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BRIEF COMMUNICATION

Notes on male and female facial patterns in bees (Hymenoptera: Apoidea), with comments on other aculeates

Charles D. Michener¹

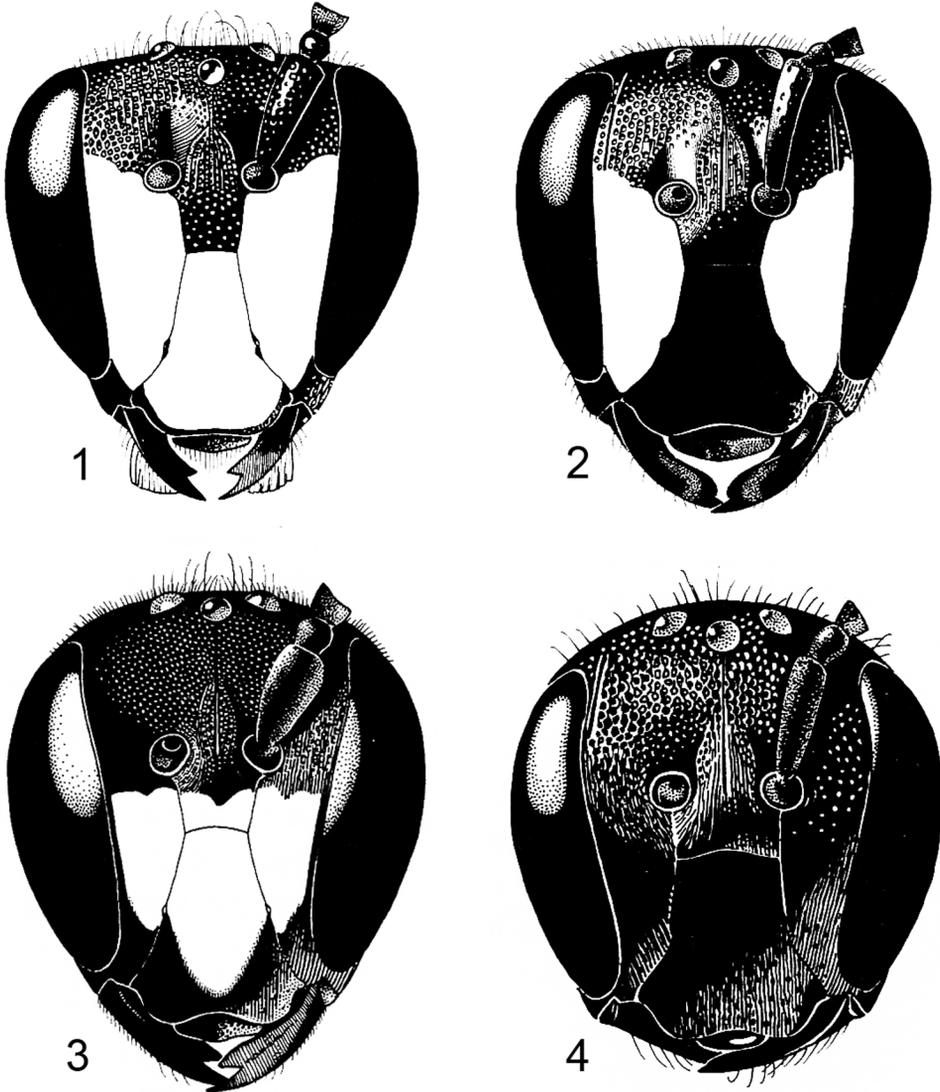
Abstract. Pallid (frequently yellow) integumental areas characterize faces of many bees and related wasps. Some species lack such markings, others lack them only in females, while others have them in both sexes. A rule applicable to thousands of species is that, if present, yellow areas are more extensive in males than in females. In different groups, yellow areas can be either expanded or reduced, both have occurred repeatedly in the Aculeata. In some groups that lack integumental yellow facial areas, males have brushes of yellow or brassy facial hairs that hide the integument. Behavior associated with presence or absence of facial yellow areas is not recognized, for mating males usually approach females from above and behind so that neither can see the face of the other. Possibly male-to-male interactions are involved.

INTRODUCTION

In many aculeate Hymenoptera, especially those with yellow, white, or reddish integumental markings on the body, the face also has such markings. For simplicity, they are termed yellow below. Such areas contrast with the commonly black background color of the head, although in some species the background color is ferruginous or yellow. In such cases the yellow areas may become unrecognizable.

The basic rule is that, if individuals of a species exhibit yellow facial marks, they will be more extensive in males than in females. For good examples, see illustrations of hylaeine bees in Houston (1975, 1981: Figs. 1–4). Thus there are species (*e.g.*, many ants) without yellow facial markings in either sex. Others have no such yellow areas in females, but have yellow areas in males, as in figures 3 and 4. Still others have yellow on the face in both sexes, but the yellow is more extensive in males than in females, as in figures 1 and 2. This basic rule is applicable to thousands of species. Yellow may occupy most of the face, but it is often restricted to the clypeus and/or to the paracocular areas where it often forms a band or line along the inner orbit of each compound eye.

¹ Division of Entomology, Natural History Museum, and Department of Ecology & Evolutionary Biology, 1501 Crestline Drive – Suite 140, University of Kansas, Lawrence, Kansas 66045, USA (michener@ku.edu).



Figures 1–4. Faces of *Hylaeus* Fabricius (Colletidae), males at left, females at right, from Houston (1981: reproduced with permission). 1, 2. *Hylaeus (Euprosopellus) chrysaspis* (Cockerell). 3, 4. *H. (Planihylaeus) trilobatus* (Cockerell).

The yellow areas are ordinarily sharply defined in bees and some other aculeate Hymenoptera. In other Hymenoptera these areas are often not sharply defined, and there is sometimes individual variation that obscures possible differences between sexes.

It is not clear whether yellow facial marks are ancestral or derived in the Aculeata as a whole. It is clear that they have appeared and been lost repeatedly. Examples suggesting such events are: (1) In the tribe Osmiini (Megachilidae), yellow integumental markings on the face are ordinarily absent in both sexes. The male of *Ochreriades fasciatus* (Friese), however, has a yellow clypeus. The male is unknown for the only

other species of *Ochreriades* Mavromoustakis. It seems very probable that *Ochreriades* was derived from black-faced ancestors. (2) In the tribe Eucerini (Apidae) and more specifically in the large genus *Melissodes* Latreille, males ordinarily have a yellow clypeus. However, in the subgenus *Psilomelissodes* LaBerge, the face is black in both sexes. Species of that subgenus were presumably derived from ancestors with a yellow clypeus in males. Similarly, the species of the large genus *Leioproctus* Smith (Colletidae) mostly lack yellow facial markings but males of the subgenus *Andrenopsis* Cockerell have such markings.

Among the bees, although presence of yellow facial markings at least in males is very widespread, there are large groups that lack such markings. Examples are *Colletes* Latreille and its relatives (Colletidae), and *Osmia* Panzer and *Megachile* Latreille and their relatives (Megachilidae). In numerous large taxa of bees, some genera or species have facial markings while others do not. For example in the Meliponini, the faces of species of *Trigona* Jurine (subgenus *Trigona*) are dark in both workers (females) and males, while faces of *Melipona* Illiger and *Paratrigona* Schwarz have rather complex yellow patterns, those of males somewhat enlarged compared to those of workers, or much enlarged in *Melipona quinquefasciata* Lepeletier de Saint Fargeau, *M. rufiventris* Lepeletier de Saint Fargeau, &c.

Among bees, exceptions to the rule are almost unknown. However, in *Exoneura* (*Exoneura*) *bicolor* Smith (Apidae) and some similar species of the same subgenus, the male has enlarged compound eyes with the inner margins convex, the face correspondingly narrow and covered with strong long hairs. Such males often have smaller facial (in this case, clypeal) marks than females. Males of these bees are known to hover in groups, unlike most other bees. Males of *Apis* Linnaeus also have large compound eyes and hover but neither sex has a distinctive facial color pattern. Males of *Xylocopa* Latreille with large compound eyes, for example *Xylocopa* (*Prosopoxylocopa*) *mirabilis* Hurd & Moure, have yellow markings that are lacking in females.

Among wasps, more irregularity in facial marking as related to gender can be found than among bees. Thus in *Philanthus* Fabricius and *Cerceris* Latreille (both Crabronidae) nearly all species have more yellow on the face of males than females, but in a few the yellow seems equal in the two sexes. In most bembicines (*Bembix* Fabricius, *Stenolia* Say, *Rubrica* Parker) and also in *Crabro* Fabricius the sexes are alike in facial markings; however, in *Bembix troglodytes* Handlirsch the male has more yellow. In Vespidae there is often no conspicuous difference between the sexes in yellow facial pattern. However, in *Polistes metricus* Say the male has more yellow on the face than the female. Species of *Sapyga* (Sapygidae) such as *Sapyga angustata* Cresson and *S. nevadica* Cresson, have more yellow on the face of the male than on that of the female.

Possible importance to the insect of the facial patterns summarized above are not known, although such features appear to be associated with recognition of individuals in *Polistes* (Sheehen & Tibbetts, 2011; Tibbetts, 2002). However, that the patterns have some importance is strongly suggested by their presence in diverse groups, and especially by the replacement of integumental coloration patterns by hair (setae). The tendency of males to have more pale hair on the face than females is common, but there are outstanding examples such as the following: In the genus *Megachile*, which always lacks integumental face markings, males of numerous species have the lower face, especially the clypeus, densely covered with yellow or golden hairs that are directed downward and hide the cuticle beneath, giving a yellow, golden, or brassy aspect to the lower face. In the genus *Hoplitis* Klug (Megachilidae), which also lacks integumental face marks, males of the subgenus *Robertsonella* Titus have the clypeus covered with

dense, erect, white hairs hiding the surface beneath, and in the subgenus *Monumetha* Cresson, males of *Hoplitis* (*Monumetha*) *albifrons* (Kirby) but not other species of the genus have the clypeus covered with minute silvery hairs that give it an aspect entirely different from areas of the body with ordinary hairs. Thus, males of taxa that produce no integumental facial markings sometimes evolve hair patterns that apparently replace integumental coloration.

The wide distribution of the facial color patterns among taxa and their apparently repeated development suggest that they probably have an importance for the insects. That they can be replaced by similarly colored hairs supports the view that they are perceived by sight; that they are regularly better developed in males than in females suggests that they may have something to do with sexual behavior. One can imagine that during courtship a female might see faces of other individuals and preferentially accept one with stronger face markings. However, in most of the few species whose courtship and mating behaviors are known, males in the presence of appropriate pheromones, pounce on females from above and behind, so that there is little opportunity for either sex to see the face of the other. Perhaps a more likely explanation is that males approaching other males, respond (aggressively or not) to one another, in some way differently, depending on facial coloration.

The objective of this 'Note' is to call the attention of observers to the (predominantly male) yellow head markings and facial hair in the hope that explanations will be suggested, and verified by behavioral observations.

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