

MATING BEHAVIOR OF *PHYSOLIMNESIA AUSTRALIS* (ACARI, LIMNESIIDAE), A NON-PARASITIC, ROTIFER-EATING WATER MITE FROM AUSTRALIA

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ABSTRACT. The diversity of sperm transfer behavior shown by water mites (Acari, Hydrachnidia) is among the highest in the Arthropoda. However, sperm transfer has been described in fewer than 10% of water mite genera, all of them being Holarctic or cosmopolitan taxa. Here I describe mating behavior in *Physolimnesia australis* (Halik 1940), the sole representative of an Australian genus. *P. australis* is unusual in having larvae that do not parasitize insects, and in including rotifers in its diet. The highly dimorphic *P. australis* male responds to female presence by taking up an "embrace" posture in which he orients his opisthosoma and legs III toward approaching females. The female is caught in the embrace and her legs IV are secured by the modified tips of the male's legs IV. The male deposits a glutinous mass on the female's back, which she grooms towards her genital opening after being released. This mode of transfer differs from members of the confamilial genus *Limnesia* Koch 1836 in which males and females do not pair.

Chelicerates show the greatest diversity of sperm transfer modes in the Arthropoda. In some taxa, males transfer sperm directly with a penis (Opiliones) or with secondarily derived genitalia (e.g., palps in Araneae). In other groups, males transfer sperm indirectly by depositing spermatophores on a substrate, and either encouraging females to move over the sperm packets (e.g., Scorpionida) or allowing females to discover and take up sperm on their own (e.g., many Pseudoscorpionida) (Proctor et al. 1995). Finally, the horseshoe crabs (Merostomata) have external fertilization of eggs (Ruppert & Barnes 1994). Within the Chelicerata, some taxa exhibit greater behavioral diversity than others. For example, all spiders pair whereas pseudoscorpions may or may not have close associations between the sexes. The greatest variety of sperm transfer behavior occurs among the mites (Subclass Acari), and within this group the most diverse behavior is shown by the water mites (Suborder Prostigmata, Hydrachnidia). With the exception of external fertilization, all possible modes of sperm transfer occur in the Hydrachnidia from direct transfer via venter-to-

venter copulation (e.g., *Midea* Bruzelius 1854, *Eylais* Latreille 1796) to complete dissociation in which the sexes never meet (e.g., *Hydrodroma* Koch 1837). Despite this amazing range of behavior, water mites have been poorly studied and mating observations have been published for only 24 of the more than 340 genera of water mites (Proctor 1992a,b). These observations have been limited almost entirely to species from North America and Europe, and there are no descriptions of sperm transfer in a non-holarctic genus. Here I describe mating behavior in a monotypic genus of Australian water mites together with casual observations of its life cycle and diet.

METHODS

Physolimnesia australis (Limnesiidae) is a small (≤ 1 mm) water mite found in the littoral zone of standing and slowly running water in Queensland and New South Wales (M. Harvey pers. comm.; Proctor pers. obs.). This species shows a strong sexual dimorphism in which males have a ventrally concave opisthosoma and flattened terminal segments of legs III and IV (Fig. 1). Females are morphologically similar to species in the confamilial genus *Limnesia* and were previously described

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as a species in this genus (*Limnesia trituberculata* Viets 1955). I collected and observed *P. australis* on two occasions in 1995: in March from Cedar Creek approximately 50 km south of Brisbane, Queensland; and in October from a large pond on the University of Queensland campus, St. Lucia. All observations were made using a dissecting microscope and took place at the Department of Entomology, University of Queensland. I separated mites according to sex and stage (adult and deutonymph) and maintained these groups in large well plates (well diameter = 35 mm, depth = 19 mm). Dipteran larvae (Culicidae, Chironomidae) and cladocerans (Moinidae) collected from a small pond on the University of Queensland campus were included as potential prey for the mites. I made behavioral observations on mites that had been collected as adults as well as those raised from deutonymphs in the lab. Voucher specimens are deposited in the University of Queensland Insect Collection, Department of Entomology, St. Lucia, Australia, 4072.

RESULTS

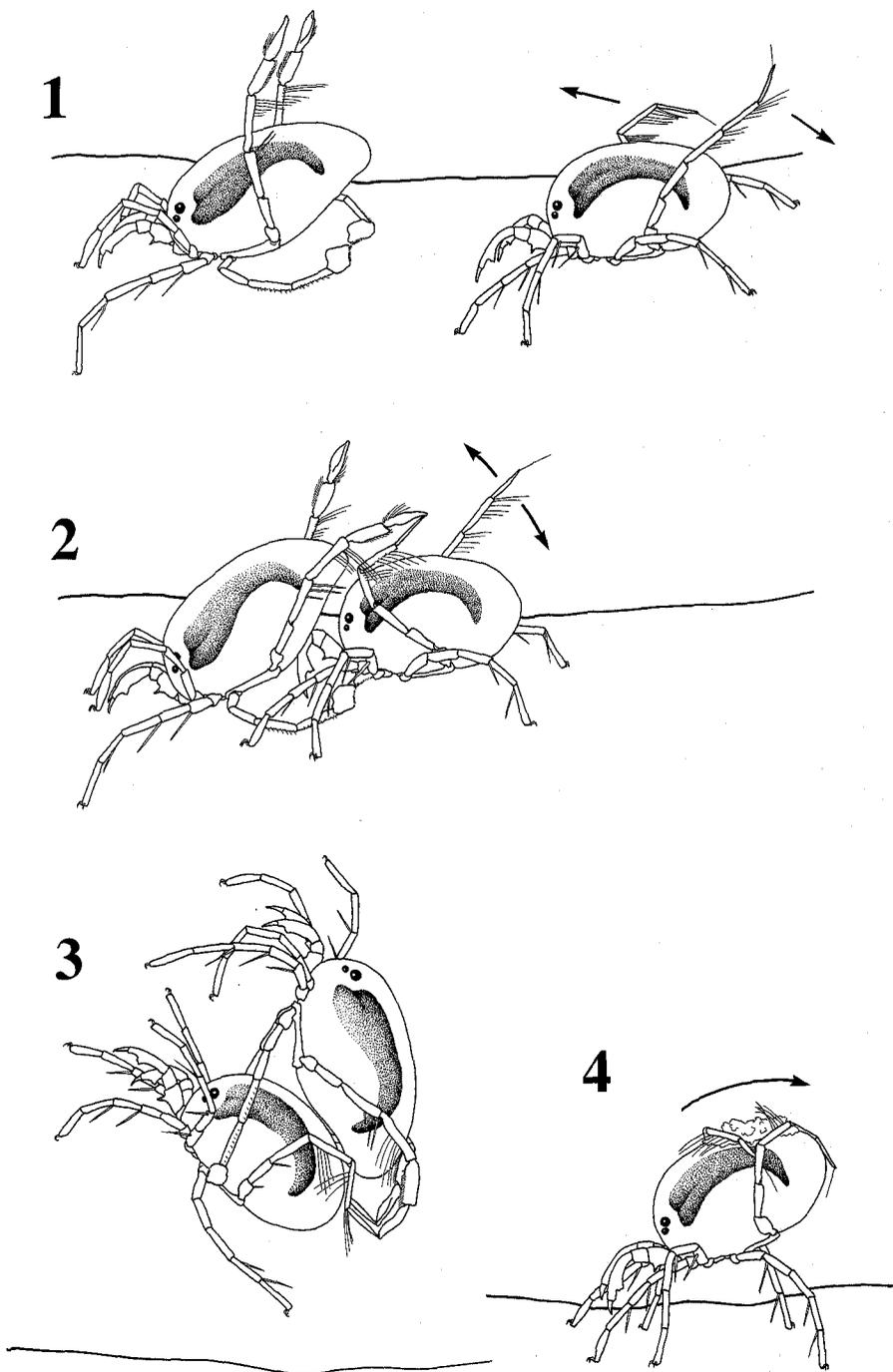
Life-cycle and predation.—Most water mites have a complex life-cycle with three active stages: the six-legged larva parasitizes adult aquatic insects, and is followed by two eight-legged predatory stages, the deutonymph and the adult (Smith & Cook 1991). *Physolimnesia australis* is an exception to this rule in that its larvae forgo the parasitic phase. Adult females collected from the field readily laid small clutches consisting of 1–8 eggs on the sides and bottoms of the wells. The eggs were large relative to the female (mean = 134 μm , SD = 8 μm , $n = 4$). I observed that *P. australis* larvae remain within the coating of the egg clutch and transform directly into predaceous deutonymphs (via the inactive protonymph).

The newly emerged *Physolimnesia* deutonymphs were very small (body length \approx 250 μm) and were unable to handle the large cladoceran and dipteran prey I provided. Nevertheless, they increased in size and transformed into adult mites. This energetic mystery was solved when I observed deutonymphs capturing and eating large phoretic rotifers that had been inadvertently introduced along with their moinid cladoceran hosts. The rotifers were identified as *Brachionus variabilis* Hempel

1896, a cosmopolitan epizootic species of 200–380 μm in length (Koste & Shiel 1987). Thus to a 250 μm deutonymph, a single rotifer would be a substantial meal. Adult male and female *P. australis* were observed eating *B. variabilis*, as well as feeding on cladocerans and dipteran larvae. Neither the deutonymphs nor the adults appeared to forcibly remove the rotifers from their moinid hosts; rather, the mites captured rotifers that had detached from the cladocerans and were swimming freely in the wells.

Mating behavior.—When a male *P. australis* was placed in a well that held females, he initially stood on the substrate and groomed himself vigorously by moving legs III and IV back over his dorsum and around to his venter. After a bout of grooming, the male was very still relative to the females, which were constantly crawling and swimming close to the substrate. In *P. australis*, as in most limnesiids (pers. obs.), crawling locomotion is accomplished by the first three pairs of legs, with legs IV moving in a constant fanning motion over the mite's back, presumably aerating the dorsal integument for gas exchange purposes. When a female bumped into the male or passed near him he immediately took up the "embrace" posture (Fig. 1). In this position the male's opisthosoma was tilted at approximately 30° to the substrate, the flattened tips of legs III were touching and pressed against the substrate (thereby forming the circular "embrace"), and legs IV were held rigidly and vertically. The male oriented his embrace towards any females that passed behind him. He also oriented towards other passing males and occasionally to swimming cladocerans. While in this posture the male was often approached by a female that -by accident or intent -crawled up behind the male and placed her capitulum over the flattened tips of the male's legs III (Fig. 2). The male responded by elevating his opisthosoma to about 50° to the substrate and attempting to capture the fanning tips of the female's legs IV in the flattened, scoop-like tips of his own fourth legs (Fig. 2). It was unclear how this capturing was achieved; possibly, the long apical seta at the tip of the female's leg IV is secured by the groove in the male's tarsus.

When the male had captured both of the female's legs she typically began to struggle.



Figures 1-4.—Mating behavior of *Physolimnesia australis*. 1, Male in the "embrace" posture with female approaching from behind; 2, Female within male's embrace, male has captured the tip of her left leg IV in the tip of his modified leg IV; 3, Male has captured both leg tips and the pair is swimming jerkily; 4, Female grooms sticky material deposited by male on her back towards her ventrally located genital aperture.

However, the male gripped the female in the region of her 2nd or 3rd coxal plates with the tips of his legs III (Fig. 3). The pair typically left the substrate at this point and swam about in a jerky fashion. I observed at least 20 pairings that reached this stage; however, all but three were terminated when the female escaped from the male's grip after a few seconds of swimming. For the pairs that continued swimming, which usually lasted less than one minute, the male rubbed the concave ventral surface of his opisthosoma on the female's dorsum. The male's genital opening is located just behind the coxal plates of legs IV, and the rubbing of his venter against the female's back probably represents deposition of the ejaculate. In two of the three complete matings observed, the male slid around backwards towards the end of the female's opisthosoma just before the pair separated. After the female escaped or was released from the male's grip, she perched on the substrate and vigorously groomed back over her dorsum and around towards her ventrally located genital opening (Fig. 4). In two of the three complete matings, I observed opaque white material on the female's dorsum after she separated from the male (Fig. 4).

DISCUSSION

The mating behavior of *Physolimnesia australis* is very different from that of species in the genus *Limnesia*, the only other limnesiid genus for which reproductive behavior is known. *Limnesia* species show no sexual dimorphism save in body size (female larger) and degree of fusion of genital plates. In *Limnesia* spp., physical or chemical contact between males and females is not required for spermatophore production and transfer (Witte 1991; Proctor 1992a). Rather, males maintained alone will deposit spermatophores on a substrate, and females that later encounter them will take up sperm if so inclined. Proctor (1992a) called this mode of sperm transfer "complete dissociation", and contrasted it with three other modes: incomplete dissociation (physical or chemical contact between the sexes required for spermatophore deposition but no pairing between the sexes); pairing, indirect transfer (male courts a given female, spermatophores deposited on substrate); and copulation (male places sperm in female's sperm-receiving structure). The transfer mode

of *Physolimnesia australis* appears to fall between the third and fourth categories, as the male places the sperm on the female (as in copulation), but she must move it to her genital opening (as in pairing, indirect transfer). This suggests that the categories of sperm transfer outlined by Proctor (1992a) may be too rigid to easily encompass all transfer behaviors.

It is not clear what motivates the *P. australis* female to enter the embrace of the male's legs. In the water mite *Neumania papillator* (Unionicolidae), the female orients towards the male's courtship signals because they resemble vibrations caused by prey (Proctor 1991). It is possible that male *Physolimnesia australis* engage in similar "sensory trapping" (*sensu* Christy 1995), perhaps by producing chemicals that mimic the scent of prey animals.

The water mite Family Limnesiidae contains 23 genera, five of which are composed of species that are strongly sexually dimorphic (*Physolimnesia*, *Timmsilimnesia* K.O. Viets 1984, *Centrolimnesia* Lundblad 1935, *Pterolimnesia* Viets 1942 and *Acantholimnesia* Viets 1954) (Cook 1974, 1980, 1986, 1988; Viets 1984). No two genera share the same types of male modifications, suggesting that sperm transfer with close contact between the sexes has evolved repeatedly in this family from an ancestral non-paired state, as has occurred in many other families of water mites (Proctor 1991).

Physolimnesia australis is an unusual water mite in other aspects of its biology. Whereas most Hydrachnidia have a parasitic larva that acts as both a feeding and a dispersal stage, the larva of *P. australis* transforms to a predatory deutonymph without parasitizing an insect host. Suppression of the parasitic phase has been recorded in 29 species scattered through distantly related families of water mites, including a few confamilials in the genus *Limnesia* (Smith & Cook 1991; Smith in press; H. Proctor pers. obs.). Like many species with non-feeding larvae, *P. australis* has a small adult body size, small clutch size and relatively large eggs for its body size (Cook, Smith & Brooks 1989; Smith in press). Although the loss of larval parasitism has independently arisen many times, it does not seem conducive to cladogenesis, as such lineages consist of single species (or populations)

whose closest relatives retain parasitic larvae (Smith in press). Although one might expect that loss of dispersal via parasitic larvae would occur in lineages that inhabited permanent water bodies, there is no apparent pattern in relation to habitat: lineages without larval parasitism occur in streams, temporary ponds, and both littoral and planktonic habitats within lakes (Smith in press). It is not clear how, or indeed if, water mites with non-feeding larvae disperse to new bodies of water.

The final strange aspect of *P. australis*' biology is the inclusion of rotifers in its diet. Confamilials in the genus *Limnesia* have been observed feeding on a variety of invertebrates (crustaceans, insects, other mites) and even vertebrate prey (fish eggs) (Proctor & Pritchard 1989); but to my knowledge, this is only the second observation of arachnids feeding on rotifers. One other species, an undescribed oribatid mite in the genus *Aquanothrus* Engelbrecht 1975 (Ameronothridae), is believed to feed on rotifers based on the presence of undigested trophi (rotifer mouthparts) in the mites' guts (R.A. Norton pers. comm.).

Note added in proof: (a) Adults and nymphs also prey on nematodes and oligochaetes. (b) It is also possible that the male deposits spermatophores on his own legs III prior to taking up the embrace posture; sperm could thereby be inserted in the female's genital opening during the "nuptial swim," and the gelatinous substance on her dorsum may be residual spermatophore material.

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