

Transvestism Hypothesis: a Cross-Sex Source of Morphological Variation for the Evolution of Parasitism Among Sweat Bees (Hymenoptera: Halictidae)?

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ABSTRACT Brood parasitism has evolved repeatedly in insects, and is especially diverse within bees. Little attention has been given to the evolution of structural modifications associated with parasitism, in contrast to behavior. Female parasitic bees tend to converge on a suite of characters, some of which may involve loss of characters associated with pollen-collecting or nest-making, whereas others may represent new characters used in a parasitic lifestyle. Certain external traits of female parasites resemble those of males, and this study compares the phenetic similarity of males and females of a social parasite, *Paralictus asteris* Mitchell, and its host, *Lasioglossum (Dialictus) imitatum* (Smith). Results are consistent with the hypothesis that some structural traits associated with parasitism may be derived from the expression of male-like traits in females.

KEY WORDS *Paralictus asteris*, social parasitism, brood parasitism, masculinization, phenocopy, sex transfer

DARWIN REMARKED THAT the evolution of parasitism in bees was “more remarkable” than in birds, because it involved both behavioral and morphological changes (Darwin 1859, p. 218). Nonetheless, compared with behavior (e.g., Wcislo 1987, Hölldobler and Wilson 1990, Cervo and Dani 1996), relatively little attention has been given to the evolutionary origins of external structural features associated with parasitism (Müller 1872, Pérez 1884, Popov 1945, Wcislo 1995).

Obligate brood parasites exploit the parental care of heterospecific individuals (hosts) to rear the parasites' offspring; this behavior presumably evolved from facultative parasitic behavior (e.g., West-Eberhard 1986, Wcislo 1987, Field 1992, Cichoñ 1996). Recurrent facultative parasitic behavior is an environmental change (sensu Wcislo 1989) that creates conditions that may selectively favor structural alterations appropriate for a parasitic lifestyle. Female parasitic bees tend to converge on a suite of morphological characters, with an enlarged, nearly quadrate head with elongate, toothless and pointed mandibles, compared with the smaller, rounded head of pollen-collecting females with shovel-like toothed mandibles. Many structures associated with pollen-collecting and nest construction are lost or reduced in female parasites (Richards 1927, Wcislo 1997, Michener 1978). Pérez (1884) and Michener (1978) noted that female parasitic bees resemble males of pollen-collecting species for a number of traits characteristic of a parasitic syndrome, providing a hint that such traits might originate as cross-

sex changes in expression of sex-linked traits, a process labeled *transvestism* by Clarke et al. (1985).

This article presents results from a study of the phenetic similarity (sensu de Quieroz and Good 1997) among males and females of parasitic *Paralictus asteris* Mitchell and nonparasitic *Lasioglossum (Dialictus) imitatum* (Smith) (Hymenoptera: Halictidae) to help account for the origins of external structural traits of parasites and draw attention to a neglected problem.

Wcislo (1997) gives an overview of the natural history of *P. asteris* and its host, *L. (D.) imitatum*. Morphological and molecular data suggest that the generic distinction between *Paralictus* and *L. (Dialictus)* is artificial (W.T.W., unpublished data; Danforth 1998); furthermore, a preliminary phylogenetic study using molecular data suggests that *P. asteris* is more closely related to *L. (D.) zephyrum* than it is to its host, *L. (D.) imitatum* (Danforth 1999).

Materials and Methods

Dried, preserved specimens of the parasite *P. asteris*, and the host, *L. (D.) imitatum*, were obtained from the Cornell University Insect Collection and my personal collection. A series of structural features were measured at 25 or 50× using an ocular micrometer fitted to a Wild M10 dissecting microscope (see Appendix 1) in a minimum of 10 males and females of both species. Variables were log-transformed and used in a principal components analysis (PCA); statistical analyses were done with SYSTAT (Wilkinson 1989).

Voucher specimens are deposited in the Cornell University Insect Collection and the Dry Reference

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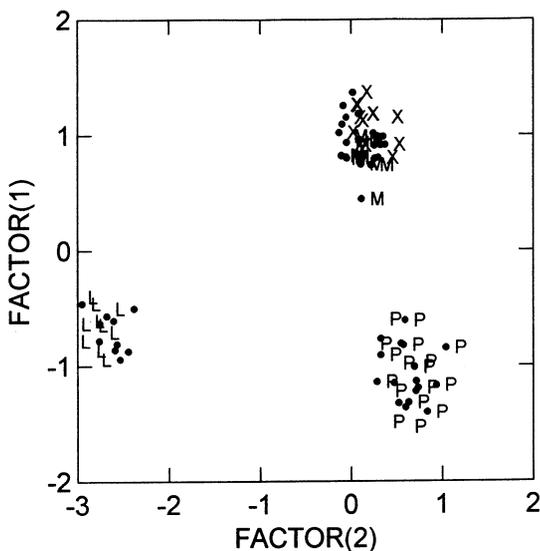


Fig. 1. Projection of scores on principal components 1 and 2. P, *Paralictus asteris* females; M, *Paralictus asteris* males; L, *Lasioglossum (Dialictus) imitatum* females; X, *Lasioglossum (Dialictus) imitatum* males.

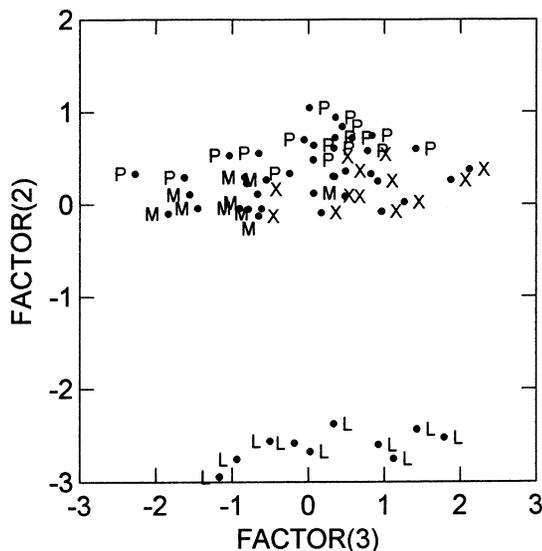


Fig. 2. Projection of scores on principal components 2 and 3. Symbols as in Fig. 1.

Collection of the Smithsonian Tropical Research Institute.

Results

The first 2 principal components together account for 88.1% of the total variation, and a plot of these factors produces a distinct cluster of female *L. (D.) imitatum*, female *P. asteris*, and a single cluster of males of both species (Fig. 1). This result merely quantifies the fact that at a glance males of either species are readily distinguished from conspecific females (e.g., the male metasoma is more slender and elongate than females, and males have longer antennae). In contrast, it is very difficult to distinguish male *Paralictus* from *Lasioglossum (Dialictus)* using external morphology. A plot of PC2 (which explains 14.9% of total variance) against PC3 (which explains 3.3% of total variance) shows that *P. asteris* females cluster with males of both species, distinctly separated from *L. (D.) imitatum* females (Fig. 2).

Paralictus asteris females also are male like in lacking external structures that nonparasitic females use in pollen-gathering or its manipulation, and in nest construction. For each of the following character states, *P. asteris* females are more similar to male *L. (D.) imitatum* than to female *L. (D.) imitatum*: female *P. asteris* have a relatively rounded labrum without keel; narrow, pointed mandible without a tooth; reduced mid-femoral brush; hind tibia and metasomal venter with fewer plumose hairs; basitibial plate with less well-defined marginal carina; pygidial plate on the 6th metasomal less distinct; and reduced penicillus of the hind basitarsus.

Discussion

Nonparasitic female *L. (D.) imitatum* possess a number of characters related to pollen-collecting and nest construction, like other bees (e.g., Wcislo and Cane 1996). Males usually play no role in parental care, and lack such structures. Similarly, *P. asteris* females play no role in parental care, and also lack these structures or they are reduced. Thus, female *P. asteris* are phenetically masculinized to some extent, although different species currently placed in *Paralictus* are less masculinized than others (e.g., *P. michiganensis* retains a manibular tooth; Michener 1978; W.T.W., unpublished data). Scant available information suggests that female parasites are male like in having to search for hosts, and have converged with respect to antennal size (Wcislo 1995). Some male-like traits in parasitic females may be advantageous for fighting with host bees, such as a narrow, pointed mandible. However, at least at nest entrances, *P. asteris* females do not use their pointed mandibles to kill guards (Wcislo 1997), whereas *Sphecodes monilicornus* Kirby (Halictidae) females routinely kill host bees, yet have unmodified, shovel-like toothed mandibles (Michener 1978). Thus, a slender, pointed mandible might be better viewed as the loss of a character used for nest construction, rather than the gain of a character used for aggression or defense. Presumably, the loss of such characters means that limited resources can be redirected elsewhere.

A phenetic relationship between sex-linked characters and brood parasitism in bees has been noted previously (Pérez 1884, Michener 1978) (also see Wheeler 1937 on ants). Cockerell (1911), for example, described a new genus of parasitic bees (*Androgynella*, Megachilidae) based on a series of females that lacked metasomal pollen-collecting hairs, which are typical of

nonparasitic female megachilids. In fact, the specimens are probably phenodeviants (intersexes) of nonparasitic *Megachile* (*Eutricharaea*) (Megachilidae) (Mitchell 1929, Michener 1965).

The expression of malelike traits in females (or vice versa) can arise from changes in gene expression or hormonal regulation, providing a source of selectable variation (e.g., Darwin 1868: 26ff.; Ferveur et al. 1995). Worker females and queens are structurally divergent to differing degrees among bee taxa (e.g., Pignata and Diniz-Filho 1996), which Kerr and colleagues attribute to differential masculinizing effects of hormones on female external morphology (Bonetti and Kerr 1985, Kerr 1987, Kerr and da Cunha 1990). Clarke et al. (1985) referred to this class of novelties as *transvestism*, based on breeding experiments that indicated that wing color patterns of a female *Papilio* butterfly result from the expression of male-typical colors.

Phenotypic effects of genetic mutations can be mimicked by subjecting a developing organism to an abnormal environment, producing phenocopies (e.g., Waddington 1961). *Stylops* (Strepsiptera) frequently affect secondary sexual characters in their aculeate hymenopteran hosts: individuals of one sex express the attributes of the other sex to differing degrees (Salt 1927) (for other parasites, see Wülker 1964). For example, styloped *Andrena* (Andrenidae) females have a reduced basitarsus with fewer hairs, finer scopal hairs and a narrowed tibia (Salt 1927), and smaller corpora allata volume (Brandenburg 1956), indicating that these effects are probably mediated by juvenile hormones (see Nijhout 1994). Mitchell (1929) noted that females with reduced pollen-collecting structures presumably would be unable to provision nests or be too inefficient, and they therefore might compensate behaviorally by parasitizing others. Mitchell (1929) speculated that stylopization or sex anomalies might contribute to the evolution of parasitism, although he correctly regarded this as a fanciful possibility because internal reproductive structures usually are damaged by the parasite. These pathologies are important, however, in revealing the potential for the expression of parasite-like structural traits in nonparasitic females.

Two caveats highlight the speculative nature of the transvestism hypothesis (sensu Clarke et al. 1985) as applied to parasitic bees. First, the need to study additional pairs of host-parasite halictid bees is impeded by the fact that *Paralictus* is undoubtedly artificial, and there is no species-level phylogenetic resolution at the species level for the natural group (Danforth 1998). Second, other comparative data are not consistent with a transvestism hypothesis. For example, as noted above, even among different *Paralictus* species or within other genera like *Sphecodes* (Halictidae), there are differing degrees of male-like forms; or in another genus of parasitic halictids (*Eupetersia*), males and females are intermediate between typical male and female halictids (Michener 1978). Nevertheless, the provisional evidence presented here may help draw more attention to an important problem that Darwin (1859) long ago flagged as remarkable.

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Appendix 1. List of morphological variables measured.

Body length	Clypeal-antennal distance
Maximum metasomal width	Interantennal distance
Forewing length	Anteno-ocular distance
Intertegular distance	Lateral interocellar distance
Head width	Ocello-ocular distance
Head length	Maximum genal width
Clypeal width	Scape length
Clypeal length	Pedicel length
Lower interorbital distance	Length of 1st antennal flagellomere
Upper interorbital distance	Width of 1st antennal flagellomere
Maximum ocular length	Length of 2nd to <i>n</i> th flagellomere (<i>n</i> = 10 in females; <i>n</i> = 11 in males)
Maximum ocular width	