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First report of gynandromorphy in *Hoplitis*: A bilateral specimen of *H.* (*Alcidamea*) *producta* (Hymenoptera: Megachilidae)

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Abstract. A bilateral gynandromorph of *Hoplitis* (*Alcidamea*) *producta* (Cresson) is described and illustrated for the first time. The specimen is notable for its nearly complete bilateral asymmetry and represents the first recorded case of gynandromorphism in *Hoplitis*. A summary of literature records on gynandromorphic bees is provided.

INTRODUCTION

Animals simultaneously displaying both male and female characteristics are commonly referred to as gynandromorphs (Akre *et al*., 1982; Narita *et al*., 2010). Individuals with such sexual abnormalities are rarely witnessed in nature and are worthy of being noted (Lucia *et al*., 2015). Because bees, like most arthropods, are sexually dimorphic, physical traits can normally be used to determine sex type (Narita *et al*., 2010). True gynandromorphs have mixed morphology consisting of genetically male and genetically female tissues, and in each cell, the genetic sex (*i.e*., sex chromosome composition) is consistent with the sexual phenotype. Gynandromorphs (gynanders) differ from intersexes, which are genetically uniform but display a sexual phenotype in some or all parts of their bodies that is opposite of their genetic sex. In many cases, the underlying genetic makeup of body tissue is unknown, and phenotypically mixed creatures are arbitrarily referred to as intersexes or gynandromorphs; however, clearly bilateral individuals are likely to be true gynandromorphs (Narita *et al*., 2010).

Michez *et al.* (2009) classified bee gynandromorphs in three categories: 1) transverse, in which sex traits are dispersed across two asymmetrical body sections; 2) bilateral, in which male and female body parts are equal and symmetrical; and 3) mosaic, in which sex features are distributed randomly across the body. The specimen of *Hoplitis* (*Alcidamea*) *producta* (Cresson) described in this work corresponds to a bilateral gynandromorph.

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A review of gynandromorph reports of wild bees, based on Michez *et al*. (2009), Hinojosa-Díaz *et al*. (2012), and additional sources (Supplemental Material, Table S1), reveals that gynandromorphy has been recorded in all Anthophila families except Stenotritidae. To date, at least 165 species across 45 genera have been recorded, excluding records of *Apis mellifera* Linnaeus, for which the literature is extensive (Hinojosa-Díaz *et al*., 2012). The family with the greatest number of species exhibiting gynandromorphy is Apidae (37%), followed by Megachilidae (31%), Halictidae (14%), Andrenidae (10%), Colletidae (6%), and Melittidae (2%). The genera with the highest number of species are *Megachile* Latreille (18%), *Xylocopa* Latreille (11%), *Andrena* Fabricius (9%), *Bombus* Latreille (7%), *Lasioglossum* Curtis (5%), *Hylaeus* Fabricius (5%), *Osmia* Panzer (5%), and *Sphecodes* Latreille (4%). This study adds the genus *Hoplitis* Klug (Osmiini) to the family of Megachilidae.

Hoplitis consists of about 390 species worldwide (Ascher & Pickering, 2020), with around 60 species in North America. More than 50 species are found in the western U.S.A. with some extending as far south as northern Mexico (Carril & Wilson, 2023). While most species are found in higher elevations and cool mesophytic areas, some are found in low-elevation and desert environments (Michener, 1944; Carril & Wilson, 2023). Nesting habits are diverse, with species building nests in preexisting wood cavities, twigs, the ground, or constructing external nests from mortar and pebbles. *Hoplitis* ranges in body shape, from elongate and slender hoplitiform to a more robust megachiliform form (Michener, 2007).

Hoplitis producta is a small (6–8 mm), black bee with distinct white tergal hair bands (Cresson, 1864; Carril & Wilson, 2023). Males are characterized by a large, steeply pointed projection on the second metasomal sternum and a narrow, triangular projection in the middle of the seventh tergum. The species is solitary, polylectic, and univoltine, with a flight period spanning from mid-April through July. It is widely distributed across most of the United States and southern Canada. *Hoplitis producta* nests in the hollow stems of pithy plants such as sumac (*Rhus* L.; Anacardiaceae), elder (*Sambucus* L.; Adoxaceae), and rose (*Rosa* L.; Rosaceae). Its nest cells are constructed from green, leafy material, which is chewed into a soft pulp and molded into plugs and partitions that harden over time (Rau, 1928; Michener, 1947).

MATERIAL AND METHODS

The gynandromorph described here was netted by M.G. on *Prunella vulgaris* L. (Lamiaceae) during sampling for the Oregon Bee Atlas at Cooper Mountain Nature Park (45.450066, -122.874181) in Beaverton, Oregon, U.S.A. (Figs. S1, S2). It was collected near a trail where the park transitions from mixed forest to oak savannah on June 25, 2021, around 11 h, on a warm and sunny day. Ethyl acetate was used to euthanize the bee, and it was later glued to an insect pin. The genitalia was not removed to preserve the specimen's integrity, which is housed in the Oregon State Arthropod Collection under the museum ID OSAC_0001309999.

Photographs were taken with a Canon EOS T3i DSLR, a Canon f/2.8 100mm macro lens, an EL-Nikkor 50mm f/2.8 reversed enlarging lens, and several microscope objectives. Photo stacking was implemented using a WeMacro stepper rail under the control of Helicon Remote. Images were combined using Helicon Focus software, and Adobe Lightroom was used for cropping and minor adjustments. The gynandromorph and reference specimens were measured using 10× and 20× eyepieces with reticles and an Amscope 4.5x stereo zoom microscope (SM-1TN-V203). Body part measurements

were taken at fixed zoom settings with specific eyepiece reticles to ensure consistency in unit lengths at each magnification level. Reticle unit measurements at the specific magnifications (30× to 90×) were converted to millimeters using calibration slides.

Seven wild male and seven wild female conspecifics, collected from the same location and time of year as the gynandromorph, were examined as baselines for comparisons. They are referred to as "references" or "typical" males and females. Male clypeal integument was largely obscured by dense hair (>2 to 3 median ocellus widths; Fig. 9), but one relatively hairless male (Fig. 10) and another with a shaved clypeus provided clear views for comparison. Body length was measured from the tip of the head to the apex of the metasoma in lateral view. Head width was measured across the widest part of the eyes, while head length was taken from the vertex to the bottom of the clypeus. The mesosoma was measured across the outer margins of the tegulae, and the metasoma was measured at its widest point across the third tergum. Clypeus length (CL) was measured from the clypeal base to the rim margin on both sides, aligned with the inner edges of the antennal sockets. Clypeus half-width (CHW) was measured from the midpoint to the lateral angles. Tarsal segments were measured laterally along their mid-axis, while scape widths and lengths were taken from an anterior-frontal view. The gynandromorph was identified using the male and female keys from Hurd & Michener (1955). Specimen description follows the morphological terminology of Michener (2007), with S and T used for metasomal sternum and tergum. Average values are provided with standard deviation.

RESULTS

Hoplitis (*Alcidamea*) *producta* (Cresson, 1864)
Gynandromorph
(Figs. 1–8)

Description: The specimen is a nearly perfectly bilateral gynandromorph, as sexual features of color, pubescence, and integument are divided asymmetrically left (female) to right (male) along the sagittal plane of its body in all three tagmata (Figs. 1–3), except for the clypeus, which appears more female-like.

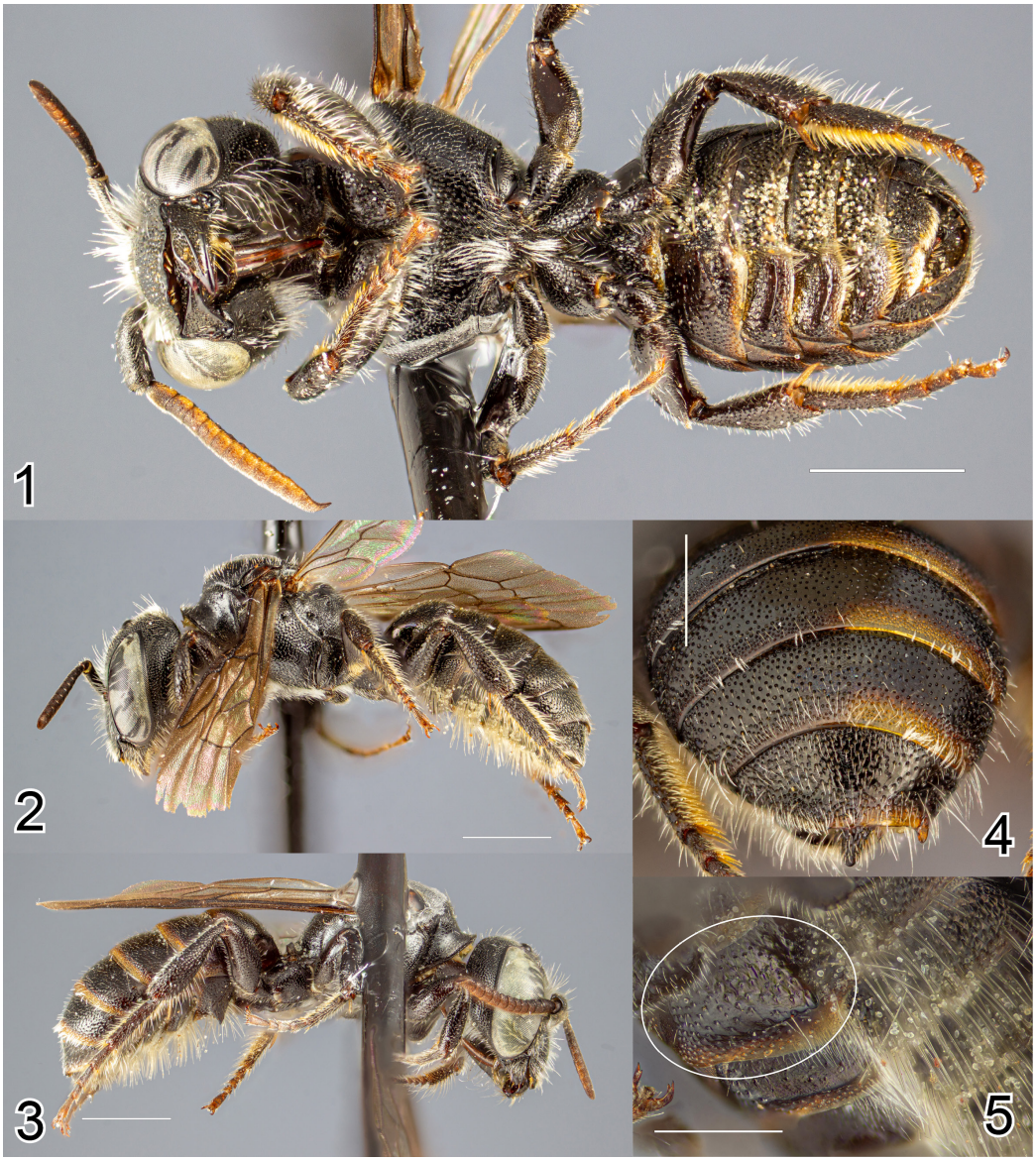
Measurements. Body length 5.6 mm; head length 1.5 mm; head width 1.7 mm; mesosoma width 1.6 mm; metasoma width 1.6 mm. In general, the gynandromorph is slightly smaller than the average female (6.20 mm, ± 0.68, $n = 7$) and male (6.44 mm, ± 0.45, $n = 6$) reference specimens, although one of the female references was shorter (5.3 mm) and another of the same length (5.6 mm). The gynandromorph pubescence is generally sparser on both the right and left sides than the reference specimens, but this may be attributable to wear. This feature is most noticeable on the male side (frontal left) of the head.

Head. Bilaterally split into male (right) and female (left) features except for the clypeus, which bears largely female traits (Figs. 6–8). The male antenna contains 13 segments with a thickened scape (L/W = 0.51/0.23) and a pointed terminal segment, while the female antenna consists of 12 segments, a narrower scape (L/W = 0.47/0.14), and a blunt terminal. The male side has a wider eye (0.47 mm) and narrower gena (0.43 mm) than the female side (0.42 mm and 0.47 mm, respectively). On the ventral side, the female side shows a 3-toothed mandible, while the male side is obscured by the opposing mandible but does show mandibular ridges consistent with typical males (Fig. 6). On the ventral side, the female hypostoma area along the ventral gena

margin has long white bristles that form a loose basket that is absent on the male side (Fig. 6). Pubescence on either side of the head generally follows typical male and female characteristics, but the male trait of thick hair on the frons and clypeus is not evident (Fig. 7). The clypeus appears structurally and dimensionally uniform, and it is not divided medially left to right like other portions of the head. The male references showed punctures on the clypeus that were oblong, closer together (< 1 puncture diameter apart centrally), smaller, and devoid of shiny interspaces (Fig. 10) compared to the female clypeus. Female references generally had shorter clypeal hairs (~1 to 2 median ocellus width) with the underlying integument displaying larger (~2×), more distinct, and rounded punctures (1 to 2 puncture diameters apart centrally) with shiny interspaces (Fig. 11). In addition, the female references had polished areas (about the width of an antenna socket) of sparse punctation in the basal-medial area of their clypeus, just below the frons (Fig. 11), while the same area in the males showed mostly dense punctation without polished integument (Fig. 10). CHW on both the left and right sides are equal (0.45 mm and 0.45 mm), as are CL of the right and left sides (0.57 mm and 0.56 mm). This differs from the reference specimens in which the male clypeus was narrower (CHW: 0.40 mm, ± 0.02, $n = 7$) and shorter (CL: 0.51 mm, ± 0.02, $n = 7$) compared to the females (CHW: 0.47 mm, ± 0.02, $n = 7$; CL: 0.60 mm, ± 0.03, $n = 7$).

Mesosoma. Typical female legs on the left and typical male legs on the right side. Tarsal claws are simple on the left legs, bifurcated on the right legs. The rear legs of the gynandromorph differ in structure. The female (left) leg has a wider basitarsus (0.26 mm) covered with short bristles, while the male (right) leg has a narrower basitarsus (0.20 mm) without bristles. The second tarsal segment of the hind leg is wider on the female side than on the male side (0.25 mm vs. 0.22 mm), as is the third tarsal segment (0.17 mm vs. 0.22 mm). The basitarsus of the left front leg is covered in erect, curving white hairs, which are the longest on this segment and taper down in length to the distitarsus. The basitarsus of the right front leg has sparse white hairs, mostly along the margins, while the other segments continuing to the distitarsus have few and scattered long hairs. Differences in scutum punctation are evident along the dorsal medial line, where the male (right) side has finer, smaller punctation (~0.67×) compared to the female (left) side (Fig. 8). The ventral mesepisternum between the mid and hind coxae exhibits dense white pubescence on the male side, which is largely absent on the female side (Fig. 1).

Metasoma. Sexual asymmetry is evident in the presence or absence of sternal scopa along the medial line (Figs. 1, 5). The left (female) sternal segments (S2–S6) are covered in fine white scopal bristles up to the midline, while these bristles are absent on the right (male) side. The right (male) sterna are shiny and mostly hairless on their discs, with white hairs along the apical margins extending to the midline; S3–S4 have longer, denser hairs medially. The typical wedge-shaped S2 projection is present on the male side but absent on the female side, resulting in a half-formed projection (Fig. 5). The left sternal margins are straight or concave and not thickened apically, whereas the right S3–S4 margins are convex, medially emarginated, and thickened apically. The T6 rim is smooth on the left side but features the typical male lateral spine on the right side (Fig. 4). T7 is visible but malformed, appearing triangular and pointed, with a straight lateral facet on the right side and a slightly convex lateral facet on the left side (Fig. 4). The specimen follows the expected pattern where male terga have brownish-hyaline apical margins (Figs. 3, 4), while female terga have black apical margins (Figs. 2, 4). The tip of a gonostylus anterior to T7 is present on the male side but is not visible in the included photos.



Figures 1–5. Gynandromorph of *Hoplitis producta*. **1**. Ventral view showing female traits on the left and male traits on the right side of the body. **2**. Left lateral displaying female traits. **3**. Right lateral displaying male traits. **4**. Metasoma showing tergal color differences between the left (female) and right (male) sides, along with a spine on T6 and malformed T7. **5.** Close-up of ventral metasoma, highlighting the S2 projection (white circle) present only on the male side. Scale bar: 1 mm in Figs. 1–3; 0.5 mm in remaining figures.

Figures 6–7. Gynandromorph (6–8), male (9, 10) and female (11) sexes of *Hoplitis producta.* **6.** Ventral view of the head showing bilateral differences in the genal basket, pubescence, antennae, eyes, mandibles, and paraocular pubescence. **7**. Frontal view of the head showing bilateral differences in the antennae, eyes, mandibles, and paraocular pubescence. **8**. Dorsal view of head. **9, 10**. Facial views of the male, showing the clypeus with and without pubescence. **11**. Facial view of the female. Scale bar: 0.5 mm.

DISCUSSION

The distinct separation of male and female traits along the longitudinal plane across all three tagmata indicates that the specimen exhibits bilaterally asymmetrical morphology, except for the clypeus. According to Narita *et al*. (2010), clearly bilateral individuals are more likely to be gynandromorphs rather than intersexes. However, confirming this is challenging due to uncertainties regarding the clypeal structure and the unknown genetic composition of the specimen's male and female tissues. Genetic analysis can help determine true gynandromorphism, which occurs when an individual's genotypic and phenotypic sexes align. This requires viable tissue samples from both male and female body parts (Michez *et al*., 2009).

Bees, like other hymenopterans, use a haplodiploid genetic system. Males develop from an unfertilized egg and remain haploid, whereas females typically develop from the union of an egg and sperm and become diploid (Michener, 2007; Heimpel *et al*., 2008). There is evidence that many hymenopterans, including some bees, use a sex determination mechanism known as "complementary sex determination" (CSD) or "single locus CSD" (sl-CSD), in which the sexual phenotype is controlled by a single gene with multiple alleles, in addition to haplodiploidy. In sl-CSD, females are heterozygous for this allele (A1, A2), while males are hemizygous (either A1 or A2, the default condition for an unfertilized egg). But another condition that can produce males is when an egg is fertilized but is homozygous for the sl-CSD gene (A1A1 or A2A2) (Michez *et al*., 2009). Such males are typically sterile and short-lived (*Apis* larvae are removed and cannibalized by workers) but can produce diploid sperm leading to triploid and sterile offspring (Page *et al*., 2002; Michener, 2007; Van Wilgenburg *et al*., 2006). In a study on sex mosaics in the honey bee, it was noted that a wide range of developmental variants can occur in haplodiploid organisms and still result in viable adults. Haplodiploidy permits almost any combination of gametes present in an egg to fuse and form a zygote, or to not combine and develop independently as haploid tissue (Aamidor *et al*., 2018).

Numerous theories have been proposed to explain the origins of gynandromorphism in Hymenoptera. Models put forward for bilateral development include the addition of a second gamete during fertilization, such as in "polyspermy" (Morgan, 1916) or "delayed fertilization of a binucleate egg" (Boveri, 1915), as well as the theory of "chromosomal elimination" (Morgan & Bridges, 1919), which postulates the loss of the CSD gene (Michez *et al*., 2009). Bilateral, transverse, and mosaic gynandromorph formations have been explained by alternative hypotheses as well. These include mutations, genetic incompatibilities, temperature, endosymbiont activity, epigenetic impacts, loss or aberration of the CSD-containing chromosome, and up/down-regulation of CSD (Michez *et al*., 2009; Narita *et al*., 2010; Sommaggio *et al*., 2021).

Knowledge of the genetic makeup of a gynandromorph's male and female bodily tissues can aid in understanding haplodiploidy, CSD, and other factors that may determine phenotypic expression (Suzuki *et al*., 2015). Assuming sl-CSD is at work, it would be fascinating to learn whether a given gynandromorph's genotype reflects the typical phenotype, in which male tissue is hemizygous (haploid) and female tissue is heterozygous (diploid). And one cannot rule out the possibility that male tissue contains diploid cells homozygous for sl-CSD or diploid cells heterozygous for sl-CSD but controlled by gene regulation or other mechanisms.

Methods for detecting ploidy levels (*i.e.*, haploid vs. diploid) via chromosome count or allelic zygosity (where heterozygous implies diploidy) could be utilized to determine the genetic gender of tissues. Genotyping of fresh tissue has been done with bees (Aamidor, 2018; Suzuki *et al*., 2015), but doing so on dried material may be more challenging. However, allelic zygosity testing has been successful on dried and aged bumble bee tissue from museum specimens aided by PCR amplification of DNA microsatellite alleles (Strange *et al*., 2009; Rohde *et al*., 2024). Although microsatellite markers may not have yet been identified for a *Hoplitis* species, some have been determined for related groups of Megachilidae, including *Megachile sculpturalis* Smith, *Osmia lignaria* Say and *O. bicornis* (Linnaeus) (Lanner *et al*., 2021; Koch *et al*., 2023; Neumann & Seidelmann, 2006; Van Eeckhoven *et al*., 2022). Such information might aid in the identification of microsatellite markers for *Hoplitis*.

Gynandromorphs are fascinating not only because of their striking body shapes but also for the insights they may provide about developmental pathways in bees and the genetic underpinnings of their phenotypic expression (Wcislo *et al*., 2004; Engel, 2007). Studies connecting phenotypes to genotypes using modern genetic tools could enlighten this area of biology.

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SUPPLEMENTAL MATERIAL

Table S1. Updated list of wild bee gynandromorph records.
Figures S1, S2. *Hoplitis producta* visiting *Prunella vulgaris* L. (Lamiaceae) at Cooper Mountain Nature Park.

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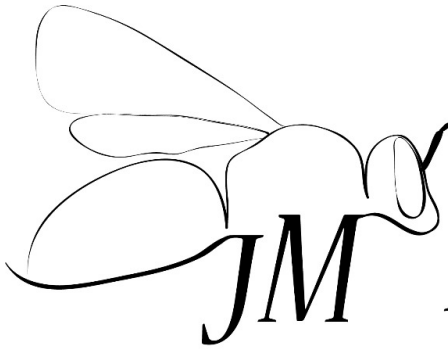

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