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RESEARCH

Species discrimination in the parasitic bee genus *Nomada* based on wing morphometrics (Hymenoptera: Apoidea: Apidae)

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Abstract
Geometric morphometrics (GM) is a series of methods that enables the quantitative analysis of shape by analysing landmarks. It is widely used to investigate morphological variation in both vertebrates and invertebrates. These methods are commonly applied to infer taxonomic affinities in wild bees, as they are easier, cheaper and less destructive than chemical and molecular analyses, while the characters are preserved in collections over time. However, GM has not yet been tested in the parasitic genus *Nomada* Scopoli, 1770 which is a genus of wild bees that mainly parasitize the nests of *Andrena* Fabricius, 1775 in a wide variety of environments. Here we demonstrate that wing morphometry can locally differentiate *Nomada* species, including the near cryptic *panzeri*-group, represented by *Nomada flava* Panzer, 1798 and *Nomada panzeri* (Lepeletier, 1841). Geometric morphometrics further confirms its effectiveness in distinguishing bees at the subgeneric level. Finally, a sexual dimorphism in wing shape and size is observed in several species.

Keywords Taxonomy · Geometric morphometrics · Wild bees · Nomad bees

Introduction

Bees (Hymenoptera: Anthophila) are a diverse and widespread group of pollinators comprising seven families and over 20,000 described species globally (Michener 2007; Michez et al. 2019; Ascher and Pickering 2020). Among them, the family Apidae has the highest species diversity, with more than 5500 described species (Michener 2007; Ascher and Pickering 2020). Within Apidae, the genus *Nomada* Scopoli, 1770 is a widespread parasitic group, containing roughly 800 described species globally and mostly targeting species of the genus *Andrena* Fabricius, 1775 as hosts (Michener 2007; Smit 2018; Ascher and Pickering 2020; Straka et al. 2024). Females of *Nomada* do not dig their own nest but instead lay their eggs in the nest of their hosts; this genus is thus referred as brood parasitic (Michener 2007; Smit 2018; Straka et al. 2024). Due to this parasitic lifestyle, *Nomada* are generally found in the same habitats as their hosts, which can be highly diverse (Michener 2007; Smit 2018).

Morphometrics quantitatively studies biological structures by measuring shape and size variation but also their covariation with other variables (Bookstein 1992; Claude 2008; Adams et al. 2013). Geometric morphometrics comprises a set of methods that statistically analyse anatomical structures by capturing and preserving the geometry of morphological structures throughout the analyses (Adams et al. 2013). Within geometric morphometrics, the Procrustes-based landmark methods analyse anatomical structures using Cartesian coordinates of landmarks after mathematically removing non-shape variations (Bookstein 1992; Claude 2008; Adams et al. 2013). This method has been widely applied to differentiate taxa across various taxonomic groups (Cardini et al. 2009; Ahmad et al. 2022; Shukri et al. 2024; Özkan et al. 2024; Casaubon and Riehl 2024), including bees (Francoy et al. 2008; Martinet et al. 2019; Dehon et al. 2019; Gérard et al. 2020). Among bees, wing vein intersections and cell apexes are commonly used to digitize landmarks (Francoy et al. 2008; Martinet et al.

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2019; Dehon et al. 2019; Gérard et al. 2020; Ghisbain et al. 2021; Soipijit and Sopaladawan 2024). Wing morphometrics is particularly valuable to discriminate taxa at the family and genus levels, but its effectiveness is more variable at lower taxonomic levels (Aytekin et al. 2007; Dehon et al. 2019). Yet, this approach has the advantage of remaining reliable even when specimens are aged, as the wings of most museum individuals are generally well-preserved for such analyses, and is more cost-effective and accessible than molecular and chemical methods such as DNA analyses, cuticular hydrocarbons, etc. (Francoy et al. 2008; Gérard et al. 2020; Soipijit and Sopaladawan 2024). As a completely non-destructive method, it also fully preserves specimens, making it highly valuable for studying historical entomological collections (Gérard et al. 2020).

This study introduces for the first time wing morphometrics as a diagnostic tool in the genus *Nomada* by exploring wing shape variations of a selection of species from Belgium (six species tested out of the 52 species of Belgium), testing this method to differentiate the studied species, including a near-cryptic group composed of *N. panzeri* and *N. flava* (Falk et al. 2022). Four other species are included in the analyses to assess wing shape divergence among genetically related but morphologically distinct species. As we analyse specimens of both sexes, the dataset further allows us to investigate sexual dimorphism in wing shape and size, and to make a first assessment of the discriminative power of wing shape at the subgeneric level in this group of bees.

Materials and methods

Dataset

Wing morphometrics was analysed in the six most abundant *Nomada* species hosted in the collection of the Laboratory of Zoology at the University of Mons (UMons). These species are included in two subgenera: *Heminomada* Cockerell, 1902 for *N. goodeniana* and *N. fucata*) and *Nomada* Scopoli, 1770 for *N. fabriciana*, *N. flavoguttata*, *N. flava* and *N. panzeri*) considering the phylogeny of Straka et al. (2024). The species were also chosen due to their variability in terms of phylogenetic relationships (i.e. their phylogenetic distances), making it useful for testing wing shape variation on various level of generic relationships. All specimens were collected in Belgium, and their number per sex and species ranged from 12 to 50, depending on their availability in the collection (Table 1). Specimens were selected to maximise the number of distinct sampling localities thus maximizing the intraspecific variation and reducing the spatial autocorrelation among specimens (Carion et al. 2026).

Table 1 Number of *Nomada* specimens studied per sex and species used to assess the differences in wing morphometry within the genus

Species	Females	Males
Nomada (*Nomada*) *fabriciana* (Linnaeus, 1767)	50	50
Nomada (*Nomada*) *flavoguttata* (Kirby, 1802)	47	48
Nomada (*Nomada*) *flava* Panzer, 1798	50	50
Nomada (*Heminomada*) *fucata* Panzer, 1798	50	50
Nomada (*Heminomada*) *goodeniana* (Kirby, 1802)	37	19
Nomada (*Nomada*) *panzeri* (Lepeletier, 1841)	39	12

Geometric morphometrics

The right forewings were photographed with a standardized millimetre scale positioned beneath them except if the wing was unusable (i.e. broken, folded, with an aberrant number of cells, or missing). In that case, the left forewing was photographed and flipped using GNU Image Manipulation Program (GIMP) 2.10.36 to mimic a right forewing (left forewings composed around 6.5% of the studied wings). The pictures were taken using an Olympus SZH10 stereo microscope equipped with a Planapo IX lens, an Olympus Highlight 3000 lamp and a Nikon D70 digital camera. In the following analyses, males and females were analysed together to assess sexual dimorphism in term of wing shape and size, in addition to the interspecific variation.

The "Tps" software suite processes .tps files, generated using wing images, for subsequent analyses (Rohlf 2013a, b). First, .tps files were created using tpsUtil32 v. 1.83. Then, eighteen landmarks were digitised on each picture following a specific pattern (Fig. 1) which was already used in similar studies on others group of bees (Wappler et al. 2012; Martinet et al. 2019; Gérard et al. 2020), and the scale was set for each picture using tpsDig232 v. 2.31. These steps produced a set of Cartesian coordinates, representing the landmark configuration for each wing. All digitising was carried out by a single trained researcher, to minimize variability.

A Procrustes superimposition was first applied to the data to minimise positional differences and standardize size, preserving it as a separate variable. This approach first scales each wing's landmark configuration to unit centroid size. Centroid size is defined as the square root of the sum of squared distances from each landmark to the centroid of a specific landmark configuration. The superimposition then translates the configuration to a common centroid, and optimally rotates the landmark configurations, minimizing the total sum of squared distances between corresponding landmarks across specimens.

Centroid size was used to estimate wing size. Wing size differences among species and between sexes were first analyzed using a one-way analysis of variance (ANOVA) with Tukey's Honest Significant Difference (HSD) post-hoc test for pairwise comparisons. Wing shape variation, as well as

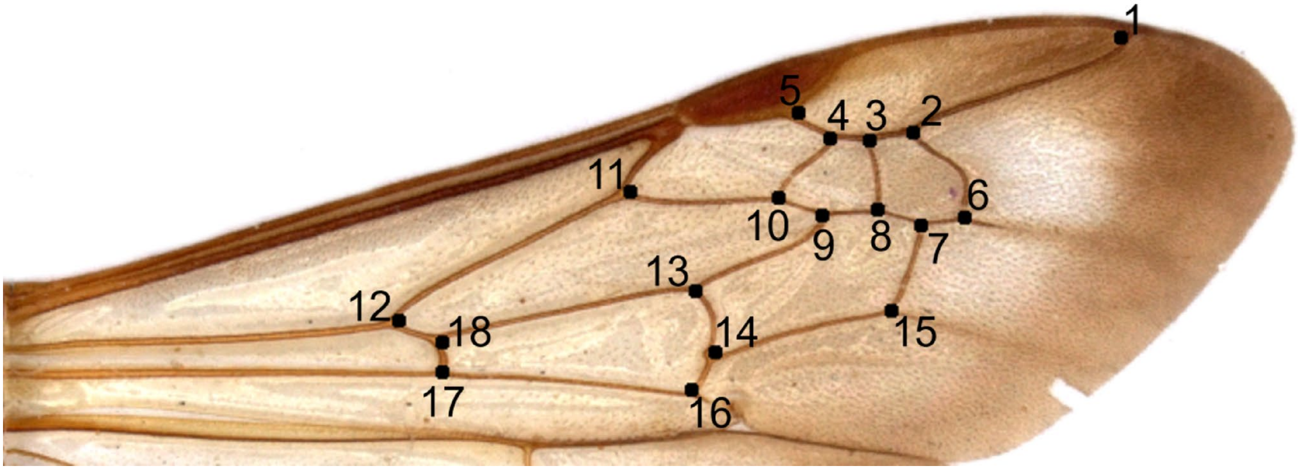

Fig. 1 Right forewing of *Nomada flava* male and the eighteen landmarks used to quantify wing shape

Table 2 Interspecific and intersexual differences in wing centroid sizes for the tested *Nomada* species based on ANOVA test

	Df	Sum Sq	Mean Sq	F value	*P* value
Species	5	442.4	88.49	612.13	<0.001**
Sex	1	11.6	11.60	80.23	<0.001**
Species and sex	5	2.5	0.50	3.49	0.004**
Residuals	490	70.8	0.14		

Df is the degrees of freedom. Sum Sq is the sum of squared differences to the group means in a hierarchical ANOVA. Mean Sq is the sum of squares divides by the corresponding degrees of freedom. F value is the ratio of explained variance to residual variance

**$p<0.01$

the clustering of species and sexes, were summarized using principal component analysis (PCA). Linear discriminant analysis (LDA) assessed the classification accuracy of wing shape, while a two factors Procrustes ANOVA evaluated the significance of shape differences.

The accuracy of the LDA was evaluated using a leave-one-out cross-validation (LOO-CV) approach. This method involves iteratively excluding each observation from the dataset and using it as a test case, while the LDA model is trained on the remaining data. The predicted species identity from the LDA is then compared to the true identity of the observation. This process is repeated for each observation, allowing for the calculation of the percentage of correct classifications for each species and sex. The LOO-CV approach provides an estimate of the model's ability to accurately classify individuals based on their wing morphometry.

All the morphometric analyses were performed using Rstudio 2024.09.1 and R ver. 4.4.2 as well as the packages geomorph (Baken et al. 2021; Adams et al. 2025), RRPP (Collyer and Adams 2018, 2024), ggplot2 (Wickham 2016), MASS (Venables and Ripley 2002) and car (Fox and Weisberg 2019).

Results

Wing size analysis

For wing size, the ANOVA reveals highly significant interspecific and intersexual differences (Table 2; Fig. 2). Almost all pairwise comparisons were significant ($p<0.001$; Online Resource 1, Fig. 2), except for the pairs *N. goodeniana*-*N. flava* and *N. panzeri*-*N.fucata*, which are not significantly different (both $p>0.1$; Online Resource 1, Fig. 2). The comparison between sexes also shows a strongly significant difference ($p<0.001$; Online Resource 1). A more detailed inspection of the pairwise contrasts reveals that most sex-species combinations are significantly different in wing size (most $p<0.05$), however the pairs of *N. flavoguttata* male-*N. flavoguttata* female ($p=0.929$), *N. fucata* male-*N. fucata* female ($p=0.324$), *N. goodeniana* male-*N. goodeniana* female ($p=0.081$) are not significantly different (Online Resource 1, Fig. 2).

Wing shape analysis

The first two principal components of the PCA on the wing shape data reveal two distinct clusters (Fig. 3). One cluster comprises *N. fucata* and *N. goodeniana*, while the second includes *N. fabriciana*, *N. flavoguttata*, *N. flava* and *N. panzeri* (Fig. 3).

For females, *N. fucata* and *N. goodeniana* form a clearly separated cluster with no overlap, whereas the second group of four species shows substantial overlap among species (Fig. 3). In contrast, males show greater overlap, especially between *N. fucata* and *N. goodeniana*. The second group displays a similar level of overlap to that observed in females (Fig. 3). Finally, males and females show partial overlap within each species (Fig. 3).

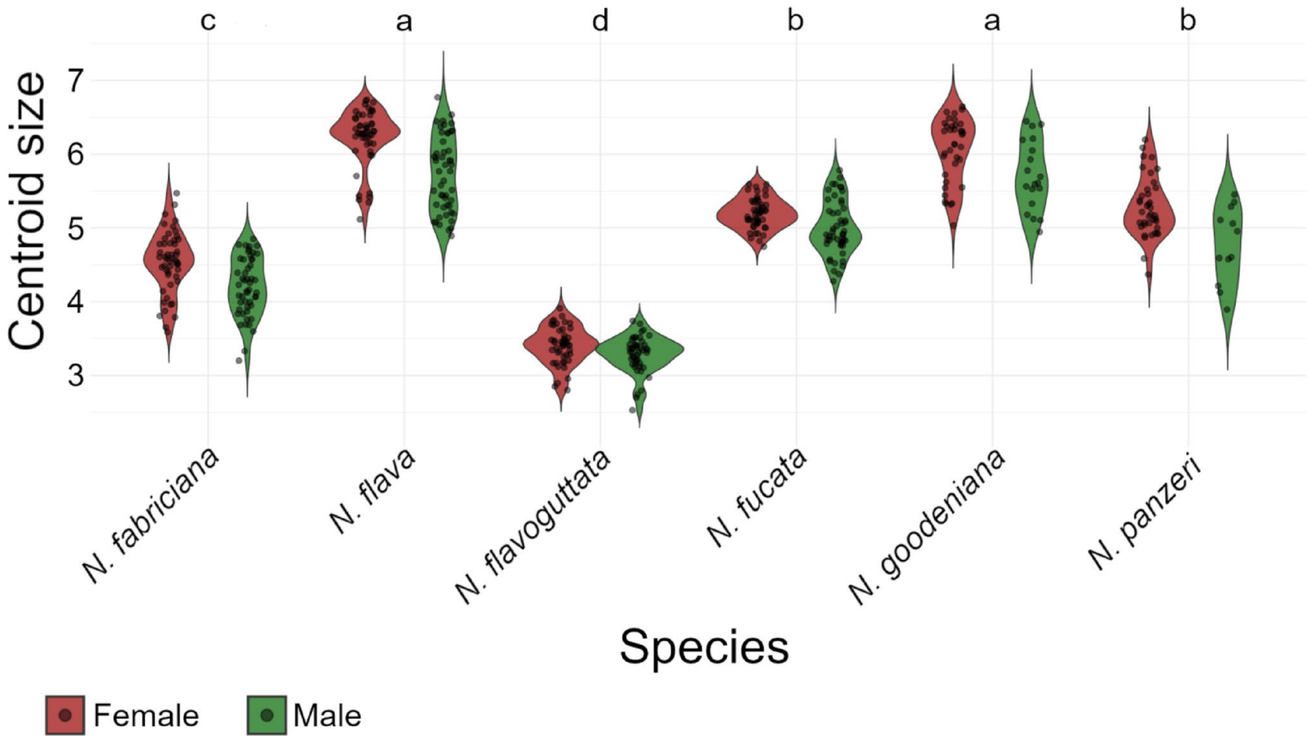

Fig. 2 Distribution of the centroid sizes for the wings of *Nomada* species for both females and males. Letters above the boxplots indicate significant interspecific differences, species sharing the same letter are not significantly different while species that do not share the same letter are significantly different

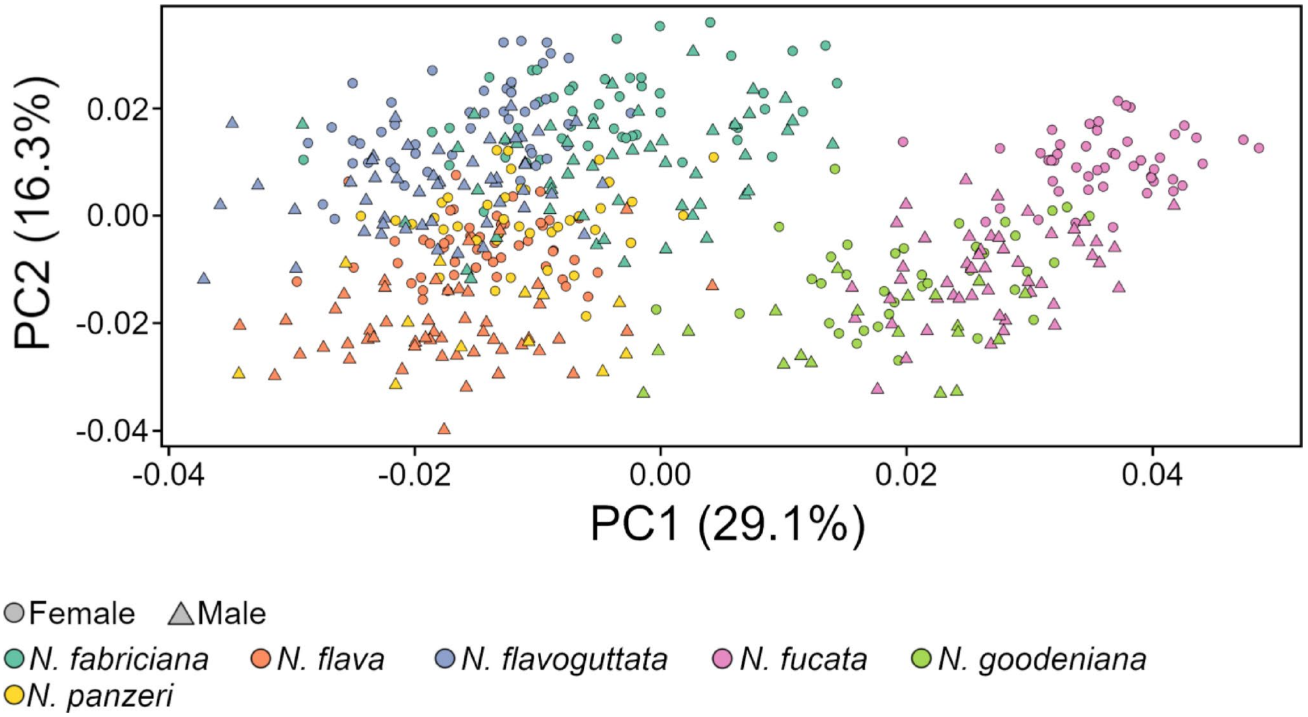

Fig. 3 Ordination of the *Nomada* species along the first two axes of the PCA reflecting wing shape variation. Specimens of both sexes in the same graph

Overall, the two factors Procrustes ANOVA shows a highly significant interspecific difference in wing shape among the studied species ($p < 0.01$; Table 3). Concerning the intersexual differences, the Procrustes ANOVA also indicates a strongly significant effect of sex on wing shape ($p < 0.01$; Table 3). Moreover, sexual dimorphism in wing shape varied significantly ($p < 0.01$; Table 3). The LDA reaches an average accuracy of 94.6% based on leave-one-out cross validation, indicating that almost all the specimens are correctly classified to their species and sex based on wing shape (Online Resource 3). Most misclassifications arise from confusion between males and females within a same species (between one and three individuals per species are; Online Resource 3). Additional misidentifications involves species-level errors: one *N. panzeri* female being misidentified as a *N. flava* female; one *N. panzeri* female being misidentified as a *N. flava* male; one *N. panzeri* female being misidentified as a *N. flavoguttata* male; one *N. flava* male being misidentified as a *N. panzeri* male and one *N. panzeri* male being misidentified as a *N. flava* male (Online Resource 3).

Discussion

This work unveils that wing morphometrics can serve as a valuable taxonomic tool to locally differentiate species within the parasitic bee genus *Nomada*, especially for the challenging and near cryptic *panzeri*-group (here represented by *N. panzeri* and *N. flava*). This method demonstrates particularly high accuracy, achieving an overall accuracy of 94.6%. Therefore, wing morphometrics can aid species identification, even if it should be used cautiously to minimise errors rather than as an absolute diagnostic criterion. However, two potential limitations should be considered regarding the intraspecific variations and the spatial autocorrelation among specimens. Firstly, although intraspecific variation was maximized by including specimens from various localities across Belgium, all studied species display a broader geographic range (Smit 2018). As such, the full extent of wing shape variation remains unknown, our knowledge being currently restricted to Belgium. Secondly, while spatial autocorrelation was minimized by the multiple localities, some species were represented by a higher number of specimens for particular sites (see Carion et al. 2026 for the precise data). This uneven sampling may lead to residual spatial autocorrelation, potentially inflating within-species similarity and, consequently, between-species differentiation.

The pattern of wing size appears to align with the observed pattern of body length, with the larger species having larger wings (Smit 2018 for the body length). Moreover, wing size appears to be generally smaller in males than females, with lower interspecific variability than in females, a pattern also present in the body length (Fig. 2; Table 2; Online Resources 1; Smit 2018). Species with non-significant intersexual differences (*N. flavoguttata*, *N. fucata* and *N. goodeniana*) tend to have a more similar body lengths between sexes than other species (Smit 2018), possibly explaining their more similar wing sizes.

The differences observed in wing shape (Fig. 3, Online Resource 2) appear to mostly align with the phylogenetic relationships recently highlighted by Straka et al. (2024) (Fig. 4). Indeed, the separation of species into two groups in both the PCA and LDA plots (Fig. 3, Online Resource 2) is likely due to the presence of two different subgenera in the analyses. In fact, *N. goodeniana* and *N. fucata* consistently cluster together across all plots and belong to the subgenus *Heminomada* Cockerell, 1902 whereas the four other species are classified within the subgenus *Nomada* Scopoli, 1770 (Straka et al. 2024). The use of wing morphometry to diagnose subgenera has already been tested in bumblebees, yielding significant results (Aytekin et al. 2007; Wappler et al. 2012). While further research is needed to confirm this result, it is thus plausible that most of the bee subgenera can be distinguished based on wing morphometry if these subgenera are clearly defined (e.g. based on genetic evidence, and not only morphological criteria). Moreover, phylogenetically close species exhibit more similar wing shapes, independent of their general morphological similarities, such as

Table 3 Interspecific and intersexual differences of wing shape for the tested *Nomada* species based on a two factor procrustes ANOVA

	Df	SS	MS	Rsq	F	Z	*P* value
Species	5	0.338	0.068	0.463	98.150	15.327	0.001**
Sex	1	0.044	0.044	0.060	63.531	9.782	0.001**
Species and sex	5	0.011	0.002	0.015	3.140	6.767	0.001**
Residuals	490	0.337	0.001	0.462			
Total	501	0.730					

Df is the degrees of freedom. SS is the sum of squared differences to the group means in a hierarchical ANOVA. MS is the sum of squared differences to the group means in a hierarchical ANOVA. MS is the sum of squares divided by the corresponding degree of freedom. Rsq is the proportion of total variance explained by the statistical model. F is the ratio of variance explained to residual variance. Z is a permutation-based standardized effect-size, calculated as the number of standard deviations the observed test is from the mean of its permutation-based sampling distribution

**$p < 0.01$

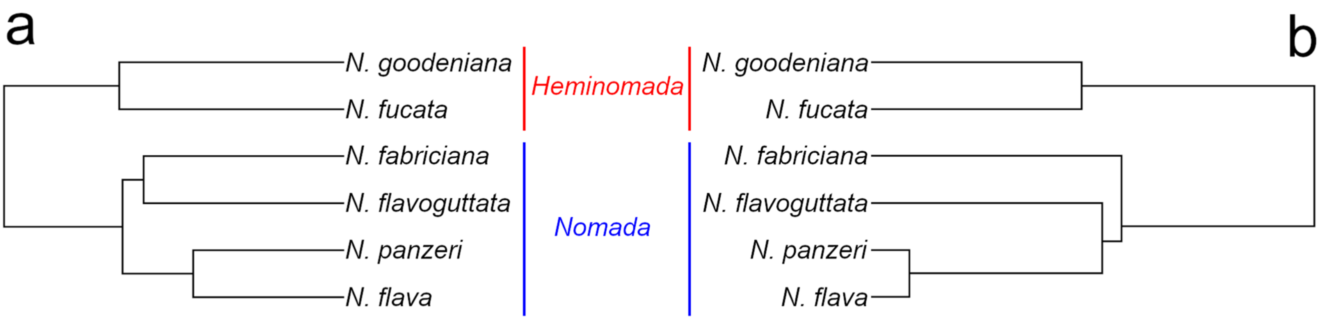

Fig. 4 Comparison between the groups established using wing morphometrics data and the phylogeny for the six studied species of *Nomada*. Corresponding subgenera highlighted at the centre of the figure. **a** Phenogram built using the wing shape data produced during the study. **b** Simplified phylogeny of the genus, containing only the six studied species, based on the phylogeny of Straka et al. (2024)

their habitus or even other specific characters (Fig. 4; Smit 2018). These results confirm existing knowledge about the relationship between wing shape and phylogeny, as highlighted in other groups (Perrard et al. 2014). The apparent phylogenetic signal in wing morphology suggests that wing shape evolution is at least partly constrained by evolutionary history. Closely related species may retain similar wing structures due to shared developmental pathways, with divergence occurring gradually along lineages (Klingenberg and Gidaszewski 2010). This pattern indicates that wing shape could provide insight into the evolutionary trajectories of species within the genus, reflecting both historical relationships and potential adaptations (Chazot et al. 2016). However, in our case, divergence in wing shape consistent with phylogenetic relationships may also arise through neutral evolutionary processes, such as genetic drift, rather than adaptive differentiation.

In addition to the significant interspecific variations found in wing shape, a significant intersexual variation was unveiled (Fig. 3, Online Resource 2, Table 3). This sexual dimorphism may reflect differences in behaviour between the sexes: females are responsible for locating host nests and laying eggs, while males search for females by patrolling near hosts nesting sites or flowers visited by females, and may even deposit pheromones on leaves to potentially attract females (Smit 2018). Consequently, wing shape may be driven by sex-specific selective pressures, related to nest-searching efficiency in females or mate-locating performances in males.

Nomada panzeri and *N. goodeniana* were represented by fewer specimens than the other species (see Table 1) particularly for males, which poses challenge for statistical analyses. Small sample sizes can increase error rates and reduce the stability of multivariate techniques, although no universal minimum number of individuals exists, as this threshold is specific to each study or sampling context (Cardini et al. 2015, 2021). In addition, the geometric morphometric analyses were based on 18 landmarks, each with x and y coordinates, yielding 36 raw variables. After Procrustes superimposition—which removes variation due to translation, rotation, and scaling—the effective number of shape variables was reduced to 32. In the smallest groups, *N. panzeri* males ($n = 12$) and *N. goodeniana* males ($n = 19$), the number of variables ($p = 32$) exceeded the sample size ($p > N$), resulting in high p/N ratios. Such ratios can present challenges for multivariate techniques like Discriminant Analysis (DA), potentially leading to overfitting and inflated classification accuracy (Cardini et al. 2019). Increasing sample sizes for these species in future studies would help validate and strengthen the promising results obtained. Furthermore, some studied wings were left wings rather than right wings, which could theoretically introduce error due to possible wing asymmetry. However, none of the misidentified specimens were left-winged, suggesting that laterality did not affect classification in this study. Further research should explicitly examine wing asymmetry in the genus *Nomada* to assess potential effects on morphometrics analyses. Additionally, assessing allometry by exploring the relationship between shape and size could provide further insights into morphological variation and help disentangle size-related shape changes from other sources of variation.

The case of *N. panzeri*, being sometimes misassigned in both males and females as *N. flava*, raises concerns, especially when the specimens are this close in wing shape to *N. flava* when compared with the other tested species (Fig. 3). The identifications of the misassigned *N. panzeri* were verified using Smit's (2018) key and characters, suggesting no misidentification. These misassignments can therefore results from either (i) the low number of *N. panzeri* used, which may have caused the analyses to underestimate overlap between species (although small number can also inflate differences between species), or (ii) an incomplete resolution of this group of species, leading to misidentifications due to weak morphological distinctive characters. Increasing the number of studied specimens for *N. panzeri* could help us get closer to reality and focus on one of the proposed hypotheses.

Concerning other inaccuracies, sex misidentifications can easily be minimised in *Nomada* due to pronounced sexual dimorphism, which is based mainly on three easily recognisable characters (Smit 2018): a difference of number of antennal articles, a difference of number of metasomal segments and a difference of the shape of the pygydial plates. Nevertheless, sex misidentifications in our study may reflect the incomplete sexual dimorphism of wing shape, possibly influenced by the co-occurrence of both sexes in the same locations during mating. This partial sexual dimorphism in wing shape warrants further investigation. The species misidentification between *N. panzeri* females and *N. flavoguttata* males is more difficult to explain, as these species are genetically distant, parasitise different hosts, and are morphologically clearly different (Smit 2018; Straka et al. 2024). These results highlights that wing morphometrics in *Nomada* should be applied cautiously and ideally in combination with other morphological characters (Smit 2018).

Regarding the selection of principal components (PCs) in the PCA, the first two PCs accounted for 45.4% of the total variance (Fig. 3). While this means that a substantial portion of variance remains in the subsequent components, the first two PCs revealed clear and well-defined clusters, with each species generally forming distinct groupings (Fig. 3). Given this, we focused our analysis on the first two PCs to maintain interpretability. Nonetheless, we acknowledge that approximately 50% of the total variance is not captured by plotting the first two PCs, and we have provided PC3 (10.3% of the total variance) and PC4 (9.1% of the total variance) to allow for a more comprehensive evaluation, even if no cluster are distinct on these further PCs (Online Resource 4).

Overall, the results of wing morphometry in *Nomada* are promising, performing as well as, or even better than similar studies on other Apidae genera (Francoy et al. 2008; Kozmus et al. 2011; Dehon et al. 2019; Gérard et al. 2020; Soipijit and Sopaladawan 2024). Broadening the geographic scope of sampling could further enhance the taxonomic utility of this method in this morphologically challenging parasitic bee genus as well as provide a better understanding of the evolution of wing shape in this group. Moreover, these findings further confirm the link between wing shape and phylogeny, highlighting the genetic basis of wing shape and its potential evolutionary constraints. This relationship could be explored in other animal groups—whether taxonomically challenging or not—to develop a cost-effective, time-efficient, and non-destructive tool to help differentiate taxa and for investigating pattern of morphological evolution over time.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00435-026-00768-0.

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Author contributions The study was conceptualized by F.C., G.G. and M.G.; Analyses were performed by F.C. and M.G.; Original draft was written by F.C.; Review and edition of the draft were made by F.C., G.G. and M.G.; The study was supervised by G.G. and M.G.

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Data availability Datasets produced during this study and used for the analyses available in .tps file on the online repository Zenodo following this DOI (Carion et al. 2026): https://doi.org/10.5281/zenodo.15345547.

Declarations

Conflict of interest The authors declare no competing interests, either financial or non-financial.

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