

A synthesis of gynandromorphy among wild bees (Hymenoptera: Apoidea), with an annotated description of several new cases

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Abstract. We here describe six new specimens of gynanders (i.e. specimens where male and female phenotypic characters occur on the same individual) from distinct families of wild bees (Hymenoptera, Apoidea). The newly described cases include *Melitta haemorrhoidalis* (Fabricius 1775) (Melittidae), *Dasygaster hirtipes* (Fabricius 1775) (Melittidae), *Anthophora plumipes* (Pallas 1772) (Apidae), *Bombus monticola rondoui* Vogt 1909 (Apidae), *Bombus vestalis vestalis* (Fourcroy 1785) (Apidae) and *Bombus vestalis sorgonis* (Strand 1917) (Apidae). Descriptions are accompanied by behavioural observations of gynanders under natural conditions before their capture for two cases. We also list 109 gynanders already described in bees and we interpret the newly described cases along these previous records. The putative origins of gynandromorphy are then discussed in the light of recent advances in the field of sex determination in Hymenoptera.

Résumé. Une synthèse sur la gynandromorphie des abeilles sauvages (Hymenoptera : Apoidea), avec la description commentée des plusieurs cas nouveaux. Nous décrivons dans le présent article six nouveaux spécimens de gynandromorphes (individu entier présentant à la fois des caractères morphologiques mâle et femelle) de plusieurs familles d'abeilles sauvages. Ces spécimens appartiennent aux espèces suivantes: *Melitta haemorrhoidalis* (Fabricius 1775) (Melittidae), *Dasygaster hirtipes* (Fabricius 1775) (Melittidae), *Anthophora plumipes* (Pallas 1772) (Apidae), *Bombus monticola rondoui* Vogt 1909 (Apidae), *Bombus vestalis vestalis* (Fourcroy 1785) (Apidae) et *Bombus vestalis sorgonis* (Strand 1917) (Apidae). Les descriptions sont complétées par des observations de comportement dans la nature pour deux spécimens avant leur capture. Par ailleurs, nous avons recensé 109 spécimens d'abeilles gynandromorphes déjà décrits dans la littérature ce qui nous permet d'interpréter les six nouveaux cas observés. Nous concluons cet article par une discussion sur les causes probables des phénomènes de gynandromorphie à la lumière des récentes découvertes réalisées dans le domaine de la détermination du sexe chez les Hyménoptères.

Keywords: Morphology, sex determination, Apoidea, gynandromorphy, deviant.

Although environmental conditions might influence the sexual phenotypic outcome in animals lacking sex chromosomes (for evidence in reptiles see e.g. Bull 1980; Janzen & Paukstis 1991a, 1991b; Ciofi & Swingland 1997), sex phenotype is usually primarily genotypic-dependent and is determined by internal factors such as gonadal hormone secretions (Agate *et al.* 2003) and sex chromosomes (Crozier 1977; Hunt & Page 1994; Beye & Moritz 1994; Hunter 1995).

It has long been reported that sex determination in Hymenoptera was exclusively achieved through a peculiar mode called *haplo-diploidy* (or *arrhenotoky*) (review see Heimpel & de Boer 2008). According to this model, females are diploid and develop from fertilised eggs, whereas males are haploid and develop

from unfertilised ovules. The genetic mechanism underlying sex determination in these insects has received much attention over the past few decades and is now becoming better understood, especially in the honeybee. As far as most Hymenoptera and bees in particular are concerned, sex phenotypes are determined by allelic variation at a so-called "single locus of complementary sex determination" (sl-CSD) (Wilgenburg *et al.* 2006). This mechanism implies that females bees are heterozygotes (A_1A_2), whereas males are hemizygotes (A_1 or A_2) (Whiting 1933, 1943; Crozier 1977; Bull 1981; Cook & Crozier 1995; Heimpel & de Boer 2008). Numerous cases of diploid males have been reported all across the order Hymenoptera (Whiting & Whiting 1925; Duchâteau *et al.* 1994; Pamilo *et al.* 1994; Cook & Crozier 1995; Zayed & Packer 2001). This unusual, or perhaps under-reported phenomenon (see e.g. Liebert *et al.* 2004), is made possible *via* homozygosity (A_1A_1 or A_2A_2) at the aforementioned sex-determining locus (Cook & Crozier 1995; Wilgenburg *et al.* 2006).

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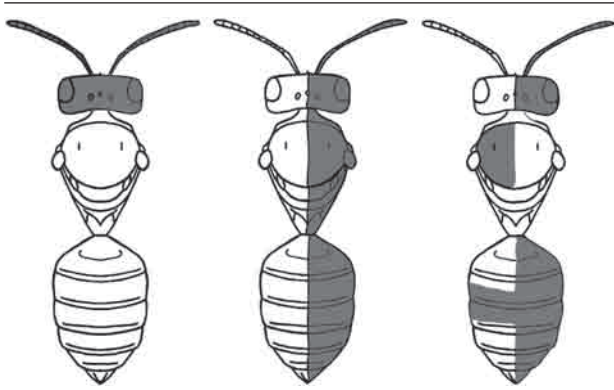


Figure 1
Schematic representation of an example of the three major categories of gynandromorphy: transversal (left), bilateral (centre), and mosaic (right). Male tissues are drawn in grey, female tissues are white.

The recent insights in this field of research have also allowed drawing new perspectives in some related areas of sex determination such as the possible mechanisms driving the rise of teratologies (morphological abnormalities) among the Hymenoptera. Gynandromorphy is one of the best known cases of teratology. Numerous reports and descriptions have been made of so-called *gynanders* [“condition in which male and female features are displayed in one individual” (Gordh & Headrick 2001)], especially in Chalcidoidea (Pintureau *et al.* 1999), Formicidae (Hall & Smith 1954; Berndt & Kremer 1983), Mutillidae (Wheeler 1910), Pompilidae (Wolf 1989; Wahis 1996) and Vespidae (Cooper 1959). This phenomenon is also well described in Apoidea with some authors like Wolf having displayed tremendous endeavour in describing new cases of gynandromorphy during the past two decades (Wolf 1982 to 2000, see all references in tab. 6).

This paper proposes an annotated description of six new cases of gynandromorphy with behavioural observations for two cases. The origin of gynandromorphism among Apoidea is then discussed in the light of both past and recent reports in the field of sex determination in Hymenoptera.

Material and Methods

Description of new gynanders

The gynander of *Dasygoda hirtipes* (Fabricius 1793) was collected on 26.VI.2003 in a wide nesting site encompassing hundreds of nests in activity at Erbisoeul, Belgium (50°30'33"N 03°54'20"E, WGS, leg. D. Michez). The gynander of *Bombus monticola rondoui* Vogt 1909 was collected on 18.VII.2000 foraging on *Rhododendron ferrugineum* L. (Ericaceae) at Evol, France (43°38'07"N 06°12'48"E, WGS, leg. P. Rasmont). Both of these bees were killed with ethyl-acetate and set on an insect pin. The genitalia and internal sterna were then extracted from the metasoma and dissected for additional observations on morphological characters.

Four others gynanders of *Melitta haemorrhoidalis* (Fabricius 1775), *Anthophora plumipes* (Pallas 1772), *Bombus vestalis vestalis* (Fourcroy 1785) and *Bombus vestalis sorgonis* (Strand 1917) were found in the collections of the Naturhistorisches Museum Wien (NMW, Austria), the Natural History Museum of London (NHM, UK) and the University of Mons-Hainaut (UMH, Belgium). The gynander of *M. haemorrhoidalis* was caught on 09.IX.1855 in Villa Opicina (Italia, Friuli-Venezia Giulia, 45°41'N 13°47'E, WGS, leg. Graeffe) foraging on *Campanula* sp. (NMW, Graeffe collection). The gynander of *A. plumipes* was caught on 09.V.1975 in Hundon (England, Suffolk, 52°06'N 00°33'E, WGS leg. Chinery), foraging on garden flowers (NHM, Main collection). The gynander of *B. vestalis sorgonis* was caught on 05.VII.1984 in Sassari, Mont Limbara (Italia, Sardinia, 40°51'N 09°10'E, leg. R. De Jonghe) (UMH). The gynander of *B. vestalis vestalis* was caught on 30.VII.1975 near Deal (England, E. of Kent, 51°13'N 01°24'E, WGS, leg. G. Else) (NHM, Else collection).

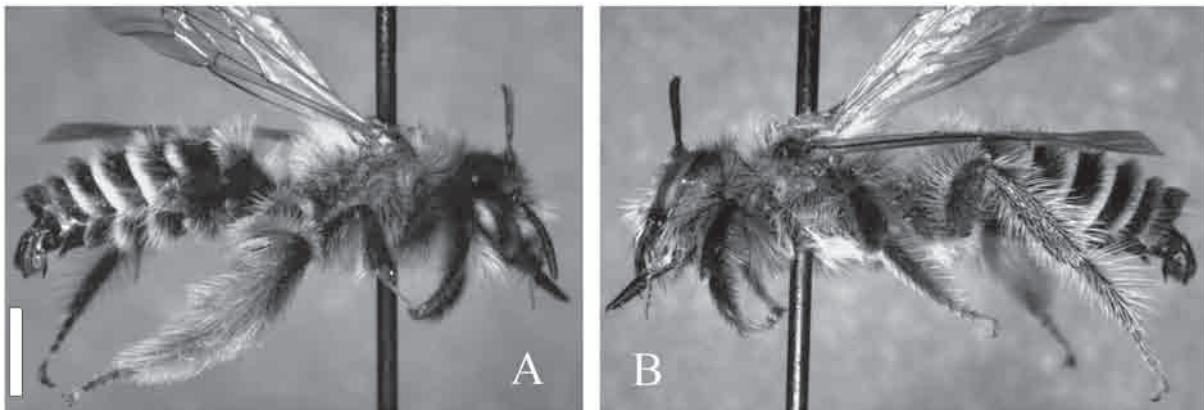


Figure 2
Dasygoda hirtipes gynander. A, left profile; B, right profile (scale = 0.3mm).

Table 1. Comparison of characters displayed by both sexes of *Melitta haemorrhoidalis* to those of the gynander.

Character	Female	Male	Gynander
Prosoma			
Clypeus	Unpunctate medially	Punctate completely	♀
Antenna	12 segments	13 segments	♀
Vertex vestiture	Black	Yellowish	♀
Mesosoma			
Scutum vestiture	Black	Brown	Right half part ♀, left half part ♂
Legs vestiture	Brown	Yellowish	Right half part ♀, left half part ♂
Posterior leg	With enlarged basitarsus and scopa	Without enlarged basitarsus and scopa	Right half part ♀, left half part ♂
Metasoma			
Exposed sterna	6	8	♂
Disc of terga	Hairless	With erected yellowish setae	♂
Sting	Present	Absent	♂
Sclerotized genitalia	Absent	Present	♂

Review of the literature on gynandromorphy in Apoidea

Each description of an Apoidea gynander found in the literature was examined and classified (when possible) into one of the three commonly accepted gynander categories: (i) bilateral if female and male body parts are equal and symmetric, (ii) transverse if sex characters are distributed in two asymmetrical parts; (iii) mosaic if sex characters are distributed randomly in the body (fig. 1). The results of this survey are reported in tab. 6. The generic classification and the morphological nomenclature reported in tabs. 1-6 follow Michener (2000).

Results

Description of the *Melitta haemorrhoidalis* gynander

Male and female tissues are distributed on two distinct areas of the body (tab. 1). The head and right part of the mesosoma present female features. The left part of the mesosoma and the metasoma present male features. These characteristics lead us to conclude that the *M. haemorrhoidalis* gynander falls within the transverse gynander category.

Table 2. Comparison of characters displayed by both sexes of *Dasypoda hirtipes* to those of the gynander.

Character	Female	Male	Gynander
Prosoma			
Clypeus	Irregularly rounded	Regularly rounded	♀
Antenna	12 segments	13 segments	♀
Vertex vestiture	Black	Red	♀
Mesosoma			
Ventral side vestiture	Brown	White	♀
Fore (a) and hind (p) legs vestiture	Brown (a) and red (p)	Red (a and p)	♀
Hind leg	Exhibiting scopae	Without scopae	Right ♀, left ♂
Metasoma			
Exposed sterna	6	8	8
Sterna vestiture	Black	Red	Red
Exposed terga	6	7	7
Tergum 2	Strip of white hairs at the apex of the uninterrupted terga in the median zone; curved black hairs at its bottom	Strip of reddish hairs at the apex of the uninterrupted terga and tousled red hairs	Right half part ♀, left half part ♂
Other terga	Strip of white hairs at the apex of the uninterrupted terga in the median zone; curved black hairs at its bottom	Strip of reddish hairs at the apex of the uninterrupted terga and tousled red hairs	♂
Sting	Present	Absent	Absent
Sclerotized genitalia	Absent	Present	Present

Table 3. Comparison of characters displayed by both sexes of *Anthophora plumipes* to those of the gynander.

Character	Female	Male	Gynander
Prosoma			
Cuticle	Black	Mandibles, labrum, clypeus, paraclypeal area, supraclypeal area and scape with yellow spots	Right half part ♀, left half part ♂
Vestiture	Black	With white setae and some black setae (mainly on vertex)	Right half part ♀, left half part ♂
Antenna	12 segments	13 segments	Right half part ♀, left half part ♂
Mesosoma			
Vestiture	Black	Ventral face with reddish setae	Right half part ♀, left half part ♂
Anterior leg	With black setae	Mainly with white setae	Right ♀, left ♂
Median leg	With short setae	With long setae	Right ♀, left ♂
Posterior leg	With scopae	Without scopae	Right ♀, left ♂
Metasoma			
Vestiture	Black	White	♀

Description of the *Dasypoda hirtipes* gynander

Male and female tissues are distributed patchily (fig. 2, tab. 2). Altogether, the prosoma, the mesosoma and five out of six legs exhibit female characters. Both the whole metasoma (including the genitalia) and the left hind leg show typical male features. The right half of the second metasomal terga displays female vestiture. These characteristics lead us to conclude that the *D. hirtipes* gynander falls within the mosaic gynander category.

The specimen was observed digging actively on the nesting site, thereby displaying exactly the same behaviour as that of conspecific mated females provisioning their brood cells with pollen and nectar (Lind 1968). Male Apoidea are known to devote most of their time searching for mates and feeding on co-occurring flower patches (Eickwort & Ginsberg 1980). They have never been observed engaging in the construction of the nest.

Description of the *Anthophora plumipes* gynander

Male and female tissues are distributed on two distinct areas of the body (tab. 3). The left half-part of the head, the left half part of the mesosoma and the left legs 1-2 present male features. Others parts of the body are female. These characteristics lead us to conclude that the *A. plumipes* gynander falls within the transverse gynander category.

Description of the *Bombus monticola rondoui* gynander

Secondary sexual characters are symmetrically distributed on the left (male) and on the right (female) half of the body (figs 3A-E, tab. 4). Of particular interest is the close examination of the internal sclera: the left part bears typical female characteristics, the right part is composed of an hemi-male genitalia showing

Table 4. Comparison of characters displayed by both sexes of *Bombus monticola rondoui*.

Character	Female (right part of gynander)	Male (left part of gynander)
Prosoma		
Mandible	Wide; no <i>barbae mandibularis</i>	Narrow; <i>barbae mandibularis</i> present
Antenna	12 segments	13 segments
Face, vertex and clypeus vestiture	Black hairs with some brownish bristles on the inner margin	Dense and yellowish vestiture on the inner side; dense and black vestiture on the outer side
Labrum	Wide	Narrow
Mesosoma		
Thorax vestiture	Collar down to the coxa	Collar stops before the coxa
Posterior legs	Scopa and pollen comb present; basitarsus enlarged	No scopa or pollen comb; basitarsus thin
Vestiture of the inner face of the median basitarsus	Red to brown on the apical half	Reddish (bristles) on its whole length
Metasoma		
Sterna vestiture	Small and white	Long and white
Genitalia	Absent	Present
Sting and sheath lobe	Present	Absent

a single penis valve and a single gonostylus (figs 3F-G). These characteristics lead us to conclude that the *B. monticola* gynander ranks within the bilateral gynander category

The *B. monticola* gynander was caught on a *Rhododendron ferrugineum* while it was collecting pollen the same way as normal workers do. The specimen was only able to collect pollen using its left hind leg which bore a pollen comb.

Description of the *Bombus vestalis sorgonis* gynander

Male and female tissues are distributed on two distinct areas of the body (tab. 5). The right half of the head and of the mesosoma (including legs) present male features. Others parts

of the body are female. These characteristics lead us to conclude that the *B. vestalis sorgonis* gynander falls within the transverse gynander category.

Description of the *Bombus vestalis vestalis* gynander

Male and female tissues are distributed patchily (tab. 5). Altogether, both mandibles, left half part of the labrum, left half part of the face, right antenna, right half part of the vertex, left half part of the mesosoma and right half part of the metasoma exhibit male characters. Others parts of the body show typical male features. These characteristics lead us to conclude that the *B. vestalis vestalis* gynander falls within the mosaic gynander category.

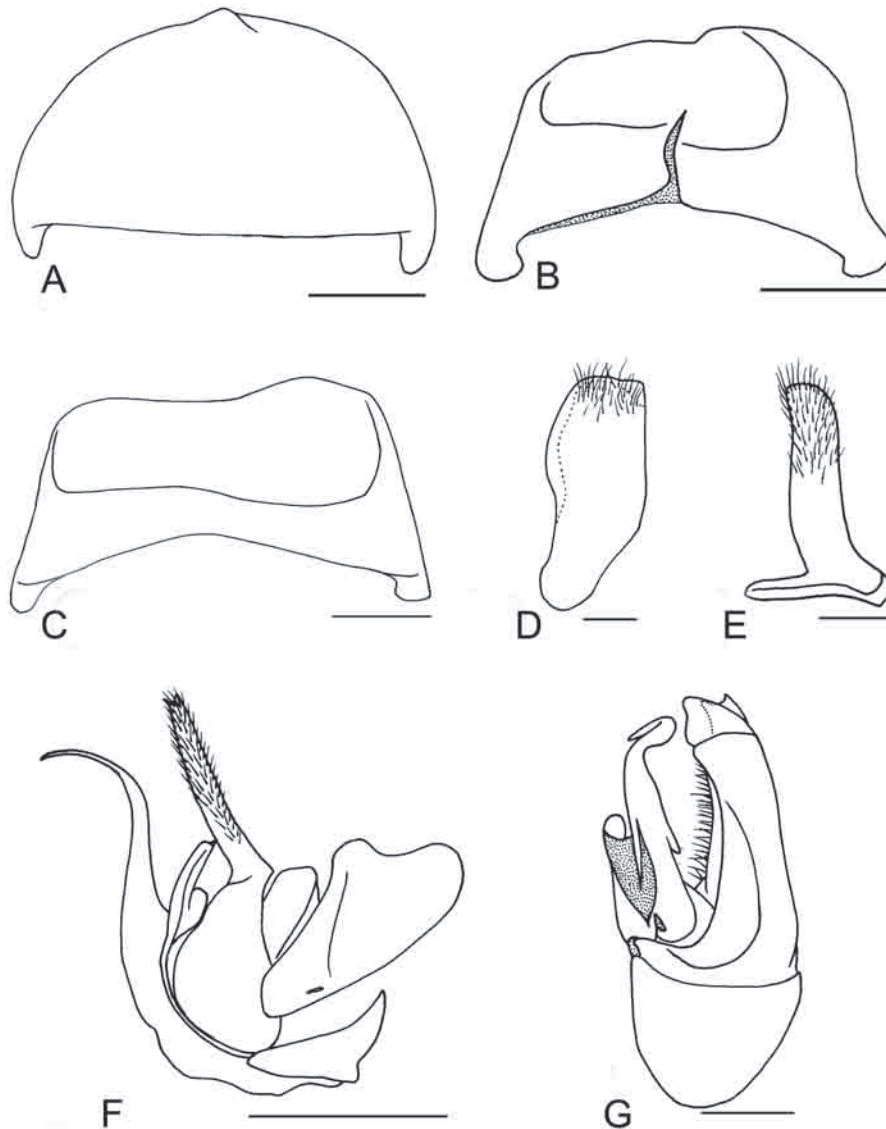


Figure 3

Bombus monticola gynander. **A**, 8th tergum, front view (scale = 1 mm); **B**, 6th sternum, front view (scale = 1 mm); **C**, 7th sternum, front view; **D**, 7th sternum, lateral view (scale = 0.5 mm); **E**, 8th sternum, front view (scale = 1 mm); **F**, right part of genitalia (scale = 1 mm); **G**, left part of genitalia (scale = 0.5 mm).

Table 5. Comparison of characters displayed by both sexes of *Bombus vestalis sorgonis* and *Bombus vestalis vestalis* to those of the gynander.

Character	Female	Male	Gynander of <i>B. v. sorgonis</i>	Gynander of <i>B. v. vestalis</i>
Prosoma				
Mandible	Wide; no <i>barbae mandibularis</i>	Narrow; <i>barbae mandibularis</i> present	Right ♂, left ♀	Both ♂
Labrum	Wide	Narrow	Right half part ♂, left half part ♀	Right half part ♀, left half part ♂
Face	With short setae	With long setae	Right half part ♂, left half part ♀	Right half part ♀, left half part ♂
Vertex	With black setae	With black and yellow setae	Right half part ♂, left half part ♀	Right half part ♂, left half part ♀
Antennae	12 segmented	13 segmented	Right ♂, left ♀	Right ♂, left abnormal
Mesosoma				
Collare	Black	With black and yellow setae	Right half part ♂, left half part ♀	Right half part ♀, left half part ♂
Scutellar	Black	With black and yellow setae	Right half part ♂, left half part ♀	Right half part ♀, left half part ♂
Posterior leg	Basitarsus enlarged	Basitarsus thin	Right ♂, left ♀	Right ♀, left ♂
Metasoma				
Genitalia	Present	Absent	♀	Right part ♂, left part ♂
Sting and sheath lobe	Present	Absent	♀	Right part ♂, left part ♂

Review of the literature on gynandromorphy in Apoidea

A total of 109 reports of gynandromorphy among Apoidea have been described so far in 6 bee families (tab. 6). Analysing the relative proportion of each gynander category found in the literature reveals that transverse gynanders are by far the most frequently reported cases (61 out of 109, i.e. 56%), followed by mosaic gynanders (38 out of 109, i.e. 33%), and by the very few cases of bilateral gynanders (10 out of 109, i.e. 9%).

Discussion

Three major hypotheses have been advanced since the early twentieth century to explain the causes of gynandromorphy, namely (i) embryonic fertilisation (Boveri 1915), (ii) polyspermy (Morgan 1916) and (iii) chromosome elimination (Morgan & Bridges 1919). The validity of these hypotheses has been thoroughly explored experimentally by Rothenbuhler (1958), who investigated the genetic mechanisms driving the rise of gynandromorphy using *Apis mellifera* L. as model species (fig. 4A). Rothenbuhler (1958) reported that a great deal of the gynanders obtained displayed father-inherited, haploid characters on the “male” body parts. These first results supported Morgan’s (1916) early hypothesis of polyspermy as the predominant mechanism causing gynandromorphy to occur. Under this scenario, the fertilised nuclei produce diploid (female) characters, while the second sperm nucleus remain haploid and result in “male” body parts (fig. 4B).

This hypothesis showed its limitations when attempting to explain how other phenotypes could

have been produced, such as gynanders with mother-inherited, haploid characters on the “male” body parts (fig. 4C). The most plausible alternative hypothesis accounting for such phenotypic abnormalities was first proposed by Boveri (1915) and concerned the phenomenon of partial fertilisation, in which the sperm is “delayed from penetrating ooplasm until cleavage commences” (Gordh & Headrick 2001). Resulting from this is the production of an embryo with fertilised nuclei becoming diploid “female” characteristics, whereas unfertilised nuclei become mother-inherited “male” tissues (fig. 4C).

The chromosome elimination hypothesis is supported by the production of specimens showing male and female diploid characters (fig. 4D–E). But Rothenbuhler (1958) remained puzzled about his observations on males displaying diploid characters, as witnessed by the question mark on the illustration of his original paper. At this time CSD and diploid males were well not understood. It is only during the past decade that studies have focused more precisely on diploid male production among Hymenoptera (see e.g. Stouthamer *et al.* 1992; Cook 1993; Duchâteau *et al.* 1994; Cook & Crozier 1995; Zayed & Packer 2001; Cowan & Stahlhut 2004). How diploid males arise is now well known (at least in honeybee): haploid males are CSD hemizygous while diploid males are commonly CSD homozygous (Cook & Crozier 1995). In gynandromorphs showing female and male diploid characters (figs 4D–E), female parts have to be CSD heterozygous while male tissues should be (i) CSD hemizygous or (ii) CSD homozygous. The former hypothesis (i) implies the loss of chromosome bearing CSD and correspond to the chromosome elimination hypothesis (Rothenbuhler 1958; Gordh & Headrick

2001). This process might take place during the stage of zygote cell division, whenever a daughter nucleus loses the chromosome bearing the CSD although the genetic cell contents is double that of all other remaining loci (Fig. 4D). The latter hypothesis (ii) implies mutation and/or inhibition that inactivate or remove part of the CSD allele but not whole chromosome (Fig. 4E). This hypothesis has not yet been proposed to explain gynandromorphism but recent studies show that repression of the CSD transcript effectively results in male traits in honeybee (Beye *et al.* 2003).

In light of the above scenarios for the origin of gynandromorphy, we may formulate hypotheses concerning the developmental pathways leading to the formation of the gynanders observed among wild bees (Tabs. I–VI). First, mosaic gynanders (e.g. presently

described *Dasygoda hirtipes* and *Bombus vestalis vestalis*) can be the immediate outcome of some independent chromosomal aberration, elimination or characteristic of CSD expression within distinct embryonic tissues during the development of the embryo (figs 4D–E). Second, transverse gynander (e.g. presently described *Melitta haemorrhoidalis*, *Anthophora plumipes* and *Bombus vestalis sorgonis*) and bilateral gynander (e.g. presently described *Bombus monticola rondoui*) result from an unique genetic accident. Bilateral gynander could result from any of the proposed developmental pathways (figs 4B–E) while a single alteration of CSD is more likely for transversal gynander (late polyspermy or embryonic fertilisation seem unlikely). Modern molecular techniques such as flow cytometry represent appropriate tools to check the ploidy level of specimen

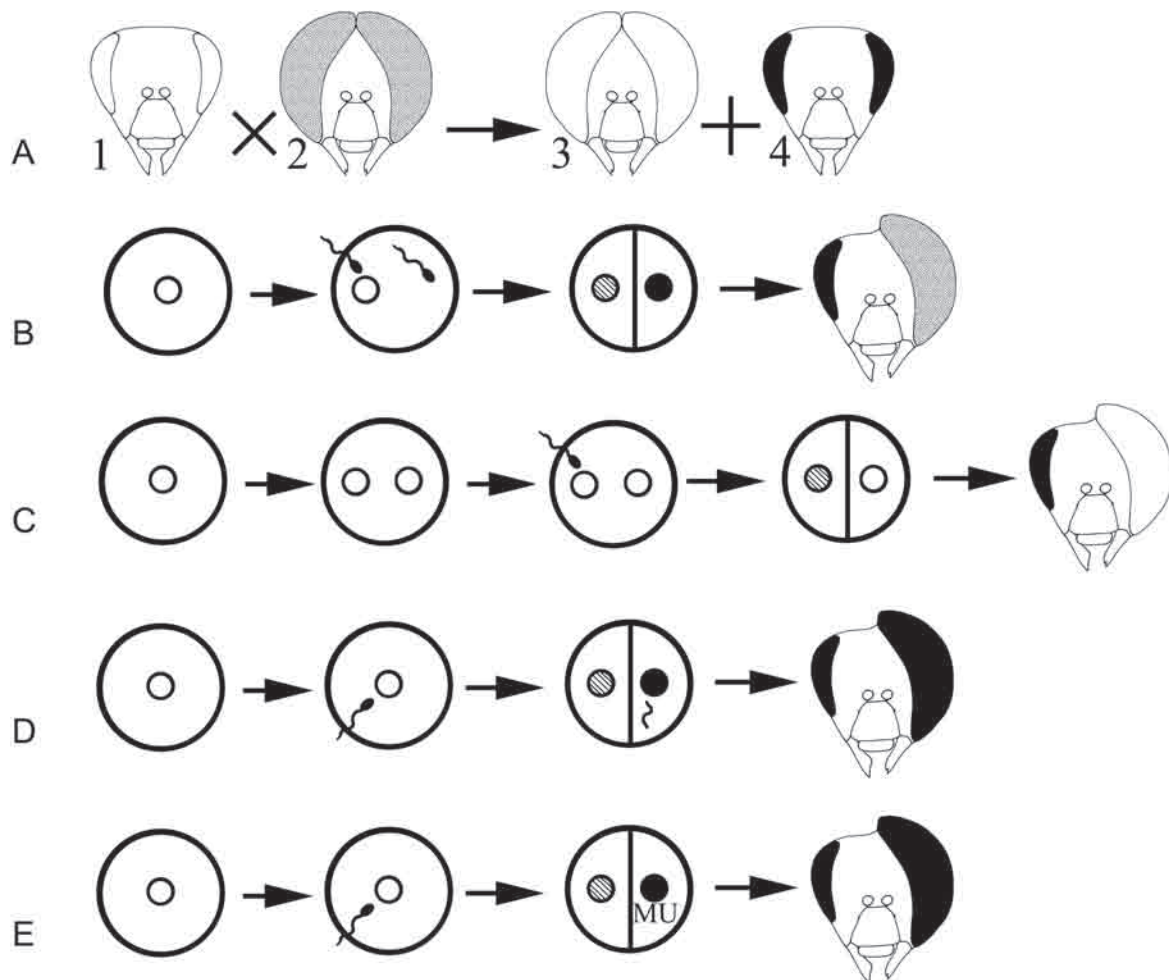


Figure 4

Testing hypotheses of Rothenbuhler (1958). **A**, mating experience (1 = Female ivory eye recessive character; 2 = Drone chartreuse eye recessive character; 3 = Drone ivory eye; 4 = Normal diploid progeny); **B–D**, phenotypes of obtained gynandromorph and hypothesis of origin: **B**, embryonic fertilisation; **C**, polyspermy; **D**, chromosome elimination.

Table 6. Cases of gynandromorphy reported from Apoidea

Species described	Gynander Category ¹	Reference	Species described	Gynander Category ¹	Reference
APIDAE			HALICTIDAE		
<i>Anthophora furcata</i> (Panzer)	Tr	Wolf (1995a)	<i>Dasygoda hirtipes</i> (Fabricius)	Tr, Mo	Wolf (1995a), present study
<i>Bombus fernaldae</i> (Franklin)	Mo	Milliron (1960)	<i>Melitta haemorrhoidalis</i> (Fabricius)	Mo, Tr	Wolf (1985), present study
<i>B. flavifrons</i> Cresson	Mo	Milliron (1962)	HALICTIDAE		
<i>B. lapidarius</i> (L.)	Tr, Mo	Sichel (1858), Stöckhert (1920)	<i>Halictus quadricinctus</i> (Fabricius)	Mo	Saunders (1901)
<i>B. pascuorum</i> (Scopoli)	Bi, 2Tr	Röseler (1962), Laidlaw (1932), Wolf (1993b)	<i>H. sexcinctus</i> (Fabricius)	Tr	Leclercq (1953)
<i>B. pratorum</i> (L.)	Tr	Wolf (1991b)	<i>H. tumulorum</i> (L.)	2 Tr, Mo	Wolf (1995a), Andrewes (1946), Hohndorf (1931)
<i>B. monticola</i> Smith	Bi	Present study	<i>Lasioglossum albipes</i> (Fabricius)	Mo	Nilsson (1987)
<i>B. ruderarius</i> Müller	Mo	Stöckhert (1924)	<i>L. calceatum</i> (Scopoli)	Mo	Plateaux-Quénu & Plateau-Quénu (1982)
<i>B. wurflenii</i> Radoskowski	Bi, Mo	Ritsema (1881), Stöckhert (1924)	<i>L. eurygnathus</i> Bluthgen	Mo	Popov (1937)
<i>Epeolus julliani</i> Pérez	Tr	Wolf (2000)	<i>L. fulvicorne</i> (Kirby)	Tr	Wolf (1987a)
<i>Partamona cupira</i> Smith	Tr	Schwarz (1929)	<i>L. lativentre</i> (Schenck)	Tr	Stöckhert (1924)
<i>Nomada fucata</i> Panzer	Mo	Schenk (1871)	<i>L. lissonotum</i> (Noskiewicz)	Tr	Wolf (1990)
<i>Nomada</i> sp.	Tr	Tsuneki (1975)	<i>L. malachurum</i> (Kirby)	Mo	Stöckhert (1924)
<i>N. laevilabris</i> Schmiedecknecht	Tr	Pérez-Iñigo Mora (1982)	<i>L. morio</i> (Fabricius)	Tr	Wolf (1986)
<i>Thyreus redaluctus</i> ? Cockerell	Bi	Engel (2007)	<i>Nomioides minutissimus</i> (Rossi)	Mo	Wolf (1997)
<i>Xylocopa brasilianorum</i> (L.)	Bi	Benoist & Berland (1935)	<i>Sphescodes albilabris</i> (Fabricius)	Mo	Wolf (1994a)
<i>X. confusa</i> Pérez	Tr	Handschin (1935)	<i>S. geofrellus</i> (Kirby)	Tr	Wolf (1987b)
<i>X. fenestrata</i> (Fabricius)	Mo	Maa (1940)	<i>S. niger</i> Hagens	Tr	Wolf (1991b)
<i>X. mendozana</i> Enderlein	Bi	Enderlein (1913)	<i>S. reticulatus</i> Thomson	Tr	Stöckhert (1924)
<i>X. micans</i> Lepeletier	Tr	Maidl (1912)	<i>S. rufiventris</i> (Panzer)	Tr	Wolf (1987b)
<i>X. nigrita</i> (Fabricius)	Tr	Carcasson (1965)	MEGACHILIDAE		
<i>X. ordinaria</i> Smith	Mo	Enderlein (1913)	<i>Anthidium oblongatum</i> Latreille	Tr	Stöckhert (1924)
ANDRENIDAE			<i>A. strigatum</i> (Panzer)	Mo	Wolf (1998a)
<i>Andrena barbilabris</i> (Kirby)	Tr	Wolf (1993b)	<i>Chalicodoma parietina</i> (Geoffroy)	Bi	Bischoff & Ulrich (1929)
<i>A. bimaculata</i> (Kirby)	Mo	Perkins (1914)	<i>Coelioxys inermis</i> (Kirby)	Tr	Wolf (1999)
<i>A. convexuscula</i> Kirby	Tr	Schenk (1871)	<i>C. rufescens</i> Lepeletier	Mo	Noskiewicz (1923)
<i>A. haemorrhoea</i> (Fabricius)	Tr	Wolf (1989)	<i>Dianthidium ulkei</i> (Cresson)	Tr	Schwarz (1926)
<i>A. fasciata</i> Wesm.	Tr	Schenk (1871)	<i>D. sayi</i> Cockerell	Tr	Hicks (1926)
<i>A. flavipes</i> Panzer	Tr	Perkins (1914)	<i>Megachile angelarum</i> Cockerell	Mo	Mitchell (1941)
<i>A. fucata</i> Smith	Tr	Loken (1967)	<i>M. bertonii</i> Schrottky	Tr	Mitchell (1929)
<i>A. fulva</i> (Müller)	2 Tr	Wolf (1990, 1993a)	<i>M. chapadiana</i> Mitchell	Mo	Mitchell (1929)
<i>A. helvola</i> (L.)	Tr, Mo	Schenk (1871), Celary & Wisniewski (2001)	<i>M. chrysopidia</i> Smith	Mo	Rayment (1935)
<i>A. humilis</i> Imhoff	Tr, Tr	Wolf (1995b), Wolf (1994b)	<i>M. curvipes</i> Smith	Mo	Mitchell (1941)
<i>A. potentillae</i> Panzer	Tr	Wolf (1982)	<i>M. deserta</i> Cockerell	Tr	Cockerell (1911)
<i>A. porterae</i> Cockerell	Mo	Linsley (1937)	<i>M. latimanus</i> Say	Mo	Mitchell (1932)
<i>A. praecox</i> (Scopoli)	Tr	Wolf (1998c)	<i>M. cf. leachella</i> Curtis	Tr	Wolf (1998d)
COLLETIDAE			<i>M. gemula</i> Cresson	Tr	Mitchell (1929)
<i>Colletes cunicularius</i> (L.)	Bi	O'Toole (1989)	<i>M. maritima</i> (Kirby)	Tr	Wolf (1993a)
<i>Hylaeus albofasciata</i> Friese	Tr	Stöckhert (1924)	<i>M. onobrychidis</i> Cockerell	Mo	Mitchell (1941)
<i>H. brevicornis</i> Nylander	Tr	Morice (1915)	<i>M. parallela</i> Smith	2 Mo	Mitchell (1929, 1941)
<i>H. minuta</i> (Fabricius)	Tr	Noskiewicz (1923)	<i>M. perihirta</i> Cockerell	Mo	Mitchell (1929)
<i>Euryglossa</i> sp.	Tr	Exley (1976)	<i>M. pilidens</i> Alken	Tr	Wolf (1998b)
MELITTIDAE			<i>M. rotundata</i> (Fabricius)	2Tr, Bi	Akre <i>et al.</i> (1982), Gerber & Akre (1969)
			<i>M. subrixactor</i> Cockerell	Tr	Cockerell (1918)
			<i>M. tapytensis</i> Mitchell	Tr	Mitchell (1929)

Table 6. (continued) Cases of gynandromorphy reported from Apoidea.

Species described	Gynander Category ¹	Reference
<i>M. uniformis</i> Mitchell	Tr	Mitchell (1929)
<i>M. vidua</i> Smith	2 Mo	Mitchell (1929)
<i>M. willughbiella</i> (Kirby)	Bi, Tr	Benno (1948), Stenton (1909)
<i>Megachile</i> sp.	Tr	Mitchell (1929)
<i>Osmia aurulenta</i> (Panzer)	Mo	Wolf (1991a)
<i>O. bicolor</i> (Schrank)	Mo	Wolf (1990)
<i>O. caerulescens</i> (L.)	Mo	Benno (1948)
<i>O. pentstemonis</i> Cockerell	Mo	Sandhouse (1923)
<i>O. rufa</i> (L.)	Tr	Noskiewicz (1923)
<i>Trachusa byssina</i> (Panzer)	Tr	Wolf (1992)

¹ Bi = bilateral gynander; Tr = transversal gynander; Mo = mosaic gynander.

tissues. This approach would allow discriminating between the process of chromosome elimination on the one hand (where all tissues are expected to be diploid), and alternative processes such as embryonic or polyspermic fertilisation on the other (where tissues can be diploid or haploid). The main limiting factor to run this method is the necessity of applying it on fresh specimens.

Observations of the “female” behaviour of two newly described gynanders provide additional insights on how such teratological individuals behave under natural conditions. The observed gynanders could be considered as originally female like most of described gynanders (Wcislo *et al.* 2004). These two cases are the first behavioural notes that have ever been published on the behaviour of wild gynander bees under natural conditions.

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