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Morphological differences between sympatric populations of the *Poecilochirus carabi* complex (Acari: Mesostigmata: Parasitidae) associated with burying beetles (Silphidae: *Nicrophorus*)

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Abstract

Adults of two sympatric populations of the parasitid mite *Poecilochirus carabi* G. & R. Canestrini, one preferring *Nicrophorus vespillo* (Linnaeus) as carrier beetle species and the other *N. vespilloides* Herbst, could be separated by differences in the form of the structures associated with the male genital orifice and the size of the female endogynum. Adults and deuteronymphs of the two populations also differed in the size of idiosomal shields and dorsal setae. On the basis of these findings, plus data from a literature review and an examination of type-material, the preference type choosing *N. vespilloides* was identified as *P. carabi* (*sensu stricto*) and that preferring *N. vespillo* as *P. necrophori* Vitzthum, a species previously synonymised with *P. carabi*.

Introduction

Deuteronymphs of the mite *Poecilochirus carabi* G. & R. Canestrini, 1882 (*sensu* Hyatt, 1980) (Mesostigmata: Parasitidae) are phoretic on burying beetles of the genus *Nicrophorus* Fabricius (Silphidae). The mites complete their life-cycle and subsequently reproduce in the beetles' brood chamber (Springett, 1968; Schwarz & Müller, 1992). The predation of *Nicrophorus* eggs by female *P. carabi* may reduce the brood size of the host beetle (Beninger, 1993).

The marked morphological variation amongst deuteronymphs of *P. carabi* has been acknowledged for many years. Indeed Vitzthum (1930) went so far as to erect the species *P. necrophori* to accommodate those deuteronymphs (larvae, protonymphs and adults were unknown at the time) with short anterior and posterior extensions to the dark transverse band of their sternal shield. This separation was followed by other workers (Willmann, 1939; Cooreman, 1943; Neumann, 1943; Belozerov, 1957; Holzmann, 1969; Micherdzinski, 1969; Karg, 1971; Davydova, 1976; Bregetova, 1977), although a number of them expressed reservations. Cooreman (1943) measured numerous deuteronymphs he identified as *P. necrophori* and found they fell into two size ranges, which he suggested was due to sexual dimorphism and not specific difference. Micherdzinski (1969) questioned whether the variability was of inter- or intraspecific significance and declared the need for an investigation into the problem. Karg (1971) discounted the reliability of Vitzthum's definitive character, instead basing his diagnosis of *P. necrophori* on differences in the lengths of deuteronymphal idiodorsal setae. He also suggested that *P. necrophori* might be a subspecies of *P. carabi*. Subsequently, Hyatt (1980), having examined large numbers of *P. carabi* deuteronymphs, concluded that the shape of the sternal band and lengths of the idiodorsal setae were so variable that they were unreliable as definite characters and he consequently synonymised *P. necrophori* with *P. carabi*. Korn (1982) was of the same opinion, but he had evidently not seen Hyatt's work because he attributed the new synonymy to himself. Neither Hyatt (1980) nor Korn (1982) attempted to correlate the variations they saw with other aspects such as host species or behaviour, but the synonymy has been followed by most authors (Haitlinger, 1988, 1990; Wise et al., 1988; Brown & Wilson, 1992; Karg, 1993).

In laboratory experiments, individual deuteronymphs of *P. carabi* have demonstrated clear preferences for different carrier species of beetle. Wilson (1982) and Brown & Wilson (1992), studying populations of

deuteronymphs from Michigan, USA, reported a preference for either *N. orbicollis* Say or *N. tomentosus* Weber. Brown & Wilson (1992) found differences in developmental time between the two types and, in principal components analyses, identified correlating differences in the lengths of the podonotal shield and certain idiodorsal setae. Two preference types have also been identified in Germany, one chooses *N. vespillo* (Linnaeus) and the other *N. vespilloides* Herbst as host carrier (Müller & Schwarz, 1990). The failure of the two forms to cross-breed provided evidence of reproductive isolation (Müller & Schwarz, 1990), while a genetic basis to the difference was shown in enzyme analyses (Schwarz et al., 1991). Differences in the duration of mating and developmental time were also observed (Schwarz & Walzl, 1996).

Preliminary examination of adults of the two *P. carabi* preference types identified by Müller & Schwarz (1990) showed that males could be consistently separated by the form of the genital opening and females by the size of the endogynum. Consequently, a detailed study was carried out to determine whether additional characters separated the adults and whether morphological differences could be used to distinguish between the deuteronymphs of the two groups. This paper presents the results of these studies which, together with data obtained from the literature concerning *P. carabi* and *P. necrophori* and examination of type-material of the two species, are used to review the taxonomic status of *P. carabi* and *P. necrophori*.

Materials and methods

Origin of the specimens

The specimens (adults and deuteronymphs) of *P. carabi* (*sensu* Hyatt, 1980) studied were predominantly from first generation laboratory cultures reared from field-caught populations (details in Müller & Schwarz, 1990). A number of alcohol-preserved deuteronymphs caught in Bielefeld, Germany on the two host beetle species (*N. vespilloides* and *N. vespillo*) were included in analyses to check whether there were any differences between field-caught and cultured mites. Adults were examined one day after the deuteronymphal moult.

The two preference types were separated in two runs of choice experiments and designated **P-vo** (those preferring *N. vespillo*) and **P-vs** (those preferring *N. vespilloides*).

The holotype of *P. carabi* (slide no. 34/22) was examined at the Berlese Acaroteca, Istituto Sperimentale per la Zoologia Agraria, Florence, Italy, and the two syntypes of *P. necrophori* (slide nos V303 & 304) were obtained for study from the Zoologische Staatssammlung, Munich, Germany.

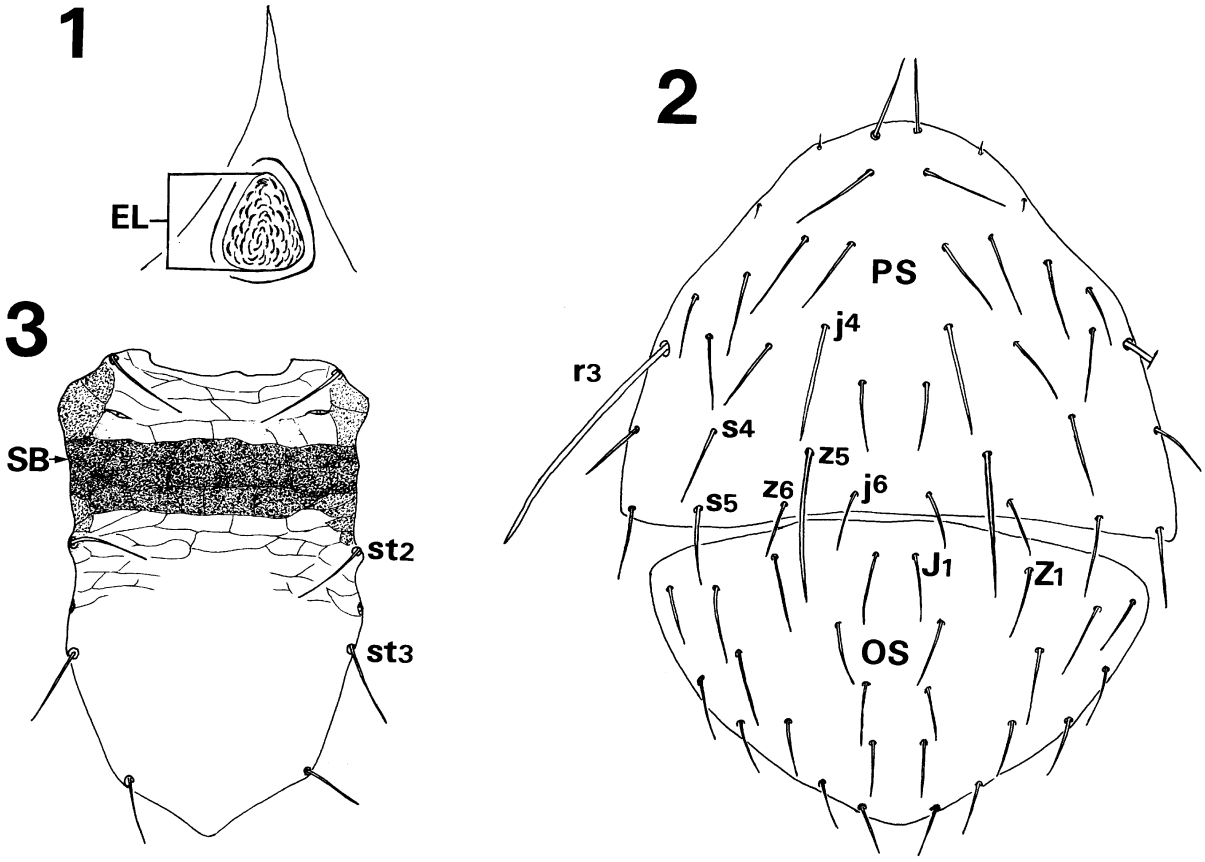
Morphological studies

Prior to examination, specimens were cleared in 60% lactic acid and slide-mounted in Hoyer's medium. Initially, a comparison of morphological structures was made in order to detect any differences in form between P-vo and P-vs mites. Specimens (numbers given in Table I) were measured using a Kontron Videoplan Image Processing System attached to a Zeiss phase contrast microscope. Characters included in statistical analyses and principal component analyses were those which could be consistently measured without distortion through curvature.

For adults, the length of the podonotal shield (to the median transverse suture in males) and five idiodorsal setae (j4, z5, s4, s5, r3) were compared (Figure 2), together with that of the endogynum for females (Figure 1).

For deuteronymphs, four measurements were made of the sternal shield (length, median depth of sternal band, distance between setae st2-st2 and st3-st3) (Figure 3), two of the idiodorsal shields (median length of podo- and opisthonotum) and the lengths of nine idiodorsal setae (j1, j6, z5, z6, s4, s5, r3, J1, Z1) (Figure 2). Principal components analyses were carried out on the untransformed data using TAXPAC statistical software (a version of a program by Davies (1971) written in BASIC by I.M. White, International Institute of Entomology, London). Only those specimens in which all characters could be measured were included in the analysis.

Certain character measurements were subjected to statistical analysis (Student's t-test) in order to determine whether differences between the two preference types were significant. In each case, a character was considered to be significantly different when $P < 0.05$.



Figures 1–3. Poecilochirus carabi G. & R. Canestrini. 1. Female genital opening. 2. Dorsal idiosomal shields and setae. 3. Deuteronymph, sternal shield. *Abbreviations*: EL,endogynal length; OS,opisthonotal shield; PS,podonotal shield; SB,sternal band; st,sternal seta.

Results

Adults

Males of the P-vo preference type (those preferring *N. vespillo* as carrier species) could be consistently separated from P-vs males (those preferring *N. vespilloides*) by the more elaborate sclerites associated with the genital orifice (Figures 4,5). Also, the podonotal shield and seta r3 of P-vo mites was significantly longer, although there was no difference in the lengths of the other setae measured (Table I).

No qualitative differences were discerned in P-vo and P-vs females, while seta r3 did not differ significantly in length. The podonotal shield and endogynum were significantly longer in P-vo mites, but setae j4, s4, z5 and s5 were significantly longer in P-vs specimens (Table I, Figures 6,7).

Deuteronymphs

No qualitative differences were detected in deuteronymphs but, in principal components analysis, two clusters representing the two preference types were separated by the first two principal components, the first axis accounting for 62% of variation and the second 10% (Figure 8). PC1 was strongly correlated with size, PC2 negatively so. The larger of the two types were the P-vo mites, the smaller P-vs; there was no separation of cultured and free-caught mites within these clusters. The greatest influence on separation, indicated by the eigenvector coefficients, were the lengths of the podosomal shield and idiosomal setae r3, s4-5, J1 and Z1; all were found to be significantly different between P-vo and P-vs mites (Table I). The length of the opisthosomal shield accounted for least separation, but the difference was still significant. The two clusters were discrete, except for one deuteronymph classified as P-vs which was positioned in the P-vo group. The syntypes of *P. necrophori*, with podonotal shield

Table I. Statistical comparison (Student's t-test) of morphological characters of sympatric *Poecilochirus carabi* complex.

Character (length)		P-vs mites		vs	P-vo mites		
		$x \pm$ S.D. (n)	Range (μm)		$x \pm$ S.D. (n)	Range (μm)	P
Males							
Seta	j4	133.4 ± 7.1(17)	123–149		129.6 ± 6.8(20)	115–149	
	z5	142.9 ± 8.6(20)	129–158		139.0 ± 7.9(20)	127–158	
	s4	115.7 ± 7.3(17)	105–133		113.0 ± 8.4(18)	105–127	
	s5	104.5 ± 6.2(15)	93–119		104.4 ± 7.0(19)	97–125	
	r3	162.2 ± 8.3(10)	152–178		174.4 ± 12.7(18)	158–186	**
Podonotal shield		552.0±23.9(19)	552-666		666.1 ± 15.4(19)	640–692	***
Females							
Seta	j4	116.6 ± 7.0(20)	100–129		95.8 ± 7.7(17)	79–103	***
	z5	126.0 ± 5.8(19)	117–137		108.1 ± 10.4(18)	89–127	***
	s4	109.7 ± 7.4(19)	89–119		85.2 ± 7.5(19)	71–103	***
	s5	111.0 ± 5.1(20)	103–119		86.7 ± 6.4(20)	79–99	***
	r3	147.9 ± 6.6(17)	139–162		143.5 ± 7.9(12)	123–152	
Endogynum		54.1 ± 3.0(16)	48–59		66.4 ± 6.1(17)	51–75	***
Podonotal shield		689.1 ± 25.6(25)	640-744		722.3 ± 25.8(21)	672–776	***
Deuteronymphs							
Seta	Z1	121.5 ± 11.1(18)	96–141		154.1 ± 6.1(15)	144–165	***
	s4	133.1 ± 9.4(18)	119–155		166.4 ± 9.8(15)	154–186	***
	J1	99.2 ± 8.7(18)	78–114		131.2 ± 7.3(15)	114–144	***
	s5	129.3 ± 8.1(18)	114–150		157.0 ± 7.6(15)	147–174	***
	z5	242.4 ± 17.6(18)	192–273		271.3 ± 6.2(15)	255–285	***
	r3	328.3 ± 18.9(18)	288–356		356.6 ±11.9(15)	338–374	***
Podonotal shield		571.5 ± 22.5(18)	510–600		610.5 ± 24.5(15)	564–660	***
Opisthonotal shield		398.0 ± 19.8(18)	360–420		436.8 ± 19.7(15)	401–482	*

Abbreviations: P-vs, mites preferring *N. vespilloides*; P-vo, mites preferring *N. vespillo*; *, $p = <0.05$; **, $p = <0.01$; ***, $p = <0.001$.

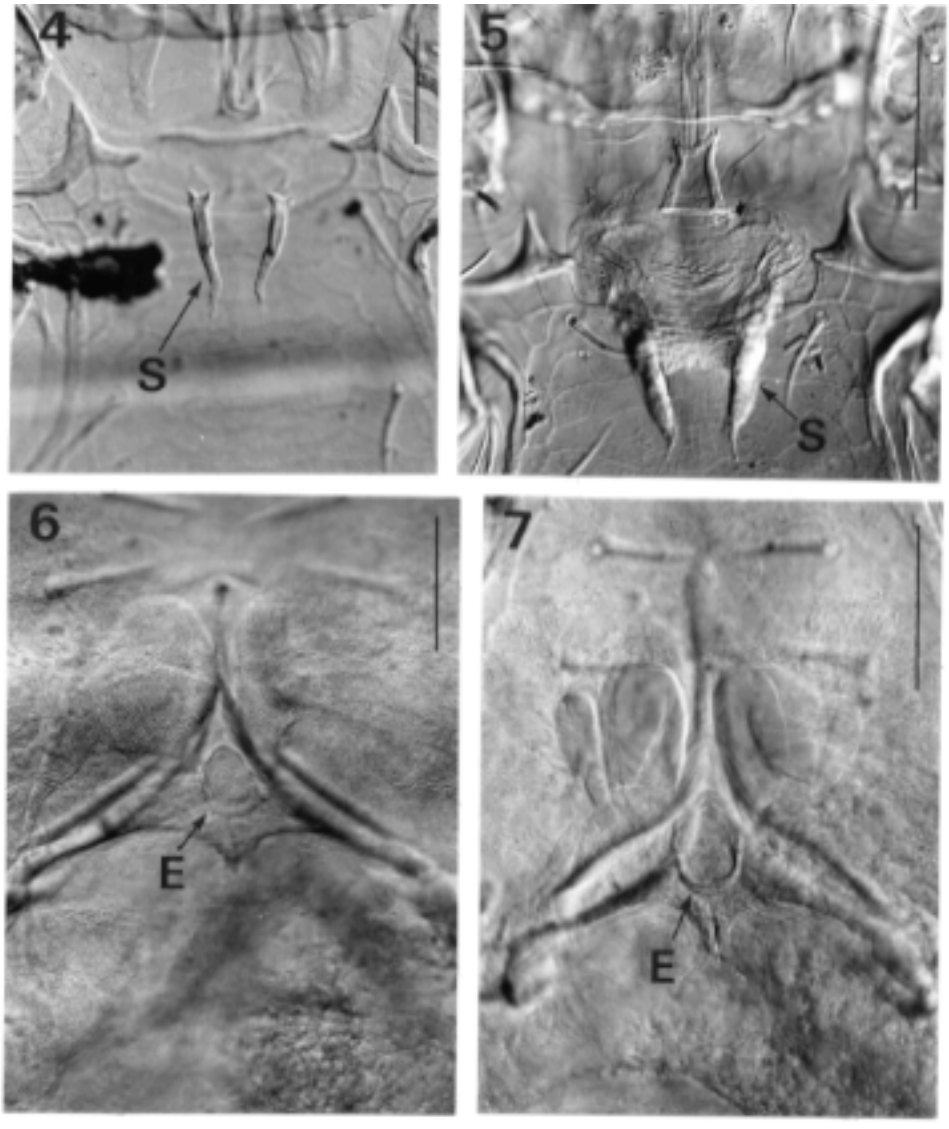
lengths of 632 and 660 μm, fell within the P-vo group range (564–660 μm), and the holotype of *P. carabi*, at 560 μm, within the P-vs range (510–600 μm).

Discussion

The results of the morphological analyses clearly show quantitative and qualitative differences between the two preference types of *P. carabi* (*sensu lato*) which correlate with those in behaviour, genetics and reproduction detected in earlier studies (Müller & Schwarz, 1990; Schwarz et al., 1991; Schwarz & Walzl, 1996).

Wilson (1982) suggested that the North American preference types of *P. carabi* he distinguished were either a single species that is genetically polymorphic for host carrier species or else a sympatric sibling species complex. However, as additional genetic, reproductive and morphological data were obtained, authors concluded that the latter case is true (Müller & Schwarz, 1990; Schwarz et al., 1991; Brown & Wilson, 1992). Morphologically similar but behaviourally, genetically or reproductively isolated species have been recognised in other mite taxa. For example, Krantz & Mellott (1972), Cicolani et al. (1981) and Cicolani & Di Sabatino (1991) all identified sibling species in the mesostigmatid family Macrochelidae, Athias-Binche et al. (1993) in the mesostigmatid *Neoseius novus* (Oudemans), Bernini et al. (1991) in the oribatid genus *Amerus* Banks and Boczek & Cross (1983) in the astigmatid genus *Acarus* Linnaeus.

What is the taxonomic status of the P-vo and P-vs preference types? Although there is a noticeable size variation given for *P. carabi*/*necrophori* in the literature, it is difficult to compare these measurements with those made in this study because authors mostly



Figures 4–7. *Poecilochirus carabi* complex, adult genitalia. 4. P-vs male (=*P. carabi* G. & R. Canestrini). 5. P-vo male (=*P. necrophori* Vitzthum). 6. P-vs female (=*P. carabi* G. & R. Canestrini). 7. P-vo female (=*P. necrophori* Vitzthum). *Abbreviations*: E,endogynum; S,sclerite. *Scale-bars*: 100 μm.

give total idiosomal lengths, which is affected by the extent of engorgement of the specimen. Also, when their material was derived from several host species, more than one *Poecilochirus* species may have been measured. The dimensions of the type-material of *P. necrophori* and *P. carabi* do fall within the range for P-vo and P-vs mites, respectively, but more useful information was obtained from descriptions of male mites. Both Holzmann (1969) and Micherdzinski (1969) illustrate *P. carabi*/*necrophori* with elaborate sclerites associated with the male genital orifice, like those found in P-vo mites. By contrast, the males of *P. carabi* studied by Hyatt (1980) have simple sclerites, as in P-vs mites. The sclerites of the male genital opening are involved in spermatophore formation (Evans, 1992), while the endogynum is thought to hold or prevent the escape of the spermatophore after its implantation (Winkler, 1888). Differences in form and/or size of these structures may act as isolating mechanisms in reproduction and, therefore, have contributed to the failure of P-vo/P-vs matings observed by Müller & Schwarz (1990).

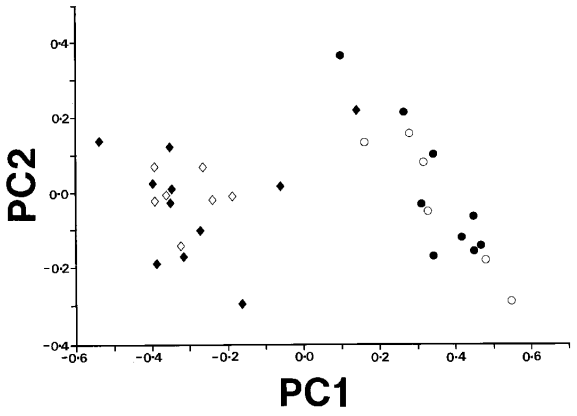


Figure 8. Principal components analysis of idiosomal shield and setal lengths of deuteronymphs of *Poecilochirus carabi* (*sensu lato*). ♦ = P-vs (cultured); ◊ = P-vs (free-caught); ● = P-vo (cultured); ○ = P-vo (free-caught).

The synonymy of *P. carabi* and *P. necrophori* by Hyatt (1980) was made on the basis that he could not recognise any trend in the variations he observed. He suggested that the difference in shape of the sternal band used by Vitzthum (1930) to define *P. necrophori* was due to the intensity of illumination used for microscopical examination. However, the present study suggests the difference is, in fact, a product of specimen size; the larger P-vo mites are more heavily sclerotised and so the extensions to the band are more obvious. The size and morphological differences identified in the current study for P-vs and P-vo mites match data for, respectively, *P. carabi* and *P. necrophori*. Hyatt's synonymy is therefore rejected, *P. necrophori* is resurrected to accommodate P-vo-type mites and *P. carabi* (*sensu stricto*) is retained for the smaller P-vs-type.

Brown & Wilson (1992) did not detail the measurements they used in analyses and only included deuteronymphs in their study. It is not, therefore, possible to determine whether the differences seen in the German populations also occur in those examined by Brown & Wilson (1992). Other synonymies have been suggested for *P. carabi*, for example, *P. eurasiaticus* Trägårdh, 1937 and *P. trebinjensis* Willmann, 1940 (see Hyatt, 1980). It is, therefore, possible that more sibling species exist and that both *P. carabi* and *P. necrophori* may be further divided in the future.

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