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Original Article

Geometric morphometrics of leaves help distinguish species from the *Bauhinia fusconervis* complex (Fabaceae-Cercidoideae)

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ABSTRACT

Bauhinia, a pantropical genus of approximately 230 species with a taxonomy principally based on reproductive characters, contains several identified species complexes including *Bauhinia fusconervis*, a group with an almost exclusively Brazilian distribution. The present study sought to investigate species delimitation in this complex using geometric morphometrics of the leaves. A total of 765 leaf images were analyzed. Images were processed and eight landmarks were applied for PCA and CVA. The results showed that five groups can be defined, three of them corresponding to the species *B. candelabriformis*, *B. curvula,* and *B. pulchella*; the other two comprehend overlapping individuals of the remaining species. The main observed variations were in the degree of fusion of the leaflets and the angle of the leaflet apices. Analyses including only species from the overlapping groups were run with populations separated by geographical area. Although some areas separate in these analyses, there was also cases where one population showed more morphological variation than all the others. This can be an indication of a morphological continuum that corresponds to a single specific entity, a reflex of recent speciation in this group, or evolutionary convergence related to habitat.

Keywords: *Bauhinia*, Brazilian flora, Cercidoideae, morphological variation, species complexes, species delimitation, taxonomy

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Data availability
The datasets generated during and/or analyzed during the current study are available in the SciElo Data repository, https://doi.org/10.48331/scielodata.OY66AA.

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Introduction

Correct species delimitation sometimes requires arguments based on evidence beyond traditional morphology (Carstens *et al.*, 2013; Galtier, 2019). This can be especially challenging in taxonomically complicated cases, known as species complexes. Such groups are formed by populations that are not yet completely separated by the speciation process, and that show large morphological variation. Thus, the overlap of morphological characters complicates the recognition of specific biological entities among populations (Pinheiro *et al.*, 2018; Jacobs *et al.*, 2019).

Among plants, species complexes are common in large genera, such as *Aristolochia* L. (Aristolochiaceae), *Bauhinia* L. (Fabaceae), *Calea* L. (Asteraceae), *Chamaecrista* (L.) Moench. (Fabaceae), *Epidendrum* L. (Orchidaceae), *Habenaria* Willd. (Orchidaceae), and *Myrcia* DC (Myrtaceae) (Vaz & Tozzi, 2003; Pessoa *et al.*, 2012; Silva & Teles, 2018; Cruz-Lustre *et al.*, 2020; Burton *et al.*, 2021; Pessoa *et al.*, 2021; Silva *et al.*, 2022; Frank, 2023). Taxonomic groups with difficult delimitation are sparsely studied but their investigation contributes to a better understanding of intra- and inter-specific morphological variation (Pinheiro *et al.*, 2018). Different methodological approaches can be applied, and their choice should be related to the characteristics of the study group and the chosen species concepts. Some of the methods commonly used with plants are molecular phylogenetics, linear and geometric morphometrics, cytogenetics, and population genetics (Pessoa *et al.*, 2012; Donnell *et al.*, 2015; Huttunen *et al.*, 2015; Mucciarelli *et al.*, 2016; Piedra-Malagón *et al.*, 2016; Simo-Droissart *et al.*, 2013; 2016; Fernández *et al.*, 2017; Herrando-Moraira *et al.*, 2017; Lambert *et al.*, 2017; Gale *et al.*, 2018; Andrade *et al.*, 2019; Menini Neto *et al.*, 2019; Jacobs *et al.*, 2019; Cruz-Lustre *et al.*, 2020; Burton *et al.*, 2021; Freitas *et al.*, 2020; Holanda *et al.*, 2021; Pessoa *et al.*, 2021; Camelo-Jr *et al.*, 2022; Araújo *et al.*, 2023; Belo *et al.*, 2023; Farias *et al.*, 2024).

Geometric morphometrics comprehends techniques that allow the description and representation of the studied shape, besides locating the parts of the structure that show significant variation and representing them graphically (Moraes, 2003). Leaf shape is commonly used in studies of plants (Viscosi *et al.*, 2009a; b; Silva *et al.*, 2012; Vieira *et al.*, 2014; Piedra-Malagón *et al.*, 2016; Nery & Fiaschi, 2019; Nery *et al.*, 2020; Freitas *et al.*, 2024), being especially interesting for groups with compound or lobed leaves. The family Fabaceae comprises 798 genera and more than 22,550 species, characterized by compound leaves (Legume Data Portal, 2025; LPWG, 2017). Among its largest genera, *Bauhinia* includes approximately 230 species exhibiting leaf morphology that ranges from entire and unifoliolate to bilobed or bifoliolate (Legume Data Portal, 2025; Sinou *et al.*, 2009; 2020). Consequently, geometric and linear morphometric approaches have proven valuable in Fabaceae studies, enabling the resolution of species complex delimitations, description of new taxa, and evaluation of biogeographic hypotheses (Meng *et al.*, 2014; Morales *et al.*, 2014; García-Lara *et al.*, 2015; Oliveira *et al.*, 2024; Lima *et al.*, 2025).

Vaz & Tozzi (2003) proposed seven species complexes for the Brazilian species of *Bauhinia* sect. *Pauletia* ser. *Cansenia*, based on both vegetative and floral traits. Two decades after this publication, no other work has investigated species delimitation in these groups. Among the seven complexes, the *B. fusconervis* (Bong.) Steud. complex (hereby BFC) is the largest, containing eight currently accepted species: *B. candelabriformis* R.S.Cowan, *B. curvula* Benth., *B. dumosa* Benth., *B. fusconervis*, *B. goyazensis* Harms, *B. malacotrichoides* R.S.Cowan, *B. pulchella* Benth., and *B. tenella* Benth. (Vaz & Tozzi, 2003).

Leaf blade traits such as shape and degree of fusion of the leaflets are traditionally used to define species in this genus (Wunderlin *et al.*, 1987; Vaz & Tozzi, 2003; Castellanos & Forero, 2019). However, these characters show significant qualitative and quantitative overlap in these species complexes with complicated taxonomy. Thus, geometric morphometrics emerges as an analytical tool with high potential to help delimit species in the genus, especially because floral traits are sometimes unavailable in herbarium specimens or fruiting individuals. Additionally, the use of this tool enables the use of the morphological species concept to test the species delimitation hypothesis. Therefore, the objective of our study was to investigate if geometric morphometrics of the leaf can distinguish species in the *B. fusconervis* (Bong.) Steud. complex and to define the points with higher variation in the leaf blade. With this method, we also tested how many species can be recognized in this complex.

Material and Methods

Species group

The BFC is distinguished from other species in *Bauhinia* sect. *Pauletia* ser. *Cansenia* by the inconspicuous stipules, tubular (clavate in *B. tenella*), smooth or subcostate floral buds, linear petals, and staminal column sericeous-tomentose internally. Leaf morphology ranges from bifoliolate (e.g., *B. curvula*, *B. dumosa*, and *B. malacotrichoides*) to bilobed unifoliolate, exhibiting diverse shapes including ovate, obovate, oblong, elliptical, ovate-elliptical, reniform, and subreniform, with either parallel or divergent apices (Vaz & Tozzi, 2003; Souza *et al.*, 2017; Cruz *et al.*, 2024; Amorim & Pessoa, 2025a) (Fig. 1). Its species are distributed mostly in the Brazilian Cerrado domain (*B. curvula* and *B. pulchella* also occur in Bolivia), but some species also occur in the Amazon (*B. curvula* and *B. pulchella*) and the Atlantic Forest (*B. fusconervis*) (Vaz & Tozzi, 2003; BFG, 2021; Vaz & Santos, 2024; POWO, 2024) (Fig. 2).



Figure 1. Leaf morphology of species of the *B. fusconervis* complex. **A.** *B. candelabriformis* (*E. Yale Dawson 14581*). **B.** *B. curvula* (*R.R. Silva s.n. & C. Spiller*). **C.** *B. dumosa* var. *dumosa* (*M.L. Fonseca 1035 et al.*). **D.** *Bauhinia dumosa* var. *viscidula* (*H.S. Irwin 11388 et al.*). **E.** *B. fusconervis* (*Vauth s.n.*). **F.** *B. goyazensis* (*R.F. Vieira 35 & J.B. Pereira*). **G.** *B. malacotrichoides* (*M.A. da Silva et al.* 1993). **H.** *B. pulchella* (*B. Wilke 5 et al.*). **I.** *B. tenella* (*E. Nunes s.n. & P. Martins*).

Bauhinia curvula occurs in Bolivia and the Brazilian states of Tocantins, Distrito Federal, Goiás, Mato Grosso, Mato Grosso do Sul, and Minas Gerais (BFG, 2021; Vaz & Santos, 2024; POWO, 2024); its type was collected in Goiás [*Wendell* 2590, Vaz & Tozzi (2003)]. *Bauhinia dumosa* is endemic to Brazil, found in the states of Bahia, Distrito Federal, and Goiás (BFG, 2021; Vaz & Santos, 2024), with its type specimen collected in Goiás [*Burchell 7790*, Vaz & Tozzi (2003)]. *Bauhinia fusconervis* occurs only in Brazil, in the states of Minas Gerais and Rio de Janeiro (BFG, 2021; Vaz & Santos, 2024), with its type specimen coming from the border between these states [*Langsdorff s.n.*, Vaz (2011)]. *Bauhinia goyazensis* is endemic to Brazil and is distributed in Tocantins, Distrito Federal, and Goiás (BFG, 2021; Vaz & Santos, 2024), with its type specimen collected in Goiás [*Glaziou 21012*, Vaz (2011)]. *Bauhinia pulchella* has been recorded in Bolivia and in the Brazilian states of Pará, Rondônia, Tocantins, Bahia, Ceará, Maranhão, Pernambuco, Piauí, Rio Grande do Norte, Goiás, Mato Grosso do Sul, Mato Grosso and Minas Gerais (BFG, 2021; Vaz & Santos, 2024; POWO, 2024); its type specimen is from Piauí [*Gardner 2150*, Vaz & Tozzi (2003)]. *Bauhinia tenella* occurs only in Brazil, in the states of Tocantins, Maranhão, and Goiás (BFG, 2021; Vaz & Santos, 2024), with type material from Tocantins [*Gardner 3701*, Vaz (2011)]. *Bauhinia candelabriformis* and *B. malacotrichoides* are endemic to Brazil and occur only in the state of Goiás (BFG, 2021; Vaz & Santos, 2024), with type specimens also collected in this state [*E. Y Dawson 14581* and *Dawson 1429,* respectively, Cowan (1957)].

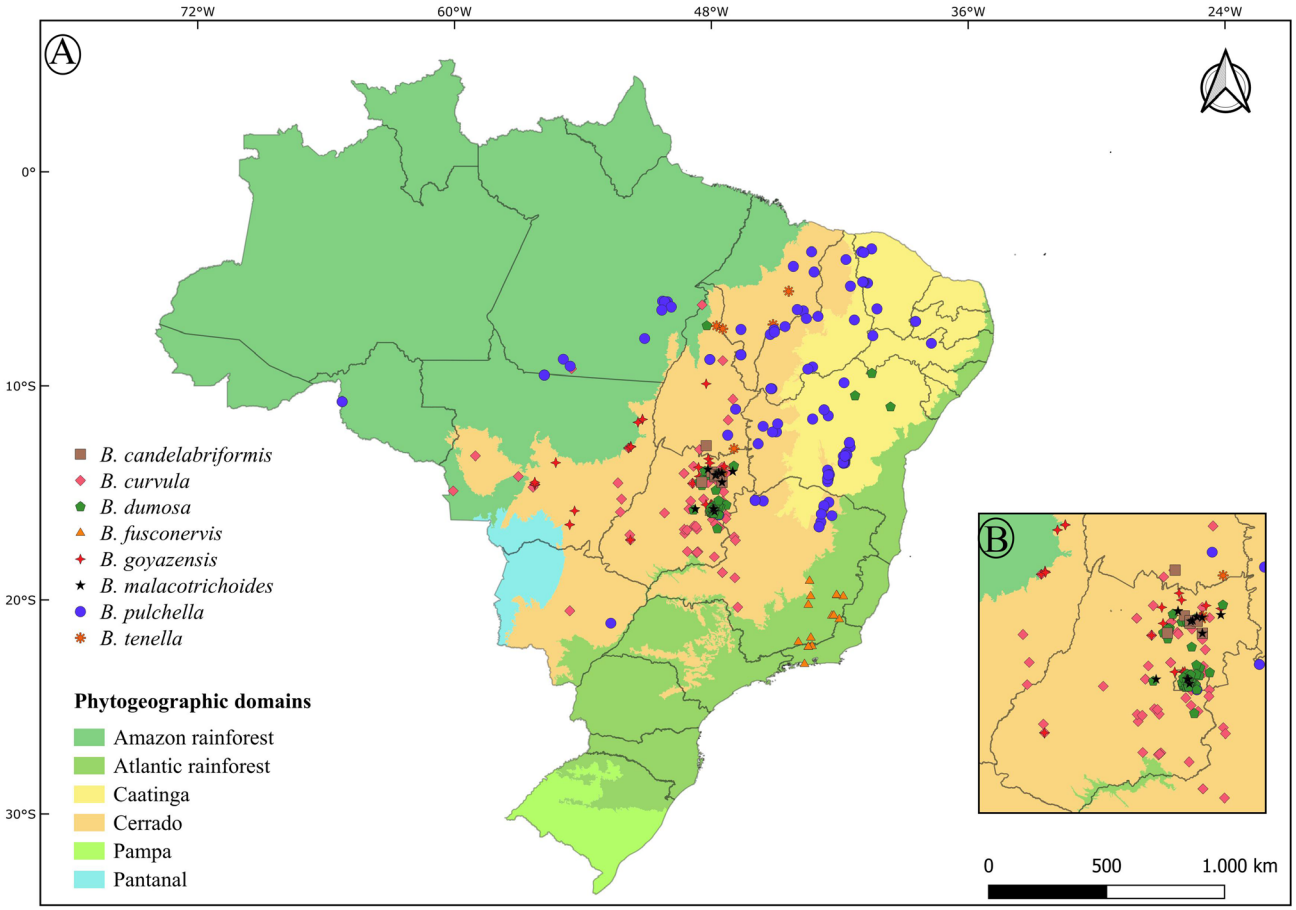


Figure 2. Geographic distributions within the *B. fusconervis* complex. **A.** Composite map of all eight species. **B.** Detail of Goiás state illustrating sympatric occurrence of four taxa (*B. curvula*, *B. dumosa*, *B. goyazensis* and *B. malacotrichoides*).

Sampling

The analysis was based on specimens deposited in the following herbaria: ALCB, BHCB, BM, BRBA, CEN, EAC, ESA, F, FLOR, FURB, GH, HCF, HEPH, HUEFS, HUFU, HVASF, IAN, IBGE, INPA, IPA, K, L, LE, M, MBM, MBML, MO, NY, P, R, RB, RSA, SLUI, SP, SPF, UB, UFMT, US, USF, VIC, and W (acronyms according to Thiers 2023, continuously updated), totaling 544 specimens (Tab. S1). Only specimens with at least one completely open leaf, without any folds, emerging below the third node of the inflorescence axis were selected. Between one and four leaves were selected for each specimen, totaling 765 leaf samples for analysis, distributed among species as follows: 16 samples of *B. candelabriformis*, 192 samples of *B. curvula*, 113 of *B. dumosa*, 56 of *B. fusconervis*, 71 of *B. goyazensis*, 20 of *B. malacotrichoides*, 261 of *B. pulchella* and 36 of *B. tenella*. We sought to cover the whole distribution of each species. Specimens were identified based on Vaz & Tozzi (2003). Specimen analysis was done through high-resolution images available online (GBIF, 2024; INCT, 2024; JSTOR, 2024; NYBG, 2024; Reflora, 2024; Tropicos, 2024), and images captured during visits to herbarium collections and during field expeditions.

Geometric Morphometrics

Leaf images with a scale were converted to the .tps format with the software tpsUtil (Rohlf, 2015). The leaf contour was converted into eight landmarks marked with the software tpsDig (Rohlf, 2010). Landmark 1 is the point of leaflet separation, representing the degree of fusion of the leaflets, landmarks 2 and 8 correspond to the leaflet apices, landmarks 3 and 7 are the widest points of the leaf blade, landmarks 4 and 6 are the leaflet bases and landmark 5 is the connection of the blade with the pulvinus and petiole (Fig. 3) (Amorim & Pessoa, 2025b).

After applying landmarks, the .tps file was imported into the software MorphoJ (Klingenberg, 2011) and submitted to Procrustes analysis, an overlapping method to remove factors related to the size and orientation of samples (Rohlf & Slice, 1990; Goodall, 1991; Viscosi & Cardini, 2011). After that, Principal Component Analysis (PCA) was carried out for an exploratory analysis of shape variation. Canonical Variate Analysis (CVA) was conducted to discriminate pre-determined groups into taxonomic categories, to verify differences between groups (Campbell & Atchley, 1981; Monteiro & Reis, 1999).

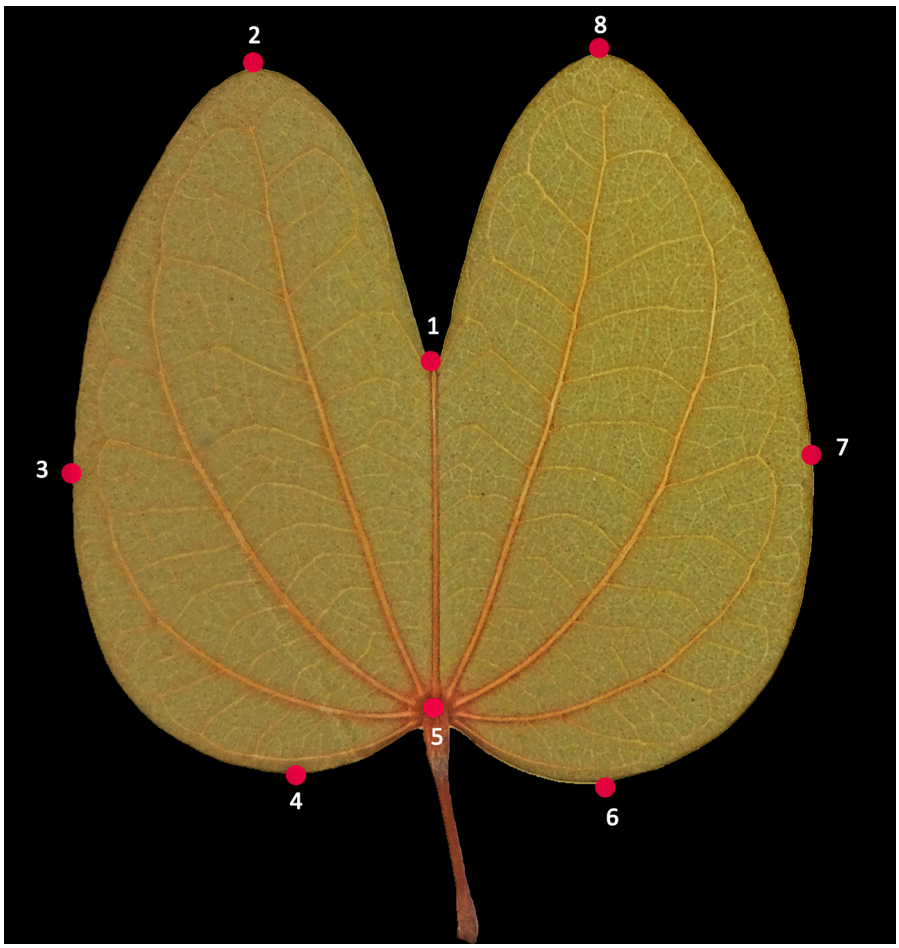


Figure 3. Landmarks applied to *Bauhinia* leaves for geometric morphometric analysis.

After an initial analysis of the eight species, new PCA and CVA analyses were carried out with the taxa showing overlap. In this second analysis, samples were organized by geographical area (Camelo-Jr *et al.*, 2022). For *B. fusconervis*, samples were divided into: 1. Minas Gerais populations and 2. Rio de Janeiro populations; for *B. tenella* they were divided into: 1. Goiás populations and 2. Maranhão–Tocantins populations; *B. dumosa*: 1. Bahia populations, 2. Distrito Federal–Goiás–Tocantins populations and 3. Minas Gerais populations, *B. goyazensis*: 1. Distrito Federal–Goiás populations and 2. Mato Grosso populations; *B. malacotrichoides* was not divided, as it occurs only in Distrito Federal and Goiás (Tab. S1).

Results

In the PCA with all eight species, the cumulative variance in the first three axes is 95.8% (PC1: 51.2%, PC2: 38.7%, PC3: 5.8%) (Tab. S2). The variation found in PC1 is mostly influenced by landmark 1, corresponding to the leaflet separation point. On the other hand, PC2 is influenced by landmarks 1, 5, 2, and 8, representing the leaflet separation point, connection of the blade with the pulvinus, and leaflet apices. All landmarks influence PC3. The ellipses overlap both in PC1+PC2 and PC1+PC3. In PC1+PC2, *B. curvula* separates from *B. pulchella*+*B. candelabriformis* and *B. tenella*+*B. fusconervis*, while the remaining species overlap. In PC1+PC3, there is a gradient of variation, starting with *B. candelabriformis* in the negative pole and ending with *B. curvula* in the positive pole (Fig. S1A–E).

In the CVA with eight species, the cumulative variance of the first two axes is 95% (CV1: 74.9%, CV2: 20.4%) (Tab. S2). CV1 variance is influenced by landmarks 1, 2, and 8, which respectively correspond to the leaflet separation point and the leaflet apices angle. CV2 variation is influenced by these same landmarks, besides 3 and 7, which correspond to the widest point of the leaf blade. It should be noted that in CV2 the variation in landmarks 2 and 8 is mainly in the opening angle, while in CV1 it is mostly in size variation. The variation found in CV1+CV2 was enough to separate five groups corresponding to: 1. *B. candelabriformis*, 2. *B. curvula*, 3. *B. pulchella*, 4. *B. dumosa*/*B. goyazensis*/*B. malacotrichoides* and 5. *B. fusconervis*/*B. tenella*. CV1 variation separated *B. pulchella* and *B. candelabriformis* in the negative pole and *B. curvula* in the positive pole, the remaining species were not strongly influenced. CV2 variation separated *B. candelabriformis*, *B. malacotrichoides*, *B. dumosa*, and *B. goyazensis* in the positive pole, and *B. fusconervis* and *B. tenella* in the negative; *B. pulchella* and *B. curvula* were not strongly influenced (Fig. 4A–C).

In the second analysis, now restricted to group 4, which includes *B. dumosa* (three areas), *B. goyazensis* (two areas), and *B. malacotrichoides* (one area), the cumulative variation in the first three PCA axis is 91.9% (PC1: 53.8%, PC2: 30.6%, PC3: 7.4%) (Tab. S2). The variation found in PC1 is influenced by landmarks 2 and 8, corresponding to the angle of leaflet apices. PC2 is more influenced by landmark 1, representing the point of separation of the leaflets. PC3 is influenced by landmarks 4 and 6, corresponding to the leaflet base. The ellipses are overlapped in the six analyzed populations both in PC1+PC2 and PC1+PC3 (Fig. S2A–E).

In the CVA restricted to group 4, the cumulative variance in the first two axes is 94.2% (CV1: 56.8%, CV2: 37.3%) (Tab. S2). CV1 variation is influenced by landmarks 1, 5, 2 8, and 4, respectively corresponding to the leaflet separation point, point of connection of the blade with the pulvinus and petiole, and base of the leaflets. All eight landmarks influence variation in CV2. The variation found in CV1+CV2 in this second analysis could not completely separate the populations organized by geographic area (Fig. 5A–C). However, the overlap is only marginal for populations of *B. goyazensis* from Mato Grosso with *B. dumosa* from Distrito Federal, Goiás, and Tocantins, and *B. dumosa* from Minas Gerais and *B. malacotrichoides*. *Bauhinia dumosa* populations from Bahia fall completely inside *B. dumosa* from Goiás and Distrito Federal, but *B. goyazensis* populations from Goiás and Distrito Federal are extremely variable and overlap with all other ellipses. In this analysis, CV1 variation separated *B. dumosa* populations from Bahia in the negative pole from populations of *B. goyazensis* from Mato Grosso in the positive poles. CV2 variation separated *B. malacotrichoides* in the positive pole from populations of *B. dumosa* from Minas Gerais in the negative.

In the third analysis, restricted to group 5, including *B. fusconervis* (two areas) and *B. tenella* (two areas), PCA showed a cumulative variance of the first three axes of 94.5% (PC1: 49.6%, PC2: 34.3%, PC3: 10.6%) (Tab. S2). The variation in PC1 is mostly influenced by landmarks 2 and 8, corresponding to the variation in the angle of leaflet apices. PC2 is influenced by landmark 1, which is the point of separation of the leaflets. PC3 is influenced by landmarks 3 and 7 and 2 and 8, respectively corresponding to the widest part of the leaf blade, and the leaflet apices angle. There was no separation of these four populations either in PC1+PC2 or PC1+PC3 (Fig. S3A–E).

In the CVA of group 5, the cumulative variance of the first two axes is 97.6% (CV1: 67.3%, CV2: 30.3%) (Tab. S2). CV1 variance is influenced by landmarks 1, 2, and 8, respectively corresponding to the point of separation of the leaflets and the angle of leaflet apices. CV2 variation is explained by landmarks 3 and 7, 2 and 8, and 1, respectively corresponding to the widest part of the leaf blade, leaflet apices angle, and leaflet separation point. The variation found in CV1+CV2 in this analysis separated *B. tenella* populations from Goiás from populations of *B. tenella* from Maranhão and Tocantins and populations of *B. fusconervis* from Rio de Janeiro (Fig. 6A–C). However, *B. fusconervis* populations from Minas Gerais have wider variation and overlap populations of *B. tenella* from Maranhão and Tocantins and populations of *B. fusconervis* from Rio de Janeiro. In this analysis, CV1 variation marginally separated *B. tenella* from Goiás in the negative pole from *B. fusconervis* from Rio de Janeiro on the positive pole. CV2 separated *B. tenella* from Maranhão and Tocantins from *B. tenella* from Goiás.

Discussion

In this study, we tested if geometric morphometrics of the leaf is useful for separating species of the *B. fusconervis* (Bong.) Steud. complex; we additionally tested which points of the leaf blade show more variation. Geometric morphometrics has been used for plants with simple, lobed and compound leaves (Viscosi *et al.*, 2009a; b; Silva *et al.*, 2012; Vieira *et al.*, 2014; Viscosi, 2015; Piedra-Malagón *et al.*, 2016; Nery & Fiaschi, 2019; Stojnic *et al.*, 2022; Freitas *et al.*, 2024) and our results indicate it can also be used for species delimitation in *Bauhinia*. The characters that showed larger variation were the degree of fusion of the leaflets (landmark 1) and the angle of leaflet apices (landmarks 2 and 8). Similarly, a study of two species of *Montrichardia* Crueg. (Araceae) (Silva *et al.*, 2012) found that landmarks related to the angle of divergence of the leaf base lobes are among those that most influence taxa separation. In *Bauhinia,* the degree of fusion of the leaflets is a character traditionally used in taxonomy (Fortunato, 1986; Wunderlin *et al.*, 1987; Vaz & Tozzi, 2003; Ramiréz-De Anda & Colín, 2007; Castellanos & Forero, 2019). Among Brazilian species, *B. cupulata* Benth., *B. pentandra* (Bong.) Dietr. and *B. vespertilio* S.Moore can be recognized by the leaflet apex morphology, their opening angle, and degree of fusion (Vaz & Tozzi, 2003; 2005; Silva, 2008; Amorim & Pessoa, 2025a). However, this character is less useful for distinguishing closely related species, such as those in species complexes, due to intraspecific morphological variation and overlaps. Here, we show that even in species groups with large variations in this character (Vaz & Tozzi, 2003), it is still important to distinguish taxa in a morphometric analysis.

Our analyses delimited five groups, three corresponding to *B. candelabriformis*, *B. curvula*, and *B. pulchella*, which were recognized in their current circumscription based on Vaz & Tozzi (2003). *Bauhinia curvula* stands out by having bifoliolate leaves, while the other two species are unifoliolate and bilobed (Vaz & Tozzi, 2003; Amorim & Pessoa, 2025a). *Bauhinia candelabriformis* and *B. pulchella* can be distinguished from each other by the flower bud apex, which is reentrant in *B. pulchella* and apiculate in *B. candelabriformis* (Vaz & Tozzi, 2003). It should be highlighted that Vaz & Tozzi (2003) hypothesized that *B. candelabriformis* is closely related to *B. goyazensis* and *B. malacotrichoides* due to their similar leaf morphology, but our results do not corroborate this initial hypothesis (Fig. 4A).

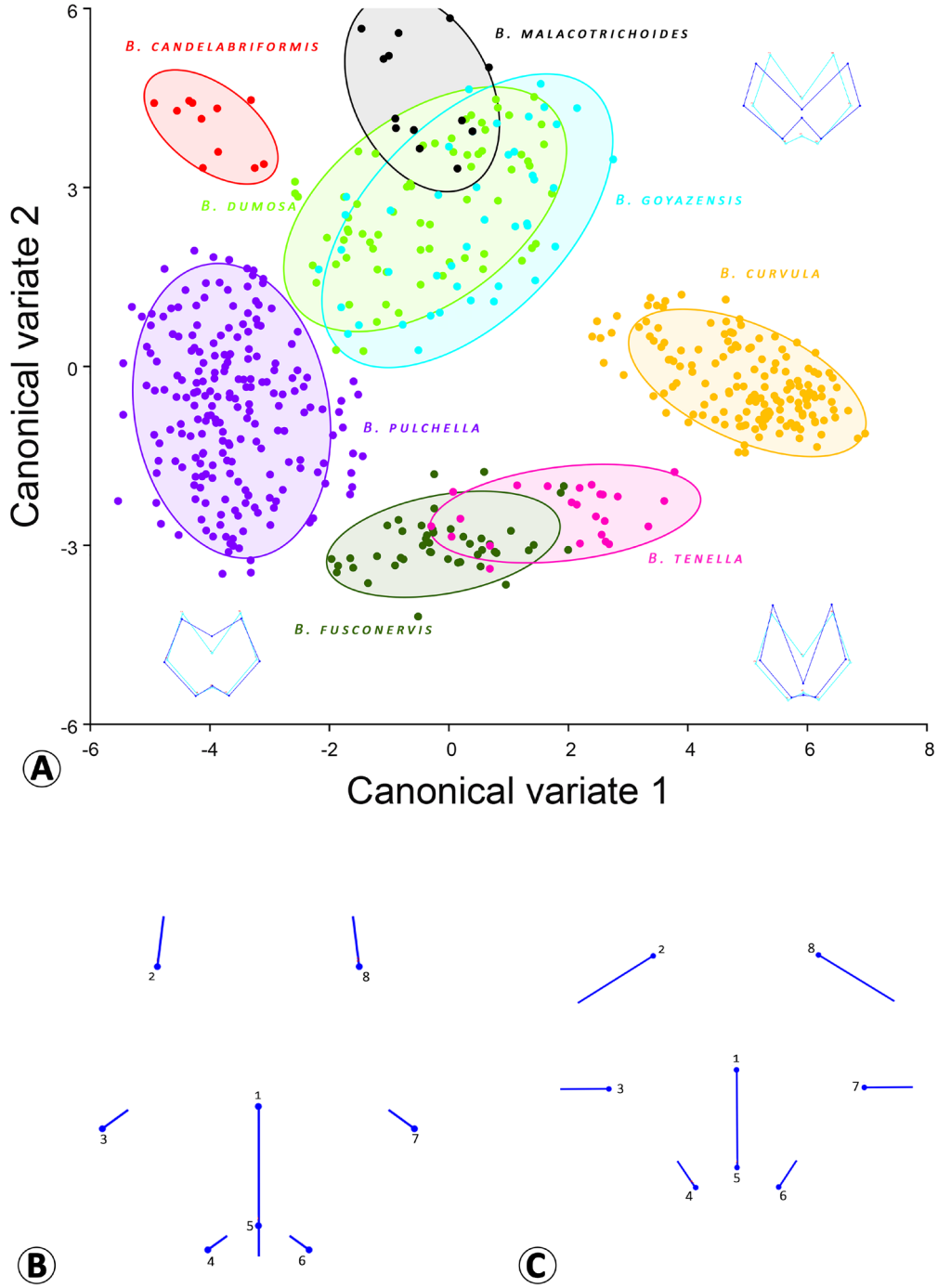


Figure 4. Canonical Variate Analysis (CVA) of morphometrics based on species of the *B. fusconervis* complex. **A.** CV1+ CV2 axis. **B.** Variation observed in CV1. **C.** Variation observed in CV2.

The other two groups correspond to *B. dumosa*/*B. goyazensis*/*B. malacotrichoides* (group 4) and *B. fusconervis*/*B. tenella* (group 5). The overlap of these species indicates that, based on leaf characters, they would not be considered distinct taxa in the current circumscription of Vaz & Tozzi (2003). Studies in *Bauhinia* after Vaz & Tozzi (2003) were local floras and checklists, descriptions of new species or new combinations (Vaz & Tozzi, 2005; Queiroz, 2006; Wunderlin, 2006; Ramirez-De Anda & Colín, 2007; Silva, 2008; Torres-Colín *et al.*, 2009; Vaz *et al.*, 2010; Wunderlin, 2010; Vaz & Lewis, 2015; Souza *et al.*, 2017; Tozzi, 2016; Castellanos & Forero, 2019; Cruz *et al.*, 2024; Amorim & Pessoa, 2025a), with most of the species complexes proposed in these works remaining unverified.

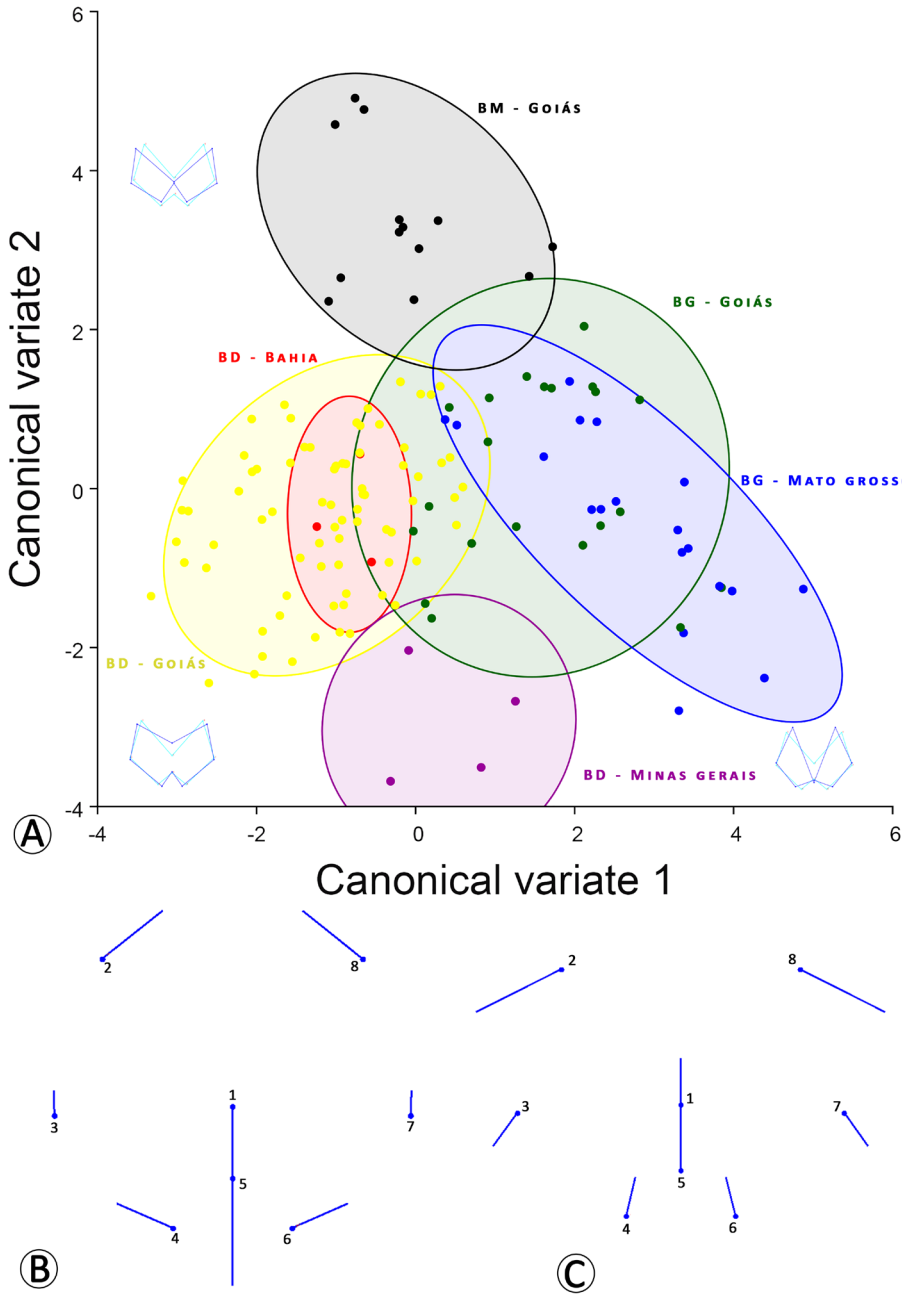


Figure 5. Canonical Variate Analysis (CVA) of morphometrics based on populations of *B. dumosa* (BD), *B. goyazensis* (BG), and *B. malacotrichoides* (BM). **A.** CV1+ CV2 axis. **B.** Variation observed in CV1. **C.** Variation observed in CV2.

The three species that form group 4 had their type specimens collected in the state of Goiás (Cowan, 1957; Vaz & Tozzi, 2003; Vaz, 2011). The literature reports large variation in leaf morphology in *B. dumosa* and *B. goyazensis*, forming a gradient from bilobed unifoliolate morphotypes to bifoliolate; the leaflets also vary in shape (ovate, elliptical, or subreniform) and the apex, which can be parallel or divaricate (Vaz & Tozzi, 2003). Our study points to an almost total overlap in the ellipses of these two species, also including *B. malacotrichoides* (Fig. 4A). By splitting *B. dumosa* and *B. goyazensis* populations by geographical area, we observed that it is possible to separate them from each other and *B. malacotrichoides*, with only marginal overlaps. However, the populations of *B. goyazensis* from Goiás and Distrito Federal overlap with all others (Fig. 5A). The literature shows confusion in the recognition of these entities, with some authors suggesting that *B. goyazensis* is a synonym of *B. pulchella*, but this has not been formally proposed (Vaz & Marquete, 1993; Vaz & Tozzi, 2003). Nevertheless, our results do not support their synonymization, as these species do not overlap in leaf morphology.

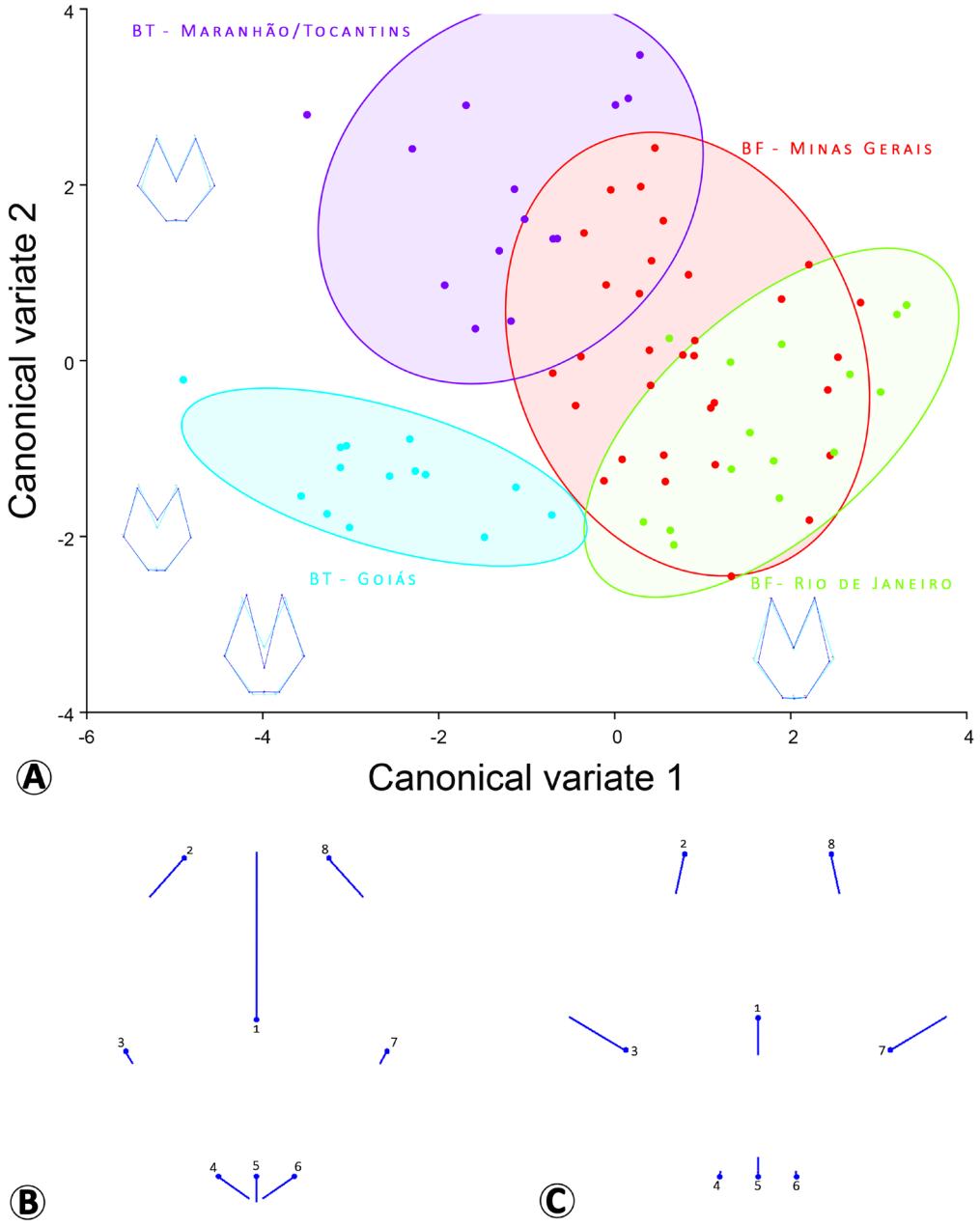


Figure 6. Canonical Variate Analysis (CVA) of morphometrics based on populations of *B. fusconervis* (BF) and *B. tenella* (BT). **A.** CV1+ CV2 axis. **B.** Variation observed in CV1. **C.** Variation observed in CV2.

By having overlapped geographical distributions, *B. dumosa*, *B. goyazensis*, and *B. malacotrichoides* share similar environmental conditions (Fiaschi & Pirani, 2009; Lima *et al.*, 2020). Genetic information on populations of *B. dumosa*, *B. goyazensis*, and *B. malacotrichoides* is needed to confirm if synonymizations are required. Nery & Fiaschi (2019), when evaluating the leaf morphology of *Hydrocotyle quinqueloba* Ruiz & Pav. and its varieties with geometric morphometrics, defined five delimited groups, contributing to a new taxonomic treatment and the necessary synonymizations. On the other hand, Viscosi (2015) concluded that the morphological variability seen in the leaf morphology of *Quercus* L. could be due to the different habitats where the species occur. Similar results were found by Stojnic *et al.* (2022) in *Fagus sylvatica* L., where the populations discriminated by geometric morphometrics showed geographical structuring, indicating that leaf shape could be influenced by the local climate. Our results can indicate a morphological continuum corresponding to a species entity, as shown by Pessoa *et al.* (2021) in some species of *Epidendrum*, with the overlap being a reflex of incipient speciation (Vargas *et al.*, 2017; Dömel *et al.*, 2019),

with taxonomic adjustments being needed, like in Nery & Fiaschi (2019). We need to also consider that the similarity in leaf shape could be due to similar habitats, as shown by Viscosi (2015) and Stojnic *et al.* (2022). Molecular data at the population level are needed for final taxonomic decisions on these taxa.

The situation of group 5, formed by *B. fusconervis* and *B. tenella,* is different. Despite the overlap found in leaf morphology variation (Fig. 4A), there are floral characters that help recognize these taxa. Among BFC species, only *B. tenella* has clavate floral buds, while the remaining have tubular floral buds (Vaz & Tozzi, 2003; BFG, 2021; Vaz & Santos, 2024). Although there is overlap, the leaf blades of *B. tenella* do not extend over 2.0 cm, while in *B. fusconervis* they reach 8.0 cm (Vaz & Tozzi, 2003). Finally, these species occur in different habitats: *B. fusconervis* in the Atlantic Forest domain, and *B. tenella* in the Cerrado domain (Vaz & Tozzi, 2003; BFG, 2021; Vaz & Santos, 2024). It is interesting to note that the analysis dividing the sampling of these species by geographical areas showed that leaf morphology overlap occurs in populations of *B. fusconervis* in Minas Gerais with populations of *B. tenella* from Maranhão and Tocantins, and although there are overlaps in the populations of *B. fusconervis* from Minas Gerais and Rio de Janeiro, our results point to a strong separation of *B. tenella* populations from the north (Maranhão and Tocantins) from those in the south (Goiás) (Fig. 6A). These results need to be further investigated in future work, as they could indicate a cryptic species within *B. tenella*. Vaz & Tozzi (2003) indicated that *B. fusconervis* is close to *B. pulchella*, but our results do not corroborate this idea (Fig. 4A).

Our study showed that geometric morphometrics of the leaf is a powerful tool that can distinguish among closely related species in *Bauhinia*. The species that show overlap still need to be better investigated with molecular data to achieve taxonomic resolution, either for synonymization, as in *B. dumosa*, *B. goyazensis*, and *B. malacotrichoides,* or to recognize new taxa, such as *B. tenella*, which in its current circumscription possibly contains a cryptic species.

Supplementary Material

The following online material is available for this article:

Table S1. Specimens and vouchers used in morphometric analysis.

Table S2. A-B Analysis 1: Eigenvalues, Variance, and Cumulative Variance of morphometric analysis based on species. A. Eigenvalues of Principal Component Analysis (PCA). B. Eigenvalues of Canonical Variate Analysis (CVA). C-D. Analysis 2: Eigenvalues, Variance, and Cumulative Variance of morphometric analysis based on populations for the *B. dumosa*, *B. goyazenis*, and *B. malacotrichoides* group. C. Eigenvalues of Principal Component Analysis (PCA). D. Eigenvalues of Canonical Variate Analysis (CVA). E-F. Analysis 3: Eigenvalues, Variance, and Cumulative Variance of morphometric analysis based on populations for the *B. fusconervis* and *B. tenella* group. E. Eigenvalues of Principal Component Analysis (PCA). F. Eigenvalues of Canonical Variate Analysis (CVA)

Figure S1. Principal Component Analysis (PCA) of morphometrics of species of the *B. fusconervis* complex. A. PC1+PC2 axis. B. PC1+ PC3 axis. C. Variation observed in PC1. D. Variation observed in PC2. E. Variation observed in PC3.

Figure S2. Principal Component Analysis (PCA) of morphometrics of populations of *B. dumosa* (BD), *B. goyazensis* (BG) and *B. malacotrichoides* (BM). A. PC1+ PC2 axis. B. PC1+PC3 axis. C. Variation observed in PC1. D. Variation observed in PC2. E. Variation observed in PC3.

Figure S3. Principal Component Analysis (PCA) of morphometrics of populations of *B. fusconervis* (BF) and *B. tenella* (BT). A. PC1+ PC2 axis. B. PC1+PC3 axis. C. Variation observed in PC1. D. Variation observed in PC2. E. Variation observed in PC3.

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Authors' Contributions

DSA: preparation of the material, data analysis, and writing of the manuscript; EMP: revision and approval of the manuscript; DSA and EMP prepared Figures 2, 3, 4, and 5; DSA prepared Figure 1 and the supplementary information Table S1, Table S2, Figure S1, Figure S2 and Figure S3.

Conflict of Interest

The authors declare no conflict of interest.

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