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Morpho-environmental characterization of the genus *Baldellia* Parl. (Alismataceae) in the Iberian Peninsula, Balearic islands and North Morocco

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Abstract

The genus *Baldellia* Parl. has always been a complex taxon. Three species and three subspecies have been proposed for the Iberian Peninsula. The morphological variation of this genus in the Iberian Peninsula, Balearic islands and northern Morocco, and its thermo-pluviometric and altitudinal correlation are the focus of this contribution. Twenty-eight morphological variables were examined and subjected to a multivariate statistical analysis. The three morphotypes observed (Form 1, which includes *B. ranunculoides* subsp. *repens* and *B. alpestris*; Form 2, which includes *B. ranunculoides* and Form 3 – for the new combination *B. ranunculoides* subsp. *ranunculoides* var. *tangerina* (Pau) J. Rocha, A. Crespi, M. García-Barriuso, R. Almeida, J. Honrado, *comb. nova* proposed here for the first time) seem to represent different reproductive strategies. Morphological variables related with the presence or absence of stolons and the architecture of the inflorescence; the size and number of fruits are the most discriminating variables. Form 1 represents the asexual morphotype; Forms 2 and 3 correspond to morphotypes for which sexual reproduction is preferential. The environmental approach revealed that the asexual form (Form 1) grows in temperate, in more humid conditions, and within a broad altitudinal range. In contrast, the two sexual forms are more common in warmer and drier conditions, and occur over a narrower interval of altitudes.

Keywords: *Baldellia*, morphotypes, Iberian Peninsula, Balearic Islands, north Morocco, biogeography

Introduction

Since its first taxonomical description, the genus *Baldellia* Parl. (Alismataceae) has been a matter of debate, especially because of its characteristic morphological variability. *Baldellia* was initially incorporated into *Alisma ranunculoides* by Linnaeus (1753) (*Plantago-aquatica minor* sensu Ray). Two decades later, Lamarck (1778) classified this species as *A. repens*, based on its capacity to develop pseudowhorl proliferations. In fact, the presence of these proliferations has been emphasised by numerous authors over the years (Gmelin 1796; Lamarck &

De Candolle 1805; Deslongchamps 1828; Bertolonii 1839; Parlatore 1858; Cosson & Saint-Pierre 1861; Nyman 1890; Lázaro e Ibiza 1906; Fiori & Paoletti 1908; Pitard 1912; Dandy 1980; Amaral Franco & Rocha Afonso 1994; Stace 1995; Kozłowski et al. 2008; Talavera et al. 2008).

The complexity of *Baldellia* classification has been clearly emphasised by Kozłowski et al. (2008), Kozłowski and Matthies (2009) and Kozłowski and Vallelian (2009), who analysed the genus as regards several ecological and biological aspects; contributions on morpho-reproductive or biogeographical aspects were also presented by Charlton (1973) and

Vuille (1998). The existence or absence of proliferous stolons, and the development of either large or small flowers have been often considered as distinctive characters. It is noteworthy that *B. repens* has been confused with *B. ranunculoides* by some authors who adopted the latter classification regardless of whether individuals exhibited proliferous stolons. The morphological variations between submerged and floating or aerial leaves have been sometimes taxonomically recognised as varieties (*A. ranunculoides* L. var. *natans* Glück, *A. ranunculoides* L. var. *zosterifolius* Fries, *A. ranunculoides* L. var. *terrestris* Glück, *A. repens* Lamk. var. *natans* Glück or *A. repens* Lamk. var. *graminifolius* Glück (Glück 1906)). Another morphological type has been identified at the south of the native area for this genus (Jahandiez & Maire 1931; Maire 1952). This morphotype, close to *A. plantago-aquatica*, which has been, in some cases, taxonomically regarded as *A. plantago-aquatica* x *Echinodorus ranunculoides* Durand & Pittier, had been previously described by Pau (1924) as *A. tangerina* Pau. The marked robustness and size were the main features suggesting the possibility of hybridisation with *A. plantago-aquatica* (Pau 1924; Molina Abril et al. 1994). Recently, another hybrid, in this case from Ireland, has been reported (Kozłowski et al. 2008).

Another taxon, initially classified by Cosson (1884) as *A. alpestris* Coss. (*E. alpestris* (Coss.) M. Micheli), was finally classified by Láinz (1960) as *B. alpestris* (Coss.) M. Láinz. This new species, according to several authors, has a morphological outline that corresponds to *B. repens* (Lam.) Ooststroom ex Lawalrée (Richter 1890; Lázaro e Ibiza 1906; Segura Zubizarreta et al. 2000; Romero Buján 2008), in disagreement with Guillén et al. (1998) and Talavera et al. (2008) who pointed out that this taxon occurs exclusively in the northern Iberian Peninsula (see also Martín Gil 2007).

Other relevant contributions are those of Talavera et al. (2008) and Talavera et al. (2011, http://www.floraiberica.es/floraiberica/texto/borradores/vol_XVII/17_161_02_Baldellia.pdf) who identified three species from the Iberian Peninsula. Moreover, recent contributions have reported the presence of *B. ranunculoides* (L.) Parl. as a rare species of wet temporary habitats in Sardinia and southern France, while Bagella et al. (2009) and Agostinelli et al. (2011) have reported *B. ranunculoides* (L.) Parl., *B. repens* (Lam.) Ooststroom ex Lawalrée and *B. alpestris* (Coss.) M. Láinz. In addition, three subspecies have been distinguished for *B. repens*: subsp. *repens*, subsp. *baetica* Talavera & Casimiro-Soriguer and subsp. *cavanillesii* (Molina Abril et al.) Talavera.

Based on the aforementioned studies, the genus *Baldellia* is represented in the Iberian Peninsula by the following three species: *B. alpestris*, *B. ranuncu-*

loides subsp. *repens* and *B. ranunculoides* subsp. *ranunculoides*. The shape of the leaves (obtuse for *B. alpestris* and acuminate for the others, as a response to environmental conditions, or “floating leaves” according to Kozłowski et al. 2008), the size of the anthers (usually less than 1 mm for *B. alpestris* and *B. ranunculoides*, and 1–2 mm for *B. repens*), the number of flowers and fruits (usually less than five for *B. alpestris* and *B. repens* subsp. *cavanillesia*, and five or more for the other species) and the surface of the fruits (smooth in *B. alpestris*, and with prominent ridges in the other taxa) represent the main morphological differences. The presence or absence of structures for asexual propagation or proliferations is considered a complementary morphological characteristic for this genus. Several Iberian authors have considered leaf shape or flower size (Brotero 1804; Willkomm & Lange 1870; Amo y Mora & Mariano del 1871; Merino 1909; Coutinho 1913; Cadevall i Diars 1933; Sampaio 1949) as the most relevant features for distinguishing the three taxa. The capacity to produce proliferations was traditionally considered to be the character that distinguished *Baldellia* from the other *Alismataceae*; indeed, Lamarck (1778) and De Candolle (1805) adopted this criterion to separate *A. ranunculoides* from the other species of this genus. However, the presence of proliferative structures has been definitely the most controversial character used to describe the apparent taxa of this genus (Láinz 1960; Molina Abril et al. 1994; Talavera et al. 2008).

The taxonomic instability of *Baldellia* cannot be explained from a phytosociological point of view. The phytosociological studies, which included *Baldellia* (Velayos et al. 1984; Carretero 1989; Velayos et al. 1989; Ursúa Sesma & Báscones Carretero 2000; Molina Abril 2001; Lence et al. 2002; Honrado 2003; Ortega et al. 2007; Dias Pereira & Silva Neto 2008; Silva et al. 2008; Silva 2009; Silva et al. 2009), consider it as a characteristic taxon of the class *Littorelletea uniflorae* Br.-Bl. et Tx. 1943 (with sporadic records in *Potametea Tüxen & Preising* ex Oberdorfer 1957 and *Scheuchzerio-Caricetea Tüxen 1937* or *Phragmitetea Tx. et Prsg. 1942* in Spain and Portugal, as pointed out by Kozłowski et al. 2008), with occurrence in dense or scarce amphibious swards or in weed communities in rice fields. *Baldellia* spp. have not been reported as a characteristic taxon of any specific association. This may be attributed to a deficient analysis of its phytosociological behaviour (Kozłowski et al. 2008), or its ecological ability to grow under widely different ecological conditions. Kozłowski et al. (2008) distinguished two taxa of this genus based on their habitats: *B. ranunculoides* subsp. *ranunculoides*, growing in “mesotrophic habitats and temporary gaps within calcareous or mildly brackish

pools”; and *B. ranunculoides* subsp. *Repens*, growing in “long-standing gaps in weakly acidic or oligotrophic water bodies”.

Our main goal was to investigate the patterns and environmental correlations of the morphological variation of *Baldellia*. This analysis was focused on the Iberian Peninsula, Balearic Islands and North Morocco (most western distribution of *Baldellia*) because of the known taxonomical variability reported for this area. A biogeographical approach, supported by an environmental analysis, was adopted in an attempt to understand the observed morphological variations. In this morpho-environmental characterisation of the genus *Baldellia*, we have adopted the hypothesis of biological corridors (Hernández Bermejo & Sainz Ollero 1984; Moreno Saiz & Sainz Ollero 1997; Rodríguez-Sánchez et al. 2008) and natural barriers to describe biogeographical mechanisms of speciation and distribution of *Baldellia* in the Iberian Peninsula. The results obtained are discussed according to the reproductive, environmental and morphological results already published for this genus.

Study area

The study area comprised the Iberian Peninsula, the Balearic islands and the northwestern Morocco. The

populations of the genus *Baldellia* analysed here occupied a very broad altitudinal interval, from sea-level (close to Alcácer do Sal, Portugal, 8° 38'W; 38° 24'N) up to 2300 m a.s.l. (Curavacas, Palencia, Spain, 4° 40'W; 42° 58'N).

Data collection and analysis

The 492 populations examined here were from 10 Iberian herbaria or field explorations (later included in the HVR herbarium). They have been designated by means of the *index herbariorum* code (Holmgren & Holmgren 1998): COI, HVR, LISE, PO and LISU in Portugal, and MA, MGC, SALA, SANT and SEV in Spain. The collections were geographically referenced to elaborate the geographic distributions of the results obtained (published in <http://www.jb.utad.pt/pt/investigacao/Morfoecologia/Locat.pdf>).

The main purpose of this analysis was the identification of morphotypes (*Forms*). The morphological analysis relied on the analysis of 18 morphological characters using 28 quantitative morphological parameters (Table I). The collected specimens were selected depending on their state of conservation in order to obtain comparable morphological data. Then, a morphological matrix per specimen measured was created.

Table I. Relation of the morphological characteristics analysed (and their respective trait codes).

Var.	Morphological description
NL	Leaf number
Ll1	Lowest length of leaves
Ll2	Highest length of leaves
Lw1	Lowest width of leaves
Lw2	Highest width of leaves
NI	Highest number of inflorescences per individual
Inn1	Lowest number of pseudowhorls per inflorescence
Inn2	Highest number of pseudowhorls per inflorescence
LEb1	Lowest length of the inflorescence peduncle
LEb2	Highest length of the inflorescence peduncle
LE1	Lowest length of the first space between pseudowhorls of the inflorescence
LE2	Highest length of the first space between pseudowhorls of the inflorescence
FNb1	Lowest number of leaves in the first pseudowhorl of the inflorescence
FNb2	Highest number of leaves in the first pseudowhorl of the inflorescence
Flp1	Lowest length of the pedicel of flowers in the first pseudowhorl of the inflorescence
Flp2	Highest length of the pedicel of flowers in the first pseudowhorl of the inflorescence
FP1	Highest length of petals
FCl	Highest length of sepals
B11	Lowest length of leaves for the first pseudowhorl of inflorescences
B12	Highest length of leaves for the first pseudowhorl of inflorescences
NF	Highest number of flowers per inflorescence
I11	Lowest length of inflorescences
I12	Highest length of inflorescences
NR	Number of pseudowhorls with roots
CW	Highest width of the flower stem
SL	Highest length of fruits
SW	Highest width of the fruits
NS	Highest number of seeds per fruit

The environmental analysis was based on the average temperature per month, average precipitation per month and altitude of the collection site. All the herbarium data, and not just the measured values of the specimens considered here, were introduced in the environmental matrix. The thermo-pluviometric values were obtained from the WorldClim layers (<http://www.worldclim.org>), proposed by Hijmans et al. (2005) and already tested for the genus *Narcissus* in the Iberian Peninsula (Hodgins & Barret 2008). In this case, an environmental matrix was established, and each population was identified according to the morphotypes obtained by the morphometric analysis.

The morphological and environmental matrices were analysed by multivariate analysis. The whole statistical analysis was carried out using STATISTICA 9.0 software (Statsoft Ltd.). From the multivariate description of the morphological matrix (Crespí et al. 2007), a similarity analysis, *via* cluster, and a classification approach were derived. Ward's amalgamation method (analysis of variance was used for evaluating the distance between clusters) and a Chebycheb distance measure (each population was *a priori* considered to be biologically different) were used to examine the similarity between the individuals, which is graphically represented in a dendrogram-type representation. Forward stepwise Canonical Discriminant Analysis (CDA) was used as an appropriate multiple discriminant analysis to reveal which variables discriminate between groups (in the present case, morphotypes). Statistical significance level was evaluated by the F , to remove values, Wilks' lambda and p -level (Morrison 1990; Hair et al. 1995). The description of the total morphological variation was performed by a biplot graphic, displayed from a Principal Component Analysis (PCA) upon a Pearson's correlation of the morphometric matrix (Morrison 1990). This methodology is a very useful tool for revealing clusters between operational taxonomic units (OTUS) and individuals (Gabriel 1971). Finally, 3D-plots for the most discriminating variables, average graphs and box-plots were used for describing the results obtained. Because of the standardisation of measurements, the units used here were designated as Structural Units.

Results

Morphometric analysis

Based on the geographical distribution of the individuals and the morphological variability, 492 populations were incorporated into the environmental matrix. For the morphological matrix, 192 specimens were selected.

The dendrogram of Figure 1 reveals three morphotypes, named (Form 1 – (F1), Form 2 – (F2) and Form 3 – (F3). *B. ranunculoides* subsp. *repens* and *B. alpestris* are represented in F1, *B. ranunculoides* var. *ranunculoides* in F2 and F3 represents the morphology described by Pau (1924) as *A. tangerina* (an annual morphotype with great robustness and a large number of flowers).

F1 is represented by the morphologies where sexual and asexual reproduction is combined. In contrast, asexual reproduction is not detected in F2 and F3 (Figure 2 shows the schematic representation of these three general morphotypes).

The CDA and the biplot PCA plots for those morphotypes confirm opposite morphological features (Figure 3a and b), with the highest F values (F to remove 34.48; Wilks' lambda = 0.211598) and the lowest p -level (p -level < 0.000 for FNb2, Table II).

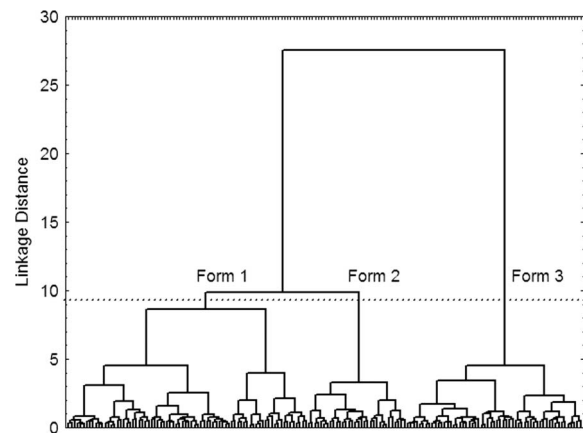


Figure 1. Dendrogram of the Pearson's correlation matrix for the morphological matrix, based on the cluster analysis. Note: Three apparent morphological tendencies or morphotypes are observed.

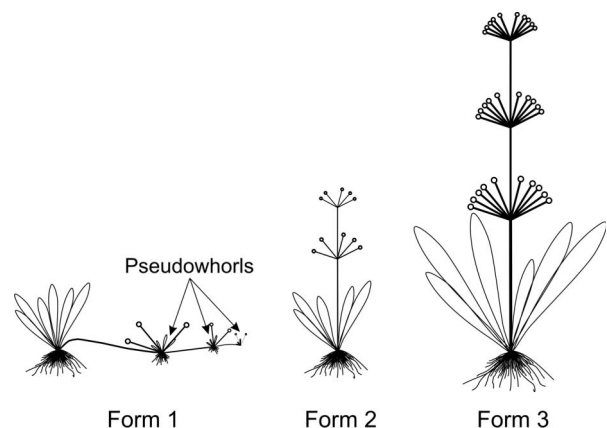


Figure 2. Schematic representations of the three Forms (morphotypes) detected for the genus *Baldellia*. Note: Proliferations with pseudowhorls are characteristics for Form 1 (*B. repens* and *B. alpestris*). Longer leaves and inflorescences, as well as a higher number of flowers and fruits, distinguish Form 3 (*B. tangerina*) from Form 2 (*B. ranunculoides*).

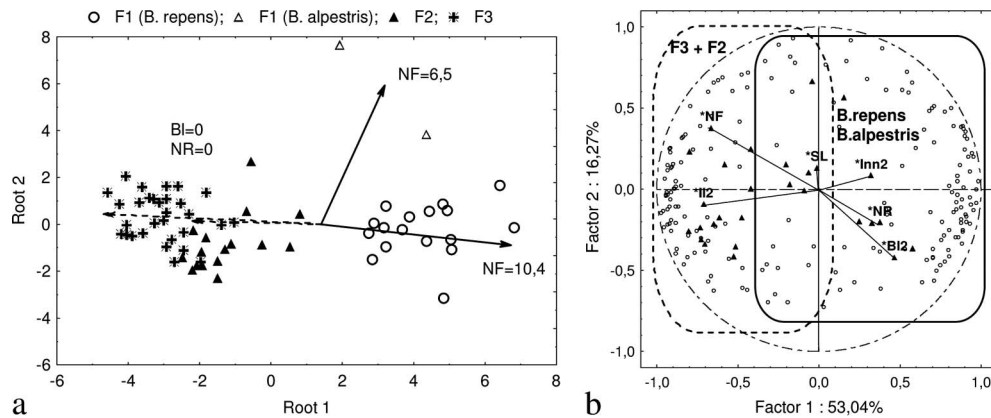


Figure 3. (a) CDA for the three forms (F1 distinguished between *B. ranunculoides* subsp. *repens* and *B. alpestris*). (b) Biplot PCA exposes the confirmation of the variables NF—highest number of flowers per inflorescence, l_2 —highest length of inflorescences, Inn2—highest number of pseudowhorls per inflorescence, NR—number of pseudowhorls with roots and BI2—highest length of leaves for the first pseudowhorl of inflorescences as the main morphological variables for distinguishing the two opposite behaviours – F1 and F2+F3 –.

The highest discrimination is obtained for the variables related to the number of flowers and the length of the inflorescence as well as the rooting capacity of the inflorescences. The 3D-plot for these variables is shown in Figure 4a and b. The morphological differences are more evident in the average plots for the more discriminating variables (Figure 4c and d).

According to these results, the genus *Baldellia* displays two extreme morphotypes: Form 1 (*B. repens* and *B. alpestris*) and Form 2 (*B. ranunculoides*) are characterised by smaller inflorescences and fewer flowers in contrast to Form 3 (larger inflorescences and a higher number of flowers); the lack of asexual reproductive structures (e.g. leaves and roots at the nodes) is characteristic for Forms 2 and 3. Based on these results and the morphological description published by Pau (1924) and confirmed by the specimens MA3597 (Tanger, Morocco, 05–1921, Pau, lectotypus of *A. tangerina* Pau), MA3614 (Isaguen, Atlantae Riphæo, 02–07–1927, Font Quer) and MA3617 (Atlas Rifain, Marécages de Isagen, 20-Jun., Sennen & Mauricio), F3 will be here recombined as *B. ranunculoides* subsp. *ranunculoides* var. *tangerina* (Pau) J. Rocha, A. Crespi, M. Garcia-Barriuso, R. Almeida, J. Honrado, *comb. nova* in order to distinguish it from *B. ranunculoides*.

A key to distinguish these three forms, based on the morphological characteristics, is as follows:

1. Plants with asexual reproductive structures (leaves, and sometimes roots, at the pseudowhorls)

Form 1

No more than two flowers per node

(*B. alpestris*)

More than two flowers per node

(*B. ranunculoides* subsp. *Repens*)

Table II. Numerical values for the CDA upon the morphological matrix classified on the basis of the apparent morphological forms.

	Wilks'	Partial	F-removed	p-level	Toler
FNb2	0.211598	0.689261	34.48847	0.000000	0.776552
CW	0.167642	0.869986	11.43246	0.000024	0.564094
BI2	0.159689	0.913319	7.26048	0.000972	0.455933
NF	0.156056	0.934576	5.35530	0.005650	0.609281
Flp2	0.151473	0.962853	2.95136	0.055252	0.554068
L11	0.150241	0.970749	2.30514	0.103200	0.609878
Inn2	0.150811	0.967079	2.60420	0.077238	0.798579
NL	0.150293	0.970413	2.33240	0.100505	0.770474
FPI	0.148973	0.979016	1.63966	0.197437	0.943837
NR	0.148046	0.985146	1.15348	0.318265	0.633740

2. Plants without asexual reproductive structures
Inflorescences < 20 cm, < 20 flowers per inflorescence; pedicels of the first pseudowhorl flowers < 5 cm; number of fruits per flower usually < 25

Form 2

(*B. ranunculoides* var. *ranunculoides*)

Inflorescences usually > 20 cm, 20 or more flowers per inflorescence; pedicels of the first pseudowhorl flowers > 5 cm; number of fruits per flower usually ≥ 25

Form 3

(*B. ranunculoides* var. *tangerina* *comb. Nova*)

Table III shows the morphological differences per Form, according to the organs analysed.

Environmental analysis

The geographical distribution of the specimens analysed per morphological form is depicted in Figure 5. Form 1 (*B. repens* and *B. alpestris*) is conspicuously concentrated in the west of the Iberian Peninsula; Form 3 spans from the north of Morocco to the east of the Iberian Peninsula, but is absent in

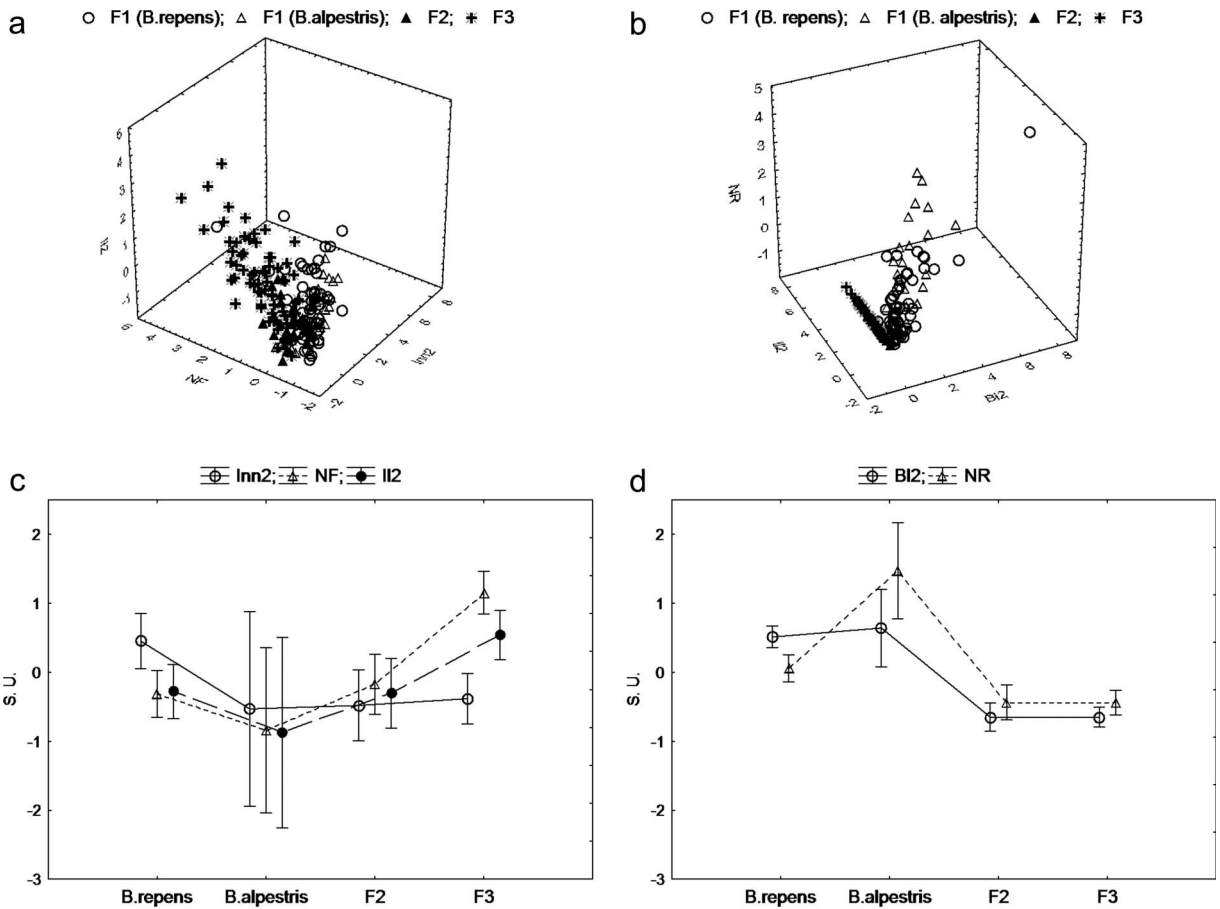


Figure 4. Three-dimensional plots for Inn2, NF and II2 (a) and BI2, II2 and NR (b) values for each population reveal two different morphological tendencies. Note: The average variations of those variables per morphological tendency (F1, here differentiated into *B. ranunculoides* subsp. *repens* and *B. alpestris*, and F2 and F3), represented in graphs (c) and (d), show the opposite reproductive behaviours in F1 and F2+F3.

Table III. Morphological differentiation of the three forms and four taxa deduced for the genus *Baldellia* (the most relevant morphological differences are specified in bold).

Morphological characteristics	Form 1		Form 2	Form 3
	<i>B. repens</i>	<i>B. alpestris</i>	<i>B. ranunculoides</i>	<i>B. tangerina</i>
Width of stems (mm)	(0.8) 0.9–1.4 (1.8)	(0.7) 0.6–1.6 (1.8)	(0.5) 1–1.5 (2.7)	(0.9) 2.1–2.5 (3.7)
Number of leaves (<i>n</i>)	(6) 7–21 (44)	(5) 6–21 (23)	(5) 12–16 (37)	(3) 12–17 (35)
Length of leaves (mm)	(16) 27–215 (321)	(10) 11–140 (192)	(11) 45–135 (327)	(2.3) 90–135 (414)
Width of leaves (mm)	(0.8) 1.3–10 (22)	(0.4) 0.6–8 (9)	(0.6) 2–6 (10)	(1) 4–9 (17)
Number of inflorescences (<i>n</i>)	(1) 2–4 (8)	(1) 1–4 (5)	(1) 2–3 (9)	(1) 2–4 (9)
Roots at pseudowhorls (<i>n</i>)	0–3 (5)	0–3 (5)	0	0
Leaves at pseudowhorls (<i>n</i>)	(0) 1–5 (10)	(0) 0–5 (15)	0 (2)	0
Length of inflorescence (mm)	(21) 48–347 (452)	(4) 11–200 (201)	(12) 75–165 (410)	(11) 180–310 (645)
Length of pedicels of flowers (mm)	(7) 15–77 (142)	(3) 6–13 (60)	(10) 20–42 (73)	(8) 55–330 (395)
Number of flowers (<i>n</i> ^o)	(2) 4–16 (46)	3–14 (15)	(3) 8–12 (32)	(7) 20–30 (67)
Length of sepals (mm)	(0.8) 2.4–4 (4.3)	(1.6) 2–4	(2) 2.5–3.5 (4.2)	(2.2) 3–3.8 (4.8)
Length of petals (mm)	(2.4) 4–9 (13)	(3.1) 3–8 (10)	(4.2) 5–8 (11.4)	(3.2) 5–8 (11)
Length of fruits (mm)	(1.6) 2–2.5 (3.7)	(1.6) 2–2.5 (3.7)	(1.7) 2–2.7 (3.3)	(1.6) 2–2.6 (3.1)
Width of fruits (mm)	(0.8) 0.9–1.4 (1.8)	(0.7) 0.8–1.6 (1.8)	(0.8) 1–1.2 (1.4)	(0.8) 1.1–1.4 (1.7)
Number of fruits per flower (<i>n</i>)	(8) 9–23 (33)	7–27 (27)	(10) 18–22 (36)	(13) 25–30 (40)

the northwest; finally, Form 2 shows intermediate occurrences between the other two forms.

The results of the environmental analysis reveal important differences between Forms 1 and 3.

Average altitudes are highest for Form 1 and lowest for Form 3 (Figure 6a). *B. alpestris* occurs at low altitudes on the western coast, and at gradually higher locations along the eastern direction (Figure 6b).

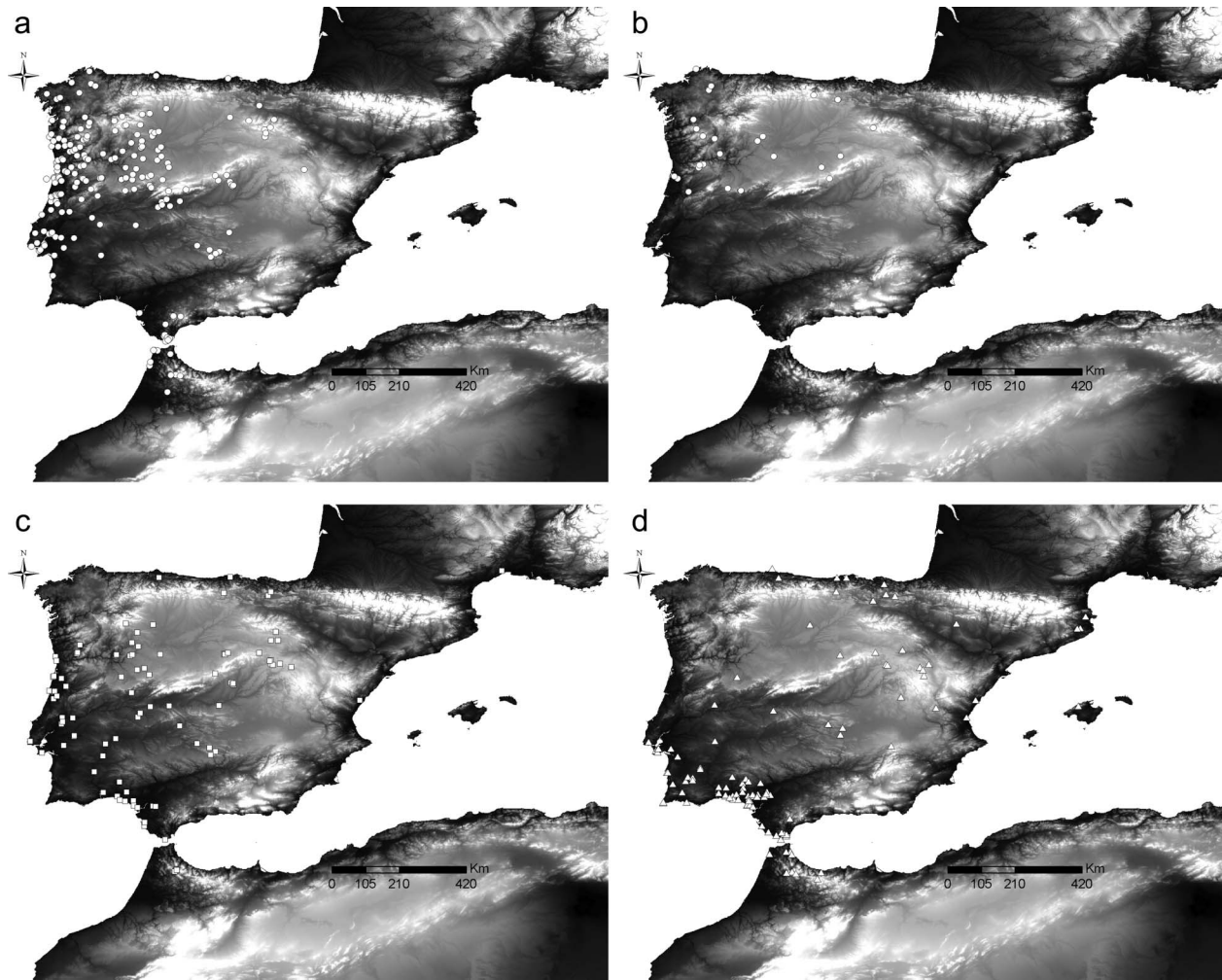


Figure 5. Distribution of (a) Form 1 (F1) *B. ranunculoides* subsp. *repens*; (b) Form 1 (F1) *B. alpestris*; (c) Form 2 (F2) and (d) Form 3 (F3) in the study area.

While lowest average temperatures are recorded for Form 1, the highest values are observed in case of Form 3 (average values per season are shown in Figure 6c). As regards average precipitations per season, these are highest for Form 1 and lowest for Form 3 (Figure 6d). The box-plots of Figure 6e show the environmentally contrasting conditions for Form 1, on one hand, and for Forms 2 and 3 on the other.

Discussion

The taxonomical difficulties in *Baldellia* Parl. have been attributed to its inherent morphological variability. Very recently their reproductive behaviour has been pointed out as the main reason for this phenotypic complexity (Kozłowski et al. 2008; Kozłowski & Matthies 2009). In the present work, a study relying on a numerical morphological comparison has been carried out with the goal of elucidating the phenologic behaviour of this genus. One of the most critical aspects that one faces when the morphology of *Baldellia* is examined is the

capacity that this plant has to radically alter its aspect depending on the reproductive strategy. In those cases where vegetative reproduction strategies are adopted, the plant transforms its inflorescences into stolons (“pseudostolons”, in accordance with Charlton 1973, or “inflorescence stolons”, according to Kozłowski et al. 2008) by developing leaves and roots in the first pseudowhorls of those inflorescences; the number of flowers and fruits per inflorescence is strongly reduced. In contrast, when the reproduction strategy is not vegetative, a clear increase in the number of flowers, an ascendant orientation of the inflorescences and a greater number of fruits per flower is observed.

Vuille (1988) and Kozłowski et al. (2008) interpreted the morphological changes developed by *Baldellia* as a function of the type of reproduction process adopted. These alterations were referred to the inflorescences, the amount of pollen produced, pollen size, number of carpels and dimension of the fruits. This phenomenon, associated with the need of heterogametic crossovers caused by a floral structure

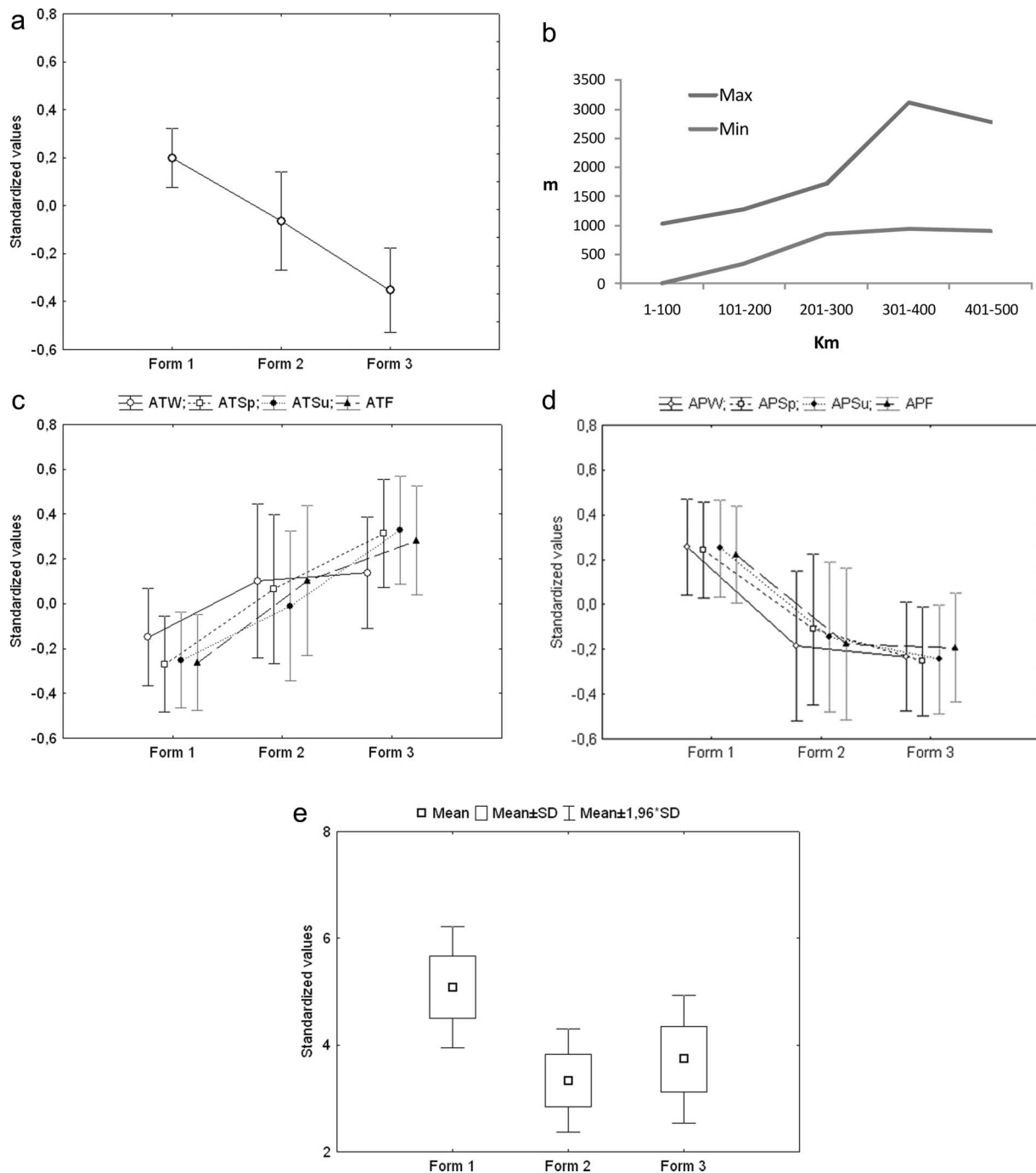


Figure 6. (a) Variation of average altitude values per morphological Form; (b) variation of highest (max) and lowest (min) altitudes for *B. alpestris*; (c) variation of average temperature values per season (ATW, average temperature for winter; ATSp, average temperature for spring; ATSu, average temperature for summer; ATF, average temperature for autumn); (d) variation of average precipitation values per season (APW, average precipitation for winter; APSp, average precipitation for spring; APSu, average precipitation for summer; APF, average precipitation for autumn); (e) box-plot of the environmental (temperature, precipitation and altitude) parameters per morphotype.

that endows these individuals with a genotypic transmission of their own (Vieira & Souza Lima 1997), could be the reason for the diverse taxonomic interpretations and many identification disagreements for *Baldellia*. The present numerical and comparative analysis of the morphology of *Baldellia* for the Iberian and Moroccan species of this genus, which avoids taxonomic issues, has turned out to be

an excellent tool to describe its apparent morphological behaviours. The taxonomical controversy could be discussed in terms of the reproductive strategy of the plant, as a response to environmental conditions.

According to the data derived from the present investigation, *Baldellia* offers three apparent morphotypes, which primarily depend on the transfor-

mation of the inflorescences into inflorescence stolons and on the number of fruits per flower. Other morphological variables show less discriminating values (e.g. aspect of the basal leaves and width of the stems) as a consequence of the reproductive morphological transformations involved. Interestingly, the most cited difference in the literature is related with *Baldellia*'s capacity to develop two opposite forms: either stoloniferous individuals (*B. ranunculoides* subsp. *repens* and *B. alpestris*) or ascending or erect individuals (*B. ranunculoides* and *B. tangerina*). Still, another question that remains open has to do with possible environmental correlations. Indeed, this factor could be seminal for a better understanding of the morphological variability of *Baldellia*.

In addition to the apparent correlation existing between the phenotypical behaviours and the reproductive strategy, the morphological characterization along thermo-pluviometric and altitudinal variations also allows to draw interesting conclusions. For instance, the environmental variability is clearly higher for Form 1. This morphotype is concentrated on the west of the Iberian Peninsula in contrast to Form 3 that is more frequent in the east. These three morphotypes (with the exception of *B. alpestris* – part of Form 1, which is just concentrated in the northern part of the Iberian Peninsula) exhibit confluent occurrences in the southwest of the Iberian Peninsula and the northwest of Morocco. According to Kozłowski et al. (2008), this area might be a possible origin for this taxon, considering its high karyological number. This possibility is also in perfect agreement with the hypothesis of Moreno Saiz and Sainz Ollero (1997), based on the existence of paleofloristic refuges on coastal zones (i.e. similarity of the endemic flora), where no frozen soil was registered during the glacial periods.

This overlapping in the occurrences of the morphotypes as well as the apparent divergence of the morphological variability observed may suggest an evolutionary path for this genus (in accordance with the hypothesis proposed by Nicholls-Vuille – and cited by Kozłowski et al. (2008)). The evolutionary path into the Iberian Peninsula would imply the expansion of *Baldellia* along the western side of the Iberian Peninsula and the Cantabrian coast, and also across the Peninsula along the Guadiana, Tejo and Douro valleys. The eastern corridor would be limited by the biological Almeria border (Hernández Bermejo and Sainz Ollero 1984). The latter hypothesis could explain the low density of individuals in this region. A similar phenomenon has been pointed out for other genera, such as *Hypochoeris* (Tremetsberger et al. 2006) or *Stauracanthus* (Pardo et al. 2008), locating their origins in the Onubo–Moroccan zone. This claim relied on the glacial-interglacial

floristic paths, which provided a dynamic and enlarged genetic flow in this zone. Although this possibility could be refuted by the abnormal polyploid number detected for the northwest of Morocco ($2n = 20$, Kozłowski et al. 2008), it must be stressed that this area has a well-known resilience, with conditions of humidity and temperature that made the development of micro-refuges possible during glacial periods (Rodríguez-Sánchez et al. 2008). Convincing proof of this phenomenon is the high concentration of taxonomic diversity in this area (Myers et al. 2000). According to Médail and Quézel (1997), it justifies its classification as a hot spot of the Mediterranean basin mainly because of the climatic transition in a heterogeneous topographic environment (Cowling et al. 1996).

Form 3 demonstrates more appropriate morphological variability at higher average temperatures, lower precipitations and lower altitudes. This behaviour is manifested along the south and east of the Iberian Peninsula. The morphological variability of Form 1 is apparently more adapted to lower average temperatures and higher precipitations and altitudes. As a consequence, its preferential occurrence takes place in the north and west of the Iberian Peninsula. Nevertheless, the environmental approach shows an important divergence in terms of thermo-pluviometry and altitude; the sexual reproductive strategy favoured the distribution of the genus into warmer and drier areas. Indeed, the variability of the average values for temperature and precipitation in the case of Forms 2 and 3 confirms this idea. Therefore, the concentration of the three forms along the northwest of Morocco and the Gulf of Cádiz is the basis for our hypothesis of the origin of the genus *Baldellia* in the Tanger-Cádiz bay. This thermo-pluviometric influence must be joined with habitat's influences. In accordance with Kozłowski and Matties (2009), more acid and organic-rich soils will characterise Atlantic influences and the occurrence of Form 1 (*B. repens* and *B. alpestris*). In contrast, a decrease in organic matter composition and higher concentrations of Ca^{2+} will stimulate Form 3 (*B. tangerina*). Differences between Form 1 and Form 2 could be explained in terms of gap periods: temporary for *B. ranunculoides* and long-standing for *B. repens* (more acid and organic-rich soils for the latter taxon). In fact, no vegetation differences were significant by these authors.

Other alternative hypothesis cannot be discarded. The confluence of the three morphotypes in the southwest of the Iberian Peninsula and the northwest of Morocco could also be the result of migrations of the morphotypes within this area during the glacial periods. This hypothesis as well as possible infra-specific variations (according to Talavera et al. 2008) will also be tested in a subsequent work.

Conclusions

The taxonomic controversy around the genus *Baldellia* is evident in the scientific literature. Diverse reproductive behaviours associated to this genus offer a large combination of morphological features. That controversy has been analysed here in terms of morphometric and environmental characterisations. Three morphotypes (designated as “Forms” in the present contribution) were detected through the morphometric analysis: *B. repens* and *B. alpestris* are represented under Form 1; *B. ranunculoides* as Form 2; and a new taxonomical combination is proposed for Form 3, based on Pau’s ancient combination *A. tangerina*, now designated as *B. ranunculoides* subsp. *ranunculoides* var. *tangerina* comb. nova. While two of these Forms are clearly opposite (Forms 1 and 3), an intermediate one exists between them (Form 2). Asexual reproduction characterises Form 1, whereas only sexual reproduction is involved in Forms 2 and 3 (these two morphotypes lack vegetative proliferative structures). The results of the morphological variability analysis performed for the three Forms revealed that a larger morphological variability is evident for Form 3 than for the other two forms. Furthermore, the environmental characterisation confirmed the importance of the reproductive strategies. In fact, the adopted thermo-pluviometric and altitudinal approach showed two distant behaviours in terms of average temperatures, precipitations and altitudes (which confirms the results obtained for the other morpho-environmental characterisations for this genus published till now). Lower average temperatures, higher average precipitations and higher altitudes are more favourable for Form 1; higher average temperatures and lower average precipitations and altitudes are preferred by Forms 2 and 3.

According to the geographical distribution of the 492 specimens observed, the concentration of the three Forms in the Tanger-Cadiz bay suggests that this location might be the origin for the genus *Baldellia* or a biological refuge in the inter-glacial periods.

Based on the results reported here, a new taxonomical combination is proposed:

B. ranunculoides subsp. *ranunculoides* var. *tangerina* (Pau) J. Rocha, A. Crespi, M. García-Barruso, R. Almeida, J. Honrado, comb. nova.

Basionym: *A. tangerina* Pau, Memorias de la Real Sociedad Española de Historia Natural 12, 389. 1924.

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