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New cases of mosaic gynandromorphy in *Habropoda laboriosa* (Apidae: Anthophorini) and *Melissodes bimaculatus* (Apidae: Eucerini)

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Abstract. We describe the first documented cases of gynandromorphy in the specialist digger bee *Habropoda laboriosa* (Fabricius) (Apidae: Anthophorini) and in the longhorn bee *Melissodes bimaculatus* (Lepeletier) (Apidae: Eucerini) from specimens collected in North Carolina and Georgia, USA. Both specimens display mosaic gynandromorphy, appearing predominantly female with patches of pale-yellow male coloration on the clypeus. These records represent the first reported case of gynandromorphy in *Habropoda* Latreille and the fifth reported case in *Melissodes* Smith.

INTRODUCTION

Gynandromorphy is a widespread phenomenon in arthropods in which genetically chimeric individuals display both male and female characteristics simultaneously (Narita *et al.*, 2010). Gynandromorphs possess distinct male and female tissues, whereas intersex individuals are genetically uniform but display a mixture of phenotypic sexual characteristics (Gorman & Best, 2025). Gynandromorphs can be classified into three categories: 1) bilateral individuals with equal and symmetric female and male sex characters; 2) transverse individuals in which sex traits are distributed in two asymmetrical parts; and 3) mosaic individuals with a random distribution of female and male features across the body (Michez *et al.*, 2009). Beyond their inherent novelty, these specimens can yield valuable insights into the developmental processes that facilitate the evolution of new phenotypes in social insects (Yang & Abouheif, 2011).

Gynandromorphy has been previously observed in at least 165 bee species worldwide, spanning six families and 45 genera, with most specimens belonging to either Apidae (~37%) or Megachilidae (~31%) (Gorman & Best, 2025). Herein, we describe the first documented cases of mosaic gynandromorphy in the specialist digger bee *Habropoda laboriosa* (Fabricius) (Apidae: Anthophorini) and in the longhorn bee *Melissodes bimaculatus* (Lepeletier) (Apidae: Eucerini). These specimens represent

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the first reported case of gynandromorphy in *Habropoda* Latreille and only the fifth reported case in *Melissodes* Smith (Cockerell, 1906; Campbell *et al.*, 2024). Other reported cases of gynandromorphy in the tribe Anthophorini include transverse specimens of *Anthophora furcata* (Panzer) (Wolf, 1995) and *A. plumipes* (Pallas) (Michez *et al.*, 2009). Four previously reported *Melissodes* specimens (two individuals each of *M. communis* Cresson and *M. trinodis* Robertson) were all mosaic gynandromorphs (Cockerell, 1906; Campbell *et al.*, 2024).

Habropoda laboriosa is a widespread oligolectic pollinator of blueberries (*Vaccinium* L.; Ericaceae) found throughout the United States of America and southern Canada east of the Mississippi River (Cane & Payne, 1988; Ascher & Pickering, 2026). This vernal species is solitary, ground-nesting, and univoltine, with adults primarily active from March to May during blueberry bloom (Cane, 1994; Ascher & Pickering, 2026). *Melissodes bimaculatus* is another solitary, ground-nesting, univoltine species, with a widespread distribution throughout the United States and northern Mexico (Giulian *et al.*, 2024; Ascher & Pickering, 2026). These bees nest gregariously in bare soil and have been recorded visiting numerous plant taxa during their summer flight season (ranging from May to October), including important commercial crops in the families Cucurbitaceae and Malvaceae (Giulian *et al.*, 2024; Trimm, 2024). As in many aculeate Hymenoptera, males of both *H. laboriosa* and *M. bimaculatus* can be recognized by elongated antennae and distinct light-colored integumental markings on the clypeus (Michener, 2013; Ascher & Pickering, 2026). By documenting the first records of gynandromorphy in these two species, we contribute to the growing body of literature on gynandromorphy in bees and help further advance our understanding of the mechanisms underlying hymenopteran sex determination.

MATERIAL AND METHODS

The *H. laboriosa* gynandromorph specimen was collected with an aerial net on the edge of a suburban forest fragment in Cumberland County, North Carolina, USA, near the town of Hope Mills (34.978252, –79.001568) on 10 March 2026. Cumberland County is located within the Carolina Sandhills ecoregion, an area known for its acidic sandy soils, fire-maintained longleaf pine (*Pinus palustris* Mill.) savannas, and high vascular plant diversity (Gilliam *et al.*, 2006; Weakley, 2022). The *M. bimaculatus* gynandromorph was collected in a blue vane trap (SpringStar Inc.) on 7 August 2023 in a privately owned early post-establishment loblolly pine (*Pinus taeda* L.) stand primarily managed for forest products in Hancock County, Georgia, USA. This specimen was collected as part of a larger study on the indirect effects of forest herbicide applications on wild bee communities in the Piedmont ecoregion of Georgia (Briggs *et al.*, 2024).

Both gynandromorphs were identified with dichotomous keys (*e.g.*, Mitchell, 1962; Ascher & Pickering, 2026), and specimen descriptions follow the morphological terminology of Michener (2007). We examined, measured, and photographed the external morphology of each specimen using a Leica Microsystems Ivesta 3 Stereo Microscope with an Integrated Camera. Typical female and male conspecifics were also photographed for visual comparison (Figs. 1–12). We report the following morphological measurements (in mm) for each gynandromorph: total body length (tip of the head to the apex of the metasoma), head width (widest point across the eyes), intertegular distance (ITD; width between the inner borders of the tegulae), metasomal width (widest point across the third tergum), scape-plus-pedicel length, and flagellum length (Table 1). We also report mean measurements from 10 female and 10 male conspecifics of each species as baselines for comparisons. Both gynandromorph specimens are housed in the Gandhi Forest Entomology Laboratory insect collection at the D.B. Warnell School of Forestry and Natural Resources, University of Georgia (Athens, Georgia, USA).

Table 1. Morphological measurements of gynandromorphs (GYN) and conspecific females and males (mean ± SE; n = 10 per sex). Antennal measurements for the *Melissodes bimaculatus* gynandromorph are given separately for the female-like right side and male-like left side. ITD, intertegular distance.

Measurement (mm)	*Habropoda laboriosa*			*Melissodes bimaculatus*		
	♀	♂	**GYN**	♀	♂	**GYN**
Total body length	16.19 ± 0.22	12.88 ± 0.20	14.25	13.02 ± 0.24	11.39 ± 0.23	12.68
Head width	5.38 ± 0.03	4.82 ± 0.04	5.35	4.58 ± 0.05	4.11 ± 0.05	4.32
ITD	3.31 ± 0.05	2.93 ± 0.09	3.36	3.38 ± 0.06	3.02 ± 0.06	3.16
Metasomal width	6.17 ± 0.08	5.87 ± 0.15	6.56	5.31 ± 0.12	4.50 ± 0.12	4.88
Flagellum length	4.20 ± 0.05	5.74 ± 0.13	4.30	3.41 ± 0.07	7.26 ± 0.10	3.40 ♀, 7.81 ♂
Scape-plus-pedicel length	1.33 ± 0.02	1.28 ± 0.04	1.28	0.89 ± 0.03	0.87 ± 0.03	0.90 ♀, 0.88 ♂

RESULTS

Habropoda laboriosa (Fabricius)
Gynandromorph
(Figs. 3–4)

Description: Mosaic gynandromorph, appearing predominantly female except for transverse pale-yellow band on apex of clypeus (Fig. 3; Table 1).

Head: Asymmetric mix of male and female traits. Antennae unelongate and female-like, with 10 flagellomeres. Facial integument mostly black, as in females, except for thin band of pale-yellow male coloration on lower clypeal margin. All-black pubescence on mandibles, labrum, clypeus, frons, paraocular area, and gena, as typical of females.

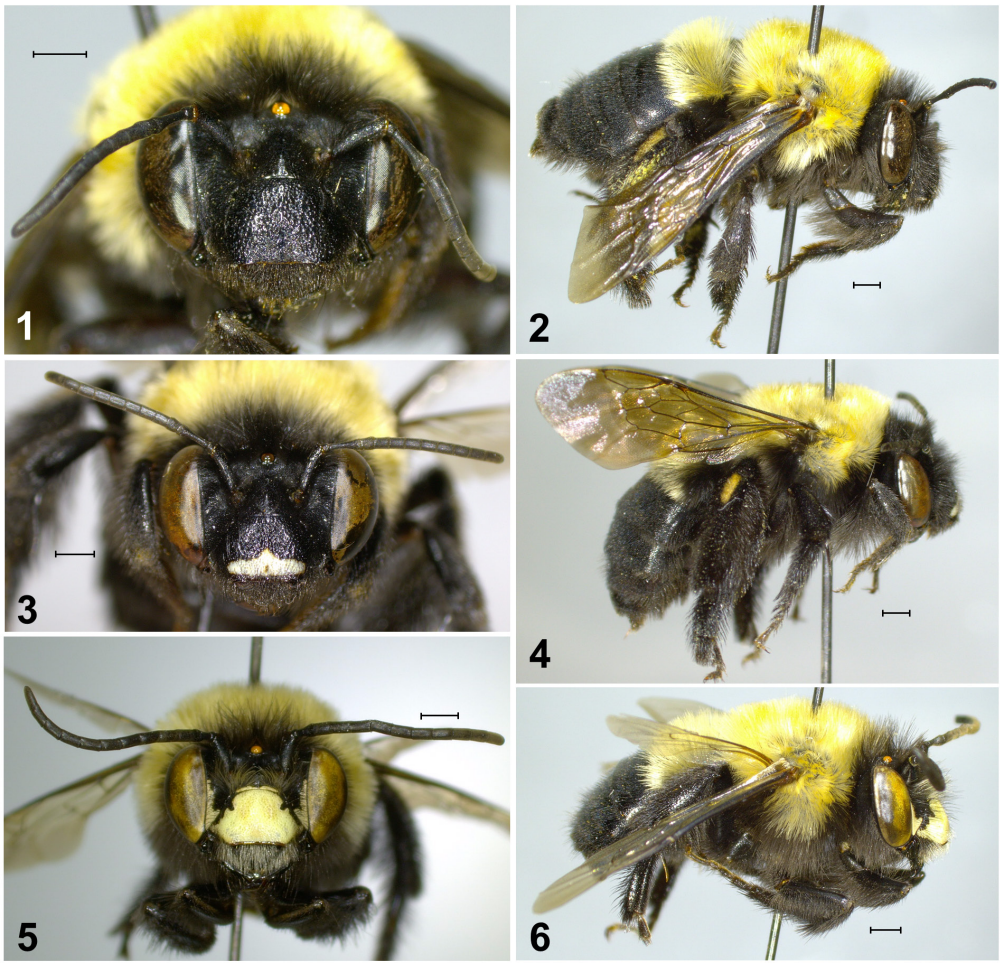
Mesosoma and metasoma: Symmetric and fully female in appearance, with six exposed terga/sterna and visible stinger. Hind legs female-like, with rounded basitibial plates and distinct elongated patches of pale pubescence immediately beyond plates. Bushy black scopal hairs present on hind tibia and basitarsus. See Mitchell (1962) for full description of female morphology.

Melissodes bimaculatus (Lepeletier)
Gynandromorph
(Figs. 9–10)

Description: Mosaic gynandromorph, appearing predominantly female save for partial bilateral split of female and male characteristics on head (Fig. 9; Table 1).

Head: Bilaterally asymmetrical. Right side with typical female features, as follows: black integument on clypeus and labrum; mandible dark; antenna black and unelongate, with 10 flagellomeres; all-black pubescence on mandibles, labrum, clypeus, frons, paraocular area, and gena. Left side with typical male features, as follows: bright yellow integument on clypeus and labrum; mandible dark, with testaceous coloration towards apex; antenna elongate, with 11 flagellomeres, as in other male Eucerini; pubescence on mandibles, labrum, and gena mostly black; long silvery-white setae on clypeus, frons, and paraocular area.

Mesosoma and metasoma: Symmetric and fully female in appearance, with six

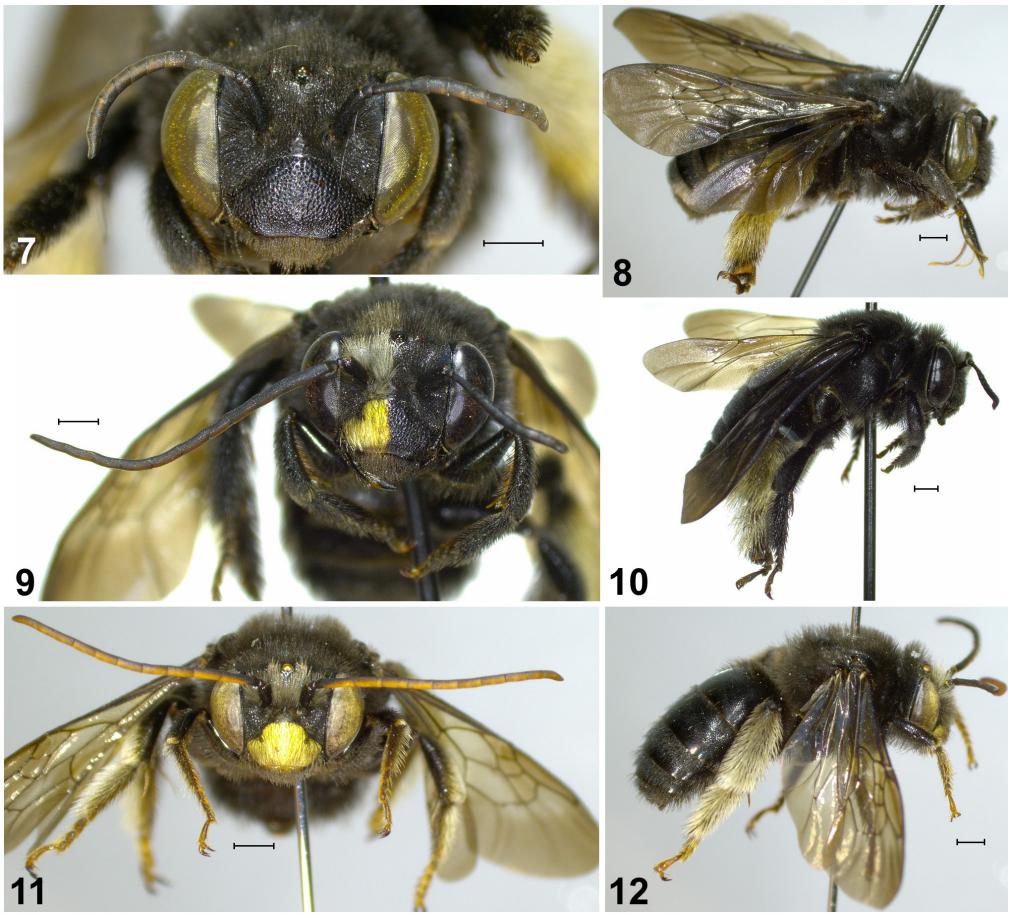


Figures 1–6. *Habropoda laboriosa*. **1.** Female, frontal view. **2.** Female, lateral view. **3.** Gynandromorph, frontal view. **4.** Gynandromorph, lateral view. **5.** Male, frontal view. **6.** Male, lateral view. Scale bars = 1 mm.

exposed terga/sterna and two apical patches of white pubescence on fourth tergum, as typical in females. Plumose white scopal hairs present on hind tibia and basitarsus. See Mitchell (1962) for full description of female morphology.

DISCUSSION

We report two new mosaic gynandromorph specimens of *H. laboriosa* and *M. bimaculatus*, representing the first reported case of gynandromorphy in *Habropoda* and only the fifth reported case in *Melissodes* (Cockerell, 1906; Campbell *et al.*, 2024; Gorman & Best, 2025). It appears that gynandromorphy may be rare in the tribes Anthophorini and Eucerini in comparison to other bee groups, with only two previously reported anthophorine specimens in *Anthophora* (Wolf, 1995; Michez *et al.*, 2009) and six other eucerine specimens belonging to the genera *Alloscirtetica* Holmberg (Urban, 1999), *Eucera* Scopoli (Dalla Torre & Friese, 1899; Masuda, 1940; Jones *et al.*, 2021), and *Florilegus* Robertson (Parys *et al.*, 2022). It is unclear whether this rarity stems from differences in rates of gynandromorphy in these taxa or sampling biases, although both tribes are



Figures 7–12. *Melissodes bimaculatus*. **7.** Female, frontal view. **8.** Female, lateral view. **9.** Gynandromorph, frontal view. **10.** Gynandromorph, lateral view. **11.** Male, frontal view. **12.** Male, lateral view. Scale bars = 1 mm.

widely distributed throughout North America and *Melissodes* species are frequently collected in regional bee surveys (Campbell *et al.*, 2024; Ascher & Pickering, 2026).

Bees exhibit a haplodiploid sex-determination system, in which females develop from fertilized diploid eggs and males originate from unfertilized haploid eggs (Heimpel & de Boer, 2008). Sex-determination errors such as gynandromorphy have multiple proposed genetic causes, including various developmental mechanisms such as chromosome elimination, egg binucleation, atypical fertilization, or polyspermy (Michez *et al.*, 2009; Narita *et al.*, 2010). Bilateral, transverse, and mosaic gynandromorphy may stem from different developmental mechanisms, with mosaic gynandromorphs potentially arising from independent chromosomal mutations within distinct tissues during embryonic development (Michez *et al.*, 2009). Sommaggio *et al.* (2021) suggested that gynandromorphy may instead be epigenetic, with mosaic sexual phenotypes explained by defects in the maintenance of regulatory signals that control sex differentiation of single-cell lineages. Future studies are needed to develop molecular approaches that allow for the characterization of single-cell ploidy levels via chromosome count or allelic zygosity (in which heterozygous implies diploidy) in both fresh and preserved gynandromorph tissues (Jones *et al.*, 2021; Gorman & Best,

2025; Dabak *et al.*, 2026). Such future studies will further our understanding of sex determination and phenotypic expression in bees and may help clarify the mechanisms underlying gynandromorphy.

Wcislo *et al.* (2004) found that gynandromorph tissues occur most frequently on the head (78% of individuals), with the majority of gynandromorphs appearing predominantly female, as in our *H. laboriosa* and *M. bimaculatus* specimens. Among *Xylocopa* Latreille species, Almada *et al.* (2022) reported that gynandromorph tissues occur most frequently in the mesosoma, with most specimens displaying a random mixture of female and male features in affected tagmata. Morphological measurements of both gynandromorphs were more similar to those of conspecific females (Table 1), but we did not dissect the genitalia of our new records to preserve the specimens, so the status of their reproductive organs is unknown. Prior to capture, the *H. laboriosa* specimen was observed visiting *Vaccinium elliottii* Chapm. (Ericaceae) flowers and displaying foraging behavior typical of females. Given the specimen's fully developed hind-leg scopa and visible stinger, the gynandromorph may have been reproductively functional. No behavioral observations were possible for the *M. bimaculatus* specimen since it was passively trapped. Some previous studies have observed gynandromorphs foraging, nest-building, and engaging in female-like behaviors (*e.g.*, Wcislo *et al.*, 2004; Michez *et al.*, 2009; Álvarez *et al.*, 2019; Jones *et al.*, 2021), while others have observed gynandromorphs exhibiting novel behavior patterns intermediate between the sexes (*e.g.*, Ugajin *et al.*, 2016; Matsuo *et al.*, 2018; Krichilsky *et al.*, 2020). Many gynandromorph specimens are first identified in museum collections, with published descriptions based solely on their external morphology (*e.g.*, Lucia & Gonzalez, 2013; Zama & Coelho, 2017). Although live observations of gynandromorphs are exceedingly rare, continued research and reporting are essential for understanding how gynandromorphy may influence bee behavior, reproductive biology, and physiological function (Krichilsky *et al.*, 2020; Lightburn *et al.*, 2022).

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