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BRIEF COMMUNICATION

The first case of gynandromorphy in *Centris pallida* (Hymenoptera: Apidae: Centridini)

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Abstract. A case of gynandromorphy is reported for the first time for *Centris pallida* Fox, a bee species found predominantly in the deserts of the southwestern United States and northern Mexico. This specimen marks only the second report of a gynandromorph within the tribe of oil-collecting bees, Centridini, and the first *Centris* Fabricius. The specimen exhibits mosaic gynandromorphy, with male and female characteristics randomly distributed throughout the body. Males of *C. pallida* are morphologically and behaviorally dimorphic (a large and a small male morph), and the male characteristics of the gynandromorph are more similar to the large male morph, which is also most similar in head width to the specimen.

INTRODUCTION

Gynandromorphy, a phenomenon found in nearly all arthropod orders, occurs when individuals display secondary sex characteristics of both sexes simultaneously (Narita *et al.*, 2010). Gynandromorphs can be categorized into three main types: mosaic, transverse, and bilateral. Mosaic gynandromorphy is described by the random distribution of sex characters throughout the body, transverse is described as the distribution of sex characters into two asymmetrical parts (typically perpendicular to the axis of symmetry), and bilateral is described as the symmetrical and equal distribution of sex characters (Michez *et al.*, 2009).

Gynandromorphy has been recorded within six of the seven bee families (all but Stenotritidae, the smallest bee family restricted geographically to Australia), showing this phenomenon to be widespread among Apoidea (Michez *et al.*, 2009). Gynandromorphy is most common in the Holarctic Region (79% of recorded cases) and within the genera *Megachile* Latreille (Megachilidae) and *Andrena* Fabricius (Andrenidae), though sampling bias in the Holarctic and taxa may account for their prevalence

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among reported cases of gynandromorphy (Michez *et al.*, 2009; Lucia & Gonzalez, 2013).

Despite numerous reports of gynandromorphs in other tribes of the family Apidae, particularly Xylocopini and Bombini, the first gynandromorph in the oil-collecting bee tribe Centridini was reported by Alvarez *et al.* (2019). The specimen was a bilateral gynandromorph of the species *Epicharis (Epicharitides) iheringi* Friese in a cerrado habitat within the Parque Nacional de Brasília in Brazil. Here, I report the second gynandromorph of this tribe, a mosaic gynandromorph of *Centris pallida* Fox from a nesting aggregation in the Sonoran Desert in Arizona, USA. Notably, *C. pallida* males utilize alternative reproductive tactics with behavioral and morphological dimorphism. Large males with light grey thorax coloration fight to dig up emerging females (and males) as they emerge from their underground brood cells. Small males, with darker brown thorax coloration more similar to the females, hover at vegetation searching for unmated females flying away from their natal nests (Alcock *et al.*, 1977). This variation in male morphology makes the case of this mosaic gynandromorph, with female and large male characteristics, particularly interesting.

MATERIAL AND METHODS

The gynandromorph of *C. pallida* was collected at Tumamoc Hill in Tucson, Arizona, near Silvercroft Wash on 3 May 2020 (N32.2232, W111.0091), where aggregations of this species have been studied since 2016. The species ranges from New Mexico in the east to southwest California in the west, south through Mexico and to a northern range limit of Utah and Nevada (Snelling, 1974, 1984; Ascher & Pickering, 2020).

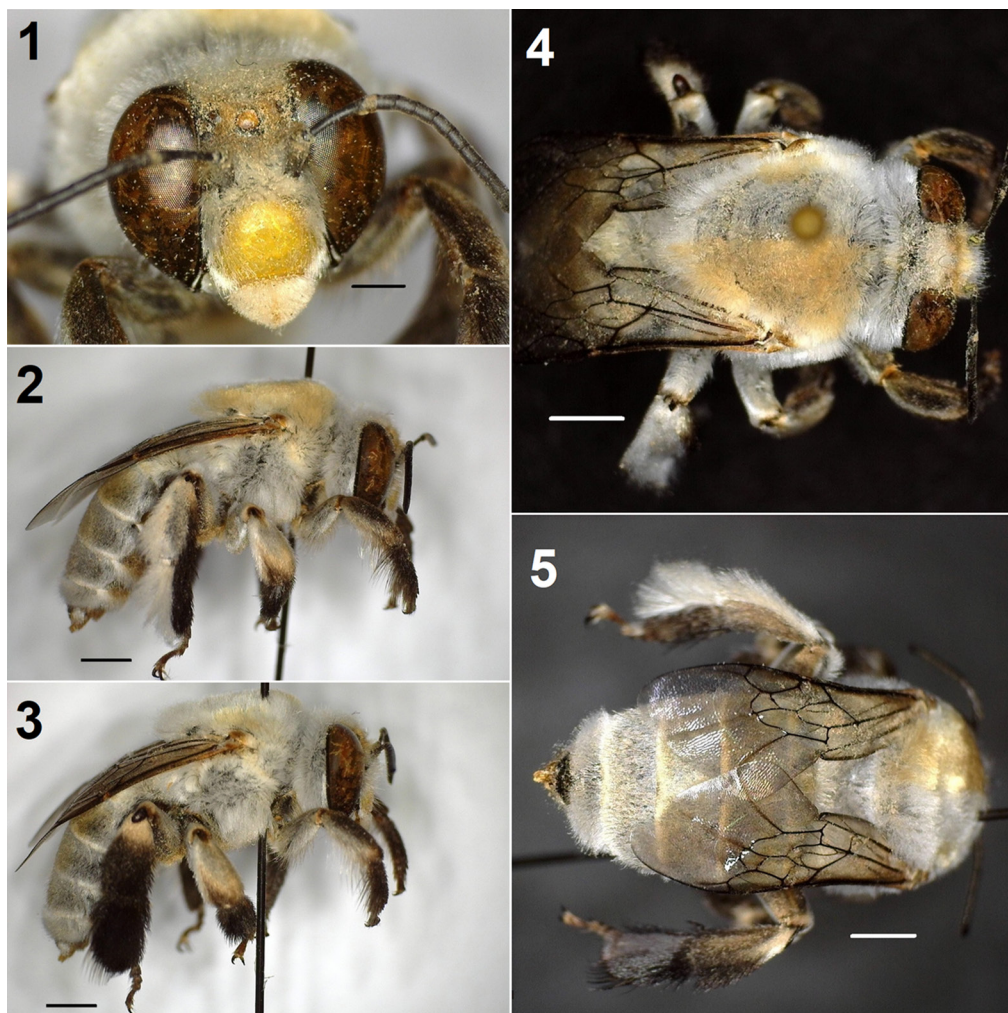
I followed morphological terminology of Michener (2007) and I photographed morphological features using a DinoLite AM4915ZT. I took measurements three times with Husky model 1467H digital calipers (accuracy 0.02 mm) and averaged them; all values are given to the nearest 0.1 millimeter. I measured total body length, mesosoma width, and metasoma width as in Alvarez *et al.* (2019). I measured head width at the widest point across the eyes, while I measured head length (height) from the vertex to the bottom of the clypeus. I used several male and female specimens I collected between 2018 and 2020, at field sites throughout Arizona, to compare the morphological variation between the gynandromorph and the normal male/female phenotypes. As males of this species are morphologically dimorphic based on body size and coloration (Alcock *et al.*, 1977), I compared the gynandromorph to male specimens most similar in head width, which corresponds to the large male morph (typical head widths range from 5.3–6.0 mm). The gynandromorph specimen is deposited in the University of Arizona Insect Collection.

RESULTS

Centris (Paracentris) pallida Fox Gynandromorph (Figs. 1–10)

DESCRIPTION: Body length 8.3 mm; head height 3.9 mm (w/labrum: 5.0 mm), head width 5.4 mm; mesosoma width 6.2 mm; metasoma width 5.9 mm.

Head. General appearance male-like; 11 flagellomeres on each antenna and clypeus yellow (Fig. 1). Pubescence mostly white on labrum, vertex, and parocular area,



Figures 1–5. Gynandromorph of *Centris pallida* Fox. **1.** Head in frontal view. **2.** Left side of body in lateral view. **3.** Right side of body in lateral view. **4.** Mesosoma and head in dorsal view (image reflected horizontally – pin is in right side). **5.** Metasoma in dorsal view. Scale = 2 mm except 1 mm in figure 1.

sides of head pale grey, pubescence on frons darker brown or tan around ocelli; no distinct morphological differences between sides (Figs. 1–4).

Mesosoma. Mix of male and female features. Bilateral split in pubescence coloration on the mesoscutum and mesoscutellum, right side generally pale in coloration like large male morph, except for a tan spot near tegula, left side pubescence tan, more similar to a small morph male or female in coloration (Figs. 2–4). Fore and middle legs generally female in appearance. Hind right leg female, hind left leg a mix of male and female features (Figs. 6–9). Medial side of leg appears female – darker colored, bushy scopal hairs on tibia and basitarsus (Fig 7). Lateral side of leg appears male – pubescence light grey and less dense in appearance on tibia and basitarsus (Fig. 8). Hind right leg with smaller than normal (for females) basitibial plate, centered towards the medial side of the tibia (Figs. 2, 4).

Metasoma. Not strongly sexually dimorphic in the first four terga/sterna, grey-



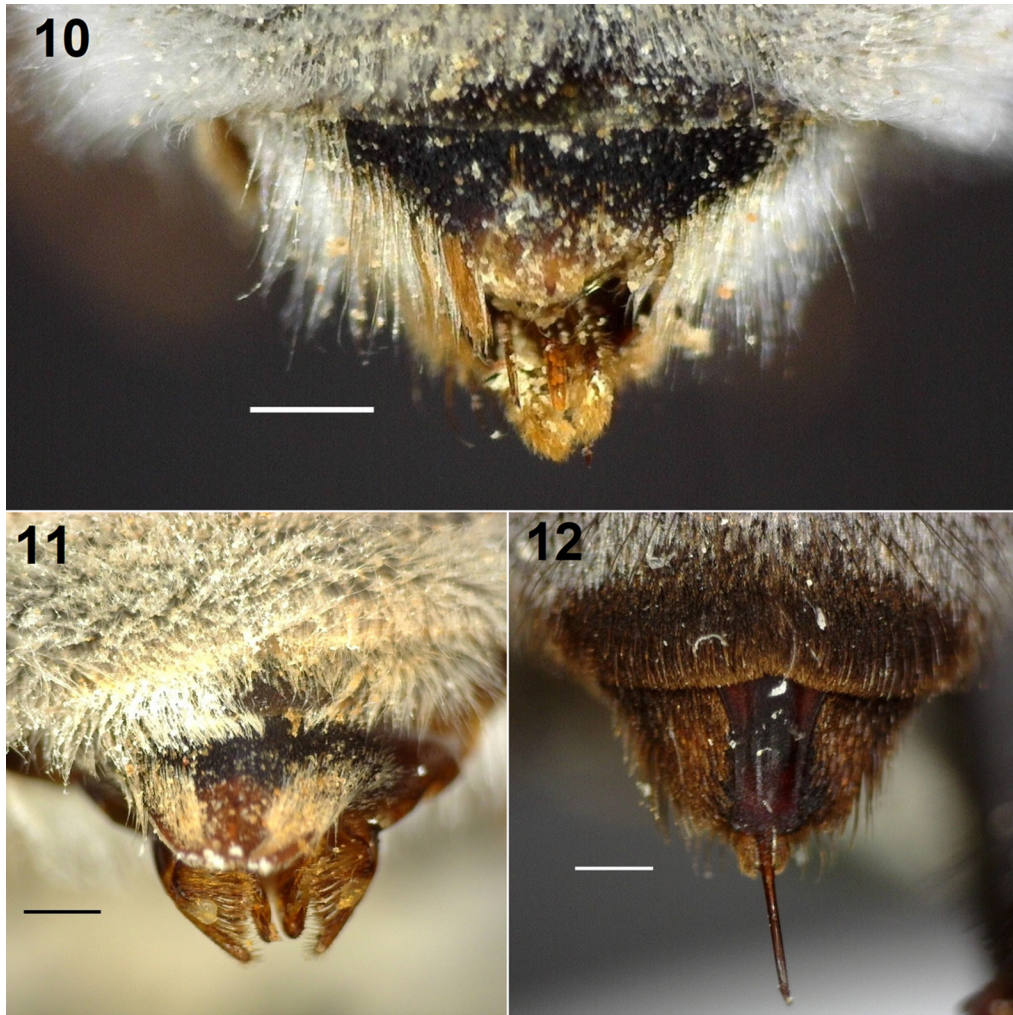
Figure 6–9. Hind legs of gynandromorph of *Centris pallida* Fox. **6.** Left hind leg in lateral view. **7.** Left hind leg in medial view. **8.** Right hind leg in medial view. **9.** Right hind leg in lateral view. Left hind leg shows partial female, partial male characteristics; right hind leg shows all female characteristics. Scale = 1 mm for all figures.

ish-brown dorsally, with overall shape, and ventral setae density pattern female-like. The specimen has seven exposed terga as in males (terga 1–5 easily visible in figure 5, terga 6 and 7 most visible in figure 10); terga 5 and 6 more closely match a male morphology, missing the heavily raised pygidial plate, and darker pygidial and prepygidial fimbria, of a female (Figs. 10–12). The genitalia appear to be female; on T6, there is a sting that may only be partially developed (recessed; Fig. 10) along with sting sheath (clearly visible surrounding the female sting in figure 12), however these could also be weakly developed male gonostyli (see figure 11 for comparison to a large male morph). To preserve the integrity of the specimen, dissection of the genitalia was not possible.

MATERIAL EXAMINED: The specimen is at the University of Arizona Insect Collection, Number UAIC1052985.

DISCUSSION

This is the first report of gynandromorphy in *Centris*, and only the second report within the Centridini (Alvarez *et al.*, 2019). With this new report, over 140 species of Apoidea from six of seven families have shown evidence of gynandromorphy (Michez *et al.*, 2009). Within the Apidae, to which the genus *Centris* belongs, records of gynandromorphs exist for the following tribes: Anthophorini, Apini, Bombini, Centridini, Epeolini, Eucerini, Euglossini, Melictini, Meliponini, Nomadini, and Xylocopini, thus covering a great diversity of life history strategies and large geographic areas (Urban, 1999; Wcislo *et al.*, 2004; Michez *et al.*, 2009; Hinojosa-Díaz *et al.*, 2012; Lucia & González, 2013; Alvarez *et al.*, 2014; Le Féon *et al.*, 2016; Onuferko, 2018).



Figures 10–12. Apex of metasoma of *Centris pallida* Fox. **10.** Gynandromorph. **11.** Large morph male. **12.** Female. Scale = 0.5 mm.

Of the cases in Apoidea compiled by Michez *et al.* (2009), 56% are transverse, 33% are mosaic, and 9% are bilateral gynandromorphs. Gynandromorphic traits occur with relatively equal frequencies across main body regions (head, mesosoma, metasoma: Wisclo *et al.*, 2004). The specimen of *C. pallida* is relatively rare because of its mosaic distribution of sex characteristics: a fully male head, bilaterally split thorax coloration, majority female legs (except the left hind leg, which shows both male and female characteristics), and a metasoma with both male and female characteristics.

Causes of gynandromorphy have not been fully determined – polyspermy, embryonic fertilization, and chromosome elimination are all possible hypotheses with varying levels of support (Boveri, 1915; Morgan, 1916; Morgan & Bridges, 1919; Rothenbuhler, 1958). Different phenotypic expressions of gynandromorphy (bilateral, transverse, mosaic) may also have different developmental and genetic causes (Michez *et al.*, 2009). It is suggested that mosaic gynandromorphs, such as the specimen described here, are the outcome of independent chromosomal mutations, chromosome

elimination, or differential expression of chromosomal sex determination genes within different tissues during embryonic development, though the specific developmental pathway can only be revealed through genetic study (Rothenbuhler, 1958, Michez *et al.*, 2009). While the specific developmental basis of the *C. pallida* male dimorphism has not been studied, larval nutrition often plays an important role in generating developmental pathways in bees, including queen versus worker in *Apis mellifera* Linnaeus, dwarf versus normal daughters in *Ceratina calcarata* Robertson, or large versus small male dimorphism in *Lasioglossum hemichalceum* (Cockerell) (Winston, 1987; Kukuk, 1996; Lawson *et al.*, 2017). Given that *C. pallida* females and large morph males are both generally larger-bodied compared to small morph males, this specimen may have received a relatively larger quantity of larval provisions while developing, and thus the male characteristics (including thorax coloration) are more similar to large morph males than small morph males.

In collecting the gynandromorph, I noted a fight among several large males, and watched the specimen emerge, presumably from its natal nest in the ground. A large male from the fighting group then attempted to mount and mate with the gynandromorph (though it did not seem to be able to make genital contact successfully, this may have been due to my quick interruption to collect the specimen). This should not be taken as confirmation that the bee was considered 'female' by the mounting male, however. Males frequently make attempts to mate with both newly emerged male and female bees, as well as (presumably) mated, older females returning from foraging trips, and will even fight over and attempt to dig up dead male and female bees (Alcock *et al.*, 1976; Barrett, pers. obs.). Other gynandromorphs have been found foraging and engaged in 'female behaviors' (Wcislo *et al.*, 2004; Alvarez *et al.*, 2019), but behavioral data are sparse for bee specimen.

More records on the interactions of gynandromorphs with other individuals of their species, and with their environment, will be useful in determining how these phenotypic differences influences behavior. The causes of gynandromorphy in bees, outside *A. mellifera*, have not been well studied, and future work looking at the genetic basis and developmental pathways of gynandromorphs in other species would provide valuable insight into the diversity of gynandromorphy seen across the Apoidea. Finally, the reproductive capacity, anatomy (*e.g.*, intraspecies sex difference in neuroanatomy), and even genital morphology of gynandromorphs are poorly studied and could provide further information about how this unique condition manifests beyond external characteristics.

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REFERENCES

- Alcock, J., C.E. Jones, & S.L. Buchmann. 1976. Location before emergence of the female bee, *Centris pallida*, by its male (Hymenoptera: Anthophoridae). *Journal of Zoology* 179(2): 189–199.
- Alcock, J., C.E. Jones, & S.L. Buchmann. 1977. Male mating strategies in the bee *Centris pallida* Fox (Anthophoridae: Hymenoptera). *American Naturalist* 111(977): 145–155.
- Alvarez, L.J., M. Lucia, P.J. Ramello, & A.H. Abrahamovich. 2014. Description of two new cases of gynandromorphs in *Paratrigona* Schwarz and *Augochlora* Smith (Hymenoptera: Apidae and Halictidae). *Zootaxa* 3889: 447–450.
- Alvarez, L.J., W.P. Silva, M. Lucia, & A.J.C. Aguiar. 2019. The first cases of gynandromorphism in oil-collecting bees (Hymenoptera, Apidae: Centridini, Tapinotaspidini). *Papéis Avulsos de Zoologia* 59: e20195936.
- Ascher, J.S., & J. Pickering. 2020. DiscoverLife bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). [http://www.discoverlife.org/mp/20q?guide=Apoidea_species; last accessed 25 June 2021]
- Boveri, T. 1915. Über die Entstehung der eugsterschen Zwitterbienen. *Archiv für Entwicklungsmechanik der Organismen* 41: 264–311.
- Hinojosa-Díaz, I.A., V.H. González, R. Ayala, J. Mérida, P. Sagot, & M.S. Engel. 2012. New orchid and leafcutter bee gynandromorphs, with an updated review (Hymenoptera, Apoidea). *Zoosystematics and Evolution* 88(2): 205–214.
- Kukuk, P.F. 1996. Male dimorphism in *Lasioglossum* (*Chilalictus*) *hemichalceum*: The role of larval nutrition. *Journal of the Kansas Entomological Society, Supplement* 69(4): 147–157.
- Lawson, S.P., S.L. Helmreich, & S.M. Rehan. 2017. Effects of nutritional deprivation on development and behavior in the subsocial bee *Ceratina calcarata* (Hymenoptera: Xylocopinae). *Journal of Experimental Biology* 220(23): 4456–4462.
- Le Féon, V., A. Le Nevé, & É. Dufrêne. 2016. Premières mentions d'un cas de gynandromorphie chez *Nomada flava* Panzer, 1798 et *Nomada lathburiana* (Kirby, 1802) (Hymenoptera, Apoidea, Apidae). *Invertébrés Armoricains* 14: 15–21.
- Lucia, M., & V.H. Gonzalez. 2013. A new gynandromorph of *Xylocopa frontalis* with a review of gynandromorphism in *Xylocopa* (Hymenoptera: Apidae: Xylocopini). *Annals of the Entomological Society of America* 106(6): 853–856.
- Michener, C.D. 2007. *The Bees of the World* [2nd Edition]. Johns Hopkins University Press; Baltimore, MD; xvi+[i]+953 pp., +20 pls.
- Michez, D., P. Rasmont, M. Terzo, & N.J. Vereecken. 2009. A synthesis of gynandromorphy among wild bees (Hymenoptera: Apoidea), with an annotated description of several new cases. *Annales de la Société Entomologique de France* 45(3): 365–375.
- Morgan, T.H. 1916. The Eugster gynandromorph bees. *American Naturalist* 50(589): 39–45.
- Morgan, T.H., & C.B. Bridges. 1919. The origin of gynandromorphs. In: *Contributions to the Genetics of Drosophila melanogaster*: 1–122, +4 pls. Carnegie Institution of Washington; Washington, D.C.; v+388 pp., +12 pls.
- Narita, S., R.A.S. Pereira, F. Kjellberg, & D. Kageyama. 2010. Gyandromorphs and intersexes: Potential to understand the mechanism of sex determination in arthropods. *Terrestrial Arthropod Reviews* 3(1): 63–96.
- Onuferko, T.M. 2018. A record of bilateral gynandromorphism in *Epeolus* (Hymenoptera: Apidae: Nomadinae). *Journal of Melittology* 76: 1–6.
- Rothenbuhler, W.C. 1958. Progress and problems in the analysis of gynandromorphic honey bees. *Proceeding of the Tenth International Congress Entomology* 2: 867–873.
- Snelling, R.R. 1974. Notes on the distribution and taxonomy of some North American *Centris* (Hymenoptera: Anthophoridae). *Contributions in Science, Natural History Museum of Los Angeles County* 259: 1–41.
- Snelling, R. R. 1984. Studies on the taxonomy and distribution of American Centridini bees (Hymenoptera: Anthophoridae). *Contributions in Science, Natural History Museum of Los Angeles County* 347: 1–69.

- Urban, D. 1999. Ginandromorfia en *Alloscirtetica brethesi* (Joergensen) (Hymenoptera, Anthophoridae). *Revista Brasileira de Zoologia* 16: 171–173.
- Wcislo, W.T., V.H. Gonzalez, & L. Arneson. 2004. A review of deviant phenotypes in bees in relation to brood parasitism, and a gynandromorph of *Megalopta genalis* (Hymenoptera: Halictidae). *Journal of Natural History* 38(11): 1443–1457.
- Winston, M.L. 1987. *The Biology of the Honey Bee*. Harvard University Press; Cambridge, Massachusetts; 281 pp.



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