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First record of gynandromorphy in *Andrena florivaga* and an additional case in *Nomada lathburiana* from Germany (Hymenoptera, Apoidea)

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Abstract

Rare developmental anomalies can provide valuable insights into the mechanisms of sex differentiation, particularly when they manifest in clearly defined morphological patterns. In this study, we describe the first recorded gynandromorph of *Andrena florivaga* and a further gynandromorphic specimen of *Nomada lathburiana* from Germany. The *Andrena florivaga* specimen shows a predominantly bilateral display of sexually dimorphic traits, with male structures largely restricted to one side of the body while female traits dominate the opposite side; the head and forelegs represent entirely the female state. This pattern continues across the mesosoma, legs, and metasoma and involves both secondary sexual characters and terminal structures.

The second specimen was identified as *Nomada lathburiana* and exhibits a mainly bilateral separation of male and female morphology, particularly in the tergites, sternites, mesosomal pubescence, and leg coloration. However, within certain body regions the assignment of traits alternates and transitions become indistinct, resulting in a bilateral gynandromorph with mosaic elements. The first recorded case of gynandromorphy in *Andrena florivaga*, together with a further morphologically distinct specimen of *Nomada lathburiana*, expands the known range of gynandromorphic phenotypes in wild bees and highlights the value of such anomalies for understanding sex differentiation and morphological pattern formation in Hymenoptera.

Keywords
Developmental anomaly, morphological asymmetry, sex differentiation, sexual mosaic, teratology

Introduction

Gynandromorphy refers to the simultaneous occurrence of male and female morphological traits within a single individual (Fusco and Minelli 2023). This phenomenon has been documented in Hymenoptera since the 19th century (Sichel 1858; Ritsema 1881) and is considered one of the most striking forms of teratological developmental anomalies (Carion et al. 2025).

In bees (Apoidea), more than one hundred cases have now been described, yet the actual incidence of gynandromorphism is considered extremely low. The comprehensive review by Michez et al. (2009) summarizes 109 published cases and distinguishes three clearly defined categories of gynandromorphic organization: bilateral, transversal, and mosaic distributions of sexual traits. It should be noted that the definition of transversal gynandromorphism used by Michez et al. (2009) differs substantially from that of Dalla-Torre and Friese (1899), whose system is still used in parts of the literature.

The causes of gynandromorphic development are mainly attributed to disturbances in the haplo-diploid sex-determination mechanisms of Hymenoptera (Heimpel & de Boer 2008). Specifically, the presence of embryonic cell lineages with different ploidy levels generates genetic mosaicism, which in turn produces phenotypic mosaicism. These patterns are generally attributed to early-embryonic events, such as chromosome loss, nondisjunction, or anomalies in fertilization leading to divergent cell lineages (Fusco and Minelli 2023). Moreover, it is hypothesized that under certain conditions reproductive manipulation by alphaproteobacterial symbionts of the genus *Wolbachia* may lead to the generation of gynandromorphs (Narita et al. 2010). Interestingly, evidence from experimental systems shows that environmental factors, such as temperature stress during early development, can elevate the incidence of gynandromorphy (Kamping et al. 2007).

Within the Apoidea, gynandromorphs have been documented across several bee families, including Megachilidae, Apidae, and Andrenidae. Numerous studies report new individual findings and continuously expand the known spectrum of gynandromorphic phenotypes. Examples include representatives of the Euglossini (Giangarelli & Sofia, 2011), the first record of gynandromorphy in the *Hylaeus* subgenus *Prosopis* (Lightburn et al. 2022), as well as historical single cases such as the completely bilateral gynandromorphy in *Xylocopa micans* (Maidl 1911).

These studies demonstrate that gynandromorphs can provide valuable insights into the development of sexually dimorphic structures, particularly when multiple body regions are affected. Cases are especially informative when gynandromorphism involves several body segments and shows a consistent bilateral or transversal division. Such specimens allow a precise functional and morphological comparison of sex-specific traits and provide important clues about the temporal dynamics of sex determination (Suzuki et al. 2015).

Here, we report the first documented case of gynandromorphy in *Andrena florivaga* and describe an additional gynandromorphic specimen of *Nomada lathburiana* from Germany. Both specimens are characterized morphologically and compared with previously published cases in order to assess their position within the known spectrum of gynandromorphic organization in wild bees.

Material and methods

Andrena florivaga

The gynandromorphic specimen of *Andrena florivaga* was collected using an insect net on 20 May 2025 in the nature reserve Schottenbruch near Niedermeiser (Hesse, Germany). The locality is a calcareous semi-dry grassland in the Diemel Valley (51°27.27'N, 9°19.20'E).

After the initial identification under a stereomicroscope, the specimen was recognized as gynandromorphic due to its striking distribution of morphological traits. For the examination of the terminal structures, the genital apparatus was carefully dissected. The morphological examination was performed using a Zeiss Stemi 508 stereomicroscope. Species identification followed Schmid-Egger and Scheuchl (1997). To confirm the species identity, DNA barcoding of the CO1 gene was performed. To preserve external morphological features, DNA was extracted from internal tissue, following the protocol described in Lanner et al. (2021). Species identification was based on a 313 bp CO1cox1 fragment, amplified with the primers mlCOIintF (Leray et al. 2013) and jgHCO2198 (Geller et al. 2013) and sequenced on an ONT MinION (R10.4.1 flow cell; SQK-LSK114 ligation sequencing kit, Oxford Nanopore Technologies 2025). Basecalling (MinKNOW; Oxford Nanopore Technologies 2024) and demultiplexing (ONTbarcoder 2.0; Srivathsan et al. 2024) were followed by a BLAST search against the NCBI nucleotide database for taxonomic assignment. The BLAST match showed 100% sequence identity and 100% query coverage to a reference sequence of *Andrena florivaga* (GenBank accession: KJ837219.1).

Nomada lathburiana

The gynandromorphic specimen of *Nomada lathburiana* was collected on 6 April 2024 in the nature reserve Moosheide near Hövelhof (North Rhine–Westphalia, Germany). The locality lies within the area known as “Wildbahn Senner Pferde”, which is grazed from spring to autumn by approximately five to seven Senner horses. The specimen was collected with an insect net along a horse trail (51°51.48'N, 8°41.79'E).

During identification under a stereomicroscope, the specimen was recognized as gynandromorphic due to its unusual combination of morphological traits. Species identification followed Amiet et al. (2007). The morphological examination was carried out using a Leica S APO stereomicroscope.

For the photographic documentation of both specimens, a Keyence VHX-7000 digital microscope (Osaka, Japan) was used. Images were taken at different magnifications and lighting angles, including the use of multi-lighting, in order to document both surface structures and the bilateral expression of sexually dimorphic traits. Terminology and structural nomenclature follow Michener (2007). Voucher specimens are currently deposited in the private collections of Marcel Kettermann (*Andrena florivaga*) and Juliana Klaren (*Nomada lathburiana*).

Results

Description of the gynandromorphic *Andrena florivaga*

The examined specimen of *Andrena florivaga* exhibits an almost completely bilateral gynandromorphic organization, with the left side of the body predominantly displaying male traits and the right side predominantly female traits (Fig. 1a, b). The head and forelegs are entirely female (Fig. 1d), indicating that the bilateral differentiation in this specimen begins posterior to the head. The differentiation becomes evident in the development of the hair fringes: the left side of the body shows short, whitish pubescence, while the right side bears short yellowish hairs. The mesonotum is chagrined on both sides and smooth and shiny medially, but differs clearly in the lateral punctation. On the left side the punctures are sparse and widely spaced (distances > 2× puncture diameter), whereas on the right side they are regular and dense (1–2× puncture diameter) (Fig. 2c).

The sexual dimorphism continues from the middle legs onwards: on the left side, the metatarsus is narrow, darkened basally and covered with yellowish-white hairs; on the right side the coxa, trochanter and femur are enlarged and female in form, the metatarsus is broadened, uniformly orange in color and displays orange-yellow pubescence. The hind legs follow the same pattern. On the left side the coxa, trochanter and femur are smaller and white-haired, the tibia is narrow and marked with orange and black spots, and the metatarsus and tarsi are orange. On the right side the segments are distinctly enlarged and yellow-haired; the tibia is broadened and carries a well-developed orange scopa (Fig. 2e, f). In addition, a well-developed yellow flocculus is present, corresponding to the female morphology.

The metasoma is also clearly bilaterally differentiated. On tergum 1, the left side is more weakly convex, with the apical margin bearing a more loosely developed fringe of hairs, and the punctation is regularly distributed with larger distances between punctures (approximately twice the puncture diameter). By contrast, the right side is more strongly convex, exhibits a more densely haired apical margin, and reveals denser punctation (< 2× puncture diameter). A similar bilateral differentiation is present on terga 2–5 (Fig. 2a), with regular punctation and weakly chagrined interspaces on the left side, while the right side shows denser punctation with partly more strongly shining interspaces.

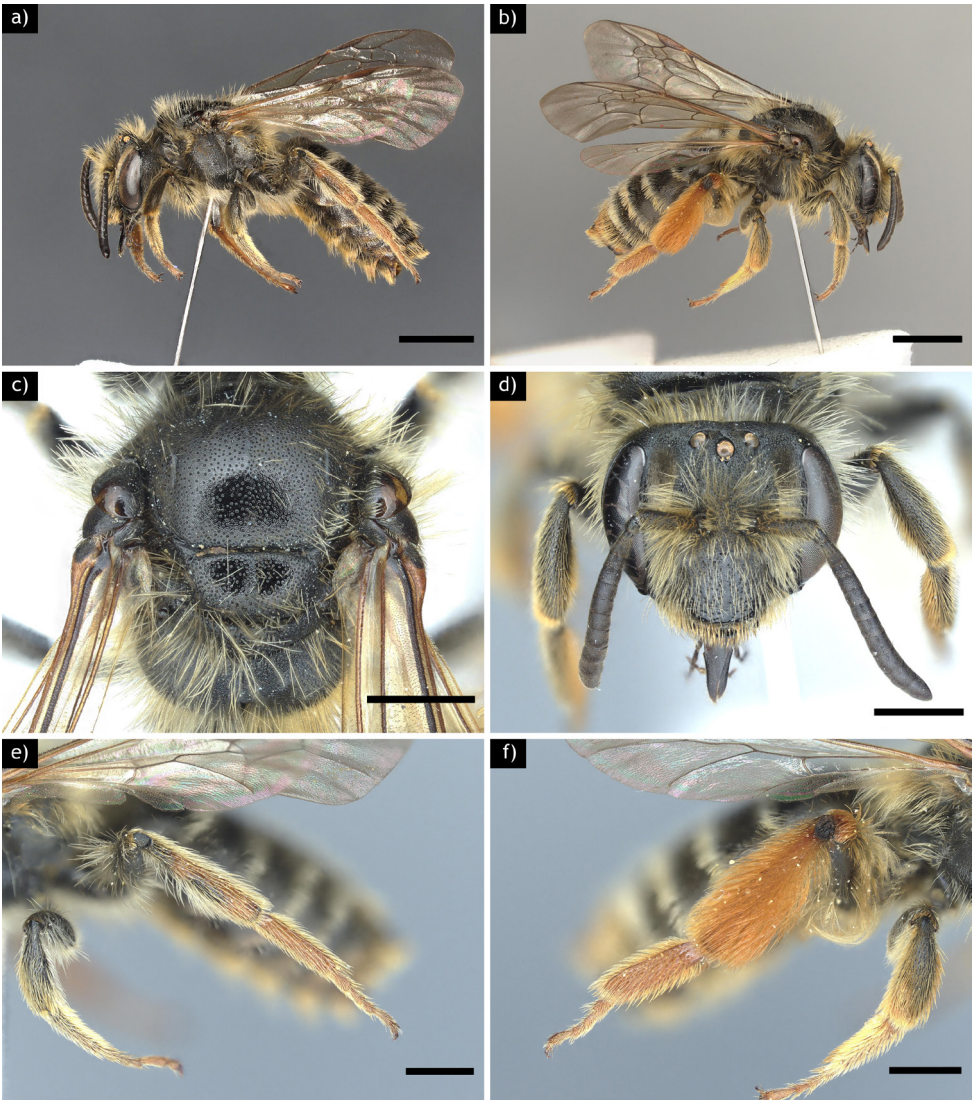

Figure 1. Gynandromorphic specimen of *Andrena florivaga* showing a predominantly bilateral expression of sexually dimorphic traits. **a** left side of the body with predominantly male characteristics **b** right side with female characteristics **c** mesosoma with bilaterally differing punctation, with larger puncture distances on the left than on the right **d** frontal view of the head showing a completely female morphology without bilateral differentiation; clypeus, labrum, and facial pubescence correspond to the female morphology **e** left hind leg with male traits **f** right hind leg with female morphology, with a densely haired orange scopa, broadened tibia, and broadened orange metatarsus. Scale bar: 1.0 mm (**a–f**).

The terminal region is also asymmetrical. On the right side a partially developed orange apical fringe is present, while it is absent on the left. The pygidium is half-developed, only visible on the right side (Fig. 2b). The sting apparatus is partially preserved

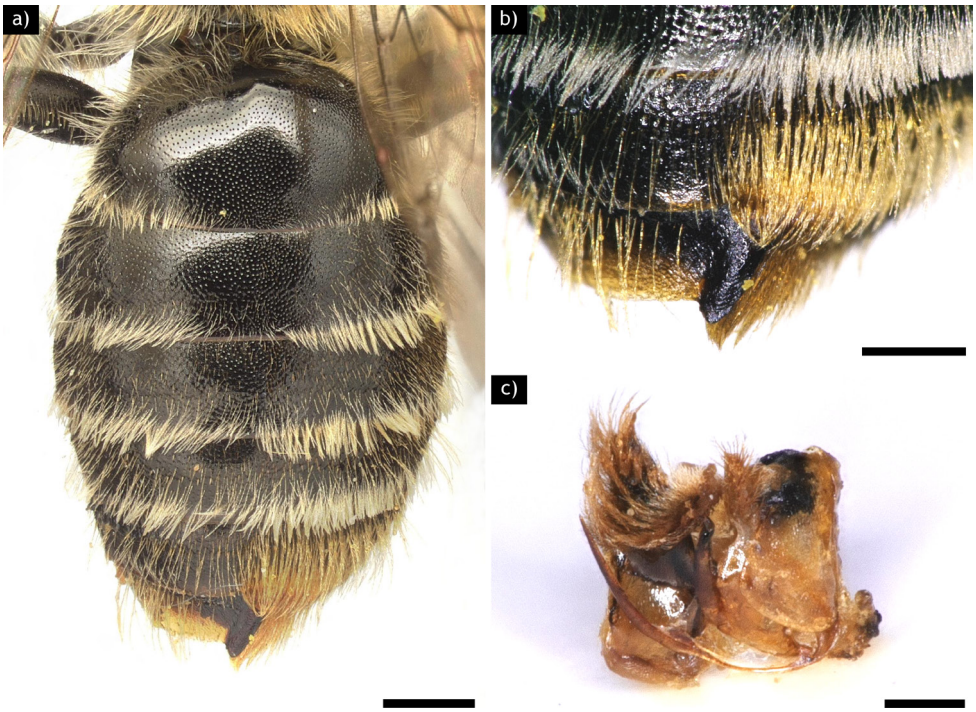

Figure 2. Detailed views of the gynandromorphic *Andrena florivaga* specimen showing bilateral differentiation of sexually dimorphic traits. **a** dorsal view of the metasoma; left side of the body with larger puncture distances on tergum 1 and looser pubescence, right side with a more strongly convex first tergite and more pronounced yellowish-white bands **b** terminal region with a partially developed pygidium and a partially preserved orange apical fringe on the right side of the body **c** genital apparatus with a deformed sternite 8 and a rudimentary sting. Scale bars: 1.0 mm (**a**); 0.5 mm (**b**); 0.25 mm (**c**).

on the right side, whereas on the left a deformed male sternite 8 is present. The genital apparatus consists of both male and female structures without a clearly recognizable bilateral boundary. A stinger with a curved, bow-like shape is present; a gonocoxite is developed but distally merges into a diffusely setose structure without a clearly defined gonostylus (Fig. 2c).

A complete overview of all diagnostically relevant characters is provided in Table 1.

Description of the gynandromorphic *Nomada lathburiana*

In the examined specimen of *N. lathburiana*, a mainly bilateral separation of male and female traits is present, particularly visible in the tergites and sternites, the mesosomal pubescence, and the coloration of the legs. However, within certain body regions alternating side assignments and indistinct transitions occur, so that the specimen can be interpreted as a predominantly bilateral gynandromorph with mosaic-like elements (Fig. 3a–c).

Table 1. Comparison of male and female characters in the gynandromorphic *Andrena florivaga* specimen.

Body region	Left body side	Right body side	Remarks
Head	With fovea (both sides)	.	Fully ♀
Pronotum (posterior margin)	Short whitish pubescence	Short yellowish pubescence	♂ left; ♀ right
Mesonotum (mesoscutum)	Chagrined, medially smooth; sparse punctation (>2× puncture diameter)	Chagrined, medially smooth; densely punctate (1–2× puncture diameter)	♂ left; ♀ right
Forelegs	Tibia slightly thickened (both sides)	.	Fully ♀
Middle legs	Metatarsus narrow, basally darkened; pubescence yellowish-white	Legs enlarged; metatarsus broadened, orange; pubescence orange-yellow	♂ left; ♀ right
Hind legs	Narrow, white pubescent; tibia orange and black	Broadened; scopa well developed	♂ left; ♀ right
Flocculus	.	Long, yellow	♂ left; ♀ right
Tergum 1	Sparsely pubescent apical margin; regular punctation (2× puncture diameter)	More strongly convex; densely punctate (<2× puncture diameter)	♂ left; ♀ right
Tergum 2–5	Sparsely pubescent apical margin	Densely yellowish-white pubescent apical margin	♂ left; ♀ right
Apical fringe	.	Present on one side	♂ left; ♀ right
Pygidium	.	Present on one side	♂ left; ♀ right
Genital	Deformed	.	No clear bilateral assignment
Sternite 8	Deformed	.	♂; no clear bilateral assignment
Sting	Present	.	♀; no clear bilateral assignment

The head is predominantly female in appearance. The pubescence of the dorsal surface and the face is reddish; the clypeus, supraclypeal area, and labrum are also red. By contrast, the area between the eyes and the clypeus as well as the mandibles are yellow, corresponding to the male condition. The underside of the genae shows a red-white mixed pubescence on both sides and exhibits a mosaic-like combination of male and female traits (Fig. 3e). The posterior margin of the eye is red on the left side and yellow on the right side. Both antennae are reddish-brown; small nodules are present on the left antenna, corresponding to the male morphology (Fig. 3f).

The mesosoma is bilaterally differentiated, particularly visible in the pubescence and in the coloration of the tegulae and the spots on the scutellum. The right side reveals red pubescence on the mesonotum, reddish-brown tegulae, and an orange spot on the scutellum, corresponding to the female morphology. The left side of the mesonotum is predominantly covered with white hairs with a few scattered red hairs and bears yellow tegulae and a yellow spot on the scutellum, corresponding to the male morphology (Fig. 4a).

The mesopleurae show a spot on the anterior margin on both sides; this spot is yellow on the left side (male) and red on the right side (female). The mesosternum, propodeum, and metapleurae reveal no externally visible differences in pubescence or coloration between the two sides.

A bilateral differentiation of sex-specific traits is restricted to the forelegs with only partial expression. Only the right fore femur is red and thus corresponds to the female

Figure 3. Gynandromorphic specimen of *Nomada lathburiana* with a predominantly bilateral, but mosaic-like mixture of sexually dimorphic traits. **a** left side of the body with male characteristics **b** right side with female characteristics **c** dorsal view **d** ventral view **e** frontal view of the head showing a predominantly female morphology but with mosaic-like distribution of male traits, including yellow coloration between the eyes and the clypeus as well as yellow-colored mandibles **f** detailed view of the antennae with male-type nodules on the left antenna (arrows). Scale bars: 2.0 mm (**a–e**); 0.5 mm (**f**).

condition, while the remaining parts of the forelegs do not allow a clear bilateral assignment. The middle pair of legs is predominantly red and therefore female in appearance. The hind legs correspond primarily to the male morphology but show slight

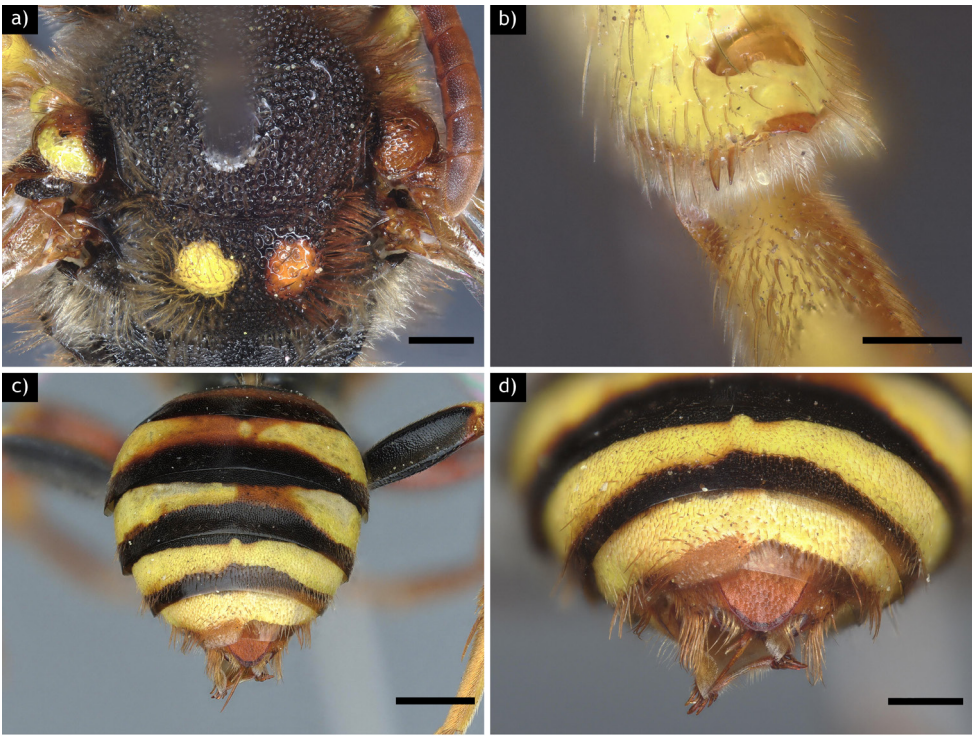

Figure 4. Detailed views of the gynandromorphic *Nomada lathburiana* specimen showing bilateral and mosaic differentiation of sexually dimorphic traits. **a** dorsal view of the mesosoma: left side with yellow tegula, yellowish-white pubescence, and a yellow spot on the scutellum (male); right side with reddish-brown pubescence, reddish-brown tegula, and an orange spot on the scutellum (female) **b** detailed view of the spination of the left femur with both transparent and dark spines **c** metasoma with terga 2–5 showing bilateral differentiation: tergum 2 with a narrow yellow spot on the left (female) and a large yellow spot on the right (male); tergum 3 with a yellow band on the left (male) and a yellow spot on the right (female); tergum 4 with a densely punctate, hairy apical margin on the left (male) and a smooth, hairless apical margin on the right (female); tergum 5 with dense bristles on the apical margin on the left (female) and a smooth apical margin on the right (male) **d** detailed view of tergum 5 with dense bristles on the apical margin on the left side (female) and a smooth, brownish translucent apical margin on the right side (male); pygidium and sting apparatus visible, with a second diverging sting tip. Scale bars: 0.5 mm (**a, d**); 0.2 mm (**b**); 1.0 mm (**c**).

darkening on the inner side of the femora. The leg spines are not typically male, as they appear stronger and darker than in normal males of *N. lathburiana* (Fig. 4b).

Gynandromorphy is also clearly visible in the metasoma, although the bilateral separation is not consistently maintained. The first tergite is crossed by a red transverse band but bears a yellow spot on the right side, typical for females. On the second tergite the left side reveals a narrow yellow spot gradually merging into a broad red transverse band, corresponding to the female morphology. The right side, by contrast,

shows a large yellow spot with a smaller red transverse band and a sharper boundary, corresponding to the male condition. On the third tergite the sexual traits are reversed: on the right side there is a yellow spot with a red transverse band (female), while on the left side a yellow band extends to the middle of the tergite (male) (Fig. 4c).

On the fourth tergite the left side is smooth, unpunctured and without hairs, and dark brown to black in color, corresponding to the male morphology. The right side is coarsely punctate and hairy, with a translucent reddish-brown apical margin, corresponding to the female condition. On the fifth tergite the left side bears dense bristles, a typical feature of female *Nomada* spp., whereas the right side reveals a smooth, translucent reddish-brown apical margin. The pygidium is fully developed, broad, rounded, and colored reddish-orange (Fig. 4d).

Sternites 1–4 are clearly divided bilaterally, with the right side red and female, and the left side yellow and male (Fig. 3d). Sternite 6 is entirely female in structure but deformed; the typical posteriorly directed and curved spines of females are present. The sting apparatus is present, however, the stinger shows a second, diverging tip.

A complete overview of all diagnostically relevant characters is provided in Table 2.

Table 2. Comparison of male and female characters in the gynandromorphic *Nomada lathburiana* specimen.

Body region	Left body side	Right body side	Remarks
Face	Red pubescent (both sides)	.	Fully ♀
Clypeus	Red (both sides)	.	Fully ♀
Supraclypeal area	Red (both sides)	.	Fully ♀
Labrum	Red (both sides)	.	Fully ♀
Area between eye and clypeus	Yellow (both sides)	.	Fully ♂
Genae	Red and white pubescence (both sides)	.	♂; ♀ mosaic
Posterior eye margin	Red	Yellow	♀ left; ♂ right
Antennae	12 antennomeres; reddish-brown with nodule	12 antennomeres; reddish-brown	Primarily ♀; nodule on left ♂
Mandibles	Yellow (both sides)	.	Fully ♂
Mesonotum	White pubescent	Red pubescent	♂ left; ♀ right
Tegulae	Reddish-brown with yellow spot	Reddish-brown	♂ left; ♀ right
Mesopleura (anterior margin)	Yellow spot	Red spot	♂ left; ♀ right
Scutellum	Yellow spot; yellow-brown pubescent	Orange spot; red pubescent	♂ left; ♀ right
Forelegs	Yellow	Right femur red	Primarily ♂; only right femur ♀
Middle legs	Red; yellow spot on femur	Red	♀
Hind legs	Dark and light spines; femur darkened internally (both sides)	.	Primarily ♂; dark spines ♀
Tergum 1	Red transverse band	Red transverse band with yellow spot	♀ left; ♂ right
Tergum 2	Narrow yellow spot	Large yellow spot	♀ left; ♂ right
Tergum 3	Yellow	Red interruption	♂ left; ♀ right
Tergum 4	Smooth apical margin; hairless	Apical margin densely punctate; pubescent	♀ left; ♂ right
Tergum 5	Apical margin with dense bristles	Smooth apical margin	♀ left; ♂ right
Pygidium	Broad; reddish-orange	.	Fully ♀
Sternite 1–4	Red	Yellow	♀ left; ♂ right
Sternite 6	With curved spines (both sides)	.	Fully ♀
Sting	Present; with second diverging tip	.	Fully ♀

Discussion

Gynandromorph of *Andrena florivaga* in comparison with other representatives of the genus

To our knowledge, this is the first documented case of gynandromorphy in *Andrena florivaga*. The specimen generally corresponds to the bilateral type of gynandromorphic organization in Hymenoptera (Michez et al. 2009). The consistent bilateral differentiation, clearly visible from the mesosoma to the metasoma, classifies the specimen as a predominantly bilaterally organized gynandromorph.

By contrast, the head and forelegs are entirely female and show no bilateral differentiation. This anterior uniformity represents a transversal deviation from the bilateral basic pattern without fundamentally altering it. Such combinations in gynandromorphic Hymenoptera are interpreted as the result of temporally offset processes of sex determination (Wcislo et al. 2004; Narita et al. 2010).

A close comparison within the genus *Andrena* is possible through the study by Xu and Cui (2007), who documented an almost perfectly bilaterally organized gynandromorph of *Andrena chengtehensis*. In that case, male traits are consistently restricted to the left and female traits to the right side of the body, while the genital structures also display a combination of male and female characters. The specimen examined here can be assigned to this bilateral basic pattern but extends it through the entirely female expression of the head and forelegs, thus documenting an additional anterior modification of the bilateral organization.

In clear contrast, several other published gynandromorphic *Andrena* specimens show gynandromorphic traits restricted to the head or to individual anterior structures. In studies on *Andrena barbilabris*, *A. humilis* and *A. praecox* (Wolf 1993, 1995, 1998) and on *A. helvola* (Celary & Wiśniowski, 2001), male traits are limited to the head region, while the mesosoma and metasoma remain completely sex-typical. These findings indicate that gynandromorphy within the genus *Andrena* has so far mostly been documented as a regionally restricted, head-focused phenomenon.

The terminal region of the specimen examined here shows both male and female structures due to its high morphological complexity, without a clearly traceable bilateral separation. This limited assignability should not be interpreted as a mosaic organization but rather reflects the limits of purely morphological analyses of complex genital structures (Xu and Cui 2007; Fusco and Minelli 2023).

Gynandromorph of *Nomada lathburiana* in comparison with published specimens

For *Nomada lathburiana*, two well-documented gynandromorphic specimens have already been reported in the studies by Le Féon et al. (2016) and Carion et al. (2025), although they exhibit clearly different organizational patterns. Le Féon et al. (2016) describe a mostly bilaterally organized gynandromorph with mosaic interruptions across several body regions, whereas Carion et al. (2025) document a case in which

gynandromorphic traits are restricted to the head, while the mesosoma and metasoma are entirely female. Against this background, the specimen examined here allows a further classification of the morphological range of gynandromorphic expressions within the same species.

The present *Nomada* specimen cannot be classified as either strictly bilaterally organized or as a gynandromorph restricted to the head. Instead, several body regions are involved, with bilateral, mosaic-like, and completely sex-typical traits combined in a complex manner. This intermediate organizational form differs clearly from both previously described cases and demonstrates that gynandromorphic patterns in *N. lathburiana* do not follow a uniform appearance.

Particularly informative is the decoupling of sex-specific traits within individual structures. Male and female characters do not occur exclusively depending on body side but are partly distributed in a mosaic-like manner within the same body region. This pattern generally corresponds to the transitional forms described by Le Féon et al. (2016), but in the present case it is less consistently organized bilaterally and is simultaneously characterized by a clear dominance of female traits. Such decouplings are interpreted as an expression of complex developmental pathways in gynandromorphic Hymenoptera (Wcislo et al. 2004; Fusco and Minelli 2023).

Conclusions

The two gynandromorphic specimens presented here show a similarly high structural complexity while belonging to different taxa, but differ markedly in the spatial organization of sex-specific traits. While the *Andrena* specimen is characterized by a consistent bilateral organization from the mesosoma onward, with an anterior transversal modification, the *Nomada* specimen exhibits an intermediate combination of bilateral, mosaic-like, and entirely sex-typical traits.

Both cases share the feature that gynandromorphic traits are not restricted to individual body regions but involve several segments and may deviate from a strictly bilateral organization. These findings highlight the considerable variability of gynandromorphic expressions in wild bees, which can occur even within a single species and are likely determined by the interaction of several temporally offset developmental processes. Both specimens therefore expand the currently known range of gynandromorphic organizational forms within the Apoidea.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

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No ethical statement was reported.

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Data availability

The DNA sequence data generated in this study have been deposited in GenBank under accession number PZ623334.