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A Remarkable Gynandromorph of *Thectochlora alaris* (VACHAL 1904) (Hymenoptera: Halictidae)

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Abstract

A remarkable bilaterally asymmetrical gynandromorph of the augochlorine bee *Thectochlora alaris* (VACHAL 1904) (Halictinae: Augochlorini) is described and figured. This is only the second documented gynandromorph for the bee tribe Augochlorini and one of the most dramatic in its complete asymmetry. Despite the deformity of the usual acarinarium present in species of *Thectochlora*, the individual was found in association with at least six deutonymphs which are likely of *Thectochloracarus neotropicalis* FAIN, ENGEL, FLECHTMANN & OCONNOR 1999.

Zusammenfassung

Eine bemerkenswerte bilateral asymmetrische Gynandromorphie der augochlorinen Biene *Thectochlora alaris* (VACHAL 1904) (Halictinae: Augochlorini) wird beschrieben und abgebildet. Es ist erst die zweite bekannte Gynandromorphie für die Tribus Augochlorini welche besonders augenscheinlich ist durch die vollständige Asymmetrie. Nichtsdestotrotz bestand bei diesem Tier eine für die Gattung typische Assoziation mit Milben von *Thectochloracarus neotropicalis* FAIN, ENGEL, FLECHTMANN & OCONNOR 1999.

Introduction

The genus *Thectochlora* comprises five species of South American halictid bees that range from Argentina to Guyana (ENGEL 2000; GONÇALVES & MELO 2006). The genus is one of the lesser studied groups of the New World tribe Augochlorini, with no investigations of its biology to date. What is known is that species are unique among modern augochlorines for the development of a prominent acarinarium on the anterior-facing surface of the first metasomal tergum in females. This small 'pocket', composed of a depressed area bordered by dense, elongate, plumose setae, is used to transport mites from nest to nest in a presumably mutualistic association (FAIN et al. 1999; ENGEL 2000). Where examined, the mites of *Thectochlora* are unique to this genus of bees, and have been described as *Thectochloracarus neotropicalis* FAIN, ENGEL, FLECHTMANN & OCONNOR (1999).

Herein we provide a brief description and discussion of a recently discovered gynandromorph of *Thectochlora alaris* (VACHAL 1904), the first such record for the genus. This is only the second gynandromorph documented for the bee tribe Augochlorini. It is hoped that this paper will stimulate others to look for these deviant phenotypes and put them on record. Morphological terminology generally follows that of EICKWORT (1969), ENGEL (2000, 2001), and MICHENER (2007). As in other studies of gynandromorphs, only those morphological deviations are described in detail (e.g., GONZÁLEZ 2004; WCISLO et al. 2004; WOLF 2006; OLIVEIRA & ANDRADE 2006a, 2006b; ENGEL 2007; CEDERBERG 2008; LUCIA et al. 2009). Photomicrographs were prepared using a Nikon D1x digital camera attached to an Infinity K-2 long-distance microscopic lens.

Systematics

Thectochlora alaris (VACHAL 1904) (Figs 1-7)

M a t e r i a l : Bilaterally asymmetrical gynandromorph (Figs. 1-3); Paraguay, Dept. Presidente Hayes, Transchaco Highway km 385, 14-v-1986 [14 May 1986], R.E. Woodruff; deposited in the Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA.

D e s c r i p t i v e n o t e s : Specimen in excellent condition, with a general female-like appearance (Fig. 1). Total body length 6.83 mm; head width 1.83 mm, length 1.72 mm; forewing length 4.84 mm; intertegular distance 1.28 mm.

Head perfectly divided between male and female halves (Figs. 4-5). Female half of head with typical dispersed pubescence not obscuring the integumental surface; apical portion of clypeus marked by brown without metallic coloration (Fig. 4); mandible reddish brown with subapical tooth (Fig. 5); labrum dark brown with rounded elevation on basal surface and narrow, poorly-developed distal process (not as well developed as in typical females; cf. EICKWORT 1969); antenna as in normally-developed females of *Thectochlora*, with more slender scape (Fig. 4) extending back to lateral ocelli and with flagellum not reaching beyond metanotum (Fig. 2). Male half of head with more dense

and plumose pubescence than on female side, partially obscuring integument on lower frons, around antennal torulus, and on lower face (Fig. 4); apical portion of clypeus marked by yellow without metallic coloration (Figs. 4-5); mandible shorter than on female half, simple, largely yellow with reddish-brown apex (Figs. 3, 5); labrum transverse and yellow; antennae with typical male development of shorter and more robust scape (Fig. 4), eleven flagellomeres thicker and longer than those of female (individual flagellomeres II-XI of roughly subequal proportions and with uniform covering of micropilosity, typical for *T. alaris* males), and extending back beyond propodeum (Fig. 3).

Mesoscutal characters of *Thectochlora* such as lamellate pronotal dorsal ridge and mesoscutal anterior lip as in normal *T. alaris* males and females (Fig. 1). Legs of female half typical for female *T. alaris*, with largely brown to amber-colored integument, well developed metafemoral scopa, poorly-defined metabasitibial plate, and pectinate inner metatibial spur with five distinct branches emanating from rachis (sensu ENGEL 2009); protrochanter without dorsal hook, with faint tubercle; mesotrochanter with pronounced dorsal hook (cf. ENGEL 2000; GONÇALVES & MELO 2006). Legs of male half typical for male *T. alaris*, with tibiae and tarsi more yellow in color (Fig. 3), without metafemoral scopa or metabasitibial plate, and inner metatibial spur serrate although there is a small tubercle proximally on the rachis in the position of where a first branch might arise were one present; protrochanter without dorsal hook (there is also no evidence of a tubercle); mesotrochanter without dorsal hook, with faint dorsal tubercle. Basal area of propodeum typical for females of *T. alaris* (EICKWORT 1969) (Fig. 1).

Metasomal terga and sterna generally female in appearance and shape (Fig. 1) except setae less developed on male side; anterior-facing surface of first metasomal tergum with male side more uniformly punctured and with more metallic coloration, that of female side more amber colored, with punctuation less developed and more pronounced imbricate surface sculpturing (Fig. 6), acarinarial setae not developed on male side and only very weakly formed on female side; sternum IV of male side with poorly formed concave apical margin (Fig. 7), presumably where this would otherwise have been developed into the concave apical margin with lateral projects in normal *Thectochlora* species (cf. EICKWORT 1969; GONÇALVES & MELO 2006).

Discussion

The gynandromorph reported here can be positively identified using characters of either side of the specimen. The male side will run to *T. alaris* in the key of GONÇALVES & MELO (2006), while the female side will run to *T. alaris/T. basiatra* (STRAND 1910). Given that the male half of the specimen has uniformly micropilosity on the antennal flagellomeres and flagellomeres that are subequal in length, we believe this safely excludes *T. basiatra* as a possibility for the species. Both species occur in the area where the single individual was collected. Interestingly, as in females of *T. alaris* and *T. basiatra* there is a mesotrochanteral dorsal hook (e.g., ENGEL 2000; GONÇALVES & MELO 2006) on the female half of the gynandromorph. Similarly, the male protrochanter lacks a dorsal hook in *T. alaris* and *T. basiatra*, as does the male side of the gynandromorph. However, the male side of the gynandromorph has a faint dorsal tubercle on the

mesotrochanter rather than a pronounced hook as in *T. alaris* or *T. basiatra*. The female protrochanter of *T. alaris* and *T. basiatra* lacks a dorsal hook, while on the female side of the gynandromorph there is a faint dorsal tubercle. If the presence of these faint tubercles is interpreted as undeveloped hooks, then the presence of such a tubercle on the protrochanter of the female side might suggest *T. hamata* GONÇALVES & MELO 2006 as a possible species identification. However, in this species the males also have a pronounced protrochanteral hook and the male side of the gynandromorph lacks any such hook or even a tubercle. Moreover, the antennal and other characters are not as in males or females of *T. hamata*. The fact that these tubercles, regardless of how faint, are expressed in the positions where otherwise developed hooks would appear may indicate some developmental flexibility in the production of trochanteral hooks in *Thectochlora* such that they can be expressed to some degree in species where they are otherwise not typically found. This flexibility could be interpreted even further to suggest that such a character is not of specific value in the genus given that 'species' which should not have protrochanteral hooks may actually have the underlying genetic architecture to develop them and that it is simply not expressed or not fully expressed in certain individuals. If such a scenario was demonstrated, then it might suggest that at least *T. alaris* and *T. basiatra* are indeed the same species, perhaps also along with *T. hamata*, and with the micropilosity of the antenna and those minor differences in the male sterna and genitalia representing mere variations. Naturally, we are not advocating this as a reason to synonymize these taxa since the proximate factors are by no means understood, but are merely attempting to propose hypotheses that could be tested using new evolutionary developmental techniques. If it were not for the presence of such an interesting gynandromorph such a hypothesis might not otherwise be considered.

It is also very interesting to note that the gynandromorph is carrying individuals of their mite associates in a very poorly developed acarinarium on the female half of the specimen (Fig. 6). There is also a single mite holding on to the first metasomal tergum on the male side, and additional mites on the dorsal surfaces of the meso- and metafemora of the male side. Thus, despite its overall abnormal morphology there has been no apparent disruption to its mutualistic association. Given that the mites are likely detecting various chemical cues in the bee's development so as to know when to position themselves on newly emerging adults, it seems that there was no significant disruption to the overall physiology of the gynandromorph as it reached adulthood.

Gynandromorphs have been implicated in the development of male-like traits in cleptoparasitic females (WCISLO 1999; WCISLO et al. 2004). An interesting possibility along these same lines is that female-like traits are expressed in males of orchid bees. For instance, the shape of the corbicula for particular *Euglossa* species is rather similar to the swollen and expanded metatibiae of their corresponding males. This expansion is not a necessity for the development of the metatibial gland since in males of the cleptoparasitic orchid bee genera *Aglae* and *Exaerete* the metatibiae are shaped similar to their associated females, which themselves are not developed into corbiculae. If the underlying development of the overall form of the metatibiae was not linked between the sexes, then there should be no tight association in male and female metatibial form. Gynandromorphs of euglossines, particularly of *Aglae* or *Exaerete*, would be immensely interesting to discover and might provide considerable insight into the development of the unique structures of orchid bees.

Gynandromorphs and intersexes provide a spectacular opportunity to understand the development and genetic architecture of phenotypic expression and to gain insights into intersexual homologies (e.g., WICSLO et al. 2004; ENGEL 2007). With the growing field of evolutionary developmental biology, the critical study of developmental mechanisms, patterns of expression, and underlying molecular genetics for bees represents a ripe opportunity for tackling interesting questions in apoid evolution (ENGEL 2011). Gynandromorphs will continue to factor into work toward understanding the origins of morphological disparity among bees, underpinning new questions and hypotheses and giving fuel to new investigative technologies.

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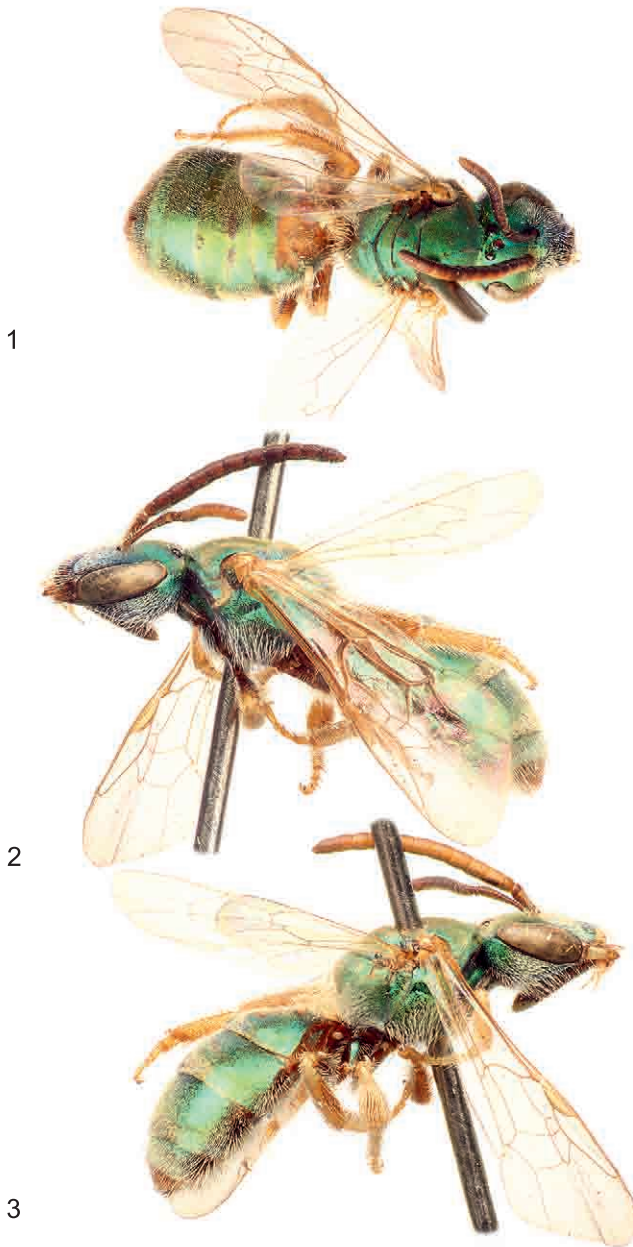
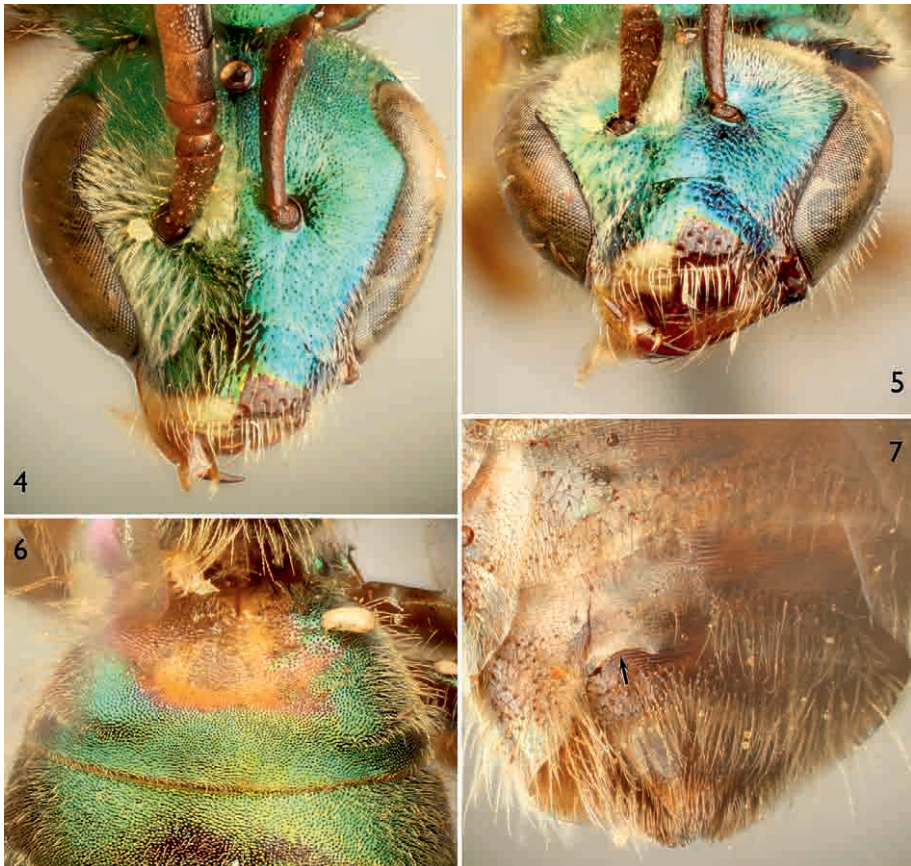


Fig 1: Gynandromorph of *Thectochlora alaris* (VACHAL 1904), dorsal aspect; left half is female, right half is male. Note mites on first metasomal tergum. **Figs 2-3:** Lateral habitus of gynandromorph of *Thectochlora alaris* (VACHAL 1904). (2) female half; (3) male half.



Figs 4-7: Photomicrographs of gynandromorph of *Thectochlora alaris* (VACHAL 1904) (in photographs of the face and terga left is female, right is male, while the reverse is true for the sternal photograph). (4) facial aspect; (5) frontal-oblique facial aspect; (6) first metasomal tergum, with associated mites; (7) metasomal sterna (arrow indicates concavity on male half of sternum IV).

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