

Are sexually-selected traits reliable species characters? Implications of intra-brood variability in *Semeiochernes armiger* (Balzan) (Pseudoscorpionida: Chernetidae)

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Summary

Characteristics of the sexually-dimorphic chelae are currently used to distinguish three species of the neotropical pseudoscorpion genus *Semeiochernes*. In Panama, we found the entire range of *Semeiochernes* "interspecific" male variability (from small chelae without lateral processes to greatly enlarged chelae with pronounced lateral processes) present in what appeared to be single populations. However, we could not exclude the possibility that we had sampled from sympatric populations of the three described species. Here, we present the results of a study in which offspring were reared in the laboratory from gravid females collected in the field. Marked differences between male siblings, in terms of chelal depth and in presence/absence and length of lateral processes, demonstrate that male variability in these populations is intraspecific rather than interspecific in origin. The results of this study clearly invalidate presence/absence and size of the chelal peg as species-level characters in *Semeiochernes*, and call into question the current organisation of the genus. The general implications of these findings for the reliability of sexually-selected traits as taxonomic characters are discussed.

Introduction

In many species, males and females exhibit pronounced sexual differences in morphology, thought to have evolved as a consequence of sexual selection through male competition or female choice (Darwin, 1871; Bradbury & Andersson, 1987). Sexually-dimorphic traits are frequently employed in systematic studies, and, indeed, characteristics of male sexually-selected traits provide the basis for species identification in several taxa (review in Eberhard, 1985: chapter 11). A growing body of evidence, however, indicates that exaggerated male traits may often exhibit extremely high levels of intraspecific variability (Grimaldi, 1987; Alatalo *et al.*, 1988; Zeh & Zeh, in press a,c). We suggest that, as a consequence, use of male sexually-selected traits may lead to erroneous species designation. In tropical arthropods, this may be a common problem, since species are often established from examination of a limited number of males. Here, we present a case in which disregard of male intrapopulation variability in sexually-dimorphic traits has led to the incorrect use of these traits as species-level characters in the pseudoscorpion genus *Semeiochernes*.

The neotropical pseudoscorpion, *Semeiochernes armiger* (Balzan) inhabits decaying trees and disperses phoretically by attachment to the giant wood-boring fly, *Pantophthalmus tabaninus* Thunberg (Zeh & Zeh, 1992). The pseudoscorpion is a large, heavily-sclerotised member of the chernetid subfamily, Hesperochernetinae. Sexual dimorphism is marked, with males possessing

greatly enlarged chelae and chelal peg-like processes, absent in females (Beier, 1933). Both *S. armiger* from Peru and Panama and *S. extraordinarius* Beier from Venezuela possess a peg-like process on the lateral surface of the chelal hand but are distinguished on the basis of process length and chelal depth (see Beier, 1933, 1954). By contrast, *S. militaris* Beier, collected from Brazil and Costa Rica, is reported to lack a chelal peg-like process (Beier, 1933, 1954; Mahnert, 1987).

In a field study carried out in Panama, we examined hundreds of specimens and found the entire range of *Semeiochernes* "interspecific" male variability (from small chelae without lateral processes to greatly enlarged chelae with pronounced lateral processes) present in what appeared to be single populations of *S. armiger* (Zeh & Zeh, 1992). After comparing our specimens from Panama with museum specimens, W. B. Muchmore suggested that "... there is probably just one very variable species involved here" (personal communication). However, we could not exclude the possibility that we had sampled from sympatric populations of the three described species. In this paper, we present the results of a study in which offspring were reared in the laboratory from gravid females collected in the field. Marked differences between male siblings in terms of presence/absence and length of lateral processes, and in chelal depth, demonstrate that male variability in these populations is intraspecific rather than interspecific in origin.

Methods

The research was conducted between December 1988 and May 1989. Seven females carrying external brood sacs were collected from under the bark of three fallen, decaying *Ficus insipida* Willd. trees in the moist tropical lowland forest of Parque Nacional Soberania, Panama. In the laboratory, these females were maintained in 30 cm³ plastic vials containing field-collected *Ficus* "sawdust" (frass). The sawdust, which is generated by larval wood-boring activity of the harlequin beetle, *Acrocisus longimanus* (L.), and the fly, *P. tabaninus*, had previously been sorted three times to remove predatory arthropods and non-experimental pseudoscorpions. The gravid females constructed brood nests of frass and silk which were monitored until protonymphs hatched from the females' brood sacs.

Approximately two days after the hatching of each brood, the sclerotised nymphs were removed from the nest and placed in vials containing *Ficus* sawdust. The number of sibling offspring per vial ranged from 3–5. Individuals were monitored and reared through the proto-, deuto- and tritonymph stages to adults on a once-per-week supply of 10–12 worker termites (*Nasutitermes* spp.) added to the vials.

In order to examine intra-brood variability in external male morphology, a comprehensive set of measurements was taken from two or more adult male offspring produced by a female. In pseudoscorpions, moulting ceases at the adult stage so that the fully-sclerotised pedipalps and cephalothorax are fixed in size (Gabbutt, 1969; Weygoldt, 1969; Zeh, 1987). Measurements were taken from photographs of live individuals restrained with pedipalps fully

extended under a glass microscope slide (see Zeh & Zeh, in press b). The negative image of each specimen was then projected on to a computer-linked digitising tablet (Summagraphics MM 1201) and the coordinates of 38 anatomical landmarks on the dorsal outline of the body and right pedipalp (plus two scale bar points) were recorded. From these coordinates, we computed the measurements of 10 traits of the pedipalps and cephalothorax: chelal movable finger length (MFL); chelal hand length (HL) and depth (HD); chelal lateral peg length (PEGL), tibia length (TL) and depth (TD); femur length (FL) and depth (FD), and cephalothorax length (CL) and posterior width (CW) (see Chamberlin, 1931). Descriptive statistics of adult morphology were carried out, using SAS (SAS Institute, 1988).

Results

Two families (II, VII) were excluded from the analysis, since in each case only a single male offspring reached the adult stage. In the remaining five families, from two to four male offspring per female completed development, giving a total of 18 individuals measured. In 12 of 42 rearing vials, no pseudoscorpions survived. In each of the remaining vials, only one individual completed development to maturity, suggesting that cannibalism among immatures may have occurred. Developmental period, from hatching to adult, varied between 103 and 154 days.

Analysis of the morphometric data demonstrated extreme variability in characteristics of the chelae, both within and between families (Table 1). When data from all families were pooled, the coefficients of variation (CV) for the sexually-dimorphic traits, HL, HD and PEGL, were 14.76%, 26.50%, and 171.53%, respectively. These compared with values of about 6–9% for the seven traits which exhibit little sexual dimorphism (Table 1).

Male siblings within three of the families (III, V, VI) included individuals with both the "pegged" chelal and "pegless" chelal morphology (see Plate 1). In the other two families (I, IV), all male offspring lacked pegs. Not surprisingly, levels of within-family variability in chelal hand traits were greatest in families possessing the two male types. In these families, coefficients of variation were comparable to those obtained from the pooled-family data.

Calculation of all possible pair-wise correlation coefficients (r) among the 10 traits revealed that PEGL is most closely correlated with the depth (HD) ($r=0.84$;

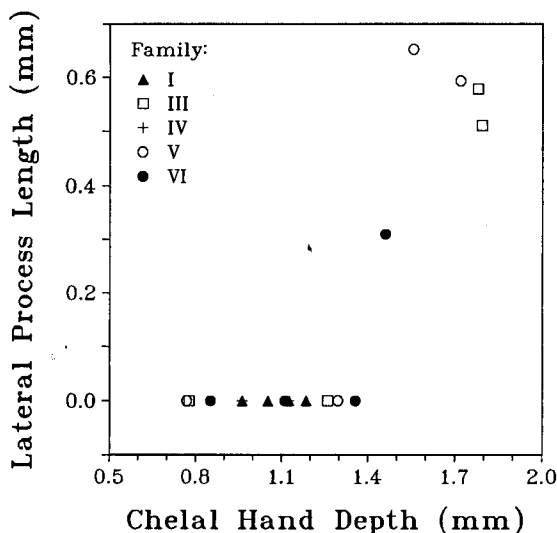


Fig. 1: Relationship between chelal depth and lateral process length in laboratory-reared *S. armiger*.

$p < 0.0001$) and length (HL) ($r=0.83$; $p < 0.0001$) of the chelal hand. By contrast, PEGL is only weakly correlated with cephalothorax length (CL) ($r=0.43$; $p=0.08$) and width (CW) ($r=0.38$; $p=0.12$). A bivariate plot of PEGL versus HD suggests that the chelal hand must exceed a threshold depth of approximately 1.45 mm for phenotypic expression of the peg (Fig. 1).

Discussion

Our results demonstrate that, in Panama, males of the species *S. armiger* exhibit the full range of *Semeiochernes* chelal morphology. Indeed, three females each produced a brood in which morphology of the male offspring varied from the pegless, *militaris*-type chela with its poorly-developed dorsal and ventral processes (Mahnert, 1987: fig. 22) to the greatly-expanded, triangular-shaped and process-bearing chela, used as the diagnostic character for *S. extraordinarius* (Beier, 1954: fig. 5). While it cannot necessarily be concluded from these findings that *Semeiochernes* is a monotypic genus, this study certainly casts strong doubt on the validity of the current division of *Semeiochernes* into the three species, *armiger*, *extraordinarius* and *militaris*. In any case, the chelal peg must clearly be discarded as a species-diagnostic character.

Previous investigators have noted the existence of high levels of intraspecific variation in continuously-varying, sexually-dimorphic traits in pseudoscorpions, particularly

Trait	Family I (N=4)			III (N=4)			IV (N=2)			V (N=4)			VI (N=4)			Pooled data (N=18)		
	Range	Mean	CV	Range	Mean	CV	Range	Mean	CV	Range	Mean	CV	Range	Mean	CV	Range	Mean	CV
MFL	1.19–1.41	1.30	7.22	1.20–1.55	1.38	12.02	1.18–1.28	1.23	5.92	1.05–1.34	1.26	10.92	1.26–1.42	1.33	5.66	1.05–1.55	1.30	8.92
HL	1.15–1.24	1.18	3.56	1.07–1.56	1.35	16.93	1.05–1.16	1.11	7.09	0.97–1.48	1.27	18.35	1.00–1.48	1.24	17.32	0.97–1.56	1.24	14.76
HD	0.96–1.18	1.08	8.87	0.78–1.79	1.40	34.55	0.96–1.13	1.04	11.04	0.77–1.72	1.34	31.09	0.85–1.46	1.20	22.69	0.77–1.79	1.23	26.50
PEGL	0.00–0.00	0.00	0.00	0.00–0.58	0.27	115.91	0.00–0.00	0.00	0.00	0.00–0.65	0.31	115.73	0.00–0.31	0.08	200.00	0.00–0.65	0.15	171.53
TL	1.18–1.26	1.23	2.49	1.11–1.44	1.29	12.72	1.21–1.26	1.23	2.98	1.13–1.33	1.23	7.09	1.18–1.33	1.24	5.26	1.11–1.44	1.25	7.01
TD	0.52–0.59	0.55	7.04	0.44–0.59	0.53	12.69	0.50–0.51	0.51	0.98	0.47–0.58	0.53	8.74	0.47–0.53	0.51	5.52	0.44–0.59	0.52	7.23
FL	1.12–1.24	1.18	4.09	1.10–1.39	1.27	9.82	1.13–1.20	1.16	4.50	1.07–1.33	1.24	9.07	1.18–1.38	1.29	7.15	1.07–1.39	1.23	7.82
FD	0.42–0.47	0.44	4.23	0.39–0.50	0.47	10.94	0.44–0.44	0.44	1.12	0.37–0.41	0.44	11.14	0.38–0.48	0.44	9.14	0.37–0.50	0.45	8.28
CL	1.26–1.36	1.30	3.76	1.13–1.41	1.30	9.80	1.24–1.29	1.27	2.51	1.17–1.41	1.27	7.72	1.20–1.41	1.30	6.74	1.13–1.41	1.29	6.32
CW	1.18–1.33	1.26	4.59	1.10–1.41	1.29	11.11	1.21–1.24	1.23	2.14	1.12–1.37	1.25	8.44	1.17–1.48	1.35	11.40	1.10–1.48	1.28	8.70

Table 1: Summary of male morphometric data from laboratory-reared broods of *Semeiochernes armiger*.

in the families Chernetidae (Mahnert, 1978), Cheliferidae (Mahnert, 1980) and Withiidae (Mahnert, 1988). In the case of *S. armiger*, our results not only document extreme male phenotypic variability, but also establish the chelal peg as a threshold trait (*sensu* Falconer, 1981: chapter 18) whose phenotypic expression is most closely linked to chelal depth. Threshold trait expression is probably responsible for discrete male polymorphisms in other arachnids such as the New Zealand opiliones of the suborder Laniatores (Forster, 1954). Indeed, threshold expression apparently occurs in many sexually-selected male traits (Eberhard & Gutiérrez, 1991), and is perhaps one of the most problematic issues confronting morphologically-based taxonomic studies. When only a limited number of specimens are available, it may be impossible to distinguish genuine species-diagnostic characters from intraspecific polymorphisms in threshold traits.

The findings of this study may well have general implications for the use of sexually-dimorphic characters in systematics. It has recently been proposed that, because of their rapid rate of evolutionary change, sexually-selected traits should often provide the most discriminating characters for distinguishing closely-related populations or species (West-Eberhard, 1983, 1984; Eberhard, 1985, 1990). However, evidence increasingly points to the existence within populations of levels of variability far higher in exaggerated male traits than in other aspects of the

phenotype (Grimaldi, 1987; Alatalo *et al.*, 1988; Zeh & Zeh, in press a,c). If males within populations are almost as variable as males from different populations, failure to take account of intrapopulation variability may lead to the kind of taxonomic *faux pas* discussed here.

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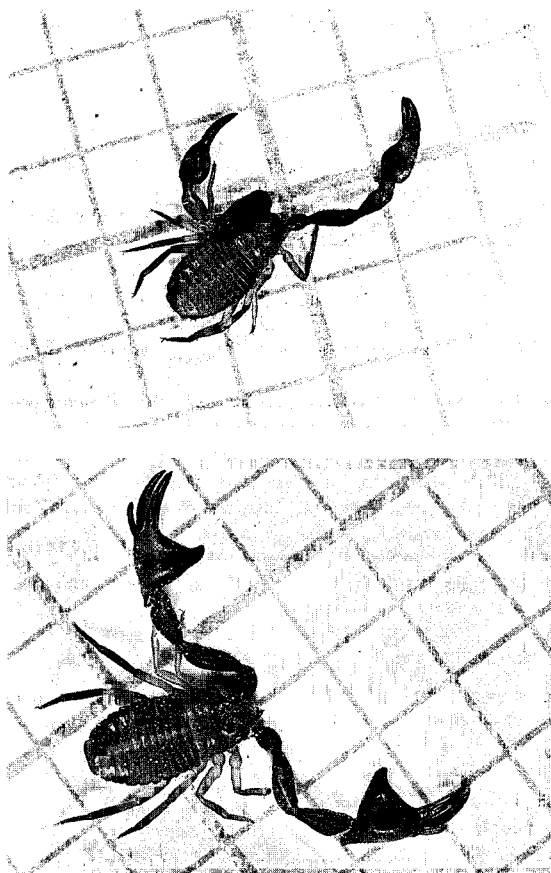


Plate I: Intra-brood variability in the morphology of male *Semeiochernes armiger* (Balzan). Smallest and largest male offspring from same brood of family II. Note complete absence of lateral peg-like process on the chelae of the small male. Background grid = 2 mm.

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The pseudoscorpion subgenus *Chthonius* (*Sigmodactylus*) Hadži, 1930: type fixation and consequent synonymy with *Pseudochthonius* Balzan, 1892 (Chelonethi, Chthoniidae)

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Summary

Chthonius (*Pseudochthonius*) *simoni* Balzan, 1892, is designated as the type species of the subgenus *Chthonius* (*Sigmodactylus*) Hadži, 1930. *Sigmodactylus* therefore becomes a junior objective synonym of the genus *Pseudochthonius* Balzan, 1892. *Microchthonius* Hadži, 1933, is returned to subgeneric rank under the genus *Chthonius* C. L. Koch, 1843.

Sigmodactylus was created by Hadži (1930: 140) as a subgenus of *Chthonius* C. L. Koch, 1843, diagnosed by the sigmoid curvature of the fixed finger and the dentition of the fingers of the chela. The heterogeneity of the group is evident from the modern familial and generic assignments of the seven species which Hadži referred to *Sigmodactylus* (see Harvey, 1991):

Chthoniidae

- Afrochthonius godfreyi* (Ellingsen)
- Chthonius* (*Chthonius*) *cavernarum* Ellingsen
- C. (C.) heterodactylus* Tömösváry
- C. (C.) raridentatus* Hadži
- C. (C.) troglodites* Redikorzev
- Pseudochthonius simoni* (Balzan)

Tridenchthoniidae

- Anisoditha curvidigitata* (Balzan)

Sigmodactylus has been either overlooked or ignored by subsequent authors, including Hadži himself (1941). Fortunately, it was included by Neave in his *Nomenclator Zoologicus* (1940).

Because Hadži (1930) did not designate a type species, *Sigmodactylus* represents a potential source of nomenclatural instability. The obvious candidates for type species would be *Chthonius heterodactylus* and *C. raridentatus*, as these are the only included species which Hadži (1930) had seen (ICZN recommendation 69B(8)). *Sigmodactylus* could then be used as a subgeneric name for the *subterraneus*-group of *Chthonius*, to which *heterodactylus* and *raridentatus* belong. However, the monophyly of this informal species-group has yet to be demonstrated. Furthermore, this might result in a synonymy with

the better-known subgenus *Chthonius* (*Microchthonius*) Hadži, 1933 (REVISED STATUS; Beier's (1963) elevation of *Microchthonius* to generic rank is not followed here). It seems likely that the species of *Chthonius* (*Microchthonius*) are closely related to those of the *subterraneus*-group.

Instead, I propose here to designate *Chthonius* (*Pseudochthonius*) *simoni* Balzan, 1892, as the type species of *Sigmodactylus*. Because *simoni* is already the type species of the genus *Pseudochthonius* Balzan, 1892, *Chthonius* (*Sigmodactylus*) becomes a junior objective synonym of *Pseudochthonius* (ICZN article 67(k)) (NEW SYNONYMY). Hence the potential threat of synonymy between *Sigmodactylus* and *Afrochthonius* Beier, 1930, *Anisoditha* Chamberlin & Chamberlin, 1945, or, perhaps, *Chthonius* (*Microchthonius*) Hadži, is removed.

Acknowledgement

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Addendum

In a paper received after this manuscript had gone to press, Gardini (1991: 173) refers to *Chthonius* (*Chthonius*) *lessiniensis* Schawaller as “appartenente al gruppo degli *Chthonius* s. str. con dito fisso dei palpi sigmoide (“subgen. *Sigmodactylus*” di Hadži, 1930)”. Although this implies a synonymy between *Sigmodactylus* and *Chthonius* (*Chthonius*), it does not have any formal status because Gardini did not select a type species for *Sigmodactylus*. Hence the synonymy with *Pseudochthonius* proposed here is unaffected.

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