

**A review of deviant phenotypes in bees in relation to brood parasitism, and a gynandromorph of *Megalopta genalis* (Hymenoptera: Halictidae)**

W. T. WCISLO\*, V. H. GONZALEZ<sup>1</sup> and L. ARNESON<sup>2</sup>

*Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancón, Panama*

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We review the occurrence of gynandromorphy in 64 species of bee, and describe the abnormal traits as deviations from the male or female wild-type. Phenodeviants occur at approximately equal frequency among the main body regions (head, thorax, metasoma). Cross-sex expression of character states occur more often among females (i.e. deviant expression of male-like traits) than among males (i.e. deviant expression of female-like traits). Such pathologies demonstrate how developmental switch mechanisms might generate novel structural traits similar to those expressed as a syndrome of brood parasitic traits. We also describe the first known gynandromorphic bee in the tribe Augochlorini, a specimen of the nocturnal bee, *Megalopta genalis*.

**KEYWORDS:** Gynandromorph, development, deviant, brood parasitism, morphology.

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**Introduction**

Developmental biologists and geneticists have used gynandromorphs and other anomalies to better understand the regulation of phenotype expression (e.g. Nesbitt and Gartler, 1971; Raff, 1996; Gehring, 1998). Some evolutionary biologists have used them to better understand patterns of natural variation (e.g. Darwin, 1868; Bateson, 1894; Goldschmidt, 1940; Michener, 1944; Waddington, 1961). Usually, however, extremely deviant phenotypes are dismissed as irrelevant monsters (e.g. Mayr, 1942). In light of recent attention to the evolution of mechanisms regulating phenotypic expression (e.g. Gerhart and Kirschner, 1997; Emlen, 2000), developmental anomalies seem important because they reveal possible phenotypic

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\*To whom correspondence is addressed at: STRI, Unit 0948, APO AA 34002-0948, USA; e-mail: [WcisloW@tivoli.si.edu](mailto:WcisloW@tivoli.si.edu).

<sup>1</sup>Present address: Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA.

<sup>2</sup>Present address: Department of Entomology, Utah State University, Logan, UT, USA.

combinations that may be favourably selected if expressed in other phenotypic backgrounds or environments (see West-Eberhard, 2003). In a posthumous work, Wheeler (1937) discussed how sexual pheno-deviants in ants could be used to understand the evolution of caste differences, and Cockerell (1911) and others discussed similar arguments for the evolution of parasitism in bees.

In this paper we provide an overview of gynandromorphs in bees, and briefly discuss the potential significance of cross-sex expression of traits in understanding aspects of the evolution of morphological features associated with brood parasitism (table 1; cf. Wcislo, 1999). We also describe the first known gynandromorphic *Megalopta* bee (Hymenoptera: Halictidae).

## Materials and methods

### *Comparative survey of gynandromorphs in bees*

Descriptions of gynandromorphs were taken from the literature, summarized in table 2, and were used to classify the overall sexual appearance of each specimen as female or male; only the anomalous characteristics are described. Earlier literature was reviewed by Dalla Torre and Friese (1899) and their specimens are not duplicated in table 2, nor are the sex anomalies associated with stylopization that are reviewed by Salt (1927). We also omitted monstrosities such as duplicate appendages that are not associated with secondary sexual characteristics (e.g. Noskiewicz, 1923). We included mosaics, whether bilateral or not, but omitted intersexes (blends). Some specimens show characters that are slightly deviant and approximate the wild-type, and are listed as showing a tendency (+) to a female- or male-like condition.

### *Overview of natural history and description of gynandromorphic *Megalopta genalis**

*Megalopta* is a genus of dark-loving bees that can be locally abundant in the Neotropics. Females live in dead, broken branches, with one to seven females per nest. Regular collections of *Megalopta* from nests and from black lights have been made as a part of an on-going study of their biology by the first author and colleagues in the Barro Colorado Nature Monument and the adjacent Soberanía National Park, Panamá Province, Republic of Panama.

The morphological description and illustrations of the gynandromorph generally follow descriptions in Eickwort (1969); terminology of surface sculpturing follows Harris (1979). The specimen is deposited in the Dry Reference Collection of the Smithsonian Tropical Research Institute, Balboa, Republic of Panama; voucher specimens of normal male and female *M. genalis* are deposited in the same

Table 1. Partial list of male-like characters of parasitic bees (female states are given in parentheses) (from Michener, 1978; Wcislo, 1999).

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- Sharp-pointed mandible without teeth (toothed mandible, broader and flattened for digging, cutting, manipulating etc.)
  - Body relatively hairless, especially legs and thorax or ventral metasoma (body often densely pubescent with thick plumose hairs, especially on legs and the ventral metasoma where pollen is transported)
  - Antennal flagella relatively long (antennal flagellar length usually noticeably shorter than male)
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Table 2. A partial survey of gynandromorphic bees.

Species	Overall sexual appearance	Gynandromorph class; and deviant phenotypic characteristics	Reference
<b>ANDRENIDAE</b>			
<i>Andrena armata</i> (Gmelin)	♀	A-P; head ♂	Wolf, 1982
<i>Andrena bimaculata</i> (Kirby)	♂	M; all legs and T5 and T6 ♀	Perkins, 1914
<i>Andrena fucata</i> Smith†	♀	A-P; scopa reduced; pubescence on T reduced	Løken, 1967
<i>Andrena fulva</i> (Müller)†	♂	M; pubescence ♀-like, coloration intermediate between both sexes	from Wolf, 1986
<i>Andrena flavipes</i> Panzer (= <i>A. fulvicrus</i> Kirby)	♂	B; left half of head and left legs ♀	Perkins, 1914
<i>Andrena porterae</i> Cockerell†	♀	M; proportions of the antennal segments, colour and structure of hind legs are intermediate	Linsley, 1937
<i>Andrena potentillae</i> Panzer	♀	A-P; head ♂	Wolf, 1982
<b>APIDAE</b>			
<b>Apini</b>			
<i>Apis mellifera</i> Linnaeus	Variable—both sexes	B; the right and left side of the eyes, antennae, mandibles, proboscis, thorax, wings, hind legs and abdomen can be either ♀ or ♂; sting can be present or not	Drescher and Rothenbuhler, 1963
<b>Bombini</b>			
<i>Bombus agrorum</i> Fabricius	B	Head, thorax (including the legs) and genitalia with left side ♂	Röseler, 1962
<i>Bombus agrorum</i> Fabricius	♂	B; left half of head ♀ (worker)	Laidlaw, 1932
<i>Bombus flavifrons</i> Cresson	♀ (worker)	M; right middle leg and hind legs with intermediate characters between ♂ and ♀; abdomen ♂	Milliron, 1962
<i>Bombus lapidarius</i> (Linnaeus)	B	Left side ♂ and right side ♀ (worker), except genital parts ♂; size ♀	Sichel, 1858
<i>Bombus lapidarius</i> (Linnaeus)	♀	M; pubescence on clypeus ♂	Stöckhert, 1920
<i>Bombus mastrucatus</i> Gerstnecker	♂	B; left side of head and thorax ♀	Ritsema, 1880 (1881)
<i>Bombus mastrucatus</i> Gerstnecker	♂	M; right antenna, right half of thorax and genitalia and all legs ♀	Stöckhert, 1924
<i>Bombus ruderarius</i> Müller	♀	M; antenna and legs on right side ♂-like	Stöckhert, 1924

Table 2. (Continued).

Species	Overall sexual appearance	Gynandromorph class; and deviant phenotypic characteristics	Reference
<i>Psithyrus fernaldae</i> Franklin <sup>‡</sup>	♀	M; pubescence on clypeus and face ♂; abdomen ♂, except for the presence of the following ♀ parts in the genitalia: furcula, second valvulae and valvifer, and stylus	Milliron, 1960
Meliponini			
<i>Partamona cupira</i> var. <i>rhumbleri</i> (Friese)	B	Left half of head and thorax ♂, other side is mostly ♀ worker; abdomen ♂	Schwarz, 1929
Nomadini			
<i>Nomada</i> sp. <sup>‡</sup>	♀	B; left half of head, mesothorax (excluding scutellum) and legs of the left side are ♂-like	Tsuneki, 1975
Xylocopini			
<i>Xylocopa fenestrata</i> Fabricius	♀	M; right half of the head and thorax (excluding legs) ♂	Maa, 1940
<i>Xylocopa brasiliatorum</i> Patton	B	Left side ♂ and right side ♀, except for the sting	Gordh and Gulmahamad, 1975
<i>Xylocopa confusa</i> Pérez	Mixed	Head ♀; left side of thorax and abdomen ♀; genitalia with sagitta, stipes and cardo reduced on the ♀ side; right side ♂	Handschin, 1935
<i>Xylocopa mendozana</i> Enderlein	Mixed	Right side head and thorax and all T ♂; left side head and thorax and all S ♀	Enderlein, 1913b
<i>Xylocopa micans</i> Lepeletier	B	Left side of head and abdomen ♂, right side ♀; thorax with sides reversed; left side of genitalia ♂, right side reduced	Maidl, 1912
<i>Xylocopa nigrita</i> Fabricius	B	Left side ♂ and right side ♀, except for the last segment of abdomen, S4–6 ♀	Carcasson, 1965
<i>Xylocopa ordinaria</i> Smith	♀	M; pubescence on clypeus and gena ♂	Enderlein, 1913a
HALICTIDAE			
Halictini			
<i>Lasioglossum albipes</i> (Fabricius)	+♀	M; left half of the head, left fore leg and left half of S1–3 ♂; first three tarsi of left middle-leg and hind metatarsi are intermediate	Nilsson, 1987

Table 2. (Continued).

Species	Overall sexual appearance	Gynandromorph class; and deviant phenotypic characteristics	Reference
<i>Lasioglossum calceatum</i> (Scop)	+♀	M; head ♂, legs intermediate	Plateaux-Quénu and Plateaux, 1982
<i>Lasioglossum morio</i> (Fabricius)	♀	B; left half of the head ♂	Wolf, 1986
<i>Lasioglossum lativentre</i> (Schenck)	♀	A-P; head ♂; smaller than normal ♀	Stöckhert, 1924
<i>Lasioglossum malachurum</i> (Kirby)	+♂	M; left antenna, pubescence and legs on right side ♂	Stöckhert, 1924
<i>Halictus eurygnathus</i> Bluthgen†	♀	M; antennal structure, colour of legs, pubescence and right side of the genitalia ♂	Popov, 1937
<i>Halictus sexcinctus</i> (Fabricius)	♂	D-V; body size and T ♀-like	Leclercq, 1953
<i>Halictus tumulorum</i> (Linnaeus)	♀	M; head ♂, thorax and abdomen intermediate	Hohndorf, 1931
<i>Halictus tumulorum</i> (Linnaeus)	♀	M; left side of the head, labrum and tip of clypeus ♂	Andrewes, 1946
<i>Halictus quadricinctus</i> Fabricius	♀	M; right antenna ♂; shape of face, clypeus and mandible are intermediate	Saunders, 1901
<i>Sphecodes reticulatus</i> Thomson‡	B	Left side ♀ and right side ♂, except S7 ♂; genitalia with sting on left side and rudimentary ♂ parts on right side; body size ♂-like	Stöckhert, 1924
<b>COLLETIDAE</b>			
<i>Hylaeus minuta</i> (Fabricius)	B	Left side of head ♂, right side ♀; thorax with left side ♀, right side ♂; abdomen ♀	Noskiewicz, 1923
<i>Hylaeus albofasciata</i> Friese	♀	Left side of head ♂	Stöckhert, 1924
<i>Hylaeus brevicornis</i> Nylander	B	Left side ♀, right side ♂, except clypeus entirely ♀	Morice, 1915
<i>Euryglossa</i> sp.	+♀	B; right side of head ♂	Exley, 1976
<b>MEGACHILIDAE</b>			
<i>Androgynella detersa</i> Cockerell (= <i>Megachile</i> )	♀	A-P; head ♂ and without metasomal scopa	Cockerell, 1911
<i>Androgynella subrixactor</i> Cockerell (= <i>Megachile</i> )	♀	A-P; head ♂ and without metasomal scopa	Cockerell, 1918
<i>Anthidium oblongatum</i> Latreille	♀	B; left half of S6 ♂	Stöckhert, 1924
<i>Coelioxys rufescens</i> Lepeletier‡	Mixed	Head ♂ except right side of clypeus; thorax mostly ♂; abdomen ♀-like; right side of genitalia ♀, left side ♂	Noskiewicz, 1923
<i>Dianthidium sayi</i> Cockerell	B	♂ characters on the right side of head and thorax; ♀ on left side; abdomen ♂	Hicks, 1926

Table 2. (Continued).

Species	Overall sexual appearance	Gynandromorph class; and deviant phenotypic characteristics	Reference
<i>Dianthidium ulkei</i> (Cresson)	♀	M; the mandibles, right half of clypeus and supraclypeal area as ♂	Schwarz, 1926
<i>Megachile parallela</i> Smith	♂	M; antennal structure and abdomen intermediate between both sexes	Mitchell, 1929
<i>Megachile parallela</i> Smith	♂	M; T6 and S ♀; sting present	Mitchell, 1941
<i>Megachile angularum</i> Cockerell	+♀	M; head (except the antennae and clypeus) and thorax ♂	Mitchell, 1941
<i>Megachile vidua</i> Smith	♂	M; antennal structure and abdomen intermediate	Mitchell, 1929
<i>Megachile vidua</i> Smith	♂	M; terminal segments of abdomen ♀	Mitchell, 1941
<i>Megachile onobrychidis</i> Cockerell	♀	M; pubescence and punctuation on clypeus ♂	Mitchell, 1941
<i>Megachile curvipes</i> Smith	Mixed	Head and abdomen with characters intermediate; thorax and legs entirely ♂	Mitchell, 1941
<i>Megachile bertonii</i> Schrottky	♂	A-P; abdomen ♀	Mitchell, 1929
<i>Megachile chapadiana</i> Mitchell	♀	M; legs intermediate and abdomen ♂-like	Mitchell, 1929
<i>Megachile chrysopyga</i> Smith	Mixed	Body size and legs as ♂; antenna and abdomen ♀	Rayment, 1935
<i>Megachile dilatata</i> Mitchell	♂	A-P; abdomen ♀	Mitchell, 1929
<i>Megachile gemula</i> Cresson	♂	M; terminal abdominal segments ♀, with normal sting	Mitchell, 1929
<i>Megachile intergradus</i> Mitchell	♀	M; front tarsi, claws distinctly cleft and punctuation of clypeus, mesonotum and abdomen are ♂-like	Mitchell, 1929
<i>Megachile intergradus</i> Mitchell	♀	M; punctuation, antennae and legs ♂-like	Mitchell, 1929
<i>Megachile intergradus</i> Mitchell	♀	M; punctuation on clypeus, pubescence colour and shape of metatarsi, and cleft of claws ♂	Mitchell, 1929
<i>Megachile latimanus</i> Say	♀	M; left half of the clypeus, S2-4 and genitalia ♂	Mitchell, 1932
<i>Megachile perihirta</i> Cockerell	Mixed	Pubescence on face and mandibles ♂; thorax (including legs) and abdomen intermediate; sting present	Mitchell, 1929
<i>Megachile rotundata</i> (Fabricius)	♀	B; without metasomal scopa on the left side of S3-6.	Akre <i>et al.</i> , 1982
<i>Megachile rotundata</i> (Fabricius)	B	Head with left side ♀, right side ♂; left side of the thorax and abdomen (including internal organs and genitalia) as ♂	Akre <i>et al.</i> , 1982
<i>Megachile rotundata</i> (Fabricius)	B	Left side ♀ and right side ♂	Gerber and Akre, 1969
<i>Megachile tapytensis</i> Mitchell	♂	A-P; abdomen ♀	Mitchell, 1929

Table 2. (Continued).

Species	Overall sexual appearance	Gynandromorph class; and deviant phenotypic characteristics	Reference
<i>Megachile uniformis</i> Mitchell	♂	D-V; number of exposed T ♀	Mitchell, 1929
<i>Megachile willoughbiella</i> (Kirby)	B	Left side ♀, right side ♂	Benno, 1948
<i>Megachile willoughbiella</i> (Kirby)	B	Right side from head through metasomal segment III ♀, left side and remaining metasomal segments ♂	Stenton, 1909
<i>Megachile</i> sp.	♂	A-P; abdomen ♀	Mitchell, 1929
<i>Osmia rufa</i> (Linnaeus)	♀	B; left side of head ♂	Noskiewicz, 1923
<i>Osmia aenea</i> (Linnaeus) (= <i>coerulescens</i> )	♀	B; right side ♂, except the antennae and legs ♀	Benno, 1948
<i>Osmia pentstemonis</i> Cockerell	B	Head and abdomen with ♂ characters on right side and ♀ on left	Sandhouse, 1923
<b>MELITTIDAE</b>			
<i>Melitta haemorrhoidalis</i> (Fabricius)	♀	M; antennae, mandible and fore and middle legs on right side are ♂	Wolf, 1985

+, With tendency to a given sex; B, bilateral asymmetry; A-P, anterior-posterior; D-V, dorso-ventral; M, mixed (see text for details); T, terga; S, sterna.

†Stylopization; ‡parasitic species.

collection, and at the Museo de los Invertebrados 'Graham Fairchild', Universidad de Panamá, and the Natural History Museum, University of Kansas, Lawrence, KS, USA.

## Results

### *Comparative survey of bee gynandromorphs*

These developmental anomalies are known in nearly all families of bees, but almost half (42%) of the 64 species with gynandromorphs listed in table 2 are in Megachilidae. It is unknown if there is something peculiar about megachilid development that renders them especially unstable. This taxonomic bias may also be explained in part by T. B. Mitchell's keen interest in the phenomenon and in megachilid bees (Mitchell, 1929, 1932, 1941); if his data are excluded then the percentage of total deviants that are Megachilidae (19%) is approximately equal to that of other large families such as Halictidae (~16%).

The expression of cross-sex characteristics occurs in numerous combinations among the diverse body regions. In this sample, most individuals are mosaics in showing no obvious patterns in the distribution of male and female features among tagmata (~48%); about 35% of the individuals show left–right *lateral* expression of male versus female traits, while *anterio-posterior* divisions are less common (~15%), and dorso-ventral *transverse* crosses are rare (~3%). Usually in the latter three classes not all tagmata are altered. Deviant phenotypes occur on all tagmata, but are most frequent on the head (78% of specimens); the thorax (with legs) and metasoma (pubescence only) are affected in 53% and 66% of specimens, respectively (table 2). Finally, cross-sex deviants are more frequent among females than among males in this sample, when one sex can be identified (table 3).

### *Description of gynandromorphic *Megalopta genalis**

The specimen was collected between 6:30 and 7:30 pm, on 11 January 1999 at a black light in the forest on Barro Colorado Island, Panama. There was nothing peculiar about the flight behaviour of the gynandromorph that drew attention to it as unusual or aberrant. The time of year, combined with the unworn wings and mandibles, suggest it was a newly active bee.

Table 3. Frequencies of deviations from normally sexual dimorphic characters involved with parasitic behaviour (from table 1), expressed as a transfer from one sex to the other (calculated per specimen from table 2, excluding Bilateral and Mixed, as well as bees with stylopization).

	Normal ♀→♂	Normal ♂→♀
Antennae	0.25	0.097
Mandible	0.25	0.042
Leg structure	0.125	0.055
Pubescence on legs or metasoma	0.111	0.069
Other	0.319	0.139

*N* = 72 tagma with cross-sex expression.

*Habitus.* Female *M. genalis* show considerable variation in body size (e.g. mean intertegular distance =  $\sim 3.0$  mm), and they are usually larger than males (mean intertegular distance =  $\sim 2.4$  mm) (Wcislo *et al.*, in preparation). Overall this specimen resembles a male due to the slender body (intertegular distance = 2.52 mm). The colour of pubescence and integument is normal.

*Head.* The head is almost completely asymmetric except for slightly swollen vertex behind ocelli (figure 3a), unlike a normal female (figure 1a) or male (figure 2a); in wild-type females it is clearly swollen (figure 1a). Male characters occur on the left side (figure 3a, b): antenna with 11 flagellomeres, scape length 0.96 mm, flagellar length 4.6 mm; compound eye converging above to other eye; mandible simple; gena not enlarged, ratio of gena: compound eye in lateral view 0.39; clypeal punctures weak, separated by less than or one puncture width, integument smooth; upper half of face with punctures strong and contiguous; pubescence dense and long. Female characters occur on the right side (figure 3a, b): antenna with 10 flagellomeres, scape length 1.4 mm, flagellar length 2.6 mm; compound eye converging above; mandible toothed; gena enlarged, ratio of gena: compound eye in lateral view 0.68; clypeal punctures separated by one to three puncture widths, with the integument and upper half of face as male; pubescence sparser and shorter than male. Distal margin of clypeus and labrum asymmetric (compare figure 3b with figures 1b and 2b), but distinct tubercles and ridges of labrum that are present in normal females (figure 1b) are not well-defined on the female side (figure 3b).

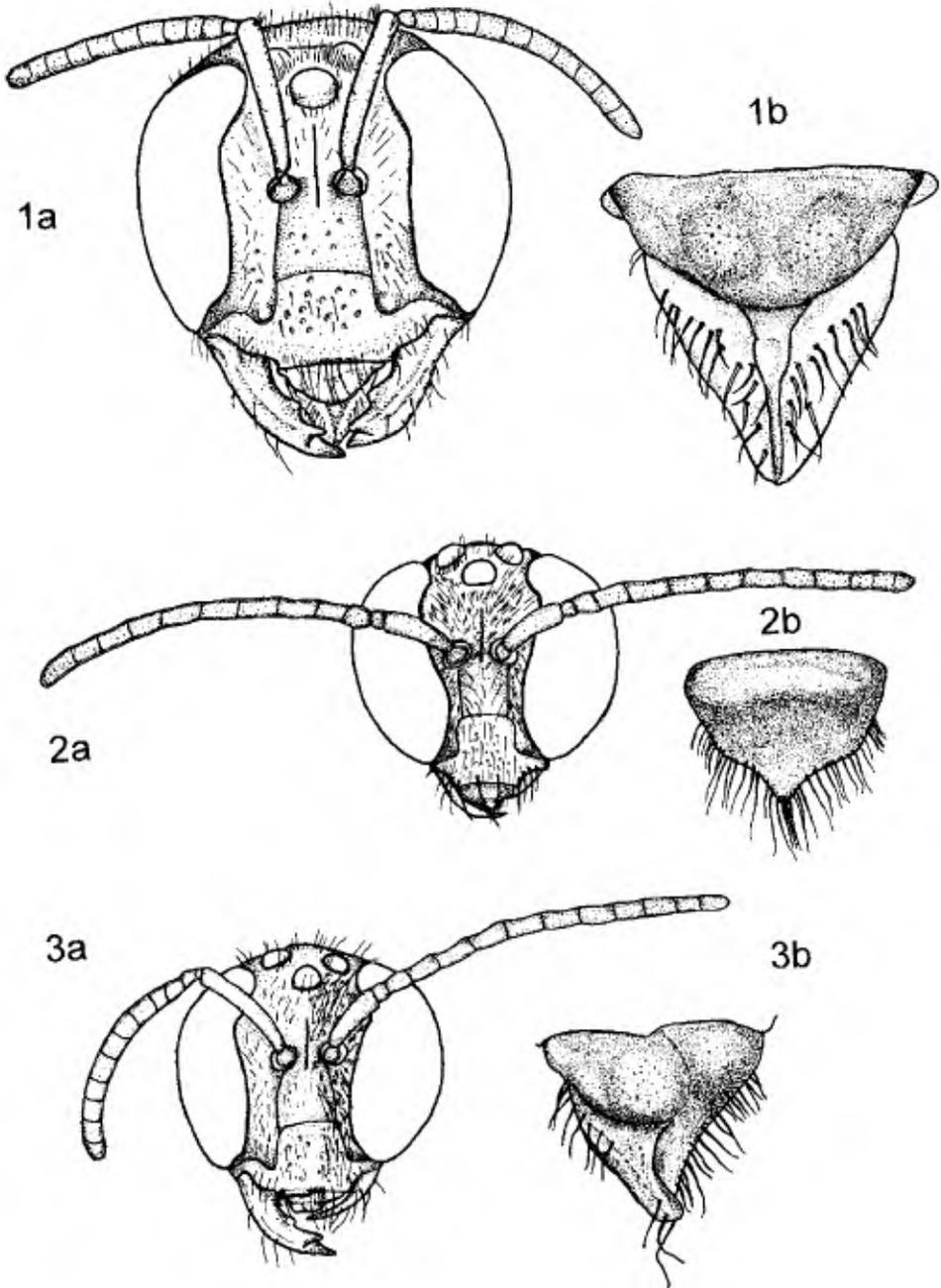
*Thorax.* The thorax is not bilaterally asymmetric. Moreover, all legs are entirely female-like; hindlegs with scopae and basitibial plates.

*Metasoma.* The metasomal (abdominal) terga and sterna are female, and internal structures (sting, ovaries, glands, digestive tract) were normal. Ovarioles on both right and left sides were moderately developed, like the 'group B' ovarioles illustrated by Michener and Wille (1961). The spermatheca was lost so we do not know if the bee was mated.

## Discussion

Dalla Torre and Friese (1899) recognized four classes of hymenopteran gynandromorphs: *lateral*, *anterio-posterior*, *transverse* (dorsal-ventral) and *mixed* (mosaics, or different combinations of the preceding three classes). The first three body axes are developmental compartments (e.g. Gerhring, 1998), and thus the first three classes are natural. According to Cooper (1959) the frequencies of these classes vary among Hymenoptera, in the order *lateral* > *mixed* = *anterio-posterior* > *transverse*. Among bees reviewed in table 2, the order is *mixed* > *lateral* >> *anterio-posterior* >> *dorso-ventral* crosses.

Müller (1872) described structural similarities between female parasitic bees and males of their hosts and their putative ancestors. Cockerell (1911) described a new genus of bees, *Androgynella* (Megachilidae), with apparent male-like females, and speculated that it might be parasitic because females had reduced metasomal



FIGS 1–3. (1) Wild-type female *Megalopta genalis*. (a) Head, width=4.16 mm; (b) labrum. (2) Wild-type male *M. genalis*. (a) Head, width=3.16 mm; (b) labrum. (3) Gynandromorph *M. genalis*. (a) Head, width=3.32 mm; (b) labrum.

scopae. According to Cockerell, females with reduced scopae might be predisposed to parasitism if they collected pollen with reduced efficiency. Cockerell (1918) later described a new congener (*A. subrixator*) that he thought might be a

gynandromorphic *Megachile*, but he re-affirmed his original interpretation of parasitic behaviour for *A. detersa*. The gynandromorph hypothesis was favoured by Mitchell (1929) and Michener (1965) for both *Androgynella* species. Mitchell (1929) studied available sex pheno-deviant *Megachile* bees and noted that some of them recalled similarities to parasitic bees, in that females possessed some male-like traits like reduced pilosity, but linking these freaks with the evolution of parasitism was regarded as a 'fanciful hypothesis'. Although it is unlikely that such freaks were themselves ancestral to a parasitic species or lineage, they point to mechanisms that might make elements of a parasite-like morphology recurrently available for selection when pollen-collecting females behave facultatively as parasites (e.g. Wcislo, 1987; Field, 1992; West-Eberhard, 1986).

In a review of the morphology and behaviour of parasitic sweat bees (Halictinae), Michener (1978) describes how some characteristics of female parasites phenetically resembled males of their hosts or close relatives (table 1), and the list could be extended by including additional traits that are found only in certain taxa (e.g. a labral keel is lacking in parasitic sweat bees and males of non-parasitic sweat bees, but is present in non-parasitic females). A multivariate analysis of structures supports this 'transsexual' hypothesis for a *Lasioglossum* (*Paralictus*) and its *Lasioglossum* (*Dialictus*) host (Wcislo, 1999). The expression of male-like characters in females is one developmental mechanism to generate novel phenotypes (West-Eberhard, 2003), such as mimicry patterns (Clarke *et al.*, 1985). The phenetic similarity between male character states and those of brood parasitic females by coincidence means that an asymmetric cross-sex expression of traits can readily produce structures that frequently are associated with obligate parasitic behaviour in insects (Wcislo, 1987, 1999).

Secondary sexual characters are well-developed in bees, with females having numerous traits associated with collecting pollen (e.g. scopae) or nest-making (e.g. a broad, toothed mandible for excavating soil). These 'female' characters may be lost in parasites, but in so doing they gain 'male' characters such as sharper, pointed mandibles, which in other insects are known to be beneficial during aggressive invasion of a closed space with only one exit (e.g. Hamilton, 1979; Wcislo, 1997). Secondary sexual characteristics of insects are usually not determined by sex hormones (Nilsson, 1987; Nijhout, 1994), and therefore mosaics with distinct male-like and female-like tissues regularly recur at frequencies that vary from 0.00013 in a mutillid wasp (Quintero and Cambra, 1994) to nearly 0.6 in an ant (Kinomura and Yamauchi, 1994), but no attempts to standardize estimates have been made. Gynandromorphs can be induced by environmental stress such as cold shock (Drescher and Rothenbuhler, 1963) and parasitism (Salt, 1927; Wülker, 1964), and their frequency of occurrence can be modified by artificial selection in strains of honey bees (*Apis*) (Rothenbuhler, 1955). Collectively, these examples indicate that a switch to regulate phenotypic expression can be readily triggered [see Cooper (1959) and Nilsson (1987) for a discussion of the cytological malfunctions that produce hymenopteran gynandromorphs; and Gehring (1998) for regulation of gynandromorphic *Drosophila*].

The nature of sex determination in insects may facilitate the evolution of parasitism because a variety of mechanisms are already in place that induce the expression of cross-sex phenotypic characteristics. Wülker (1964) reviews parasite-induced morphological changes in insects, and points out that the most common manifestation of the parasite is damage to secondary sexual characters. Some are

phenetically gynandromorphs (e.g. *Andrena fulva* in table 2; also Salt, 1927; Wülker, 1964). Salt (1927) studied a number of *Andrena* bees parasitized by Strepsiptera, insects which have wingless internal female parasites. Salt recognized that parasites altered the expression of secondary sexual characters, producing phenocopies of gynandromorphs. Internally, parasitized females also have weakly developed corpora allata (Brandenburg, 1955, 1956), a key neuroendocrine gland in insect development (Nijhout, 1994). Manipulating gland function provides yet another potential mechanism for generating novel phenotypes (Kerr and da Cunha, 1990; West-Eberhard, 2003). Usually there are striking morphological differences between males and females in bees, relative to other insects, and this divergence may make cross-sex expression of traits especially likely to facilitate the origins of parasitism in bees.

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