Descriptions of new gynandromorphs of *Xylocopa augusti* Lepeletier (Hymenoptera: Apidae: Xylocopini) from Argentina

Valentin Almada¹²⁴; Pablo José Ramello¹²⁵; Victor Hugo González³⁶ & Mariano Lucia¹²⁷

¹ Universidad Nacional de La Plata (UNLP), Facultad de Ciencias Naturales y Museo (FCNyM), División Entomología, Laboratorios Anexo Museo de La Plata. La Plata, BA, Argentina.
² Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). La Plata, BA, Argentina.
³ University of Kansas (KU), Department of Ecology & Evolutionary Biology (EEB), Undergraduate Biology Program. Lawrence, KS, United States.
⁴ ORCID: https://orcid.org/0000-0003-0317-9256. E-mail: almada.valentin@fcnym.unlp.edu.ar
⁵ ORCID: https://orcid.org/0000-0003-2539-2939. E-mail: pramello@fcnym.unlp.edu.ar
⁶ ORCID: https://orcid.org/0000-0002-4146-1634. E-mail: vhgonza@ku.edu
⁷ ORCID: https://orcid.org/0000-0001-8019-6768. E-mail: mlucia@fcnym.unlp.edu.ar (corresponding author)

Abstract. Gynandromorphs are individuals that display both male and female features throughout the body and are rarely found in nature. We document and describe two new gynandromorphs of the large carpenter bee *Xylocopa* (*Neoxylocopa*) *augusti* reared from a trap-nest in La Plata, Buenos Aires, Argentina. In addition, based on a literature review, we assessed the frequency of the different types of gynandromorphs, and the body part affected, among large carpenter bees. Both gynandromorphs were assigned to the mixed category, the most common category reported in the literature (22 of 25 specimens). The remaining three specimens exhibit a bilateral pattern in all tagmata. The presence of both sexes’ secondary sexual characteristics occurred more frequently on the mesosoma than on the head or metasoma. Trap nests used in bee hotels promote the conservation and study of wild bees and might facilitate the discovery of rare cases of gynandromorphs that would remain unknown otherwise under normal nesting conditions in the wild.

Keywords. Anthophila; Carpenter bees; *Neoxylocopa*; Gynandromorphism.

INTRODUCTION

Numerous morphological aberrations have been described in bees, but the most distinctive is gynandromorphism, when individuals display secondary characters of both sexes throughout the body (Michener, 1943; Wcislo *et al.*, 2004; Engel, 2007; Hopwood, 2007). To date, gynandromorphs have been found in more than 143 species and 37 genera belonging to all families of bees except Stenotritidae (Reviewed in Wcislo *et al.*, 2004; Michez *et al.*, 2009; Hinojosa-Díaz *et al.*, 2012; Fateryga *et al.*, 2019; Barrett, 2021). Gynandromorphs may go undetected by researchers in bee groups that exhibit little sexual dimorphism in terms of pilosity or coloration. However, for taxa with strong sexual dimorphism, as in the case of large carpenter bees of the genus *Xylocopa* Latreille subgenus *Neoxylocopa* Michener, where females are black and males are yellow, gynandromorphs are detected easily in the field or among specimens in insect collections. Indeed, half of gynandromorphs of *Xylocopa* are in that neotropical subgenus (9 of 18 species) (Lucia & Gonzalez, 2013; Lucia *et al.*, 2015; Villamizar, 2020).

Here, we document two gynandromorphs of *Xylocopa* (*Neoxylocopa*) *augusti* Lepeletier de Saint-Fargeau, which were detected during on-going studies of the biology of this species using trap-nests in Argentina. The first gynandromorph of *X. augusti* was recorded by Lucia *et al.* (2015), who described a mixed specimen from Pehuen-Có, Buenos Aires, Argentina. In addition, based on a literature review, we also explored the occurrence of gynandromorphism in *Xylocopa* and the distribution of different sexual characteristics among tagmata.

MATERIAL AND METHODS

The gynandromorph described here was reared from a trap nest of *X. augusti* built inside an internode of cane (*Arundo donax* L., Poaceae) and collected on 12-XII-2018 in the Unidad Vivero...
Forestal, Facultad de Ciencias Agrarias y Forestales of the Universidad Nacional de La Plata (34°54’39"S, 57°55’37"W, 18 m.a.s.l.), La Plata, Buenos Aires province, Argentina. To document brood development, we transported the nest to the laboratory, opened it lengthwise and secured both halves with tape (Fig. 1a), which allowed us to monitor it on daily basis. We studied and measured bee external morphological features using a Nikon SMZ 745T stereomicroscope with an ocular micrometer and took images with a Canon T6 digital camera attached to a stereomicroscope using a 60 mm Oshiro Macro lens. Multiple photographs taken at different depths were then merged using the Combine ZMT software package. Morphological terminology generally follows that of Hurd & Moure (1963) and Michener (2007). We measured total body length from the head to the apex of metasoma in lateral view, forewing length from the apex of the costal sclerite to the wing apex, mesosoma width between the outer borders of the tegulae, and metasoma width across the second tergum using a stereomicroscope with an ocular micrometer. In the descriptions, we used T and F for metasomal terga and flagellar segments. To facilitate comparisons, we followed the classification of gynandromorphs by Dalla Torre & Friese (1899) as follows: bilateral (divided in left-right), antero-posterior, transverse (dorsal-ventral), and mixed (mosaics or different combinations).

To assess the occurrence of gynandromorphism in Xylocopa and the distribution of the female and male features among tagmata, we reviewed the literature (supplementary material; table 1) and classified each gynandromorph in bilateral (symmetrical distribution of male and female features) or mixed (mosaic of male and female features) due to its features and their body part affected. To evaluate differences between types of gynandromorphs and among body parts, we used the Chi-Square goodness of fit test at a 5% significance level. Tests were analyzed using the statistical software R version 4.0.5 (R Core Team, 2021).

RESULTS

_Xylocopa (Neoxylocopa) augusti_
Lepeletier de Saint Fargeau, 1841

**Gynandromorph 1 (Figs. 1b-f)**

**Description:** Body length 22.1 mm, head length 5.1 mm, head width 7.1 mm, mesosoma width 9.5 mm, metasoma width 10.7 mm. The specimen displays female and male traits distributed irregularly along the body (mixed). **Head:** (Fig. 1b) with a mixture of female and male characteristics. The left half of the supraorbital area, vertex, frons, paraocular area, supraclypeal area and clypeus with yellow integument and pubescence as in the male. The right half with integument and pubescence dark brown to black, female-like, except male-like yellow integumental maculations as follows: frons, lower side of clypeus and left upper and lateral parac-
Figure 1. Gynandromorph of *Xylocopa* (*Neoxylocopa*) *augusti* Lepeletier de Saint Fargeau: (A) Sagittal section of a trap nest showing different developmental stages and pupa of Gynandromorph 1, which is indicated by the arrow in the third cell. (B) Head in frontal view. (C) Habitus in lateral view. (D) Habitus in ventral view. (E) Genitalia in ventral view; (F) Genitalia in lateral view. Scale bars: (A) 2 cm; (B) 2 mm; (C-D) 1 cm; (E-F) 1 mm.
gynandromorph had the general aspect of a female except for its head (mesosoma and metasoma female-like). Based on a photograph (Fig. 2), we could characterize its head. **Head:** left eye, left half of the supraorbital area, vertex, frons, paraocular area, supraclypeal area, clypeus, and labrum with integument and pubescence as in the male, right side of the head female-like.

**Frequency of gynandromorph types in Xylocopa**

Both gynandromorphs described here are in the mixed category, the most common type recorded in *Xylocopa*. Among the 25 gynandromorphs reported for *Xylocopa* (Villamizar, 2020; supplementary material; table 1), the overall proportion of mixed to bilateral types is 7 to 1. No specimen shows the transverse or anterior-posterior types, according to Michez *et al.* (2009). Mixed phenotypes are recorded in at least a tagma of 22 specimens recorded to date. The remaining three specimens exhibit a bilateral pattern in at least a tagma. Although the mixed pattern occurs in at least a tagma (head 45.5%, mesosoma 68.2% and metasoma 47.6%), it was significantly more common on the mesosoma ($\chi^2 = 6.36, \text{df} = 1, \ p < 0.01$; Fig. 3) than in other tagmata. The head and metasoma showed a similar tendency to display a mixed pattern (head $\chi^2 = 0.22, \text{df} = 1, \ p = 0.63$; metasoma $\chi^2 = 1.67, \text{df} = 1, \ p = 0.19$). The bilateral condition exhibited different proportions among tagmata, as well as in the occurrence of female and male features on each side of the body.

**Figure 2.** Gynandromorph 2 in frontal view inside the trap nest. This individual was not captured.
The number of gynandromorphs documented in *Xylocopa* has increased in recent years. Including the new specimens described here, there are 25 cases of gynandromorphism in *Xylocopa* belonging to 18 species. Half of them have been found in the subgenus *Neoxylocopa* Michener. The gynandromorphs described in this paper have a mixture of female and male features in at least a tagma, and thus they can be assigned to the mixed category. This is, by far, the most common pattern among *Xylocopa*, accounting for 88% (22/25) of gynandromorphs (Villamizar, 2020; Table 1; Supplementary material). We found that the presence of both sexes' secondary sexual characteristics occurred more frequently on the mesosoma. The underlying mechanisms that explain such a pattern are unknown. However, we believe that the presence of large appendages (legs) in this body region can make it easier for scientists to observe and describe gynandromorphy, at least superficially and without dissection, compared to head appendages or genitalic structures. Trap nests and bee hotels are extraordinary tools to promote the conservation and study of wild bees while engaging the public (McNally et al., 2018). In addition, these tools might facilitate the discovery of rare cases of gynandromorphs, as demonstrated here, that would remain unknown otherwise under normal nesting conditions in the wild.

**AUTHORS’ CONTRIBUTIONS:** VA, ML: Methodology; VA, ML, VG: Conceptualization, Writing – review & editing; PJR: Software, Data curation, Formal analysis. All authors actively participated in the discussion of the results, they reviewed and approved the final version of the paper.

**CONFLICTS OF INTEREST:** Authors declare there are no conflicts of interest.

**FUNDING INFORMATION:** Financial support was provided to ML by the Consejo Nacional de Investigaciones

---

**DISCUSSION**

The number of gynandromorphs documented in *Xylocopa* has increased in recent years. Including the new specimens described here, there are 25 cases of gynandromorphism in *Xylocopa* belonging to 18 species. Half of them have been found in the subgenus *Neoxylocopa* Michener. The gynandromorphs described in this paper have a mixture of female and male features in at least a tagma, and thus they can be assigned to the mixed category. This is, by far, the most common pattern among *Xylocopa*, accounting for 88% (22/25) of gynandromorphs (Villamizar, 2020; Table 1; Supplementary material). We found that the presence of both sexes’ secondary sexual characteristics occurred more frequently on the mesosoma. The underlying mechanisms that explain such a pattern are unknown. However, we believe that the presence of large appendages (legs) in this body region can make it easier for scientists to observe and describe gynandromorphy, at least superficially and without dissection, compared to head appendages or genitalic structures. Trap nests and bee hotels are extraordinary tools to promote the conservation and study of wild bees while engaging the public (McNally et al., 2018). In addition, these tools might facilitate the discovery of rare cases of gynandromorphs, as demonstrated here, that would remain unknown otherwise under normal nesting conditions in the wild.

**AUTHORS’ CONTRIBUTIONS:** VA, ML: Methodology; VA, ML, VG: Conceptualization, Writing – review & editing; PJR: Software, Data curation, Formal analysis. All authors actively participated in the discussion of the results, they reviewed and approved the final version of the paper.

**CONFLICTS OF INTEREST:** Authors declare there are no conflicts of interest.

**FUNDING INFORMATION:** Financial support was provided to ML by the Consejo Nacional de Investigaciones

---

**Figure 3.** Frequency of gynandromorph types among tagmata in *Xylocopa*.

**Table 1.** Gynandromorph records of *Xylocopa augusti* Lepeletier. To explore gynandromorph records of *Xylocopa* Latreille, 1802, see Villamizar (2020) and Supplementary material.

| Species                  | Category | Phenotype                                                                 | Locality                  | Repository | Reference                      |
|--------------------------|----------|---------------------------------------------------------------------------|---------------------------|------------|---------------------------------|
| *Xylocopa* (Neoxylocopa) | Mixed    | Mixture of ♂ and ♀ features in all tagmata                               | ARGENTINA, Buenos Aires   | MLP        | Lucia et al. (2015)             |
| *Xylocopa* (Neoxylocopa) | Mixed    | Mixture of ♂ and ♀ features only in the head region. Head: left male and   | ARGENTINA, Buenos Aires   | MLP        | This paper                     |
| *Xylocopa* (Neoxylocopa) |          | right female, Labrum with integument and setae as in the male, except   |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | for a small apical portion on its right side with integument and features |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | Female-like, except right mandible with a small yellow spot basally,     |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | similar to that of the male. Mesosoma: ♀ = like, Metasoma:               |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | predominantly ♀ = like.                                                  |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | Gynandromorph 1: General aspect of a female except for its face. Left    |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | eye, left half of the supraorbital area, vertex, frons, paraclypeal      |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | area, supercypeal area, clypeus, and labrum with integument and           |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | pubescence as in the male.                                               |                           |            |                                 |

---

**Figure 3.** Frequency of gynandromorph types among tagmata in *Xylocopa*.

**Table 1.** Gynandromorph records of *Xylocopa augusti* Lepeletier. To explore gynandromorph records of *Xylocopa* Latreille, 1802, see Villamizar (2020) and Supplementary material.

| Species                  | Category | Phenotype                                                                 | Locality                  | Repository | Reference                      |
|--------------------------|----------|---------------------------------------------------------------------------|---------------------------|------------|---------------------------------|
| *Xylocopa* (Neoxylocopa) | Mixed    | Mixture of ♂ and ♀ features in all tagmata                               | ARGENTINA, Buenos Aires   | MLP        | Lucia et al. (2015)             |
| *Xylocopa* (Neoxylocopa) | Mixed    | Mixture of ♂ and ♀ features only in the head region. Head: left male and   | ARGENTINA, Buenos Aires   | MLP        | This paper                     |
| *Xylocopa* (Neoxylocopa) |          | right female, Labrum with integument and setae as in the male, except   |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | for a small apical portion on its right side with integument and features |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | Female-like, except right mandible with a small yellow spot basally,     |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | similar to that of the male. Mesosoma: ♀ = like, Metasoma:               |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | predominantly ♀ = like.                                                  |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | Gynandromorph 1: General aspect of a female except for its face. Left    |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | eye, left half of the supraorbital area, vertex, frons, paraclypeal      |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | area, supercypeal area, clypeus, and labrum with integument and           |                           |            |                                 |
| *Xylocopa* (Neoxylocopa) |          | pubescence as in the male.                                               |                           |            |                                 |
ACKNOWLEDGMENTS: We are indebted to Amy R. Comfort and two anonymous reviewers for comments and suggestions that improved this manuscript. Also, Unidad Vivério (FCNYM, UNLP) and Unidad Vivério Forestal (FCAyF-UNLP) for the permission to conduct part of this study.

REFERENCES

Alvarenga, L.J.; Silva, W.P.; Lucia, M. & Aguiar, A.J. 2019. The first cases of gynandromorphism in oil-collecting bees (Hymenoptera, Apidae: Centridini, Tapinotaspidini). Papéis Avulsos de Zoologia, 59(36): 1-5. https://www.scielo.br/j/paz/a/7Krvn64VZmB5ZsPf3Hc5k7D/?format=pdf&lang=en.

Barrett, M. 2021. The first case of gynandromorphy in Centris pallida (Hymenoptera: Apidae: Centridini). Journal of Melittology, 104: 1-8. https://doi.org/10.17161/jom.i104.13782.

Dalla Torre, K.W. & Friese, H. 1899. Die hermaphroditen und gynandromorphen hymenopteren. Berichte des Naturwissenschaftlich-medizinischen Vereins in Innsbruck, 24: 1-96.

Engel, M.S. 2007. A Lateral Gynandromorph in the Bee Genus Thyreus and the Sting Mechanism in the Melectini (Hymenoptera: Apidae). American Museum Novitates, 3553(1): 1-11.

Fateryga, A.V.; Ivanov, S.P. & Filatov, M.A. 2011. Gynandromorphs of Megachile picicornis (Morawitz, 1877) and Megachile deceptoria (Pérez, 1890) (Hymenoptera, Megachilidae) and their evolutionary interpretation. Russian Entomological Journal, 20(3): 261-264.

Hinojosa-Díaz, I.A.; Gonzalez, V.H.; Ayala, R.; Mérida, J.; Sagot, P. & Engel, M.S. 2012. New orchid and leaf-cutter bee gynandromorphs, with an updated review (Hymenoptera, Apoidea). Zoosystematics and Evolution, 88(2): 205-214. https://onlinelibrary.wiley.com/doi/abs/10.1002/zoos.201200017.

Hopwood, J.L. 2007. A “cyclops” of the bee Lasiosglossum (Dialictus) bruneri (Hymenoptera: Halictidae). Journal of the Kansas Entomological Society, 80(3): 259-261.

Hurd, P.D. & Moure, J.S. 1963. A classification of the large carpenter bees (Xylocopini) (Hymenoptera: Apoidea). University of California Publications in Entomology, 29: 1-365.

Lucia, M. & Gonzalez, V.H. 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: 853-856.

Lucia, M.; Villamil, S.F. & Gonzalez, V.H. 2015. A gynandromorph of Xylocopa augusti and an unusual record of X. iris from Brazil (Hymenoptera: Apidae: Xylocopini). Journal of Melittology, 53: 1-7.

McNally, X.; Goulson, D. & Fowler, R. 2018. Air Bee n’ Bee: a citizen science study of man-made solitary bee hotels as a conservation approach. In: European Congress of Conservation Biology, 5th. Jyväskylä, Finland. https://doi.org/10.17011/conference/eccb2018/107813.

Michener, C.D. 1943. Sex anomalies in the genus Ashmeadiella (Hymenoptera) with notes on the homologies between male and female genital appendages. The Pan-Pacific Entomologist, 19(3): 96.

Michener, C.D. 2007. The Bees of the world. 2. ed. Baltimore, Johns Hopkins University Press. xvi + i + 953 pp. + 20 pls.

Michez, D.; Rasmont, P.; Terzo, M. & Vereecken, N.J. 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.

R: A Language and Environment for Statistical Computing (R Core Team). 2021. R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing. Available: https://www.r-project.org.

Villamizar, G. 2020. A new case of gynandromorphism in Xylocopa frontalis (Olivier) (Hymenoptera: Apidae), with an updated review of records in Xylocopinae Latreille. Revista Chilena de Entomología, 46(2): 189-200.

Vicario, W.T.; Gonzalez, V.H. & Arneson, L. 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. https://doi.org/10.1080/0022293031000153322.
SUPPLEMENTARY MATERIAL

REFERENCES

(Literature reviewed of gynandromorphs of Xylocopa Latreille, 1802)

Almeida, R.P.S.; Leite, L.A.R. & Ramos, K.D.S. 2018. Two new records of Gynandromorphs in Xylocopa (Hymenoptera, Apidae s.l). Papéis Avulsos de Zoologia, 58.

Benoist, R. & Berland, L. 1935. Trois cas de Gynandromorphisme chez les Hyménoptères aculéates. Archives du Museum d’Histoire Naturelle, 12: 435-438.

Bonnet, B. 1952. Xylocopa varipuncta gynandromorph. Proceedings of the Hawaiian Entomological Society, 14: 359.

Carcasson, R.H. 1965. A remarkable gynandrous carpenter bee. Journal of the East Africa Natural History Society, 25: 75.

Enderlein, G. 1913a. Ein hervorragenden zwitter von Xylocopa mendozana aus Argentinien. Stett. Deutsche Entomologische Zeitschrift, 74: 124-140.

Enderlein, G. 1913b. Zur Kenntnis der Xylocopen Südamerikas und über einen Zwitter von Xylocopa ordinaria. Archiv für Naturgeschichte, 7: 156-170.

Gordh, G. & Gulmahamad, H. 1975. A bilateral gynandromorphic Xylocopa taken in California (Hymenoptera: Apidae). Proceedings of the Entomological Society of Washington, 77: 269-293.

Guershon, M. & Ionescu-Hirsch, A. 2012. A review of the Xylocopa species (Hymenoptera: Apidae) of Israel. Israel Journal of Entomology, 41-42: 145-163.

Krauss, N.H. 1928. Xylocopa varipuncta Patton. Proceedings of the Hawaiian Entomological Society, 7: 22.

Lucia, M. & Gonzalez, V.H. 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: 853-856.

Lucia, M.; Abrahamovich, A.H. & Alvarez, L.J. 2009. A Gynandromorph of Xylocopa nigrocincta Smith (Hymenoptera: Apidae). Neotropical Entomology, 38: 155-157.

Lucia, M.; Alvarez, L.J. & Abrahamovich, A.H. 2012. Gynandromorphism in Xylocopinae Bees (Hymenoptera: Apidae): description of four new cases. Zootaxa, 3401: 37-42.

Lucia, M.; Villamil, S.F. & Gonzalez, V.H. 2015. A gynandromorph of Xylocopa augusti and an unusual record of X. iris from Brazil (Hymenoptera: Apidae: Xylocopini). Journal of Melittology, 53: 1-7.

Maa, T.C. 1940. On the monstrosity of certain Xylocopa species (Hymenoptera: Xylocopidae). Lingnan Science Journal, 19: 83-85.

Prashantha, C.; Lucia, M. & Belavadi, V.V. 2019. Two new cases of gynandromorphism in Xylocopinae bees (Hymenoptera: Apidae) from India. Oriental Insects, 53(2): 291-297.

Zama, P.C. & Coelho, I.R. 2017. New cases of gynandromorphism in Xylocopa LATREILLE, 1802 (Hymenoptera: Apidae). Papéis Avulsos de Zoologia, 57: 313-319.