs 2a, 2c).

Pygmodispus (*A.*) *pavidus* possesses a plate on the inner edge of trochanter IV that can cover the distal part of the retracted leg (Figs 2, 4e). The trochanter IV of *L. ornatus* has an expanded spine at the same position (Figs 3a, 3b, 3c, 4a). This process is, however, comparatively small and not large enough to cover the retracted leg IV. Apparently, leg IV cannot be totally withdrawn in *L. ornatus* (Fig. 3c). When playing dead, the mites nestle most segments of leg IV to the tergite C; the tibiotarsus and the long tarsal setae seem to be pressed towards the sternal plate but remain uncovered. The tarsal setae of *P.* (*A.) pavidus* are comparatively short and therefore do not protrude from the trochanter plate when leg IV is retracted (Fig. 2c).

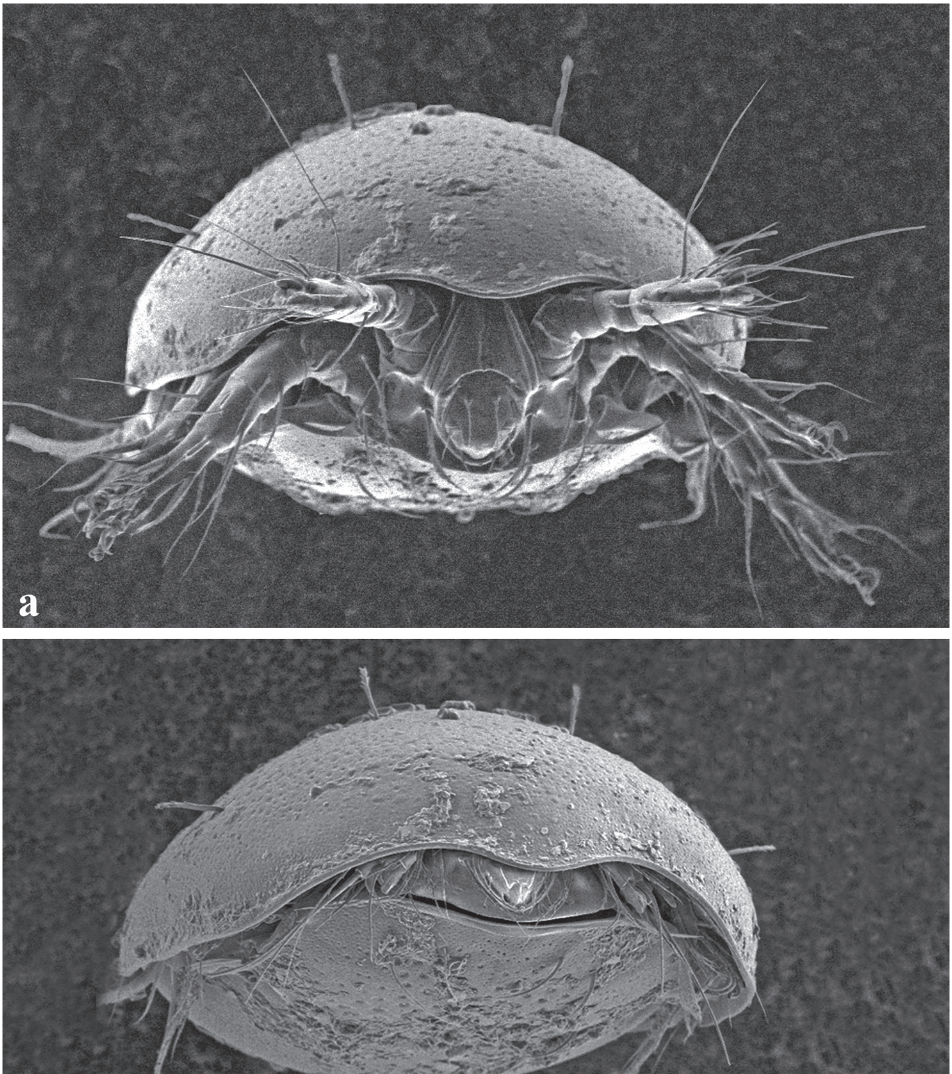

Fig. 1 Scanning electron micrographs of *Lamnacarus ornatus* females, frontal view. **a**: Female with legs stretched out; **b**: Legs concealed.

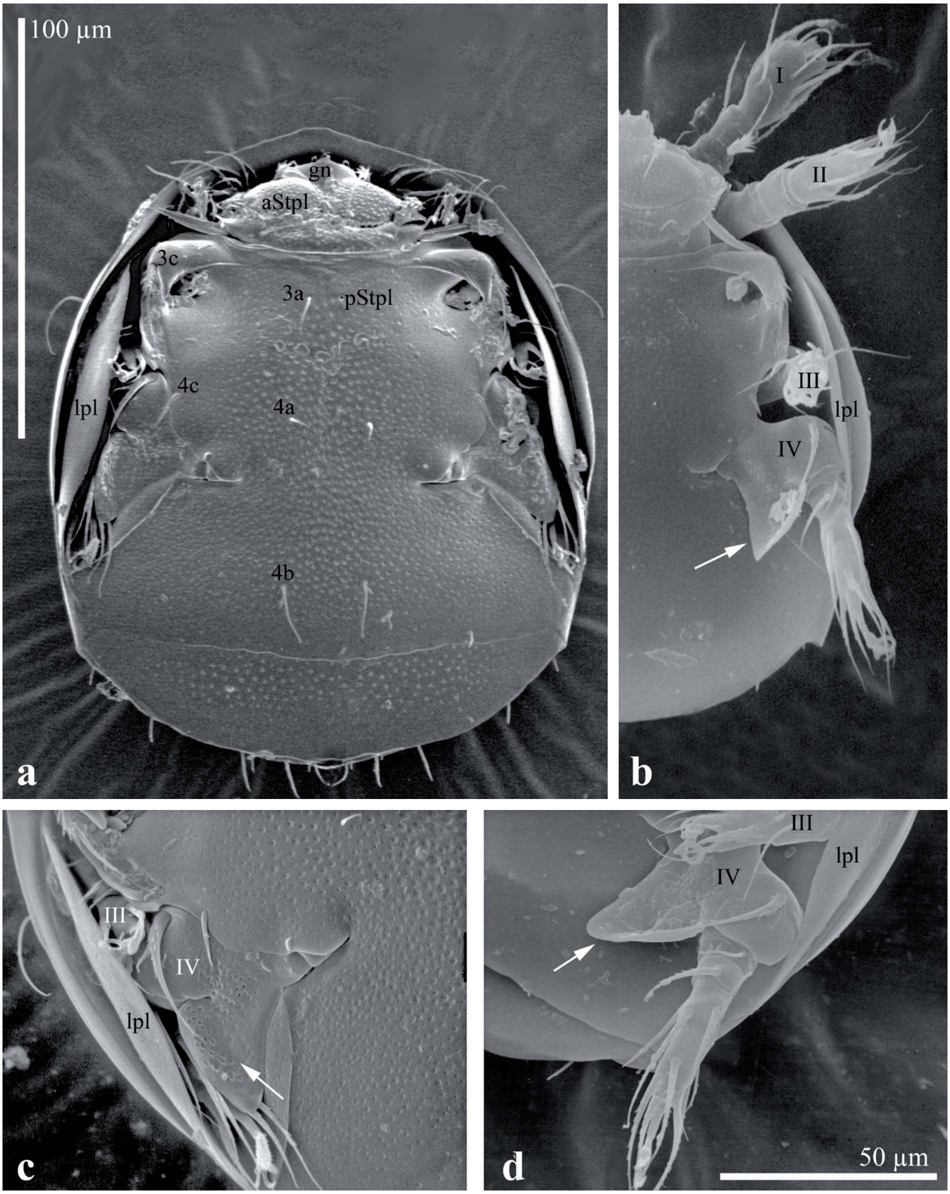

Fig. 2 Scanning electron micrographs of *Pygmodispus* (*Allodispus*) *pavidus* females, ventral view. **a**: All legs concealed, **b**: Active mite, all legs stretched out, **c**: detail of the retracted legs III and IV, **d**: Detail of the outstretched leg IV.

aStpl - anterior sternal plate, gn - gnathosoma, lpl - 'lateral plate', pStpl - posterior sternal plate, 3a–4c - setae on the pStpl. Arrows point to the process on trochanter IV.

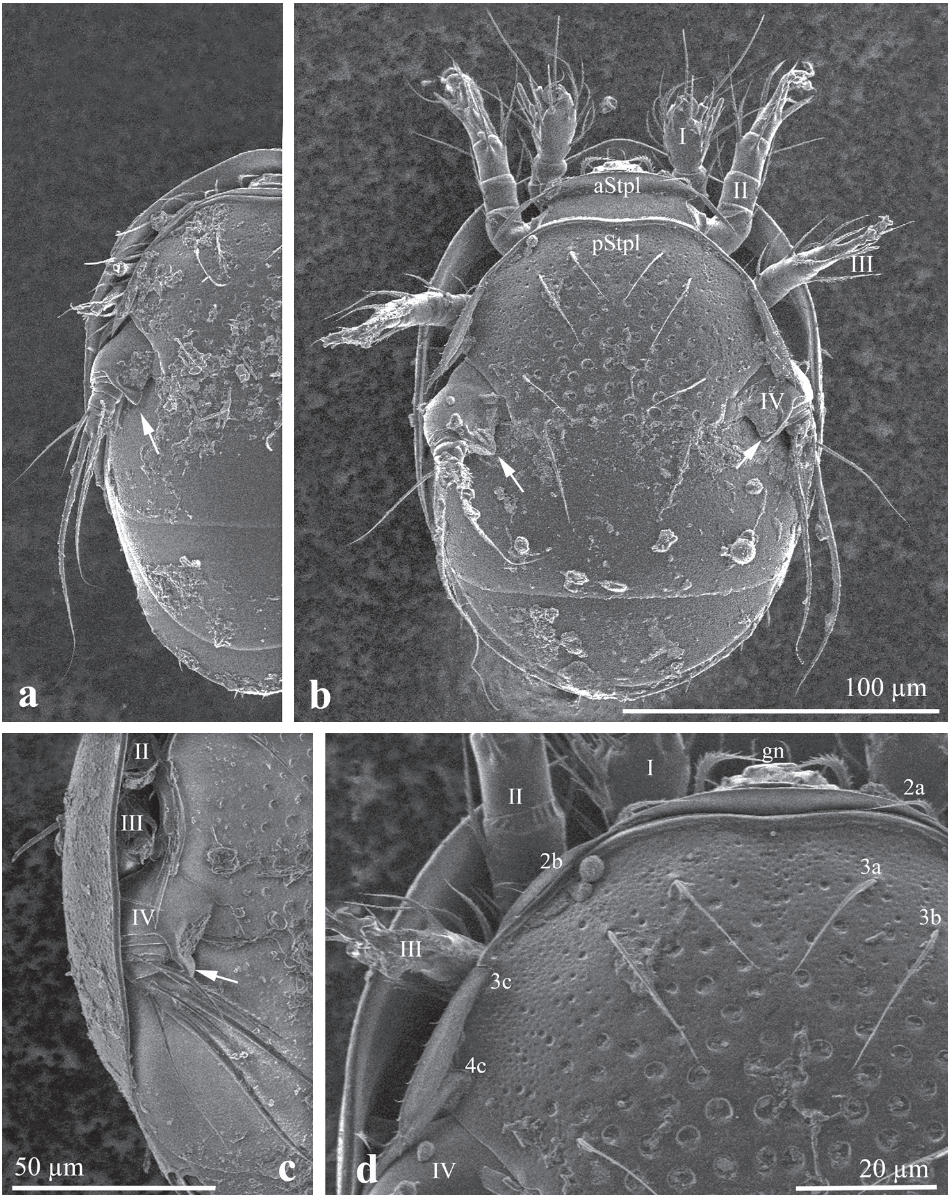

Fig. 3 Scanning electron micrographs of *Lamnacarus ornatus* females, ventral view. **a**: Mite with retracted legs I–II, **b**: Active mite, all legs stretched out, **c**: Detail of the retracted leg IV, **d**: Morphological adaptions to thanatosis on the ventral side, broadened setae 2b, 3c and 4c, enlarged pStpl.

aStpl - anterior sternal plate, gn - gnathosoma, pStpl - posterior sternal plate; 2a, 2b - setae on the aStpl; 3a–4c - setae on the pStpl. Arrows point to the process on trochanter IV.

4. Discussion

The strategies for performing thanatosis appear extremely similar in *L. ornatus* and *P.(A.) pavidus* at first sight, since both species are able to withdraw and subsequently cover their legs. Both possess a similarly enlarged posterior sternal plate, which makes the withdrawal of the limbs possible. The morphological adaptions for covering the retracted legs, however, include different parts of the body (broadened ventral setae 2b, 3c and 4c in *L. ornatus*, 'lateral plates' in *P. (A.) pavidus*).

In the genus *Pygmodispus*, comprising the subgenera *Allodispus* and *Pygmodispus*, there are different levels of development in the morphological adaptations to thanatosis. The posterior sternal plate is enlarged only in the subgenus *Allodispus*. The 'lateral plates' that can cover the withdrawn legs are always present, though they are more pronounced in the subgenus *Allodispus*. Most descriptions of *Pygmodispus* species lack information about the genus-specific 'lateral plates', but our reinvestigations showed that they nonetheless are always present. No similar structures are known in other scutacarid genera.

The morphological adaptations on the trochanter of leg IV range from pre-adaptive structures in the form of small spines in the subgenus *Pygmodispus*, e.g. *Pygmodispus* (*P.*) *baloghi* Mahunka, 1972, *Pygmodispus* (*P.*) *equestris* Paoli, 1911, *Pygmodispus* (*P.*) *zicsii* Mahunka, 1964 (Fig. 4b), to more or less extensive plate-like structures in the subgenus *Allodispus*, e.g. *Pygmodispus* (*A.*) *pavidus* (Fig. 4e), *Pygmodispus* (*A.*) *mancus* Mahunka, 1967 (Fig. 4f), *Pygmodispus* (*A.*) *stefaninii* Paoli, 1911. Intermediate stages – spurs or small plates on the trochanter of leg IV – can be found in both subgenera, whereas they are consistently formed as plates in *Allodispus*, e.g. *Pygmodispus* (*P.*) *calcaratus* Paoli 1911, *Pygmodispus* (*P.*) *montanus* Mahunka 1964, *Pygmodispus* (*P.*) *similis* Mahunka, 1968 (Fig. 4c), *Pygmodispus* (*A.*) *angulosus* Mahunka, 1979, *Pygmodispus* (*A.*) *latisternus* Paoli, 1911 (Fig. 4d) and *Pygmodispus* (*A.*) *pseudocoprophilus* Mahunka, 1979.

Since some species of the genus *Pygmodispus* are rare, it is difficult to obtain living specimens for behavioural experiments. Thus we could so far detect that *P.* (*P.*) *zicsii*, a species that does not possess morphological adaptations to thanatosis on leg IV, does not display 'playing dead' behaviour. *Pygmodispus* (*P.*) *calcaratus*, which has a spur on the trochanter of leg IV, does not perform thanatosis either. *Pygmodispus* (*A.*) *latisternus*, *P.* (*A.*) *pavidus* and *P.* (*A.*) *stefaninii* – all of which possess plates on the trochanter of leg IV – show thanatosis.

The size of the plate on the trochanter of leg IV of *L. ornatus* matches that of *Pygmodispus* species with intermediate size plates. Other *Lamnacarus* specie – *Lamnacarus baloghi* Mahunka, 1967, *Lamnacarus calcaratus* Mahunka, 1971 and *Lamnacarus expansus* Mahunka, 1973 – also possess similar plates on the trochanter. They also have an enlarged posterior sternal plate. Presumably all members of the genus are capable of withdrawing their legs. As they are only available as microscope slides so far, it is not known whether they indeed show thanatosis.

We assume that *Crenatoplaxa diademata* Mahunka, 1972 is another scutacarid species performing 'playing dead' behaviour since it has morphological adaptations to thanatosis: a pronounced plate-like process on the trochanter on leg IV (Fig. 4g) and an enlarged posterior sternal plate.

Species of the genus *Heterodispus* display processes on trochanter IV as well. However, tarsus and pretarsus IV of this genus are long and the appendages on the trochanter would not be suitable for covering a retracted leg. No additional morphological structures like lateral plates that could be interpreted as adaptations to thanatosis are present. Indeed, death feigning behaviour has not been observed in living specimens of *Heterodispus* so far (Ebermann, unpublished).

In the genus *Scutacarus*, no species possesses structures that could be interpreted as morphological adaptations to thanatosis. Some species did, however, perform the behaviour in previous experiments (Ebermann, unpublished): *Scutacarus longipes* Rack, 1975, *Scutacarus quadrangularis* Paoli, 1911 and *Scutacarus carinthiacus* Ebermann, 1979. In these species, the females react to touch stimuli by retracting their legs and pressing them against their ventral side. Doing so, they remain immobile for up to one minute. Because of the tortoise-like habitus typical for Scutacaridae, the mites can cover their legs to some degree even without special morphological adaptations.

A morphological feature shared by all scutacarid species showing thanatosis or possessing the characteristic morphological adaptations to the behaviour is the existence of short or even very short dorsal setae. The short setae could be interpreted as another passive defence against predators, since smooth tergites without any long dorsal setae offer no point of attack.

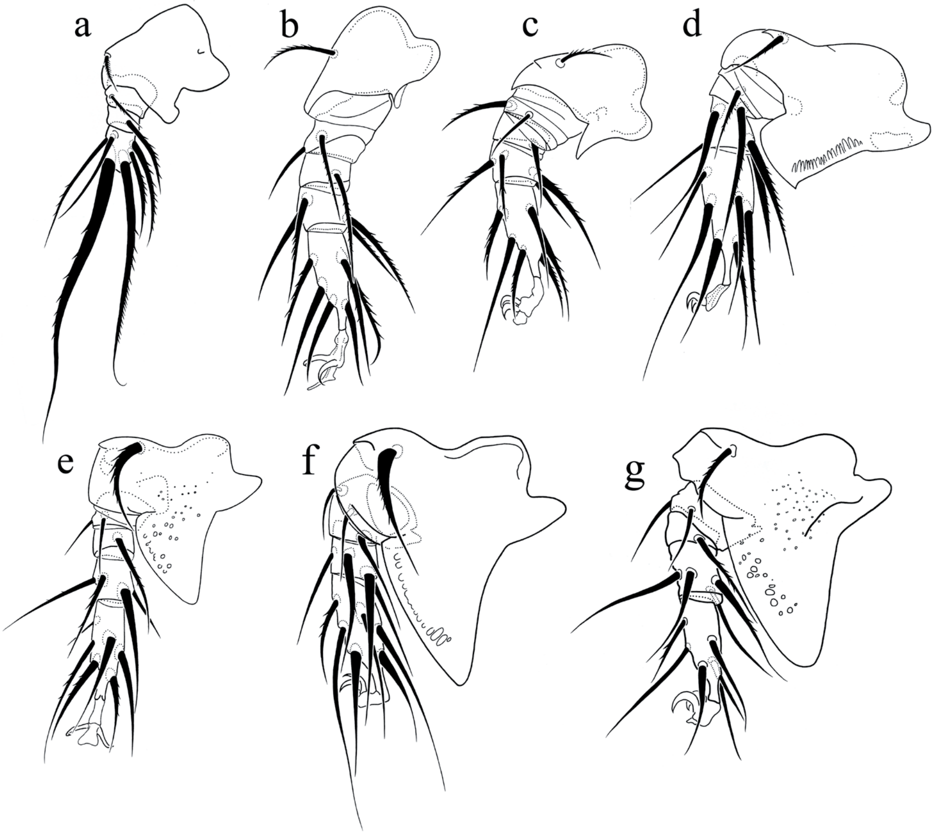

Fig. 4 Leg IV of different scutacarid species. **a**: Lamnacarus ornatus; **b–f**: Increasing perfection of morphological adaptations to thanatosis on the trochanter of leg IV in the genus *Pygmodispus* [**b**: *Pygmodispus* (*Pygmodispus*) zicsii, **c**: *Pygmodispus* (*P.*) *similis*, **d**: *Pygmodispus* (*Allodispus*) *latisternus*, **e**: *Pygmodispus* (*A.*) *pavidus*, **f**: *Pygmodispus* (*A.*) *mancus*, **g**: *Crenatoplaxa diademata*].

Thanatosis presumably is a successful method of reacting to predator pressure for female scutacarid mites. They appear to be predestined for this behaviour because of their body form. Still, the majority of scutacarid species do not exhibit it. Most mites react to touch stimuli by keeping immobile for few seconds, if at all, and then trying their luck in fleeing. *Imparipes dispar* Rack, 1964 can even jump to evade enemies (Ebermann 1995). Larvae and males of scutacarid mites, which in contrast to the females possess a soft cuticle, always move away rapidly when touch stimuli are applied.

In other mite groups, thanatosis is known in Holothyrida (Walter & Proctor 1998), Uropodina [the legs can be withdrawn into so-called pedifossae (Krantz & Walter 2009)] and several lineages of Oribatida. The latter developed extremely effective morphological adaptations to thanatosis: 'box mites' can fold themselves up like pocket knives because of their ptychoid body form. In Brachypylina, 'pteromorphs', structures on the notogaster that can conceal all parts of retracted legs, can be present (Krantz & Walter 2009).

We were able to demonstrate thanatosis in the scutacarid genera *Scutacarus*, *Lamnacarus* and *Pygmodispus* and found morphological adaptations for the behaviour in *Lamnacarus*, *Pygmodispus* and *Crenatoplaxa*. The monotypic genus *Crenatoplaxa* is similar to *Pygmodispus* (*Allodispus*) in many respects, but their relationship still has to be clarified (Ebermann 1997). Preliminary phylogenetic reconstructions based on morphological characters (Jagersbacher-Baumann 2011) showed a close relationship between *Scutacarus* and *Lamnacarus*, but not between these genera and *Pygmodispus* and *Crenatoplaxa*. Thus, the morphological adaptations to thanatosis presumably developed convergently. Since thanatosis can be performed without any morphological adaptations for withdrawing the legs, we assume that the behavioural trait of 'playing dead' itself is plesiomorphic. The evolution of those 'similar' structures in the compared genera is supposed to be caused by the same selection pressure. The driving force could be the existence of predators that use special hunting strategies or are extremely numerous.

The natural enemies of Scutacaridae are largely unknown and have not yet been studied. In our recent experiments, we could not identify any predators. So far, we could only accidentally observe gamasid mites feeding on scutacarids in laboratory cultures. Adult Staphylinidae, which serve as phoretic host for *Scutacarus longipes* (a species performing thanatosis), also occasionally captured and ate the mites (Ebermann, unpublished).

5. Acknowledgements

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