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Mate guarding in the genus *Zwickia* (Astigmata: Histiostomatidae), a natatorial inhabitant of the fluid-filled pitchers of *Nepenthes* (Nepentheaceae)

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Summary

Species in the histiostomatid genus *Zwickia* inhabit the fluid-filled pitchers of plants in the genus *Nepenthes*, and are adapted for movement on solid substrates as well as through a fluid medium. Males can actively move about while mate guarding, securely transporting a tritonymphal female. Adaptations for dual locomotory behaviors restrict the clasping of tritonymphs to the male's first pair of legs. Legs I are therefore highly modified, with tarsal adaptations to firmly clasp the tritonymph around the bases of her third pair of legs. The tritonymph is therefore held more anteriorly rather than directly beneath the male, an adaptation to reduce drag while swimming. Male legs II are also elongate, thereby allowing the tritonymph to be held off the substrate while walking.

Key words: *Zwickia*, *Nepenthes*, precopulatory mate guarding, mating behavior.

Introduction

The ultimate measure of a male's success is the number of offspring sired. Toward achieving that goal, an individual male's reproductive success can be advanced by (1) inseminating the partners of other males and (2) preventing his own sexual partners from being inseminated by rival males (Parker, 1970). The latter is often accomplished by means of precopulatory and/or postcopulatory mate guarding (Alcock, 1994; Choe and Crespi, 1997). Precopulatory mate guarding is commonly observed in the astigmatic family Histiostomatidae, especially those species inhabiting the fluid of phytotelmata. One such phytotelm habitat is the pitchers of species of *Nepenthes*, a carnivorous plant genus of over 100 species that ranges from India to Northern Australia, as well as the Seychelles and

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Madagascar. Several histiostomatid genera are obligatory inhabitants of *Nepenthes* pitchers and adapted to withstand digestive enzymes produced by the plant. Like most histiostomatid species, males seek quiescent tritonympal females and guard them from other males. Upon ecdysis to the adult, mating takes place. Successful mate guarding prevents other males from gaining access to a virgin female and thereby insures the guarding male's paternity of resultant offspring**.** The Histiostomatidae is a very large and diverse family, and this diversity is reflected in both behavioral and morphological adaptations associated with mate guarding. While most species inhabiting *Nepenthes* pitchers are solely ambulatory, moving about on decomposing arthropods in the pitcher, natatory behavior is observed in two genera. Species in the genus *Creutzeria* are solely natatory (Fashing *et al*., 1996), whereas those in the genus *Zwickia* are ambulatory as well as natatory. Swimming is a more laborious task than walking, requiring extensive modification of legs (Fashing *et al*., 1996). This in turn imposes restrictions in male adaptations for mate guarding. The following account describes precopulatory mate-guarding in the genus *Zwickia*.

Materials and Methods

Fluid-filled pitchers were collected from *Nepenthes rafflesiana* Jack at numerous localities in Brunei Darussalam, and transported back to the laboratory at the Universiti Brunei Darussalam. Pitcher contents were placed in petri dishes and behavioral observations made using a stereomicroscope. To examine the morphological adaptations associated with mate guarding, phase contrast and interference microscopy as well scanning electron microscopy (SEM) were used. For SEM preparation, specimens were dehydrated in ethyl alcohol, dried using the critical point procedure, affixed to stubs using double-sided sticky tape, and coated with gold palladium in a sputter coater. SEM microscopy was performed on an AMR-1810. Mensural data were collected on idiosomal, leg and tarsal lengths of males, females and tritonymphs collected from *N. rafflesiana* pitchers in Singapore.

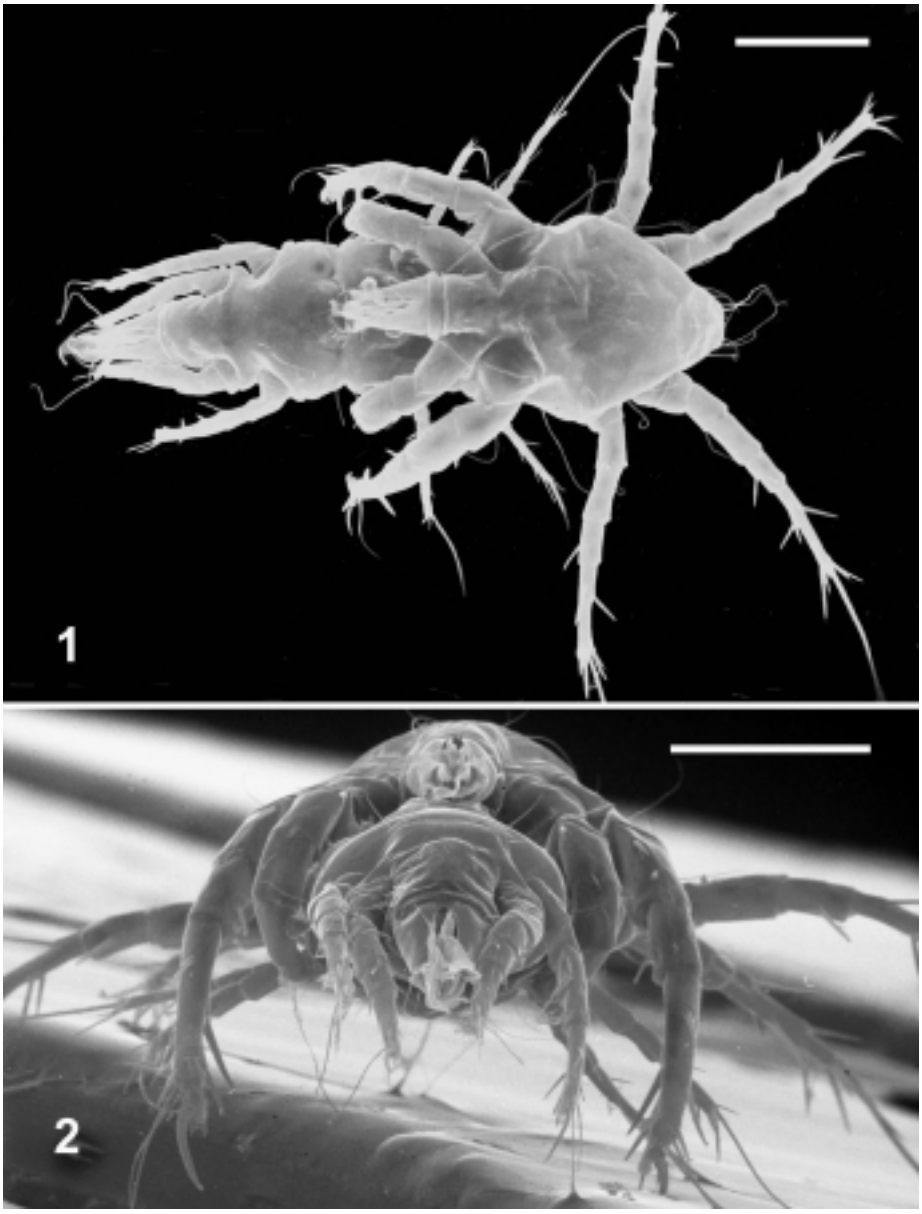
Results and Discussion

Most histiostomatid genera inhabiting *Nepenthes* pitchers are ambulatory, moving about on decomposing arthropods in the pitcher. When mate guarding, males of these species typically climb onto the dorsum of a tritonymphal female and utilize their legs to firmly clasp her idiosoma. In some species, males are not adapted to locomote when guarding a potential mate and simply ride about on her dorsum. In other species, two pair of legs clutch the female; the other two pair are very long, thereby al-

lowing the male to walk about while holding the securely clasped female off the substrate. Species in the genus *Zwickia*, on the other hand, are natatory and propel themselves through the fluid using legs III, legs highly modified for swimming. Legs IV are morphologically similar to legs III, but simply trail behind while swimming and probably function as rudders. Individuals are also adapted for movement on solid substrate, using legs I and II for grasping and pulling. Mate guarding by males poses a problem since the guarded tritonymph must be held in front of the male to minimize fluid resistance (drag) while swimming. Since legs II are used for moving about on solid substrate, only legs I are available for mate guarding rather than two pair as in solely ambulatory species. Although all male legs are longer and more robust in respect to idiosomal size than the corresponding legs of tritonymphs and females, legs I and II are especially so (tab. 1, fig. 1). The robustness of legs II-IV is thought to be associated with the fact that males require stronger and more efficient legs since they must transport tritonmyphs as well as themselves while mate guarding. Legs I of males function almost exclusively in mate guarding, and are therefore exceptionally modified for this purpose. In comparison to those of tritonymphs and adult females, they are not only longer (tab. 1) but also more massive (figs 1-3), a feature indicative of their increased musculature and therefore strength. The tarsi are longer than in other instars (tab. 1), and ventral setae *ra* and *s* are stout and broadly flattened laterally (fig. 4). These two setae, combined with the concave nature of the region between them, form a deep groove (figs 4, 5). Upon encountering a female tritonymph, the male mounts dorsally and slides the "grooved" regions of his tarsi over her third femora (fig. 5), thereby securely clasping them. The male's muscular legs I also tightly clasp the tritonymph's idiosoma (figs 1-3), and stout, cone-shaped femoral setae (*vF*) help anchor the bases of his legs to her idiosoma. The tritonymph is also modified to facilitate mate guarding; a waist-like constriction between the propodosoma and hysterosoma allows the male to more easily clasp and hold her in place (figs 1, 3). This constriction is not found in other instars. Clasping the tritonymph by her third pair of legs allows the male to hold her more anteriorly rather than directly beneath

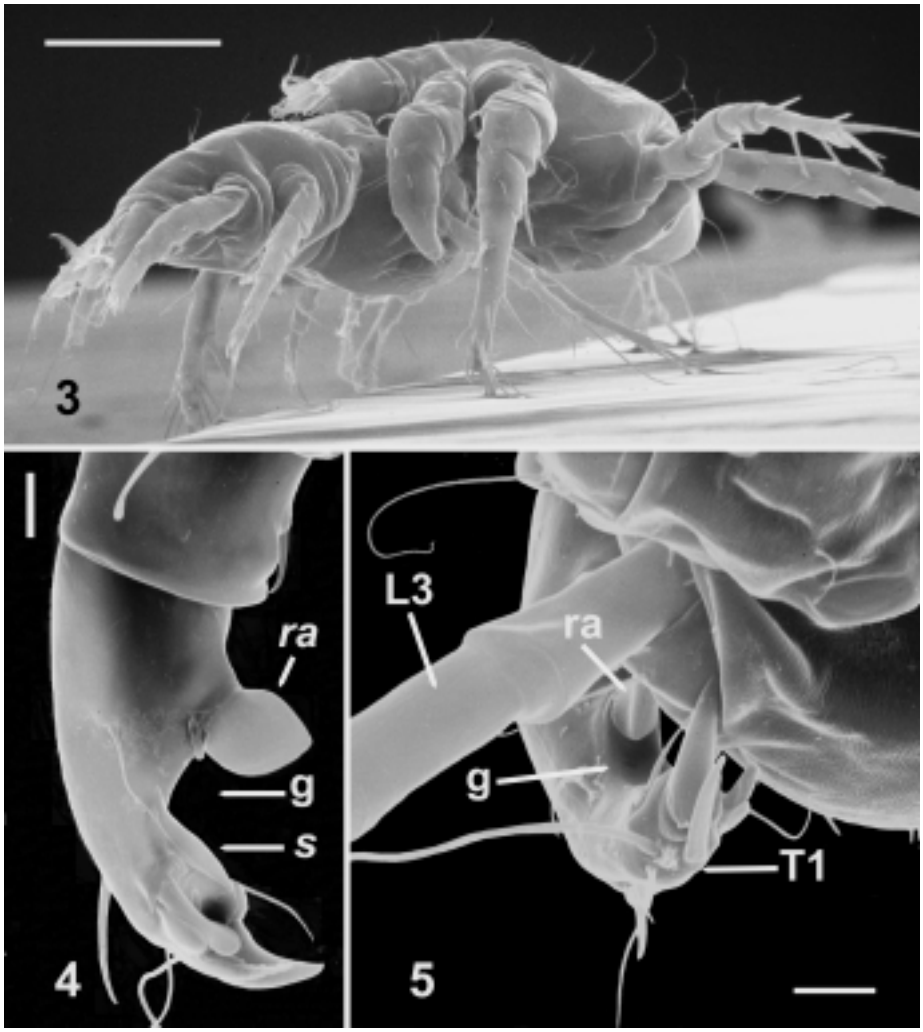
Table 1 - Measurements of tritonymphs, males, and females from Singapore. Means and their standard errors (in micrometers) for idosomal length, and for total leg length (upper) and tarsal lengths (lower). Sample size equals 10 for males and females and 6 for tritonymphs.

	Idiosoma	**Leg I**	**Leg II**	**Leg III**	**Leg IV**
Tritonymph	314 ± 5.27	122 ± 2.64	145 ± 9.61	135 ± 11.41	166 ± 13.64
		35 ± 2.25	48 ± 3.67	39 ± 3.72	69 ± 6.42
Male	300 ± 4.80	185 ± 3.48	244 ± 17.78	212 ± 12.94	236 ± 16.05
		50 ± 3.88	89 ± 4.52	69 ± 4.17	94 ± 3.62
Female	390 ± 11.25	164 ± 2.16	197 ± 14.05	188 ± 9.09	227 ± 12.48
		51 ± 1.84	68 ± 3.69	60 ± 3.31	96 ± 5.85



Figs 1-2 - *Zwickia* sp. (Brunei Darussalam). Male (upper mite) in amplexus with tritonymph. Scale bar = 100 mm. 1. Dorsal view. 2. Anterior view. Note idiosomal constriction between legs II and III of tritonymph.

his idiosoma (figs 1-3), thereby decreasing resistance by the fluid while swimming. Long legs II also allows the male to hold the guarded tritonymph above a solid substrate while locomoting (fig. 2). While mate



Figs 3-5 - *Zwickia* sp. (Brunei Darussalam). Scale bar: 1 = 100 mm; 4, 5 = 10 mm. 3. Frontal/lateral view of male (upper mite) in amplexus with tritonymph; 4. Ventral view of male tarsus I; 5. Posterior view of male tarsus I approaching leg III of tritonymph for engagement. g = groove, L3 = leg III of tritonymph, T1 = tarsus I of male.

guarding, males in the genus *Zwickia* can therefore readily move about on solid substrate or swim through fluid substrate, a trait not observed in other histiostomatid genera.

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