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MATING BIOLOGY RESOLVES TRICHOTOMY FOR CHELIFEROID PSEUDOSCORPIONS (PSEUDOSCORPIONIDA, CHELIFEROIDEA)

Mating behavior and spermatophore morphology have provided phylogenetically useful information for both vertebrate and invertebrate taxa (*e. g.*, Proctor 1992a; Alberti *et al.* 1991; Prum 1990). However, because they are transitory phenomena that cannot be observed in preserved specimens, behavior and fragile ejaculates are seldom employed in phylogenetic studies. This is unfortunate because they often contain characters potentially helpful for resolving po-

Table 1.—Spermatophore morphology, mating behavior and male morphology in cheliferoid pseudoscorpions. (+) = character present; (–) = character absent.

		Characters				
Family	Species	Spermatophore droplet	♂ pulls ♀ over spermatophore	Ram's horn organs	♂ pushes sperm in ♀'s genital opening	Reference
Chernetidae	*Epactiochernes tumidus* (Banks)	+	+	–	–	Weygoldt 1966a
	Chernes cimicoides (Fabricius)	+	+	–	–	Weygoldt 1966b
	Dendrochernes morosus (Banks)	+	+	–	–	Weygoldt 1970
	Lustrochernes pennsylvanicus (Ellingsen)	+	+	–	–	Weygoldt 1970
	Americhernes oblongus (Say)	+	+	–	–	Weygoldt 1970
	Parachernes litoralis Muchmore & Alteri	+	+	–	–	Weygoldt 1970
Cheliferidae	*Dactylochelifer latreillei* (Leach)	+	–	+	+	Weygoldt 1966b
	Chelifer cancroides (Linnaeus)	+	–	+	+	Weygoldt 1966b
	Rhacochelifer disjunctus (Koch)	+	–	+	+	Weygoldt 1970
	Hysterochelifer meridianus (Koch)	+	–	+	+	Weygoldt 1970
	Hysterochelifer tuberculatus (Lucas)	+	–	+	+	Weygoldt 1970
	Parachelifer superbus *Hoff*	+	–	+	+	Weygoldt 1970
Atemnidae	*Paratemnoides braunsi* (Tullgren)	–	+	–	–	Weygoldt 1970
	Atemnus politus (Simon)	–	+	–	–	Weygoldt 1969a
Withiidae	*Withius subpiger* Simon	–	+	–	–	Weygoldt 1969b

lychotomies that have proven intractable to traditional morphological approaches. As well, unlike the usual alternatives of electrophoretic or DNA analyses, characters resulting from studies of mating biology are evolutionarily interesting in themselves.

Because of the diversity of sperm transfer behavior and spermatophore morphology present in pseudoscorpions (Weygoldt 1969a), this group is likely to respond well to phylogenetic resolution using mating characters. In his recent cladistic study, Harvey (1992) ascribed two reproductive synapomorphies to the superfamily Cheliferoidea: production of spermatophores with complex rather than simple sperm masses and transfer of sperm during mating dances rather than without pairing between the sexes. Within the Cheliferoidea, the families Cheliferidae, Chernetidae and Atemnidae were differentiated from the Withiidae by synapomorphies of leg morphology; however, Harvey found no characters to resolve the trichotomy formed by the first three families. In recent literature reviews (Proctor 1992b) I turned up several features of cheliferoid mating biology that both help to resolve this trichotomy and suggest adaptive scenarios for the evolution of mating behavior in this superfamily.

Table 1 lists characteristics of spermatophore morphology, male anatomy and mating behavior for species in the four families of the Cheliferoidea. Spermatophore stalks of the Chernetidae and Cheliferidae apomorphically possess a large droplet of apparently hypotonic liquid that causes the sperm packet to swell and expel its contents into the female genital atrium (Weygoldt 1975). This synapomorphy allows the Cheliferoidea to be resolved from Harvey's (1992) arrangement of [Withiidae (Cheliferidae + Chernetidae + Atemnidae)] to [Withiidae (Atemnidae (Cheliferidae + Chernetidae))]. Other aspects of mating biology provide phylogenetic and evolutionary insight. Males of the Cheliferidae apomorphically possess genital sacs (ram's horn organs) that are everted after spermatophore deposition to attract the females, presumably through pheromones on their surface (Weygoldt 1969a). Concomitant with the evolution of ram's horn organs is loss of the male behavior of pulling females over spermatophores, which is present in the other three cheliferoid families (Table 1). This suggests that pheromonal attraction of the female replaced physical manipulation in the Cheliferidae and raises the possibility that chemical guidance has some advantage over physical contact for these males (*e. g.*, reduced likelihood of palp damage, greater guarantee of female interest in mating). Another apotypic behavior in the Cheliferidae is the male's use of his forelegs to push sperm into the female genital opening after she has mounted the spermatophore (Table 1); no other cheliferoids do this, although there is often extended contact between male and female after the female takes up sperm (*e. g.*, Weygoldt 1970). Adaptive explanations for these and other reproductive characters will be possible only after studying their effects on male fitness.

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