

RESEARCH ARTICLE

Taxonomic reassessment of *Tolpis* (Asteraceae) in the Azores and Madeira archipelagos with description of new species

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Abstract *Tolpis* (Asteraceae) is a recently diversified genus of flowering plants, centered in the Macaronesian region, where it exhibits striking morphological variation and high levels of endemism. In this study, we focus on the archipelagos of Madeira and the Azores (Portugal). The Azores are divided into three biogeographically distinct island groups—western, central, and eastern sub-archipelagos—which provide a natural framework for studying insular diversification. The number and identity of endemic *Tolpis* taxa in these islands remain poorly understood. To address this, we integrated recent molecular evidence with a comprehensive morphometric dataset, including 349 specimens from 137 locations across both archipelagos. Based on 61 quantitative and qualitative morphological characters, we re-circumscribe previously described taxa and formally describe seven new endemic species from the Azores. Consistent morphological differences support the recognition of *Tolpis succulenta* as endemic to Madeira. Within the Azores, both *T. succulenta* and *T. azorica* in their current circumscription display island-level morphological variation, leading to the recognition of seven newly described endemic taxa.

Keywords Azores; endemic species; Macaronesia; Madeira; morphological traits; *Tolpis*

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

The Asteraceae represent one of the largest plant families, with c. 24,700 species distributed across c. 1620 genera (Palazzesi & al., 2022). The Global Compositae Database (Compositae Working Group, 2025) currently recognizes over 33,000 accepted species names, reflecting ongoing taxonomic updates.

The family is one of the most abundant on oceanic islands, both in terms of species richness and number of endemic and native species (Lenzner & al., 2017).

The Macaronesian region comprises 32 Atlantic Ocean islands forming the Azores, Canaries, Cape Verde, Madeira, and Selvagens archipelagos, with geological ages between 0.18 and 21 Ma (Mitchell-Thomé, 1985; Carracedo, 1994;

Carracedo & Troll, 2021). The region is distinctive from other oceanic insular systems in two biogeographic features: first, they exhibit a wide range of distances from the nearest continental areas, i.e., 100 km from Fuerteventura (the second-largest island in the Canary Islands archipelago) to the southern coast of Morocco, and 1890 km from Corvo (the smallest and westernmost island in the Azores archipelago) to mainland Portugal; second, there is a wide geographical separation of approximately 3000 km between the northernmost (Azores) and southernmost (Cape Verde) archipelagos.

The genus *Tolpis* Adans. (Cichorioideae: Cichorieae: Cichoriinae) (Susanna & al., 2020), is biogeographically remarkable because many of its species are Macaronesian endemics (Jarvis, 1980). The number of species placed in

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Tolpis ranges from 12 (Jarvis, 1980) to 20 (Tomb, 1977; Bremer, 1994). The genus is also distributed in other regions, such as Europe, Turkey, the Middle East, and Africa. According to Jarvis (1980) 10 of the 12 species occur in insular settings, with 6 of these being strictly island endemics (Jarvis, 1980), while the remaining 2 are continental species (Crawford & Stuessy, 2016).

Despite the extensive morphological and ecological variation within *Tolpis*, earlier attempts to resolve phylogenetic relationships within the genus and among archipelagos using a limited number of molecular markers were largely ineffective (Moore & al., 2002; Mort & al., 2003, 2007, 2010; Archibald & al., 2006; Gruenstaeudl & al., 2013, 2017). However, recent phylogenomic approaches based on target enrichment and next-generation sequencing have provided much greater resolution, effectively clarifying most *Tolpis* clades within Macaronesia and improving the understanding of relationships among archipelagos (Mort & al., 2015, 2022). According to Mort & al. (2022), *Tolpis macrorhiza* (Banks ex Hook.) DC., endemic to Madeira, is sister to the remainder of *Tolpis*. Within the remaining *Tolpis* species, the Madeiran populations of *T. succulenta* (Dryand. ex Aiton) Lowe are closely related to the Azorean populations currently treated as *T. succulenta* and *T. azorica* (Nutt.) P.Silva, together forming a Madeira-Azores clade. This clade is sister to *Tolpis* species from the Canary Islands, Cape Verde and the continent.

Ancestral range reconstruction based on Mort & al. (2022) suggests that a primary dispersal event from the continent to Madeira occurred, and from there, *Tolpis* probably colonized the Azores, followed by the Canaries. The youngest common ancestor of Azorean *Tolpis* and Madeiran *Tolpis succulenta* indicates equal probabilities for the Azores or Madeira as the ancestral area. From the Canary Islands, there was a dispersal to Cape Verde, as well as a back-dispersal to the continent, as previously postulated by Moore & al. (2002). The divergence of *Tolpis* species in Macaronesia is due to single-island radiations and interisland dispersal (Mort & al., 2022).

Tolpis includes annuals and herbaceous perennials, with mostly rosulate leaves, capitula arranged in corymbs or panicles, yellow florets, short styles, ribbed and glabrous cypselae, and a pappus with a few to many long scabrid setae interspersed with minute scales (Jarvis, 1980). The fruits seem well suited for wind dispersal, and wind squalls may have been particularly important in the dispersal of *Tolpis*, since the cypselae of many of its members possess long pappus setae (Jarvis, 1980).

There are currently three described species of *Tolpis* in the Azores and Madeira archipelagos: *T. azorica*, *T. macrorhiza*, and *T. succulenta*. *Tolpis azorica* has been traditionally recognized as the only species endemic to the Azores (Schaefer, 2003, 2005; Silva & al., 2010). It occurs on seven of the nine islands of the archipelago, being absent from Santa Maria and Graciosa (Borges Silva & al., 2016), and typically inhabits the mountainous, very humid inland regions. *Tolpis succulenta* has been listed for all the Azorean islands (Silva & al., 2010). According to Mort & al. (2015) and Borges Silva

& al. (2016), it is also present on Madeira, Porto Santo, and the Desertas Islands. It typically grows on dry coastal cliffs, rocks, and rocky banks up to 1000 m, and occasionally up to 1500 m in open habitats in Madeira (Jarvis, 1980; Schaefer, 2005). *Tolpis macrorhiza* is an endemic species restricted to Madeira Island (Mort & al., 2015; Borges Silva & al., 2016).

According to Lack (1981), who conducted an extensive synonymy revision of *Tolpis azorica* and *T. succulenta* (see “Taxonomic Treatment”), there is one endemic *Tolpis* in the Azores (*T. azorica*) and one endemic species shared between Madeira and the Azores (*T. succulenta*). The holotype of *T. azorica*, collected by Hochstetter (son) in 1838, is a specimen from Pico and is held at the TUB Herbarium. All other types of different synonyms are from the Central or Western groups of islands. The holotype and all isotypes of *T. succulenta* can be found at BM and were obtained from cultivated material at Kew from seeds collected on Madeira Island by Masson (1777) (Jarvis, 1980; Lack, 1981; Francisco-Ortega & al., 2008). Lack (1981) observed that unusual plants of *T. azorica*, collected on the islands of São Miguel and Santa Maria, had long hairs at the base of the cypselae and an odd distribution of leaves along the stem, indicating that the systematic position of these conspicuous variants needed further analysis. According to Lack (1981), *T. azorica* is isolated in the genus *Tolpis* with its foliar stem and conspicuous brown cypselae. Similar stems and cypselae can be found in *T. macrorhiza*, an endemic species from Madeira. However, both species are quite different in cypselae and pappus morphology and in pericarp anatomy (Jarvis, 1980). According to this author, *T. succulenta* is probably not closely related to *T. macrorhiza* from Madeira (different morphology of cypselae and pappus and different cypselae anatomy) and has a closer relationship to Canarian taxa.

Recent molecular studies (Borges Silva & al., 2016; Mort & al., 2022) have clarified the genetic structure of *Tolpis* in Macaronesia, consistently identifying four main lineages: *T. macrorhiza* and *T. succulenta* from Madeira, and *T. azorica* and *T. succulenta* from the Azores.

Within the Azores, *Tolpis succulenta* populations show additional structure, with distinct groups occurring in Santa Maria, Graciosa, and São Miguel, whereas *T. azorica* displays three geographically coherent subclades corresponding to the Eastern (São Miguel), Central (Faial, Pico, São Jorge, Terceira), and Western (Corvo, Flores) Island groups.

These genetic patterns provide the framework for the present morphometric reassessment, aimed at evaluating morphological congruence with the molecular lineages.

This spatial genetic pattern, consistently recovered in both simple sequence repeat (SSR) and phylogenomic datasets (Borges Silva & al., 2016; Mort & al., 2022), supports strong regional differentiation across the Azores and Madeira. Taking this evidence into account, we reviewed all previously available data including field observations, newly collected and existing herbarium specimens, and molecular data to reassess the taxonomic diversity of *Tolpis* in these archipelagos.

Based on this previous knowledge, we developed a new morphometric dataset to address two key questions: (1) How many endemic *Tolpis* taxa occur in the Azores and Madeira? (2) What are their corresponding taxonomic ranks and respective distributions across the archipelagos?

In order to address these questions, the specific objectives of this study were as follows: (1) expand population-level sampling of *Tolpis* spp. from Madeira and the Azores, (2) detect phenotypic clusters in Azorean and Madeiran *Tolpis* species using morphological characters, (3) evaluate whether variation in *Tolpis* across the archipelagos supports the recognition of additional taxonomic entities in the Azores and Madeira, and (4) provide formal taxonomic descriptions for the newly identified endemic *Tolpis* species from the Azores.

■ MATERIALS AND METHODS

Study site. — The study was conducted in two Macaronesian archipelagos: the Azores and Madeira (Figs. 1, 2). The Azores (36°55'N and 39°42'N, 25°00'W and 31°30'W) are situated about 1500 km west of mainland Portugal, 942 km northwest of Madeira and 3380 km east from North America (Fig. 1A). This archipelago covers a total area of 2323 km² and comprises nine inhabited volcanic islands, dispersed over three geographical groups (also referred to as sub-archipelagos): the Eastern group (Santa Maria, São Miguel), the Central group (Faial, Graciosa, Pico, São Jorge, Terceira) and the Western group (Corvo, Flores). The maximum spacing between the islands corresponds to the distance between Corvo and Santa Maria and exceeds 630 km (Fig. 1B). The maximum elevation of the islands varies from 402 m in Graciosa to 2351 m at Pico Mountain, the highest point of Portugal. Contrasting with the rest of the archipelago, 16% of Pico Island's area is above 800 m. The archipelago is geologically young compared to other Macaronesian archipelagos, with the oldest island, Santa Maria (6.03 Ma, Ramalho & al., 2014), and the youngest, Pico Island (0.18 Ma, Costa & al., 2015). The Madeiran archipelago (between 30°01'N and 33°07'N, 15°51'W and 17°30'W), is in the Atlantic Ocean, southwest of the Iberian Peninsula, about 870 km from mainland Portugal, 700 km from the West African coast and between 450 and 550 km from the Canary Islands (Fig. 2A). The archipelago consists of Madeira Island (7 Ma, Ramalho & al., 2015) and the older Porto Santo (18.8 Ma, Mata & al., 2013). Several small islets are situated NE of the archipelago as well as two smaller uninhabited groups of islands (Desertas, Selvagens) (Fig. 2B). Madeira is the largest island (750 km²), with the highest peak 1861 m.

Sampling and morphological data collection. — Field work was conducted between July 2009 and July 2021. A total of 349 specimens were collected from 137 sampling locations across the Azores (103) and Madeira (34) archipelagos (Figs. 1, 2; Appendix 1). One or two representative voucher specimens per population were collected, pressed, mounted, and stored at the AZB Herbarium's Azorean Flora DNA Bank.

In addition to the AZB Herbarium specimens collected, 97 specimens on loan were included from AZ (16), AZU (7), BM (10), EMU (9), LISI (14), LY (14), MO (23), OFX (3), and TUB (1) (Appendices 2–11). Several additional specimens were examined from images provided by BR, COI, GB, LISE, LISU, MANCH, P, and W (Appendices 2–11). A gift from the McGregor Herbarium (KANU) was also added, composed of 33 specimens germinated and reared in greenhouses at the University of Kansas from seeds of two wild *Tolpis* species collected in Graciosa Island (Kerbs & al., 2020).

A total of 349 specimens from the Azores and Madeira were measured (Appendices 2–11): *Tolpis azorica* sensu lato (Azores) – 168 specimens: 7 from Corvo (4 AZB, 2 BM, 1 LISI); 13 from Faial (4 AZB, 2 AZU, 2 BM, 2 EMU, 2 LISI, 1 MO); 15 from Flores (1 AZ, 9 AZB, 1 BM, 1 LISI, 3 MO); 32 from Pico (29 AZB, 1 BM, 1 LISI, 1 TUB); 10 from São Jorge (9 AZB, 1 LISI); 73 from São Miguel (13 AZ, 32 AZB, 1 BM, 6 EMU, 2 LISI, 6 LY, 11 MO, 2 OFX); and 18 from Terceira (15 AZB, 2 AZU, 1 LISI).

Tolpis succulenta sensu lato (Azores) – 123 specimens: 3 from Corvo (1 AZ, 1 BM, 1 MO); 2 from Faial (1 EMU, 1 LISI); 4 from Flores (1 AZ, 1 LISI, 2 MO); 36 from Graciosa (35 AZB, 1 BM); 22 from Santa Maria (3 AZU, 11 AZB, 1 BM, 1 LISI, 3 LY, 2 MO, 1 OFX); 1 from São Jorge (1 LISI); 51 from São Miguel (45 AZB, 4 LY, 2 MO); and 4 specimens from Terceira (1 AZB, 1 LISI, 1 LY, 1 MO). *Tolpis succulenta* sensu lato (Madeira and Porto Santo) – 58 specimens: Madeira (35 AZB), Porto Santo (23 AZB).

Vouchers were geo-referenced, and a sampling maps generated with these data, using Quantum Gis Desktop 3.16-Hannover (Figs. 1, 2).

Compilation and standardization of morphological characters for *Tolpis*. — Sixty-one morphological characters, encompassing quantitative and qualitative traits from both reproductive and vegetative organs (see suppl. Table S1), were compiled based on classical taxonomic treatments of *Tolpis* (e.g., Aiton, 1789; Nuttall, 1841; Seubert, 1844; Lowe, 1868; Menezes, 1914, 1926; Palhinha, 1966; Jarvis, 1980; Lack, 1981) and standard glossaries (e.g., Hickey & King, 2000). The selection was based on three complementary criteria: (1) prior taxonomic relevance, with characters cited in the literature for their diagnostic value in *Tolpis* and other Asteraceae; (2) observed morphological variation, specifically traits showing consistent differences among individuals from the four main genetic lineages identified by SSR and phylogenomic data (Borges Silva & al., 2016; Mort & al., 2022); and (3) diagnostic potential, referring to characters with high resolution expected to discriminate among closely related taxa. Those initially selected morphological variables were retained at this preliminary stage because they represent complementary aspects of morphological variation. This integrative approach allowed us to capture the full spectrum of biologically and taxonomically meaningful differentiation prior to any statistical dimensionality reduction.

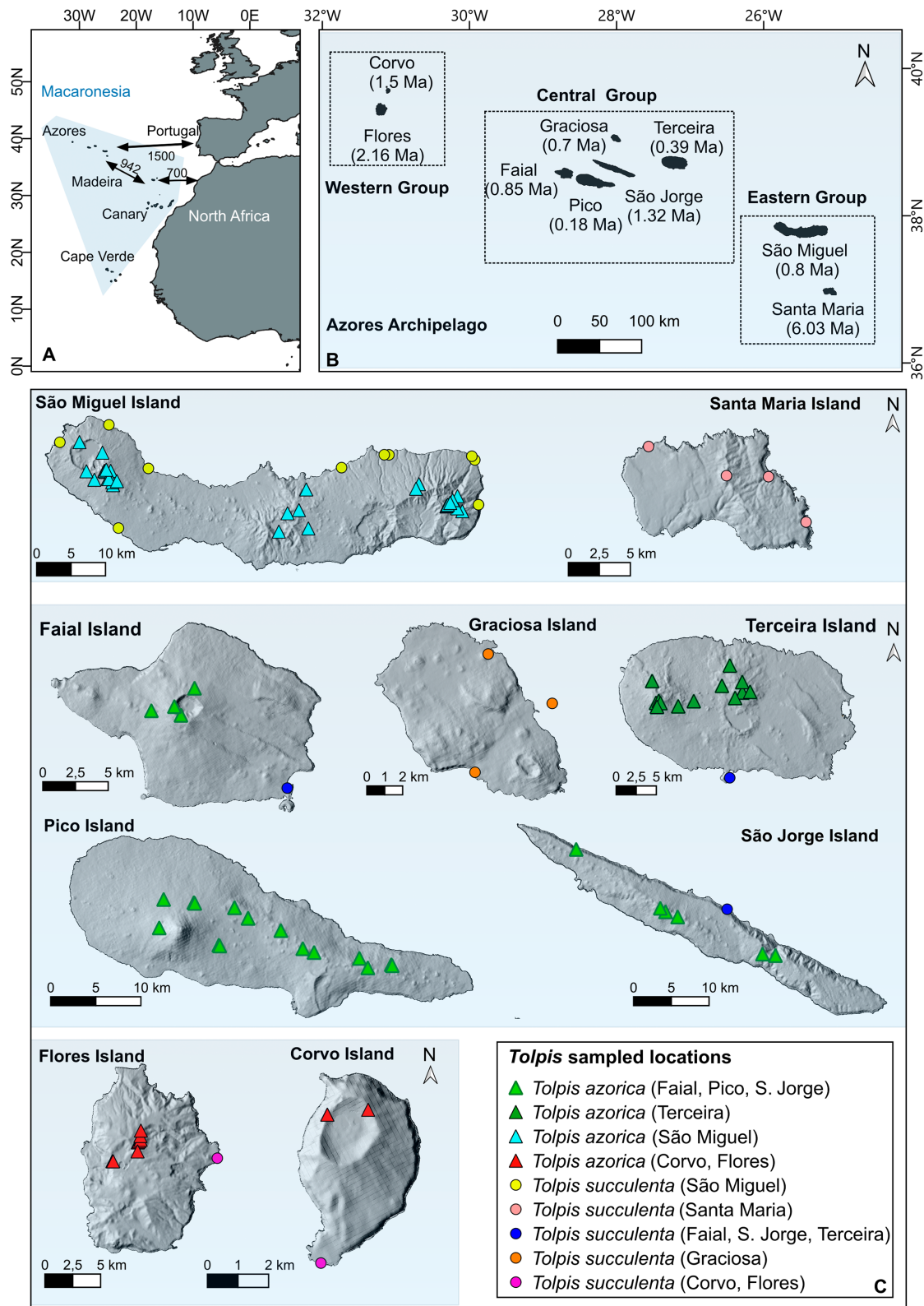


Fig. 1. Location of the Azores archipelago (Portugal) and the distribution of the 103 *Tolpis* locations sampled: **A**, Distances among archipelagos and the mainland (kilometres); **B**, Geological age estimates for the islands; **C**, *Tolpis* locations sampled: *T. azorica* (Faial, Pico, S. Jorge) by light green triangles; *T. azorica* (Terceira) by dark green triangles; *T. azorica* (São Miguel) by light blue triangles; *T. azorica* (Corvo, Flores) by red triangles; *T. succulenta* (São Miguel) by yellow circles; *T. succulenta* (Santa Maria) by pink circles; *T. succulenta* (Faial, São Jorge, Terceira) by dark blue circles; *T. succulenta* (Graciosa) by orange circles; and *T. succulenta* (Corvo, Flores) by purple circles. — Note: European Digital elevation models, version 1.1 generated in the Copernicus programme (copernicus@eea.europa.eu).

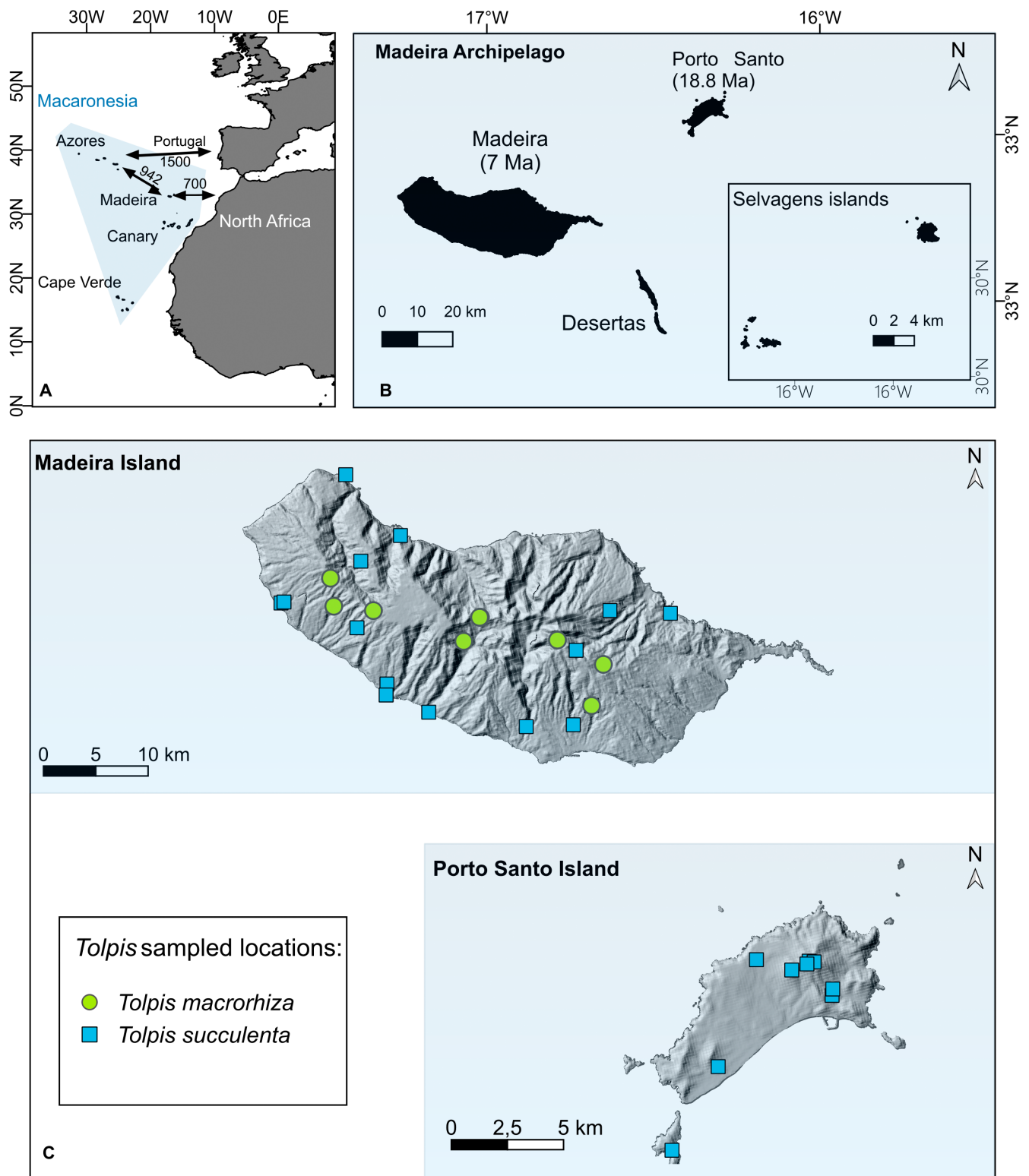


Fig. 2. The distribution of the 34 *Tolpis* locations sampled in the Madeira archipelago (Portugal): **A**, Distances among archipelagos and the mainland (kilometres); **B**, Estimated geological ages of the islands; **C**, *Tolpis* locations sampled – *Tolpis macrorhiza* by circles and *Tolpis succulenta* by squares. — Note: European Digital elevation models, version 1.1 generated in the Copernicus programme (copernicus@eea.europa.eu).

Statistical analyses. — The statistical workflow followed a two-phase structure corresponding to the preliminary and final datasets.

Preliminary dataset and exploratory analyses. — An exploratory morphometric dataset comprising 61 morphological characters, encompassing both qualitative and quantitative traits from reproductive and vegetative organs (as defined in suppl. Table S1), was assembled using 132 herbarium specimens available at AZB (Appendices 2–11). Three measures (replicates) for each quantitative trait were taken per specimen.

This preliminary dataset was part of the Master's thesis by Borges Silva (2012). Morphological characters were scored to evaluate variation and assess correspondence with the four main genetic lineages identified: (i) *T. macrorhiza* from Madeira, (ii) *T. succulenta* from Madeira, (iii) *T. succulenta* from the Azores, and (iv) *T. azorica* from the Azores (Borges Silva & al., 2016; Mort & al., 2022) (see suppl. Fig. S1, suppl. Tables S2, S3).

To explore major patterns of morphological variation, a principal coordinates analysis (PCoA) was conducted using the preliminary dataset, which incorporated both qualitative and quantitative traits related to reproductive and vegetative morphology.

Qualitative traits were tested for association with the genetic groupings using chi-square tests, and quantitative traits were assessed via one-way ANOVA followed by Tukey HSD post hoc tests. The assumptions of normality and homogeneity of variance were checked using Shapiro-Wilk and Levene's tests, respectively.

Final dataset and multivariate analyses. — Following the exploratory phase, the number of studied specimens was significantly expanded to 349 through the inclusion of field material newly collected in the Azores and Madeira archipelagos and herbarium loans from other institutions (Appendices 2–11). The original set of 61 morphological characters was subsequently re-applied to this broader sample to enable a more comprehensive assessment of morphological variation across the Azores and Madeira archipelagos.

To optimize the dataset for downstream analyses, a step-wise character selection was carried out based on data availability, statistical performance, and biological relevance. Characters showing substantial levels of missing data, limited discriminatory power among genetic groups (ANOVA, $p > 0.05$), or high redundancy (high pairwise correlation, $|r| > 0.8$) were excluded during data curation. This filtering resulted in a final dataset of 13 quantitative reproductive and vegetative characters for downstream multivariate analyses. This character selection did not replace, but rather built upon, the exploratory phase conducted with the smaller herbarium dataset. The increased sample size provided a stronger statistical basis to reassess trait relevance and to focus on the most informative and robust characters.

This final dataset of 13 quantitative reproductive and vegetative characters (suppl. Table S1) was then used in downstream multivariate analyses to assess morphological

differentiation among Azorean and Madeiran populations. One-way ANOVA followed by Tukey HSD post hoc tests was applied to evaluate trait differences among genetic groups. Traits retained for discriminant function analysis (DFA) were selected based on their statistical significance ($p < 0.05$ in ANOVA). A DFA was then conducted, and the resulting biplots were used to visualize separation among genetic groups. To improve the readability of the charts, scores of each variable were multiplied by a factor of 10 in the canonical functions.

The morphometric dataset underlying the analyses is provided as suppl. Table S4.

Statistical analyses were performed with SPSS Statistics for Windows Version 26.0 (Armonk, NY, IBM Corp.).

■ RESULTS

Morphological differentiation. — From the total of 61 morphological characters (suppl. Table S1) assessed in the exploratory dataset (Borges Silva, 2012), only those found to be statistically significant are presented (Tables 1, 2). These include qualitative vegetative and reproductive traits that showed significant associations with the previously defined genetic lineages (see suppl. Fig. S1, suppl. Tables S2, S3; for the complete analysis, see figs. 2–4 and table 4 in Borges Silva & al., 2016), as well as selected quantitative traits that differed significantly among groups according to chi-square and ANOVA tests, respectively. These results are summarized in Tables 1 and 2, which present the distribution of significant qualitative traits across the following taxonomic units: (i) *Tolpis azorica* from São Miguel; (ii) *T. azorica* from Faial, Pico, São Jorge, Terceira; (iii) *T. azorica* from Corvo and Flores; (iv) *T. succulenta* from Graciosa, Santa Maria and São Miguel; (v) *T. succulenta* from Madeira and Porto Santo; and (vi) *T. macrorhiza* from Madeira. These group numbers are used consistently throughout this results subsection to facilitate cross-reference between the text, tables, and figures.

Eight vegetative (Table 1) and seven reproductive (Table 2) qualitative characters were significant by chi-square test. Lamina shape was significantly different between the above groups (Table 1). Additionally, *Tolpis succulenta* from group v and *T. macrorhiza* exhibited cauline and basal leaves contrary to *T. succulenta* from group iv and *T. azorica* from groups i, ii, iii, which mostly exhibited only cauline leaves (Table 1).

Regarding qualitative reproductive characters, morphological differences among *Tolpis* species were observed (Table 2). The peduncle form varies, with most species having narrow peduncles, while *T. succulenta* from group iv feature a clavate peduncles. The involucre indumentum is predominantly farinose but varies within species, especially in all *T. succulenta* groups, where there are both pubescent and glabrous individuals (Table 2). The bract shape in the first series also shows variation, within Azorean species from group i and ii having triangular bracts, while group iii has oblong bracts.

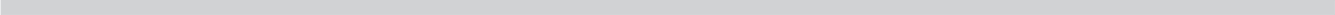


Table 1. Variability found between preliminary groups obtained in the preliminary analysis of *Tolpis* spp.

Vegetative variable	i) <i>Tolpis azorica</i> (São Miguel - Azores)		ii) <i>Tolpis azorica</i> (Faial, Pico, São Jorge, Terceira - Azores)		iii) <i>Tolpis azorica</i> (Corvo, Flores - Azores)		iv) <i>Tolpis succulenta</i> (Graciosa, Santa Maria, São Miguel - Azores)		v) <i>Tolpis succulenta</i> Madeira and Porto Santo		vi) <i>Tolpis macrorrhiza</i> Madeira		N	P-value
	N		N		N		N		N		N			
Growth form	chamaephyte	11	chamaephyte	17	chamaephyte	5	hemicryptophyte	15	hemicryptophyte	60	hemicryptophyte	23	<0.001	
Stem surface	striate	11	striate	17	striate	5	rugose	15	rugose	60	striate	23	<0.001	
Insertion (cauline leaf)	alternate	11	alternate	17	alternate	4	alternate	6	alternate	30	alternate	22	<0.001	
					rosette	1	rosette	2	rosette	17				
Lamina shape (cauline leaf)	lanceolate	10	ovate	14	ovate	5	lanceolate	13	lanceolate	4	lanceolate	23	<0.001	
	ovate	1	elliptic	3			linear	1	linear	19				
							spatulate	1	filiform	4				
									spatulate; ligulate	3; 6				
									pinnatisect; pinnatifida	18; 3				
Lamina shape (base leaf)	–	–	–	–	–	–	–	–	ligulate	6	spatulate	5	<0.001	
									filiform	11				
									pinnatifida	6				
Lamina apex (cauline leaf)	acute	9	acute	10	acute	2	acute	2	acute	27	acute	16	<0.001	
	acuminate	2	acuminate	5	rounded	3	acuminate	13	acuminate	33	acuminate	6		
			rounded	2							rounded	1		
Lamina bases (cauline leaf)	cuneate	6	cuneate	5	cuneate	1	cuneate	15	cuneate	20	obtuse	18	<0.001	
	obtuse	5	obtuse	12	obtuse	4			obtuse	18	acuminate	5		
									acuminate	17				
									acute	5				
Leaf margins (cauline leaf)	dentate	8	dentate	16	dentate	1	dentate	8	dentate	7	dentate	23	<0.001	
	denticulate	1	serrate	1	serrate	4	accentuate dentate	2	entire	20				
	accentuate dentate	2					entire	4	incized	33				
							incized	1						

Adapted from Borges Silva (2012) for qualitative vegetative characters with significant differences ($p < 0.001$) according to the results of chi-square test.

[illegible]

Adapted from Borges Silva (2012) for qualitative reproductive characters with significant differences ($p < 0.001$) according to the results of chi-square test.

In the remaining groups, *T. succulenta* from the Azores and Madeira archipelagos and *T. macrorrhiza*, the bracts are mainly linear. In the bracts of the second and third series, *T. azorica* from groups i and ii maintain triangular or oblong shapes, while *T. succulenta* from group v and *T. macrorrhiza* predominantly feature linear or lanceolate bracts. The variation in indumentum also suggests adaptations to different environmental conditions, with groups i, iv, and v having pubescent individuals, but *T. macrorrhiza* being more glabrous. *Tolpis azorica* from group iii stands out with tomentose individuals (Table 2).

According to the groups that resulted from the molecular analysis (see suppl. Fig. S1, suppl. Tables S2, S3; for complete analysis, see figs. 2–4 and table 4 in Borges Silva & al., 2016), ANOVA showed that there were significant differences between those groups for quantitative vegetative traits namely: cauline leaf length ($df = 5$, $F = 8.874$, $P = 0.000$); cauline leaf width ($df = 5$, $F = 19.593$, $P = 0.000$); cauline leaf ratio (W:L) ($df = 5$, $F = 12.327$, $P = 0.000$); and petiole length ($df = 5$, $F = 4.461$, $P = 0.001$). Regarding cauline leaf length significant difference was found between *Tolpis azorica* from group i with the highest mean value and *T. succulenta* from group v with the smallest mean. Significant differences in leaf width were found between *T. azorica* from group iii with the largest mean width and *T. succulenta* from group iv from São Miguel, Santa Maria and Graciosa, *T. succulenta* from Madeira archipelago and *T. macrorrhiza* with the smallest width. Additionally, the average leaf width:length ratio exhibited the following differences: *T. azorica* groups i (0.38 ± 0.02), ii (0.68 ± 0.03), and iii (0.70 ± 0.05); *T. succulenta* groups iv (0.74 ± 0.11) and v (0.29 ± 0.05); and *T. macrorrhiza* group vi (0.31 ± 0.02), which are in concordance with preliminary data analyses (Table 1). Regarding petiole length significant differences were found between *T. succulenta* from group iv, which exhibited the longest petiole and *T. macrorrhiza*, which showed the shortest.

Furthermore, there were significant differences between the studied groups regarding the quantitative reproductive traits namely: peduncle length ($df = 5$, $F = 10.648$, $P = 0.001$); peduncle bract number ($df = 5$, $F = 3.084$, $P = 0.012$); peduncle bract length ($df = 5$, $F = 4.884$, $P = 0.000$); capitula number ($df = 5$, $F = 8.200$, $P = 0.000$); capitula diameter including corolla ($df = 5$, $F = 3.152$, $P = 0.012$); bract width 1st series ($df = 5$, $F = 19.989$, $P = 0.000$); bract length 2nd series ($df = 5$, $F = 2.854$, $P = 0.019$); bract width 2nd series ($df = 5$, $F = 8.459$, $P = 0.000$); bract number 3rd series ($df = 5$, $F = 7.939$, $P = 0.000$); bract width 3rd series ($df = 5$, $F = 6.244$, $P = 0.000$); pappus element number ($df = 5$, $F = 6.713$, $P = 0.000$); pappus length ($df = 5$, $F = 4.454$, $P = 0.001$).

Regarding peduncle length, significant differences were found among groups with the greatest lengths recorded in *Tolpis azorica* from group i and in *T. succulenta* from group iv, the shortest in *T. azorica* from group iii and in *T. macrorrhiza*. For peduncle bract number, the largest values

were found in *T. azorica* from group ii and the smallest in *T. azorica* from group i. As for peduncle bract length, a significant difference was found with the largest length observed in *T. azorica* from group iii, while the smallest were found in group i and in *T. succulenta* from the Madeira archipelago. As for the capitula number, a significant difference was found in *T. azorica* from group iii with the largest number, while the largest mean values of capitula diameter including corolla were found in *T. azorica* from groups ii and iii. For the bract width 1st and bract length 2nd series, a significant difference was found with the largest width observed in *T. azorica* from group iii and the smallest in *T. macrorrhiza*. For the bract width 2nd series, the largest value was observed in *T. azorica* from group ii and the smallest in *T. macrorrhiza*. Finally, for pappus element number, a significant difference was found in *T. macrorrhiza* and *T. succulenta* from the Madeira archipelago with the largest and smallest mean values respectively, and for pappus length the largest was found in *T. macrorrhiza* and the smallest in *T. azorica* from group ii.

Results of discriminant analysis based on quantitative and qualitative (vegetative and reproductive) traits for *Tolpis* spp. in the Azores and Madeira islands grouped accessions into six clusters, according to their geographical location within the archipelagos, except for some individuals from Santa Maria Island, which form a distinct cluster separate those of São Miguel and Graciosa islands (Fig. 3). The first two canonical analysis functions explained 80.2% (function 1) and 8.7% (function 2) of the total variance, respectively (Fig. 3).

Morphological variability between and within the Azores and Madeira archipelagos: *Tolpis succulenta* (sensu lato). — ANOVA and Tukey HSD test (Table 3) revealed significant differences in the quantitative characters screened for Azorean accessions previously grouped in *Tolpis succulenta* (i.e., from Faial, Graciosa, Santa Maria, São Jorge, São Miguel, and Terceira Islands) and *Tolpis succulenta* from Madeiran accessions, namely, for leaf (width and ratio), inflorescences (capitulum diameter including corolla, bract length and width 1st series, bract length 2nd series, ligule length, peduncle length and peduncle bract number) and fruits (cypsela length, width and pappus number). The Azores material showed wider leaves and a higher width/length ratio (Table 3), which are concordant with preliminary data analyses (Table 1), in which Azorean accessions previously grouped in *T. succulenta* (i.e., from Graciosa, Santa Maria, and São Miguel) showed a lanceolate shape, while *T. succulenta* from Madeira Islands revealed a filiform/linear shape (Table 1, Fig. 3).

The Azores accessions were significantly different from Madeira specimens in inflorescence traits (Table 3, Fig. 4). Madeira and Porto Santo specimens had larger capitulum diameters, while Azorean plants had longer and wider 1st series bracts, longer ligules, and longer peduncles (Table 3, Fig. 4). Madeiran material had longer and wider cypselae, while the Azorean specimens had a higher number of pappus elements (Table 3, Fig. 4).

Furthermore, Madeira and Porto Santo material revealed differentiation for the above cited traits namely, for leaf (width and ratio), inflorescence (capitulum diameter including corolla, bract length and width 1st series, bract length 2nd series, ligule length, peduncle length and peduncle bract number), whereas Porto Santo accessions showed higher values than Madeiran ones (Table 3).

Regarding the morphological variability within the Azorean accessions, ANOVA and Tukey HSD test (Table 4) showed significant differences in the quantitative characters screened in Graciosa, Santa Maria and São Miguel Islands accessions namely, for leaf (length, width, ratio W:L, external and internal area), inflorescence (capitulum diameter including corolla, bract length and width 1st series) and fruit (cypsela length, pappus element number). Santa Maria Island material showed longer and wider leaves, Graciosa accessions shorter and narrower leaves, while São Miguel accessions revealed intermediate values for leaf width and length (Table 4, Fig. 4). Regarding to leaf ratio W:L, Santa Maria, Graciosa and São Miguel accessions showed higher, lower, and intermediate values respectively (Table 4, Figs. 3, 4).

Regarding the inflorescence traits, Graciosa material revealed a significant difference from Santa Maria and São Miguel accessions, but these two eastern islands showed no differences from each other (Table 4), thus Graciosa material had on average a smaller capitulum diameter than Santa Maria and São Miguel accessions. Fruit traits from Graciosa material showed lower values for cypsela length than Santa Maria and São Miguel material (Table 4), and cypsela width revealed, respectively, lowest, higher, and intermediate values for Graciosa, Santa Maria, and São Miguel specimens (Table 4).

For most of the analyzed characteristics, Tukey HSD test and discriminatory analysis revealed that individuals from the two Graciosa locations (Table 4), for most of the analyzed traits, showed no significative differences. However, the leaf length is similar to São Miguel accessions, also cypsela length and cypsela width, similar to Santa Maria and São Miguel accessions (Table 4, Fig. 4).

Furthermore, in addition to the Graciosa specimens, we also included coastal specimens from the Central islands (Faial, São Jorge, and Terceira) and from the Western islands (Corvo and Flores) (Table 5). Material from the Central islands (Faial, São Jorge and Terceira) revealed smaller inflorescence traits (capitulum diameter including corolla, bract length and width 1st series and bract width 2nd series), and Graciosa specimens shorter and narrower leaves.

Results of discriminant analysis based on quantitative (vegetative and reproductive) traits for all Azorean accessions previously grouped in *Tolpis succulenta* (i.e., from Corvo, Faial, Flores, Graciosa, Santa Maria, São Jorge, São Miguel, and Terceira Islands) and *T. succulenta* from the Madeira archipelago grouped accessions into separate clusters, with Madeira and Porto Santo in a separate group (Fig. 4). Within the Azores archipelago, accessions were grouped into five separate clusters: (1) Graciosa Island; (2) Santa Maria Island; (3) São Miguel Island; (4) Corvo, Flores Islands; and (5) Faial, São Jorge, and Terceira Islands (Fig. 4). The first two canonical functions explained 81.2% (function 1) and 11.5% (function 2) of the total variance, respectively (Fig. 4). A scatter plot again showed that Azores material was associated with wider leaves and larger values of width/length ratio (Figs. 3, 4).

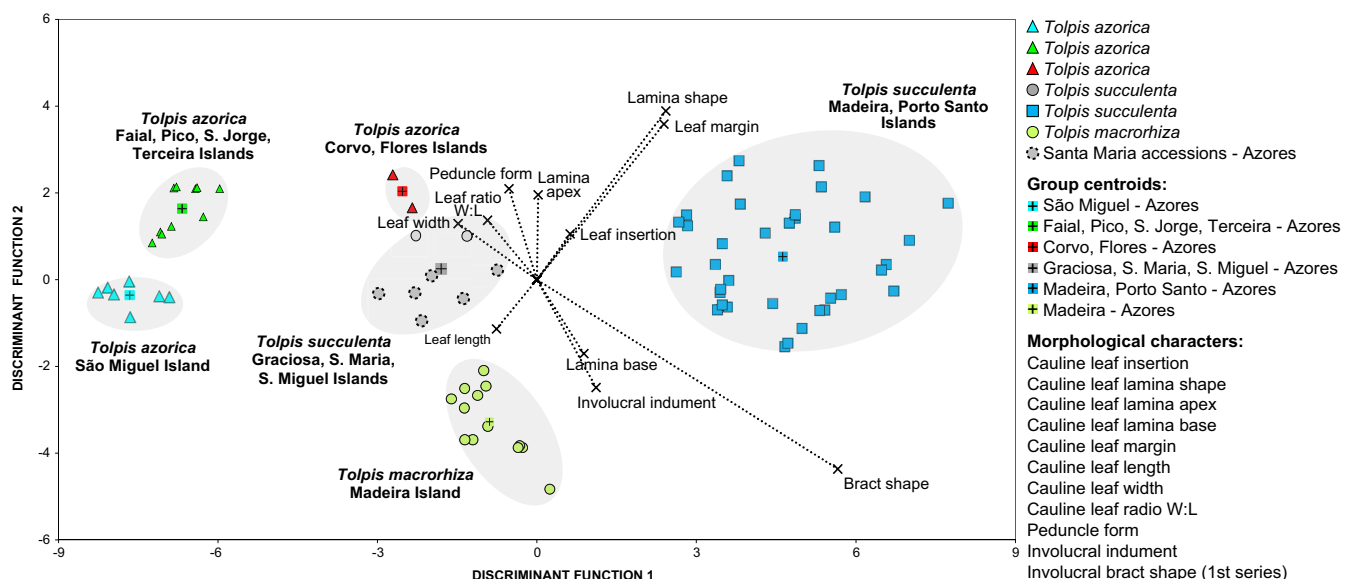


Fig. 3. Analysis of quantitative vegetative and reproductive traits characters by preliminary groups obtained in the preliminary analysis of the Azores and Madeira archipelagos. Biplot resulting from a discriminant analysis representing individuals and variables based on two canonical functions. Scores of all variables were multiplied by 10 to increase plot legibility. The obtained groups: (i) *T. azorica* (São Miguel Island); (ii) *T. azorica* (Faial, Pico, São Jorge and Terceira Islands); (iii) *T. azorica* (Corvo and Flores Islands); (iv) *T. succulenta* (Graciosa, Santa Maria and São Miguel Islands); (v) *T. succulenta* (Madeira archipelago); and (vi) *T. macrorrhiza* (Madeira Island).

Table 3. Average variability in quantitative (vegetative and reproductive) *Tolpis succulenta* (sensu lato) characters found between specimens from Madeira, Porto Santo and the Azores (Faial, Graciosa, Santa Maria, São Jorge, São Miguel and Terceira Islands).

Characters	Madeira			Porto Santo			Azores (Faial, Graciosa, S. Maria, S. Jorge, S. Miguel, Terceira)				ANOVA			Post-hoc			
	N	Mean ± SD	SE	Min–Max	N	Mean ± SD	SE	Min–Max	N	Mean ± SD	SE	Min–Max	df	F	P	Group	
Cauline leaf width (cm)	35	0.37 ± 0.38	0.06	0.08–1.72	23	0.45 ± 0.25	0.05	0.15–1.13	123	1.38 ± 0.64	0.06	0.46–3.70	2	178	59.300	0.000	a a b
Cauline leaf ratio W:L	35	0.08 ± 0.08	0.01	0.01–0.33	23	0.10 ± 0.07	0.01	0.04–0.31	123	0.25 ± 0.09	0.01	0.07–0.50	2	178	73.618	0.000	a a b
Capitulum diameter (cm)	35	1.93 ± 0.46	0.08	1.10–3.10	22	2.13 ± 0.61	0.13	1.20–3.10	104	1.57 ± 0.36	0.03	0.50–2.70	2	158	20.829	0.000	b b a
Bract length 1st series (mm)	35	1.51 ± 0.88	0.15	0.16–3.79	21	2.24 ± 0.44	0.10	1.45–3.32	99	3.54 ± 1.58	0.16	1.21–9.15	2	152	32.517	0.000	a a b
Bract width 1st series (mm)	35	0.38 ± 0.23	0.04	0.04–0.83	21	0.54 ± 0.15	0.03	0.31–0.88	99	0.52 ± 0.16	0.02	0.20–0.95	2	152	8.415	0.000	a b b
Bract length 2nd series (mm)	35	4.03 ± 2.97	0.50	0.14–9.61	20	5.14 ± 2.70	0.60	2.14–9.04	76	6.50 ± 1.70	0.19	2.13–9.40	2	128	14.889	0.000	a a b
Cypsela length (mm)	21	1.80 ± 0.20	0.04	1.45–2.15	20	1.60 ± 0.28	0.06	0.09–1.87	89	1.31 ± 0.28	0.03	0.65–1.97	2	127	33.130	0.000	c b a
Cypsela width (mm)	21	0.56 ± 0.13	0.03	0.41–0.90	20	0.53 ± 0.14	0.03	0.23–0.71	87	0.45 ± 0.13	0.01	0.20–0.71	2	125	7.248	0.001	b ab a
Pappus number	33	4.11 ± 3.30	0.57	0.00–12.67	20	4.67 ± 2.80	0.63	1.33–10.33	87	11.77 ± 3.73	0.40	4.00–19.33	2	65	4.069	0.022	a a b
Peduncle length (cm)	31	4.69 ± 2.39	0.43	1.63–9.80	23	5.34 ± 2.42	0.50	2.34–11.77	15	7.44 ± 1.66	0.43	3.84–9.23	2	137	74.016	0.000	a a b
Peduncle bract number	31	6.22 ± 4.16	0.75	0.67–17.00	23	9.60 ± 6.79	1.42	2.25–22.14	14	5.58 ± 1.98	0.53	2.33–9.00	2	66	7.573	0.001	ab b b
Peduncle bract length (mm)	31	1.11 ± 0.69	0.12	0.11–2.38	23	1.63 ± 0.45	0.09	0.79–2.58	14	1.26 ± 0.35	0.09	0.77–1.80	2	65	5.769	0.005	a b ab
Ligule length (mm)	27	6.59 ± 4.30	0.83	0.61–13.90	21	10.98 ± 3.42	0.75	5.98–22.74	5	15.45 ± 22.33	9.99	4.87–55.39	2	50	4.115	0.022	a ab b

Mean, standard deviation, standard error and results of the one-way ANOVA test and Tukey's honest significant difference (HSD) post-hoc test for the significative traits.

Morphological variability within the Azores archipelago: *Tolpis azorica* (sensu lato). — ANOVA and Tukey HSD test (Table 6) showed significant differences in quantitative characters screened for accessions previously grouped in *Tolpis azorica* (i.e., from Corvo, Faial, Flores, Pico, São Jorge, São Miguel, and Terceira Islands), namely, for leaf width and leaf ratio W:L, inflorescence (capitula number, capitulum diameter including corolla, bracts width 1st and 2nd series, peduncle length, peduncle bract length) and fruits (cypsela length and width) (Table 6, Fig. 5).

Corvo and Flores accessions showed longer and wider leaves, while Faial, Pico, São Jorge, and Terceira material showed intermediate and São Miguel Island lower values for leaf width (Table 6). Regarding the leaf W:L ratio, Corvo and Flores revealed higher values, Faial, Pico, São Jorge, Terceira intermediate values and São Miguel Island showed lower values (Table 6, Fig. 5). These ratios were complementary and support the preliminary results (Table 1) where São Miguel accessions showed a lanceolate shape while Corvo, Faial, Flores, Pico, São Jorge, and Terceira Islands accessions revealed ovate/elliptic shape (Table 1, Fig. 3).

Regarding the inflorescence traits, ANOVA and Tukey HSD test revealed that Corvo and Flores material showed the highest values for capitula number, but the lowest for capitulum diameter, while Faial, Pico, São Jorge, Terceira, and São Miguel Island accessions showed the highest values for capitulum diameter, bract width 1st series and bract width 2nd series (Table 6). However, São Miguel accessions revealed

longer peduncles, while Corvo and Flores accessions revealed shorter peduncles (Table 6). São Miguel material had longer cypselae, Corvo and Flores shorter, and Faial, Pico, São Jorge, and Terceira accessions had intermediate and higher values of cypselae length and width (Table 6, Fig. 5).

Results of discriminant analysis based on quantitative (vegetative and reproductive) traits grouped accessions into in three separate groups: (6) São Miguel Island, (7) Corvo and Flores Islands; and (8) Faial, Pico, São Jorge, and Terceira Islands (Fig. 5). The first two canonical functions explained 83% (function 1) and 16.2% (function 2) of the total variance, respectively.

A scatter plot again showed that Corvo and Flores material was associated with wider leaves and larger values of width/length ratio, and capitula number, and São Miguel was associated with larger cypselae and longer peduncles (Figs. 3, 5).

Regarding Faial, Pico, São Jorge and Terceira accessions, and contrary to the ANOVA and Tukey HSD results, discriminant analyses revealed, for Terceira leaf material, some level of differentiation from the other three islands of the Central group (Fig. 5).

DISCUSSION

Taxon circumscription and distribution of Azorean and Madeiran *Tolpis succulenta* (sensu lato). — Our study resolved two distinct groups of *Tolpis succulenta* (sensu lato),

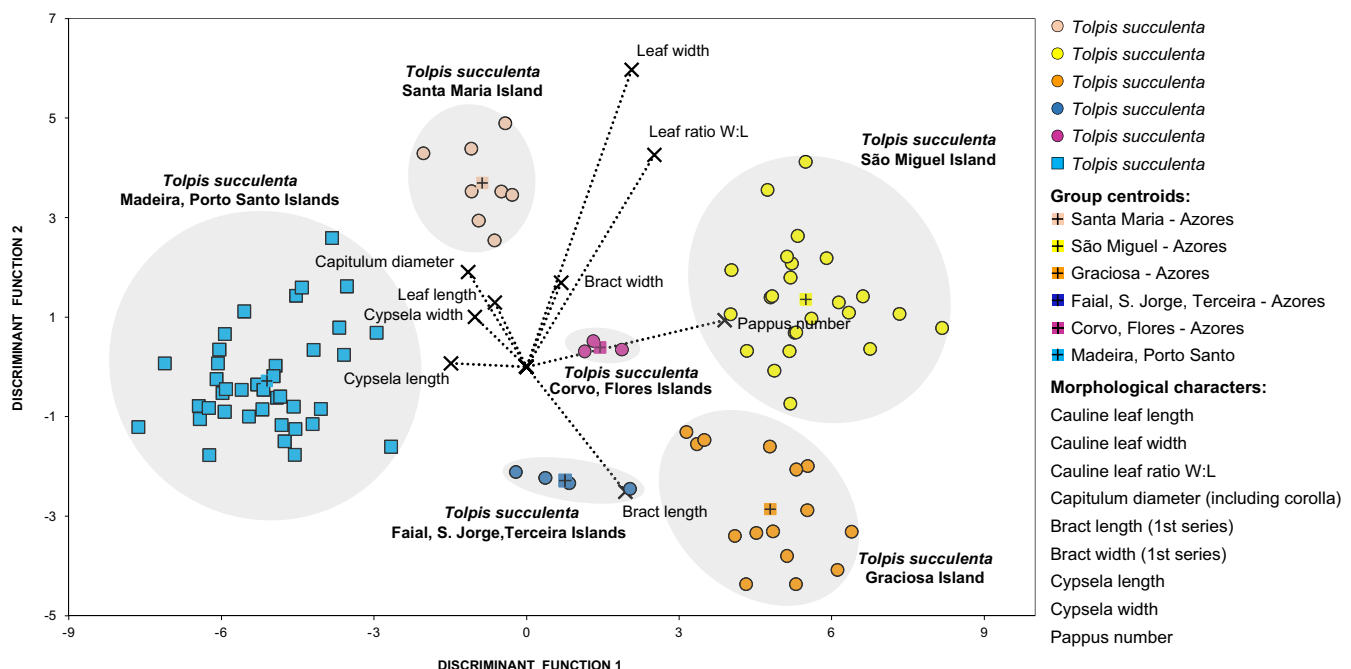


Fig. 4. Analysis of quantitative vegetative and reproductive traits characters by obtained groups for the Azores and Madeira archipelagos analysis. Biplot resulting from a discriminant analysis representing individuals and variables based on two canonical functions. Scores of all variables were multiplied by 10 to increase plot legibility. The obtained groups: *T. succulenta* (Graciosa Island); *T. succulenta* (Santa Maria Island); *T. succulenta* (São Miguel Island); *T. succulenta* (Corvo and Flores Islands); *T. succulenta* (Faial, São Jorge and Terceira Islands); and *T. succulenta* (Madeira archipelago).

Table 4. Average variability in quantitative (vegetative and reproductive) *Tolpis succulenta* (sensu lato) characters found between Azores specimens from Graciosa, Santa Maria and São Miguel Islands.

Characters	Graciosa Baía do Filipe-Beira Mar da Luz					Graciosa Santa Cruz, Quitadouro					Santa Maria					São Miguel					ANOVA			Post-hoc	
	N	Mean	SE	Min–Max	Mean ± SD	N	Mean	SE	Min–Max	Mean ± SD	N	Mean	SE	Min–Max	N	Mean ± SD	N	Mean ± SE	Min–Max	Min–Max	df	F	P	Group	Group
Cauline leaf length (cm)	23	5.15 ± 1.73	0.36	2.71–9.15	3.85 ± 0.66	11	3.85 ± 0.66	0.02	2.56–4.79	6.47 ± 0.94	22	6.47 ± 0.94	0.20	5.27–8.90	51	5.15 ± 1.70	51	5.15 ± 1.70	2.95–10.04	2.95–10.04	3	103	8.095	0.000	ab a c ab
Cauline leaf width (cm)	23	0.95 ± 0.38	0.08	0.53–2.07	0.83 ± 0.26	11	0.83 ± 0.26	0.08	0.52–1.27	2.03 ± 0.59	22	2.03 ± 0.59	0.13	1.00–3.70	51	1.51 ± 0.60	51	1.51 ± 0.60	0.46–3.35	0.46–3.35	3	103	20.542	0.000	a a c b
Cauline leaf ratio W:L	23	0.18 ± 0.03	0.01	0.11–0.25	0.21 ± 0.04	11	0.21 ± 0.04	0.01	0.16–0.26	0.31 ± 0.06	22	0.31 ± 0.06	0.01	0.18–0.42	51	0.30 ± 0.08	51	0.30 ± 0.08	0.14–0.50	0.14–0.50	3	103	20.028	0.000	a a b b
Cauline External area (mm ²)	18	340.82 ± 252.91	59.61	108.07–1141.81	233.77 ± 79.64	10	233.77 ± 79.64	25.18	127.69–361.23	944.97 ± 199.73	4	944.97 ± 199.73	99.87	791.06–1238.00	42	587.46 ± 463.41	42	587.46 ± 463.41	71.51–1921.76	71.51–1921.76	3	70	5.279	0.002	a a b ab
Cauline Internal area (mm ²)	18	310.83 ± 201.10	47.4	93.18–921.45	210.11 ± 74.50	10	210.11 ± 74.50	23.56	108.18–337.66	775.87 ± 155.62	4	775.87 ± 155.62	77.81	650.82–996.35	42	519.79 ± 402.12	42	519.79 ± 402.12	62.05–1619.58	62.05–1619.58	3	70	4.853	0.004	a a b ab
Capitulum diameter (cm)	15	1.38 ± 0.19	0.05	1.10–1.70	1.27 ± 0.26	11	1.27 ± 0.26	0.08	1.00–1.75	1.81 ± 0.32	18	1.81 ± 0.32	0.08	1.50–2.57	45	1.72 ± 0.28	45	1.72 ± 0.28	1.40–2.70	1.40–2.70	3	85	14.432	0.000	a a b b
Bract length 1st series (mm)	18	4.45 ± 1.50	0.35	2.16–7.51	5.53 ± 1.28	11	5.53 ± 1.28	0.38	2.08–7.01	3.01 ± 0.59	14	3.01 ± 0.59	0.16	2.07–4.22	43	3.12 ± 1.50	43	3.12 ± 1.50	1.65–6.15	1.65–6.15	3	82	12.093	0.000	b b a a
Bract width 1st series (mm)	18	0.51 ± 0.15	0.03	0.34–0.82	0.59 ± 0.14	11	0.59 ± 0.14	0.04	0.31–0.78	0.64 ± 0.24	14	0.64 ± 0.24	0.06	0.37–0.95	43	0.50 ± 0.12	43	0.50 ± 0.12	0.26–0.82	0.26–0.82	3	82	3.896	0.012	ab ab b a
Cypsel length (mm)	16	1.12 ± 0.16	0.04	0.80–1.43	1.17 ± 0.37	7	1.17 ± 0.37	0.14	0.72–1.77	1.25 ± 0.25	13	1.25 ± 0.25	0.07	0.85–1.54	43	1.41 ± 0.27	43	1.41 ± 0.27	0.65–1.97	0.65–1.97	3	75	5.607	0.002	a ab ab b
Cypsel width (mm)	16	0.41 ± 0.13	0.03	0.21–0.68	0.37 ± 0.14	7	0.37 ± 0.14	0.05	0.23–0.58	0.52 ± 0.10	12	0.52 ± 0.10	0.03	0.38–0.68	43	0.45 ± 0.11	43	0.45 ± 0.11	0.23–0.66	0.23–0.66	3	74	3.608	0.017	ab a b ab
Pappus number	16	10.61 ± 1.67	0.42	5.67–12.67	10.67 ± 1.62	7	10.67 ± 1.62	0.61	9.33–14.00	5.83 ± 1.20	12	5.83 ± 1.20	0.35	4.00–8.00	43	14.22 ± 2.93	43	14.22 ± 2.93	7.67–19.33	7.67–19.33	3	74	40.570	0.000	b b a b

Mean, standard deviation, standard error and results of the one-way ANOVA test and Tukey's honest significant difference (HSD) post-hoc test for the significative traits.

Table 5. Average variability in quantitative (vegetative and reproductive) *Tolpis succulenta* (sensu lato) characters found between Azores specimens from Graciosa, Faial, São Jorge, Terceira; and Corvo and Flores Islands.

Characters	Graciosa				Faial, São Jorge, Terceira				Corvo, Flores				ANOVA			Post-hoc	
	N	Mean ± SD	SE	Min–Max	N	Mean ± SD	SE	Min–Max	N	Mean ± SD	SE	Min–Max	df	F	P	Group	
Cauline leaf length (cm)	35	4.76 ± 1.64	0.28	2.56–9.15	7	6.20 ± 1.05	0.40	4.99–8.00	7	7.26 ± 0.97	0.37	6.27–8.70	2	45	9.429	0.000	a ab b
Cauline leaf width (cm)	35	0.87 ± 0.28	0.05	0.52–1.72	7	0.95 ± 0.39	0.15	0.50–1.50	7	1.24 ± 0.35	0.13	0.59–1.63	2	45	4.184	0.022	a ab b
Capitulum diameter (cm)	26	1.33 ± 0.22	0.04	1.00–1.75	6	0.96 ± 0.38	0.15	0.50–1.51	7	1.50 ± 0.14	0.05	1.22–1.62	2	36	8.697	0.001	b a b
Bract length 1st series (mm)	28	4.87 ± 1.52	0.29	2.08–7.51	5	2.44 ± 1.13	0.51	1.21–3.39	7	2.53 ± 0.44	0.17	2.00–2.90	2	37	12.704	0.000	b a a
Bract width 1st series (mm)	28	0.53 ± 0.15	0.03	0.31–0.82	5	0.30 ± 0.07	0.03	0.20–0.37	7	0.42 ± 0.03	0.01	0.40–0.46	2	37	7.627	0.002	b a ab
Bract width 2nd series (mm)	8	0.61 ± 0.14	0.05	0.38–0.77	5	0.39 ± 0.08	0.04	0.30–0.49	7	0.53 ± 0.03	0.01	0.50–0.57	2	17	7.486	0.005	b a ab
Cypsela width (mm)	22	0.38 ± 0.12	0.02	0.21–0.58	4	0.38 ± 0.18	0.09	0.20–0.60	4	0.58 ± 0.10	0.05	0.45–0.70	2	27	4.322	0.024	a a b
Pappus number	22	10.86 ± 1.23	0.26	9.33–14.00	4	10.12 ± 0.25	0.13	10.00–10.50	4	12.50 ± 2.08	1.04	10.00–15.00	2	27	3.762	0.036	ab a b

Mean, standard deviation, standard error and results of the one-way ANOVA test and Tukey's honest significant difference (HSD) post-hoc test for the significant traits.

Table 6. Average variability in quantitative (vegetative and reproductive) *Tolpis azorica* (sensu lato) characters found between Azores specimens from São Miguel; Faial, Pico, São Jorge, Terceira; and Corvo and Flores Islands.

Characters	São Miguel				Faial, Pico, S. Jorge, Terceira				Corvo, Flores				ANOVA			Post-hoc	
	N	Mean ± SD	SE	Min-Max	N	Mean ± SD	SE	Min-Max	N	Mean ± SD	SE	Min-Max	df	F	P	Group	
Cauline leaf length (cm)	73	8.42 ± 2.18	0.26	4.33–13.30	73	7.02 ± 1.87	0.22	3.47–12.26	22	8.52 ± 2.31	0.49	3.86–12.54	2	165	9.76	0.000	b a b
Cauline leaf width (cm)	73	3.42 ± 0.89	0.10	1.27–5.50	73	4.25 ± 1.00	0.12	2.43–6.70	22	5.61 ± 1.62	0.35	2.84–9.07	2	165	38.00	0.000	a b c
Cauline leaf ratio W:L	73	0.41 ± 0.07	0.01	0.25–0.61	73	0.62 ± 0.13	0.02	0.41–1.17	22	0.66 ± 0.11	0.02	0.53–0.88	2	165	90.20	0.000	a b b
Peduncle length (cm)	54	7.82 ± 2.36	0.32	3.69–14.80	51	6.03 ± 1.59	0.22	1.83–10.93	15	2.81 ± 0.73	0.19	1.50–4.29	2	117	42.20	0.000	c b a
Peduncle bract length (mm)	35	1.53 ± 0.49	0.08	1.12–4.00	19	1.94 ± 0.56	0.13	1.27–3.28	5	2.38 ± 0.42	0.19	1.80–2.90	2	56	8.36	0.001	a ab b
Capitula number	61	9.92 ± 7.47	0.96	1.00–33.00	61	10.33 ± 10.25	1.31	1.00–49.00	13	38.62 ± 26.48	7.34	12.00–82.00	2	132	34.86	0.000	a a b
Capitulum diameter (cm)	45	2.30 ± 0.41	0.06	1.73–3.75	43	2.68 ± 0.52	0.08	1.60–4.00	13	1.67 ± 0.28	0.08	1.48–2.52	2	98	26.34	0.000	b c a
Bract width 1st series (mm)	42	0.44 ± 0.10	0.02	0.27–0.71	46	0.68 ± 0.25	0.04	0.35–1.95	9	0.63 ± 0.13	0.04	0.40–0.76	2	94	17.68	0.000	a b b
Bract width 2nd series (mm)	43	0.75 ± 0.18	0.03	0.42–1.14	46	0.93 ± 0.28	0.04	0.41–1.87	9	0.84 ± 0.25	0.08	0.60–1.38	2	95	6.33	0.003	a a a
Cypsela length (mm)	30	1.49 ± 0.15	0.03	1.00–1.76	36	1.26 ± 0.20	0.03	0.79–1.60	7	0.83 ± 0.16	0.06	0.70–1.16	2	70	43.18	0.000	c b a
Cypsela width (mm)	30	0.46 ± 0.14	0.03	0.22–0.75	36	0.52 ± 0.11	0.02	0.23–0.76	7	0.38 ± 0.16	0.06	0.19–0.65	2	70	4.69	0.012	ab b a

Mean, standard deviation, standard error and results of the one-way ANOVA test and Tukey's honest significant difference (HSD) post-hoc test for the significant traits.

one in the Azores and another from Madeira. The most discriminant characteristics between Azores and Madeira specimens were leaf characters, namely, Azorean specimens showed entire and lanceolate leaves, while those from Madeiran taxa displayed elongate leaf shapes ranging from irregularly lobed to pinnatifid. Regarding the inflorescence, Azorean specimens revealed longer and wider 1st series bracts, longer ligules, and longer peduncles. As for fruits, Madeiran material had longer and wider cypselae.

The distinctiveness between *Tolpis* taxa from the Madeira and Azores archipelagos is in accordance with our previous population genetic study (Borges Silva & al., 2016). Azorean and Madeiran individuals revealed a clear geographic separation (Borges Silva & al., 2016). This is in agreement with the very low levels of gene flow that was generally found between the Madeira and Azores archipelagos *Tolpis* individuals (Borges Silva & al., 2016) and with the molecular phylogenies produced so far (Moore & al., 2002; Gruenstaedl & al., 2013; Mort & al., 2015, 2022; Crawford & Stuessy, 2016; Crawford & al., 2019; Kerbs & al., 2020; Gibson & al., 2020). Mort & al. (2022) used genomic markers and robust population sampling in Madeira and the Azores in a phylogenetic study that resolved populations from the two archipelagos in two clades, indicating that *T. succulenta* is polyphyletic, and provided strong support for the recognition of distinct species in the two archipelagos (Mort & al., 2022). Accordingly, a new species is formally described here. Also, mean pollen fertility of hybrids between plants referred to *T. succulenta* from the two archipelagos is 32% (4 crosses, 21 plants), as compared

to 64% for hybrids between different populations on Madeira (Crawford & al., 2016).

Azorean accessions of *Tolpis succulenta* (sensu lato) are composed of five well-defined morphological groups, each of which occurs on one or more of the following islands: (1) Graciosa; (2) Santa Maria; (3) São Miguel; (4) Corvo and Flores; and (5) Faial, São Jorge, and Terceira Islands. The most discriminant characteristics for the Azorean accessions were leaf characters, inflorescence, and fruit traits. Graciosa populations have narrower leaves, Corvo and Flores populations wider, whereas populations from Santa Maria, São Miguel, and the group of Faial, São Jorge, and Terceira show intermediate leaf widths. Individuals from Santa Maria and São Miguel have larger capitulum diameters, while Graciosa plants are smaller, whereas the remaining islands exhibited intermediate values. Santa Maria individuals have larger capitula than those from Graciosa (smallest); this is in accordance with Crawford & al.'s (2019) findings that the self-compatible (SC) plants of *T. succulenta* from Graciosa Island exhibit a tendency towards the selfing syndrome (Ornduff, 1969; Slotte & al., 2012), with smaller capitulae and lower pollen:ovule ratios than those found in self-incompatible (SI) and pseudo-self-compatible (PSC) populations of *T. succulenta* from Santa Maria Island and in SI *Tolpis* from other islands in Macaronesia (Crawford & al., 2008, 2015). For fruit lengths, Santa Maria Island plants have longer fruits than those on Graciosa, contrary to what was reported previously by Crawford & al. (2019). This can be explained by the fact that the individuals from these populations were

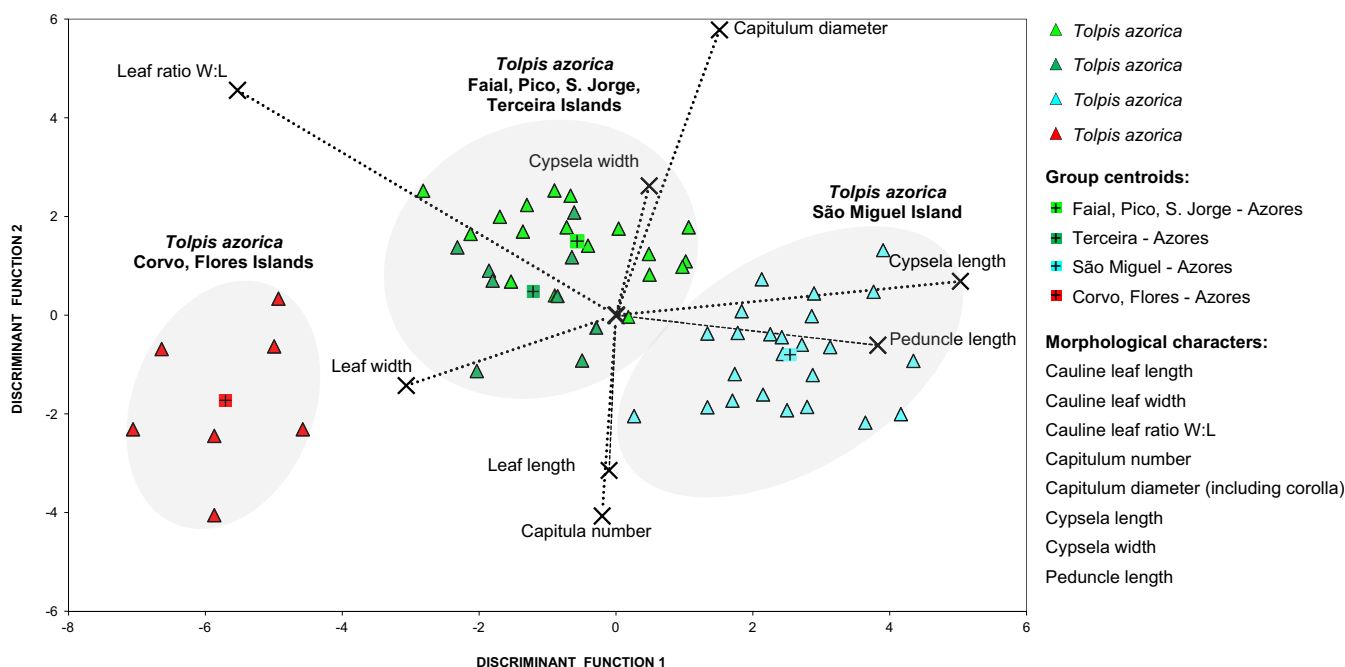


Fig. 5. Analysis of quantitative vegetative and reproductive traits by obtained groups for the Azores archipelago analysis. Biplot resulting from a discriminant analysis representing individuals and variables based on two canonical functions. Scores of all variables were multiplied by 10 to increase plot legibility. The obtained groups: *Tolpis azorica* (São Miguel Island); *Tolpis azorica* (Corvo and Flores Islands); and *Tolpis azorica* (Faial, Pico, São Jorge and Terceira Islands).

grown in greenhouse conditions at the University of Kansas (see fig. 3 in Crawford & al., 2019).

Borges Silva & al. (2016) detected very low genetic diversity (e.g., mean number of alleles per locus, mean number of polymorphic loci and expected heterozygosity) at SSR loci in Graciosa SC populations. By contrast, SI populations from Santa Maria and one SI population from São Miguel were found to have much higher genetic diversity (Borges Silva & al., 2016). These authors also showed that the two Graciosa populations were distinct and clearly separated from those of the Eastern group. According to Crawford & al. (2019), these two populations from Graciosa form a strongly supported clade sister to SI populations of *Tolpis succulenta* (Crawford & al., 2019), which further provides support for taxonomic recognition. Several factors could account for the low diversity in the two Graciosa populations, including founder effect, small population size and/or selfing (Crawford & al., 2019). In the *T. succulenta* SSR dataset (Borges Silva & al., 2016), the first-order barrier was located between the Graciosa Island populations and the second-order barrier was located between Graciosa and São Miguel and Santa Maria Islands. This agrees with an absence of gene flow between Graciosa populations, and between Graciosa populations and all other Azorean populations (Borges Silva & al., 2016). This is in contrast with the high level of gene flow obtained between two populations from Santa Maria (Maia and Pico Alto).

Our results, in conjunction with previous studies, support the recognition of five distinct taxa within the Azorean accessions previously assigned to *Tolpis succulenta*. These correspond to accessions from: (1) Graciosa; (2) Santa Maria; (3) São Miguel; (4) Corvo and Flores; and (5) Faial, São Jorge, and Terceira Islands. These entities are morphologically and geographically distinct, warranting formal description as endemic species (see Taxonomic Treatment below for further details).

Taxon circumscription and distribution within Madeiran *Tolpis*. — The Madeiran endemic *Tolpis macrorrhiza* is sister to the rest of *Tolpis* (Mort & al., 2022).

The Madeiran endemic *Tolpis succulenta* revealed some degree of differentiation between Madeira and Porto Santo Islands (leaf, inflorescences, fruits). However, the Tukey test and the discriminant analysis did not show significant differences.

Tolpis macrorrhiza is a perennial with large rhizomes (rare in *Tolpis*) and annual stems (Jarvis, 1980; Mort & al., 2022). As reported by previous authors (Jarvis, 1980; Hansen & Sunding, 1993; Crawford & al., 2015, 2022), we found that *T. macrorrhiza* has smaller capitula and lower pollen/ovule ratios than Macaronesian SI species of *Tolpis*. While this species does not exhibit a highly evolved selfing syndrome, certain floral characters (i.e., smaller capitula and fewer flowers) tend toward those seen in the SC *T. coronopifolia* (Desf.) Biv. (Soto-Trejo & al., 2013; Crawford & al., 2015).

Synthetic F1 hybrids between *Tolpis macrorrhiza* and *T. succulenta* from Madeira exhibit low pollen fertility (mean = 26% for 12 progenies from three independent

crosses; Crawford & al., 2016), indicating the presence of postzygotic reproductive barriers between the two species. In addition, *T. macrorrhiza* displays an unusual reproductive trait characterized by variation in selfing success among different flowering branches of the same individual, which may represent a distinctive feature within Asteraceae and possibly among angiosperms more broadly.

Taxon circumscription and distribution of Azorean *Tolpis azorica* (sensu lato). — Within the Azores, accessions of *Tolpis azorica* (sensu lato) were resolved into three well-supported groups: (6) São Miguel Island; (7) Corvo and Flores Islands; and (8) Faial, Pico, São Jorge, and Terceira Islands.

The resolution of Azorean *Tolpis* into three groups obtained in the present study is concordant with the genetic structure analysis for *T. azorica* (Borges Silva & al., 2016). Similar relationships received strong support in the phylogenetic study of Mort & al. (2022).

Tolpis azorica species from Azores revealed spatially structured genetic patterns, consistent with limited gene flow among populations from the three sub-archipelagos (i.e., Western, Central, Eastern Islands) (Borges Silva & al., 2016).

The most discriminant characteristics were leaf characters, inflorescence, and fruits traits. São Miguel accessions showed a lanceolate leaf shape while Central Islands (Faial, Pico, São Jorge, and Terceira) and Western Islands (Corvo and Flores) accessions revealed ovate/elliptic shape. Corvo and Flores populations showed higher capitula number but the lowest capitulum diameter. Fruits from São Miguel showed longest cypselae, and Corvo and Flores plants had shortest cypselae.

Specimens from Terceira Island revealed an incipient level of morphological differentiation. This is in accordance with previous results (Borges Silva & al., 2016), where Terceira individuals were demonstrated to be genetically distinct. This pattern was also found in other Azorean endemic angiosperm groups, such as *Euphrasia azorica* and *E. grandiflora* (Moura & al., 2018), and *Myosotis azorica*, restricted to Corvo and Flores but genetically divergent within the archipelago (Weissmann & Schaefer, 2018). The genetic pattern obtained for Terceira may be explained by the geographical location and the volcanic history of the island and its intense effect on plant populations (Dias & al., 2014; Borges Silva & al., 2016). A similar explanation was also hypothesized by Silva & al. (2011) regarding the genetic pattern found in Terceira for *Juniperus brevifolia* (Seub.) Antoine accessions.

Concerning *Tolpis* within São Miguel Island, and contrary to a previous molecular study with SSR markers (Borges Silva & al., 2016), morphological traits did not reveal a significant difference between Western, Central and Eastern specimens.

Previous revisions (Jarvis, 1980; Lack, 1981) grouped these accessions under the name *Tolpis azorica*. However, our results support the recognition of three distinct species, two of which are newly identified Azorean endemics: (6) a newly identified endemic species restricted to São Miguel Island; (7) a newly endemic species confined to the Western

Islands (Corvo and Flores); and (8) *Tolpis azorica*, endemic to Faial, Pico, São Jorge, and Terceira Islands (see Taxonomic Treatment for further details).

■ TAXONOMIC TREATMENT

Here we present a taxonomic and nomenclatural revision of Azorean *Tolpis*, recognising seven new species: (1) *T. graciosensis* from Graciosa Island, formerly included as *T. succulenta*; (2) *T. mariensis* from Santa Maria Island, formerly included in *T. succulenta*; (3) *T. maritima* from São Miguel Island, formerly included in *T. succulenta*; (4) *T. maritimoccidentalis* from Corvo and Flores Islands, formerly included in *T. succulenta*; (5) *T. maritimocentralis* from Faial, São Jorge, and Terceira Islands, formerly included in *T. succulenta*; (6) *T. micalensis* from São Miguel Island, formerly included in *T. azorica*; and (7) *T. occidentalis* from the western group of islands, formerly included in *T. azorica*. The synonymy of *T. azorica* and *T. succulenta*, according to Lack (1981), is also provided for reference in the present treatment. Taxa are listed below, in alphabetical order by species.

Tolpis azorica (Nutt.) P.Silva in Palhinha, Cat. Pl. Vasc. Açores: 129. 1966 $\equiv$ *Caladonta azorica* Nutt. in Trans. Amer. Philos. Soc., n.s., 7: 448. 1841 – **Lectotype (designated here)**: Açores. Fayal, Caldeira, s.d., Nuttall s.n. (BM barcode BM 000033338!).

= *Tolpis nobilis* Hochst. ex Seubert, Fl. Azor.: 33, t. 11. 1844 – Holotype: Açores. Pico, Pic de Pico, alt. c. 3000', 18 Jul 1838, C. Hochstetter 3365 (TUB barcode TUB 011219!).

= *Tolpis nobilis* var. *petiolaris* Trel. in Rep. (Annual) Missouri Bot. Gard. 8: 125, pl. 33. 1897 $\equiv$ *Tolpis azorica* var. *petiolaris* (Trel.) P.Silva in Palhinha, Cat. Pt. Vasc. Açores: 129. 1966 – Syntypes: Açores. Flores, Trelease 470 (MO No. 126634 [barcode MO-2071217!]), Trelease 471 (MO No. 126635 [barcode MO-2071218!]), Trelease 475 (MO No. 126633 [barcode MO-1889017!]).

Description. – *Growth form* chamaephyte. *Stem* erect, woody at the base, pubescent somewhat tomentose. *Leaf* 3.47–12.26 $\times$ 2.43–6.70 cm, variable in shape from ovate, broadly obovate, rounded, to lanceolate or elliptical, with acute, acuminate or rounded apex, cuneate to obtuse base, and clasping the stem, deeply serrated or dentate along the margin, glabrous. *Petiole* short or absent. *Peduncles* 1.50–4.29 $\times$ 1.83–10.93 cm are elongated, rigid, erect, white, and fluffy, often exceeding the main axis. *Inflorescence* simple cyme or bostryx, ranging from 1 to 49 capitula per plant, with the corolla included measuring 1.60–4.60 cm. *Involucre* diameter 1.3–1.5 cm, bracts series from 2 to 4. *Bracts* glabrous or pubescent. *Cypselae* 0.79–1.60 $\times$ 0.23–0.76 mm.

Distribution and habitat. – *Tolpis azorica* is present in the central group of Faial, Pico, São Jorge and Terceira Islands at high altitudes. Found in natural forests (*Ilex*, *Laurus*,

Juniperus, *Juniperus* with peat bogs), margins of permanent and semi-natural pastures. Natural meadows (*Holcus*, *Festuca*, *Deschampsia*), wet meadows, lake shores and watercourse margins, young lava flows with pioneer vegetation, roadside slopes, strongly exposed areas, steep slopes, ravines and craters. Altitudinal limits can reach below 530 m (Serra do Labaçal, Terceira Island) and above 1217 m (Montanha do Pico, Pico Island).

Conservation status. – Although the most widespread of the eight Azorean *Tolpis* species, *T. azorica* occupies fragmented areas of native vegetation in the central group and is threatened by grazing rabbits, sheep, goats and cows and the increasing expansion of invasive plants (*Hedychium gardnerianum* and *Hydrangea macrophylla*) and transformation of natural vegetation into pastures. Thus, according to the IUCN classification, and based on the estimated number of plants, *T. azorica* would be considered as Endangered (EN) according to criteria: B1ab(i,ii,iii,iv)+2ab(i,ii,iii,iv) (Roxo & al., 2026).

Representative specimens examined. – Appendix 2.

Tolpis graciosensis Borges Silva & M.Moura, sp. nov. – Holotype: PORTUGAL. Azores: Graciosa, Beira Mar da Luz, Baía do Filipe, 412815, 419730 UTM, 22 m, 12 Jul 2010, Moura, Dias TS-GRBL-001 (AZB No. 1314!).

The holotype is shown in Fig. 6.

Description. – *Growth form* hemicryptophyte herb. *Stem* surface rugose. *Leaf* 2.56–9.15 $\times$ 0.52–2.07 cm, alternate and rosulate, lanceolate, base acute or acuminate, apex acuminate or rounded, coarsely dentate, nearly to entire. *Leaf indument* with generally simple trichomes in upper leaf surface to glabrous. *Petiole* 0.5–6.0 mm or absent. *Peduncles* 2.80–9.20 cm, narrow, with bracts, erect to curved ascendant and descendent. *Inflorescence* simple cyme or bostryx, ranging from 1 to 24 capitula per plant, with the corolla included measuring 1.00–1.75 cm. *Bracts* glabrous, pilose or tomentose. *Cypselae* 0.72–1.77 $\times$ 0.21–0.58 mm.

Distribution and habitat. – Present only on Graciosa Island. Found exclusively near the coast, in coastal basaltic rocks, and in ignimbrite walls. They are found in areas of sparse vegetation. Altitudinal limits: sea level.

Conservation status. – *Tolpis graciosensis* is endemic to Graciosa Island and has a very small population size and significant habitat degradation. The total population of this species is estimated at 150 mature individuals, with the largest population comprising approximately 50 individuals. The species faces multiple threats, including habitat degradation, invasion by alien species, herbivory, collecting, trampling, tourism-related disturbance of sensitive areas. Populations found in roadsides are highly vulnerable to maintenance operations. Its low population density, isolation of subpopulations, and reduced habitat area further increase its vulnerability. Given its extremely restricted range, small and fragmented population, and continuing decline in habitat quality and population size, *T. graciosensis* qualifies as Critically Endangered

(CR) under the IUCN Red List criteria B1ab(i,ii,iii,iv,v); C2a(i) (Roxo & al., 2026).

Representative specimens examined. – Appendix 3.

Etymology. – The *graciosensis* epithet reflects the fact that this taxon is restricted to Graciosa Island.

Tolpis macrorrhiza (Banks ex Hook.) DC., Prodr. 7: 87. 1838 – Type: not found.

Representative specimens examined. – Appendix 4.

Tolpis mariensis Borges Silva & M.Moura, **sp. nov.** – Holotype: PORTUGAL. Azores: Santa Maria, Maia, 2 Jul 2009, 673328, 4094599 UTM, Moura, Silva TS-MASL-004 (AZB No. 1198!; isotype: AZB No. 1199!).

The holotype is shown in Fig. 7.

Description. – *Growth form* hemicryptophyte herb. *Stem* surface rugose. *Leaf* 5.27–8.90 × 1.00–3.70 cm, alternate and rosulate, spatulate to lanceolate, base acute or acuminate, apex acuminate or rounded, coarsely dentate.

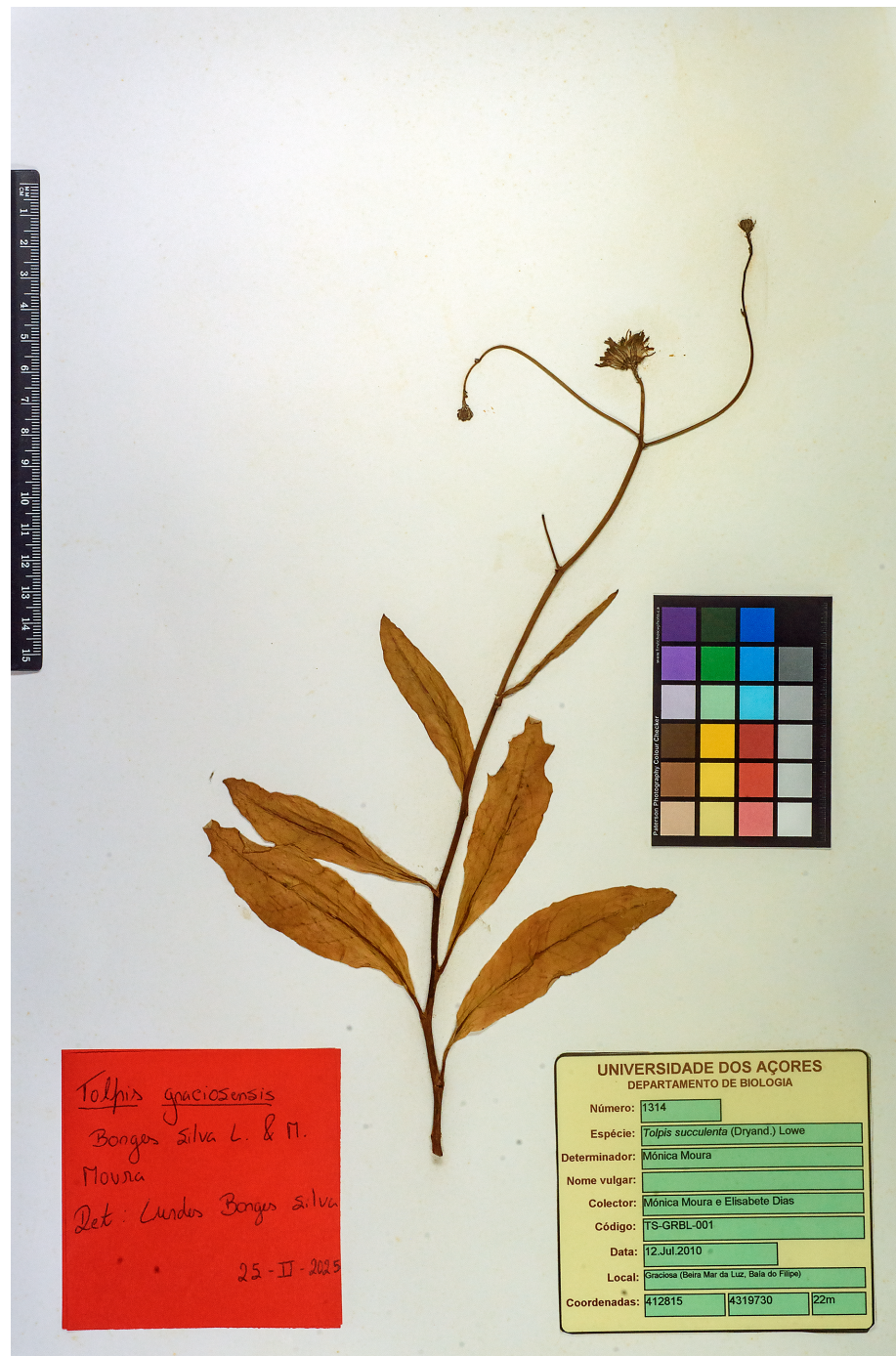


Fig. 6. Holotype of *Tolpis graciosensis* Borges Silva & M.Moura; Açores, Graciosa, Beira Mar da Luz, Baía do Filipe, 22 m, 12 Jul 2010, Moura & Dias TS-GRBL-001 (AZB No. 1314).

Leaf indument with generally simple trichomes in upper leaf surface. *Petiole* 0.5–6 mm. *Peduncles* 3.84–9.23 cm, with bracts, erect. *Inflorescence* 1.5–2.57 cm, capitula number ranges from 1 to 25. *Bracts* glabrous, pubescent, pilose and tomentose. *Ligule* 5.44–5.98 × 2.19–1.85 mm, yellow. *Cypselae* 0.85–1.54 × 0.38–0.68 mm.

Distribution and habitat. – *Tolpis mariensis* is endemic and widely distributed on Santa Maria Island. Found near the coast, in dry and strongly exposed areas, coastal rocks and

cliffs, coastal lava flows, coastal scrubland (*Erica*, *Morela*, mixed), *Erica* scrubland, steep roadside slopes and rocks. At high altitudes appear in disturbed areas, pioneer vegetation, roadside slopes, strongly exposed areas, steep slopes, and ravines. Altitudinal limits from sea level up to 600 m (Pico Alto, Santa Maria Island).

Conservation status. – *Tolpis mariensis* is endemic to Santa Maria Island, where it grows from the coast to the island's highest elevations. Its populations are highly



Fig. 7. Holotype of *Tolpis mariensis* Borges Silva & M. Moura; Açores, Santa Maria, São Lourenço, 2 Jul 2009, Moura & Silva TS-MASL-004 (AZB No. 1198).

localized and widely separated, leading to significant fragmentation. Major threats to this species include habitat degradation, changes in land use, invasion by non-native species, herbivory, trampling, and tourism. Given its restricted range, fragmented distribution, and ongoing habitat degradation, *T. mariensis* qualifies as Endangered (EN) under the IUCN Red List criteria B2ab(ii,iii,iv,v) (Roxo & al., 2026). Additionally, as it often grows along roadsides, it faces periodic disturbances from routine maintenance and cleaning operations, which can result in individuals being cut down.

Representative specimens examined. – Appendix 5.

Etymology. – The *mariensis* epithet refers to this taxon's restriction to Santa Maria Island.

***Tolpis maritima* Borges Silva & M.Moura, sp. nov.** – Holotype: PORTUGAL. Azores: São Miguel, Porto Velho das Capelas, 27 Jul 2010, 615586, 4189037 UTM, 0 m, Moura, Sardos, Borges Silva TS-SMPC-001 (AZB No. 1491!; isotypes: AZB Nos. 1327!, 2351!, 2352!). The holotype is shown in Fig. 8.

Description. – *Growth form* hemicycryptophyte herb. *Stem* surface rugose. Procumbent to ascending, woody at base,



Fig. 8. Holotype of *Tolpis maritima* Borges Silva & M.Moura; Açores, São Miguel, Porto Velho das Capelas, 0 m, 6 Jul 2010, Moura, Sardos & Borges Silva TS-SMPC-001 (AZB No. 1491).

glabrous. *Leaf* 2.95–10.04 × 0.47–3.35 cm. Alternate and rosulate, elliptic to lanceolate, base acute or acuminate, apex acuminate or rounded, entire or coarsely dentate. Leaf indument generally with trichomes on upper and/or lower leaf surface. *Petiole* 3–8 mm. *Peduncles* 3.84–8.93 cm, with bracts, erect to curved ascendant and descendent. *Inflorescence* wide simple cyme, ranging from 1 to 73 capitula per plant, with the corolla included measuring 1.0–2.7 cm. *Involucre* diameter 1.2–1.8 cm, bracts series vary from 2 to 4. *Bracts* glabrous, pubescent, pilose and tomentose. *Ligule* 4.87–8.89 × 1.76–4.94 mm yellow. *Cypselae* 0.65–1.97 × 0.23–0.66 mm, surface with 5–8 transverse striae, light brown to maroon. *Pappus setae* biseriate, first series 4.05 mm, second series 2.11 mm.

Distribution and habitat. – Present only in São Miguel. Found exclusively along the coast. Dry and strongly exposed areas, coastal rocks and cliffs, coastal lava flows, coastal scrubland (*Erica*, *Morela*, mixed). *Erica* scrubland. Steep roadside slopes and rocks, especially in sea wind exposed places. Altitudinal limits from sea level up to 90 m (Porto da Ajuda Bretanha, São Miguel Island).

Conservation status. – The species *Tolpis maritima* is endemic to São Miguel Island, where it occurs throughout the coast. The populations of this taxon are highly localized and geographically distant from one another, resulting in severe fragmentation. The primary threats include habitat degradation, changes in land use, invasion by alien species, herbivory, trampling, and touristic activities. Additionally, some populations show low density (Capelas, Lombo Gordo, Porto da Ajuda; Borges Silva & al., 2016). Given its restricted range, fragmented distribution, and ongoing habitat degradation, *T. maritima* would qualify as Endangered (EN) under the IUCN Red List criteria B1ab(iii,iv,v)c(iii)+2ab(iii,iv,v)c(iii) (Roxo & al., 2026). Because this taxon is found along roadsides, it is subject to periodic disturbance, with individuals being cut down during routine roadside maintenance and cleaning operations.

Representative specimens examined. – Appendix 6.

Etymology. – The epithet is derived from *maritima* (sea), indicating that this species is a coastal taxon.

***Tolpis maritimoccidentalis* Borges Silva & M.Moura, sp. nov.** – Holotype: PORTUGAL. Azores: Corvo, Vila, 10 m, 20 Jul 1972, *Gonçalves 4172* (BM barcode BM001172022!; isotype: BM barcode BM013856302!).

Description. – *Growth form* hemicryptophyte herb. *Stem* surface rugose. *Leaf* 6.27–8.70 × 0.59–1.63 cm. Alternate and rosulate, lanceolate, base acute or acuminate, apex acuminate, entire or coarsely dentate. *Petiole* absent or when present is longer. *Peduncles* a clavate to dilated, erect to curved ascendant and descendant. *Inflorescence* wide simple cyme or bostryx, ranging from 6 to 18 capitula per plant, with the corolla included measuring 1.22–1.62 cm. *Cypselae* 0.45–0.70 × 1.00–1.60 mm.

Distribution and habitat. – Present in the western group of Islands (Corvo and Flores). Found exclusively near the coast, in basaltic rocks; in areas of sparse vegetation.

Conservation status. – *Tolpis maritimoccidentalis* is endemic to Corvo and Flores Islands and has an extremely small total population, estimated at fewer than 50 mature individuals, with the largest subpopulation containing approximately 10 individuals. Major threats to the species include habitat degradation, invasion by alien plant species, herbivory, collection, trampling, tourism-related disturbance, and damage to sensitive areas. The very low population density, isolation of subpopulations, and reduced habitat area further increase its vulnerability. Given its extremely restricted range, very small and fragmented population, and continuing decline in habitat quality and population size, *T. maritimoccidentalis* qualifies as Critically Endangered (CR) under the IUCN Red List criteria B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v); C2a(i); D (Roxo & al., 2026).

Representative specimens examined. – Appendix 7.

Etymology. – The epithet is derived from *maritimo* (sea) and *occidentalis* (western), indicating that this species is a coastal taxon found exclusively on the western islands of Flores and Corvo.

***Tolpis maritimocentralis* Borges Silva & M.Moura, sp. nov.** –

Holotype: PORTUGAL. Azores: Terceira, Monte Brasil, 17 Jun 2021, 480722, 4277907 UTM, 19 m, *Elias TS-TEMB-001* (AZB No. 4277!).

The holotype is shown in Fig. 9.

Description. – *Growth form* hemicryptophyte herb. *Stem* surface rugose. *Leaf* 4.99–8.00 × 0.50–1.50 cm, alternate, lanceolate, base acute, apex acuminate, entire or dentate. *Petiole* absent or when present is longer. *Peduncles* a clavate to dilated, erect to curved ascendant and descendant. *Inflorescence* wide simple cyme or bostryx, ranging from 3 to 22 capitula per plant, with the corolla included measuring 0.50–1.51 cm. *Cypselae* 1.00–1.54 × 0.20–0.60 mm.

Distribution and habitat. – Present in Faial, Pico, São Jorge, and Terceira Islands from central group. It is found exclusively along the coast in dry, heavily exposed habitats such as crevices in coastal cliffs and in stone deposits. It also appears on stone walls and ramparts. The species is found only in a few places and generally with few scattered individuals, in areas of sparse vegetation. In Pico Island, it appears in coastal scrubland (*Erica*, *Morela*, mixed). In Faial it is found at Caldeirão, with a typically coastal vegetation, in a small crater situated above 300 m a.s.l. situated between Cabeço do Canto and Cabeço Verde north of Capelo at an altitude of 320 to 350 m.

Conservation status. – *Tolpis maritimocentralis* is endemic to the islands of Faial, Pico, São Jorge, and Terceira, where it occurs mainly along the coast. The populations are highly localized and geographically distant from one another, resulting in severe fragmentation. Major threats include habitat degradation, changes in land use, invasion by alien species, herbivory, trampling, and disturbance from touristic activities. Given its restricted distribution, fragmented populations, and the continuing decline in habitat quality, this taxon would

qualify as Endangered (EN) under the IUCN Red List criteria B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v). The combination of limited range, small population size, and persistent threats justifies its classification as Endangered (EN) (Roxo & al., 2026).

Representative specimens examined. – Appendix 8.

Etymology. – The epithet is derived from *maritimo* (sea) and *centralis* (center), indicating that this species is a coastal taxon found exclusively on the central islands of

the Azores archipelago, specifically Faial, São Jorge, Pico, and Terceira.

Tolpis micalensis Borges Silva & M.Moura, **sp. nov.** – Holotype: PORTUGAL. Azores: São Miguel, Lagoa das Éguas (Norte e Sul), 607743, 4187394 UTM, 819 m, 11 Sep 2010, *Borges Silva TA-SMLE-023* (AZB No. 1405!; isotypes: AZB Nos. 1403!, 1404!, 1406!). The holotype is shown in Fig. 10.



Fig. 9. Holotype of *Tolpis maritimocentralis* Borges Silva & M.Moura; Açores, Terceira, Monte Brasil, 17 Jun 2021, *Elias TS-TEMB-001* (AZB No. 4277).

Description. – *Growth form* chamaephyte. *Stem* with striated surface, erect, woody at base, glabrous. *Leaf* 4.30–13.30 × 1.27–5.50 cm, alternate, lanceolate to ovate, base cuneate to obtuse, apex acute, often deeply dentate and glabrous. *Petiole* short or absent. *Peduncles* 3.69–14.80 cm, with bracts, erect to curved ascendant and descendent, thin to clavate. *Inflorescence* wide simple cyme or bostryx, ranging from 1 to 33 capitula per plant, with the corolla included measuring 1.73–3.75 cm. *Involucre* diameter 1.3–1.5 cm, bracts series from 2 to 4. *Bracts* glabrous or pubescent. *Ligule*

5.60 × 2.15 mm, yellow. *Cypselae* 1–1.76 × 0.22–0.75 mm, surface with 4 to 12 transverse striae, light brown to dark brown. *Pappus* biseriate, with a length of 4.80 mm.

Distribution and habitat. – *Tolpis micalensis* occurs only at high altitudes on São Miguel Island. Found in natural forests (*Ilex*, *Laurus*, *Juniperus*, *Juniperus* with peat bogs) and in *Cryptomeria japonica* forests, margins of permanent and semi-natural pastures and in the openings of the native scrubland (*Calluna vulgaris*), also in open grassland, on cuttings through sandy deposits and on cliffs. In crevices on

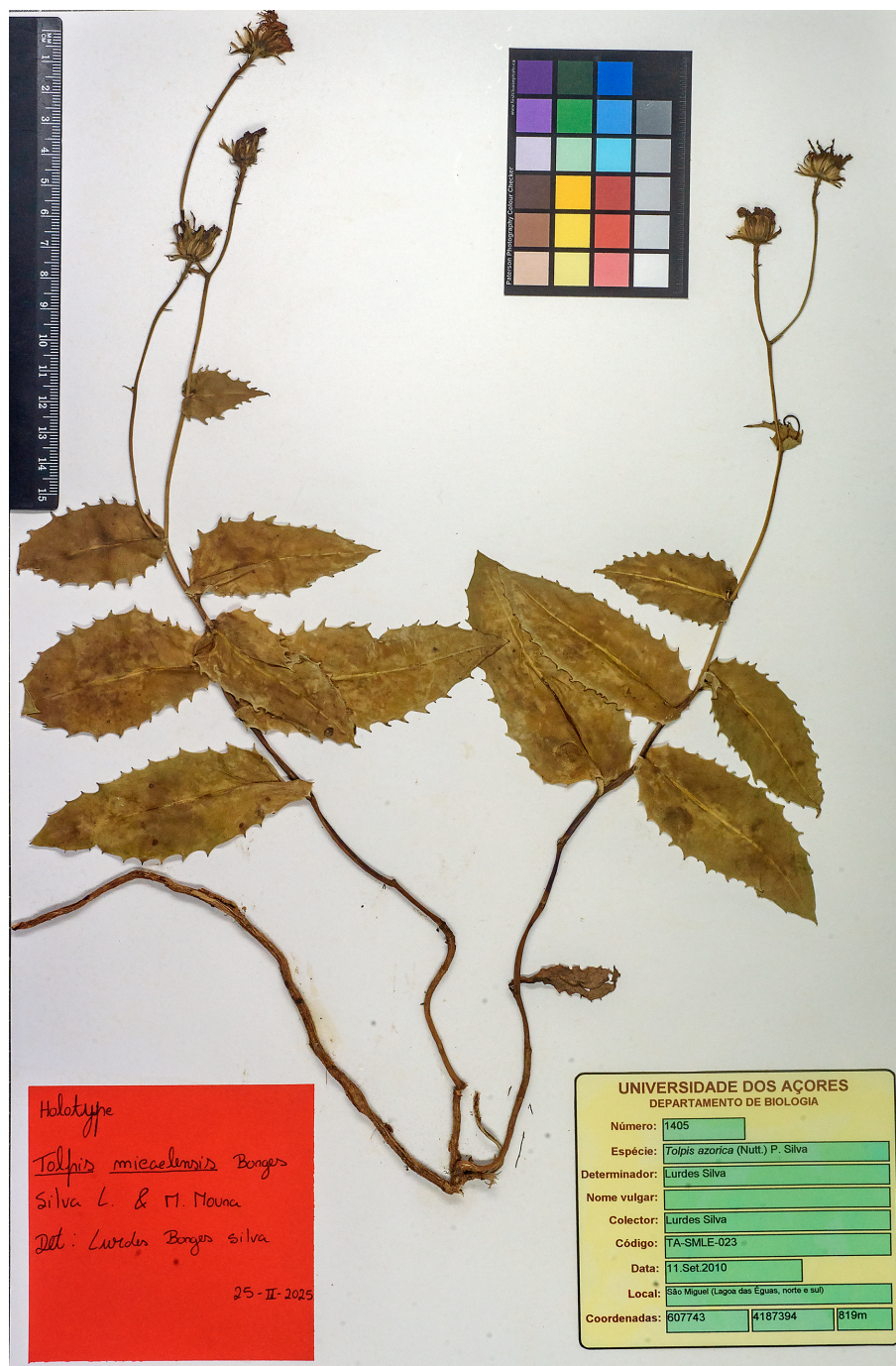


Fig. 10. Holotype of *Tolpis micalensis* Borges Silva & M.Moura; Açores, São Miguel, Lagoa das Éguas Norte e Sul, 819 m, 11 Sep 2010, *Borges Silva* TA-SMLE-023 (AZB No. 1405).

vertical cliffs and on dense humus layers or *Sphagnum* spp. carpet on slopes in ravines and craters, also associated with or *Deschampsia foliosa*. Lake shores and watercourse margins. Roadside slopes. Altitudinal limits 437 m (Caldeira do Alferes-Sete Cidades) and 1103 m (Pico da Vara).

Conservation status. – *Tolpis micaelensis* is endemic to São Miguel Island and has a small and fragmented population, with ongoing habitat degradation and severe threats from invasive species, nomadic grazing, and trampling by tourists. The species is subject to population decline caused by grazing from rabbits, cattle, feral goats, and sheep. Invasive plants such as *Crocsmia ×crocsmiflora*, *Dicksonia antarctica*, *Gunnera tinctoria*, *Hedychium gardnerianum*, *Hydrangea macrophylla*, and *Leycesteria formosa* are increasingly dominating its habitat and displacing native vegetation. Given its restricted distribution, fragmented populations, and the continuing decline in habitat quality, this taxon would qualify as Endangered (EN) under the IUCN Red List criteria B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v). The combination of limited range, small population size, and persistent threats justifies its classification as Endangered (EN) (Roxo & al., 2026).

Representative specimens examined. – Appendix 9.

Etymology. – The *micaelensis* epithet reflects the restricted distribution of this taxon on São Miguel Island.

Tolpis occidentalis Borges Silva & M.Moura, **sp. nov.** – Holotype: PORTUGAL. Azores: Flores, Ribeira da Badanela, 654175, 4370558 UTM, 800 m, 20 Jul 2010, Silva TA-FLRB-001 (AZB No. 1353!).

The holotype is shown in Fig. 11.

Description. – *Growth form* chamaephyte. *Stem* with striated surface, woody at base. *Leaf* 3.86–12.54 × 2.84–9.04 cm, alternate or rosette, broadly ovate, base cuneate to obtuse, apex acute to acuminate, dentate to serrate along the margin, glabrous. *Petiole* short or absent. *Peduncles* 1.50–4.29 cm. *Inflorescence* simple cyme or corymb, ranging from 12 to 82 capitula per plant, with the corolla included measuring 1.48–2.52 cm. *Involucre* diameter 1.3–1.5 cm, bracts series from 2 to 4. *Bracts* glabrous or pubescent. *Cypselae* 0.70–1.16 × 0.19–0.65 mm, brown to dark brown. *Pappus setae* biseriate, with a length of 4.94 mm.

Distribution and habitat. – *Tolpis occidentalis* is present only at high altitudes on Corvo and Flores Islands. Found in natural forests (*Laurus*, *Juniperus*, *Juniperus* with peat bogs), margins of permanent and semi-natural pastures. Present in natural meadows (*Holcus*, *Festuca*, *Deschampsia*). Lake shores and watercourse margins, young lava flows with pioneer vegetation, roadside slopes, strongly exposed areas, steep slopes, ravines and craters. Altitudinal limits from below 300 m (Cumieira do Caldeirão, Corvo) to above 914 m (Morro Alto, Flores).

Conservation status. – *Tolpis occidentalis* is endemic to the islands of Corvo and Flores and has a small and fragmented population, facing ongoing habitat degradation and severe threats from invasive species and nomadic grazing. Population decline is largely driven by grazing from rabbits, cattle,

feral goats, and sheep. Invasive plants such as *Hedychium gardnerianum* and *Hydrangea macrophylla* are increasingly dominating its native habitat, displacing native vegetation and altering ecosystem dynamics. This species occurs in steep slopes, ravines, volcanic craters, rocky outcrops, coastal cliffs, and waterfalls, at elevations up to 900 m. Given its restricted distribution, fragmented populations, and the continuing decline in habitat quality, this taxon would qualify as Endangered (EN) under the IUCN Red List criteria B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v). The combination of limited range, small population size, and persistent threats justifies its classification as Endangered (EN) and underscores the urgent need for conservation action (Roxo & al., 2026).

Representative specimens examined. – Appendix 10.

Etymology. – The epithet is derived from *occidentalis* (western) and reflects the fact that this taxon is restricted to the western group of islands of the Azores archipelago (Corvo and Flores).

- Tolpis succulenta*** (Aiton) Lowe, Man. Fl. Madeira 1: 525. 1868 ≡ *Crepis succulenta* Aiton, Hort. Kew. 3: 128. 1789 – **Lectotype (designated here):** A cultivated specimen in Hortus Kewensis, labelled “Hort. Kew 1779” on the reverse and “*Crepis succulenta* Mss.” in Dryander’s handwriting on the front. S. loc., 1777, Masson s.n. (BM barcode BM000829786!; isolectotypes: BM barcode BM000829785!, S No. S-G-1715!).
- = *Crepis filiformis* Aiton, Hort. Kew. 3: 128. 1789 ≡ *Tolpis filiformis* (Aiton) DC., Prodr. 7: 87. 1838 ≡ *Schmidtia filiformis* (Aiton) Sch.Bip. in Webb & Berthelot, Hist. Nat. Iles Canaries 3(2), Phytogr. 2: 399. 1847–48 ≡ *Tolpis succulenta* subsp. *filiformis* (Aiton) Menezes, Fl. Madeira: 99. 1914 ≡ *Tolpis succulenta* [subsp. *vulgaris*] var. *filiformis* (Aiton) Menezes in Brotéria, Sér. Bot. 22: 185. 1926 – Isotype: A cultivated specimen in Hortus Kewensis, labelled “Hort. Kew.” on the reverse and “*Crepis filiformis* mss.” in Dryander’s handwriting on the front. Madeira, s.d., Masson s.n. (S No. S-G-1704!).
- = *Schmidtia fruticosa* Moench, Suppl. Meth.: 217. 1802 – Type: “Im Marburger Botanischen Garten kultivierte Pflanze” (not found).
- = *Hieracium fruticosum* Willd., Sp. Pl. 3: 1591. 1803 ≡ *Tolpis fruticosa* (Willd.) Schrank, Pl. Rar. Hort. Monac.: 46. 1819 ≡ *Tolpis succulenta* subsp. *fruticosa* (Willd.) Menezes, Fl. Madeira: 99. 1914 ≡ *Tolpis succulenta* [subsp. *succulenta*] var. *fruticosa* (Willd.) Menezes in Brotéria, Sér. Bot. 22: 135. 1926 – Lectotype (designated by Lack in Willdenowia 11: 235. 1981, as “holotype”): Hb. Willd. 14724 (B [on three sheets] barcodes B -W 14724 -01 0!, B -W 14724 -02 0!, B -W 14724 -03 0!).
- = *Crepis pectinata* Lowe in Trans. Cambridge Philos. Soc. 4: 24. 1831 ≡ *Tolpis pectinata* (Lowe) DC., Prodr. 7: 87. 1838 ≡ *Tolpis succulenta* subsp. *pectinata* (Lowe) Menezes, Fl. Madeira: 99. 1914 ≡ *Tolpis succulenta* [subsp. *vulgaris*] var. *pectinata* (Lowe) Menezes in Brotéria, Sér. Bot. 22: 134. 1926 – Syntypes: Sloane Herbarium.

Hortus siccus 5:4 (planta dextra) (not found); A specimen collected during Cook's first circumnavigation, labelled "Crepis tenuifolia Ms. Madera". s. loc., s.d., *Sloane s.n.* (BM barcode BM000589002!).

= *Tolpis succulenta* var. *multifida* Lowe, Man. Fl. Madeira 1: 527. 1868 – Type: Not found.

= *Tolpis succulenta* var. *ligulata* Lowe, Man. Fl. Madeira 1: 527. 1868 – Type: Not found.

= *Tolpis succulenta* var. *linearifolia* Lowe, Man. Fl. Madeira 1: 528. 1868 – Type: Not found.

= *Tolpis succulenta* var. *oblongifolia* Lowe, Man. Fl. Madeira 1: 528. 1868 – Type: Not found.

= *Tolpis succulenta* [subsp. *succulenta*] var. *propinqua* Menezes in Brotéria, Sér. Bot. 22: 135. 1926 – Type: Madeira. Magdalena. *J.G. da Costa* (COL, not found).

Description. – *Growth form* hemicryptophyte herb. *Stem* brownish, glabrous, becoming woody with a smooth, slightly glossy bark, rugose with age; branches erect, ascending or decumbent, bearing leaf-rosettes with short axes in the leaf-axils. *Leaf* 1.70–12.73 × 0.08–1.72 cm narrowly to broadly elliptic



Fig. 11. Holotype of *Tolpis occidentalis* Borges Silva & M. Moura; Açores, Flores, Ribeira da Badanela, 20 Jul 2010, *Silva TA-FLRB-001* (AZB No. 1353).

or oblanceolate, entire or simply dentate to pinnatifid or bipinnatisect, with 2–7 teeth or lobes, herbaceous to somewhat succulent, glabrous, or occasionally somewhat woolly-floccose. *Petiole* glabrous to somewhat white-farinose at the base. *Peduncles* 1.63–11.77 cm, with bracts, erect to curved ascendant and descendent. *Inflorescence* wide simple cyme or bostryx, ranging from 1 to 57 capitula per plant, with the corolla included measuring 1.0–3.10 cm. *Involucre* diameter 1.0–1.8 cm across, white-tomentose at base, inner bracts 5–12 mm, longer than the outer, white-tomentose along the scarious margins. *Ligule* 0.63–22.74 × 0.13–2.72 mm, yellow, with an olive band on the outer face. *Cypselae* 0.91–2.15 × 0.23–0.90 mm, subcylindrical, glabrous, dark brown to black. *Pappus setae* number 1–13, whitish.

Distribution and habitat. – Common in Madeira, Porto Santo, and throughout the Desertas, this species thrives on sea cliffs, rocks, and rocky banks at elevations up to 1000 m, and occasionally up to 1500 m in open habitats.

Conservation status. – *Tolpis succulenta* is classified as Least Concern (LC) because it has large, stable, and continuous populations throughout the Madeira archipelago, indicating that the species is not facing immediate danger from population decline. The fact that these populations are widespread across the islands and show no significant fragmentation or isolation adds to the overall stability and resilience of the species. While there are several human-induced threats, such as urbanization, expansion of agricultural and the introduction of invasive species, these factors have not yet severely impacted the species to the point of causing rapid declines. The presence of threats suggests that *Tolpis succulenta* is not entirely free from risk, but the risk is not currently intense enough to push the species into a higher-risk category.

Representative specimens examined. – Appendix 11.

■ IMPLICATIONS FOR CONSERVATION

The identification of several Azorean endemic *Tolpis* species underscores the conservation guidelines already suggested by Borges Silva & al. (2016). The morphological data presented in this study are crucial for conserving the genetic diversity of the rare *Tolpis* species. By examining the morphological differences between populations, we can identify key characteristics for effective monitoring and management, contributing to the preservation of their genetic diversity.

These findings suggest a Linnaean Shortfall in the Azores, with many species, particularly endemic taxa, yet to be described due to cryptic diversity (Schaefer & al., 2011). For example, on Graciosa Island, the SC populations are rare and cryptic, with uncertainty about the number of existing populations. Two natural populations were identified in this study: one in Baía do Filipe Beira Mar da Luz (coastal basaltic rocks, sheltered by a man-made rock wall), and the other in Quitadouro (northern part of the island, isolated on an ignimbrite wall near Santa Cruz village, surrounded by pastures) (Crawford & al., 2019).

Tolpis maritimocentralis faces a similar situation, with populations being very rare, as well as *T. maritimoccidentalis*, which has only one remaining population on Terceira Island, primarily on the walls of a 16th-century fortress. This population has been significantly reduced due to cleaning by municipal workers, despite efforts to alert authorities about its importance.

This suggests that many newly described Azorean endemic coastal *Tolpis* species are at risk of extinction. *Tolpis* distributed in coastal areas face multiple threats, including coastal development, recreational activities, debris accumulation, and competition from invasive species such as *Aptenia cordifolia* (L.f.) Schwantes, *Arundo donax* L., *Carpobrotus edulis* (L.) L.Bolus, and *Cyrtomium falcatum* (L.f.) C.Presl (Silva & al., 2008, 2009). Also, plant invaders such as *Erigeron karvinskianus* DC., *Hedychium gardnerianum* (L.f.) C.Presl, *Leycesteria formosa* Wall. and *Hydrangea macrophylla* (Thunb.) Ser., the latter regrettably often used as a tourist symbol of the Azores, should be locally removed, since they can develop into monospecific stands directly outcompeting herbaceous species such as *T. azorica* (sensu lato) (Silva & al., 2008, 2015); furthermore, all species previously listed as top invasive species in the Azores (Silva & al., 2008). Thus, there is a need for urgent eradication of invasive alien species, which are becoming increasingly common. Effective control measures for this invasive plant species should be implemented, and management plans for coastal areas should be prioritized to conserve habitats where populations of endemic and native species continue to thrive (Silva & al., 2009). Also, control measures for herbivores should be considered as a priority in areas devoted to the preservation of the endemic flora. Among the invasive species are rabbits and goats, the latter often feral, that roam in areas where remains of native vegetation persist, such in Corvo, São Miguel and Pico Islands (Borges Silva & al., 2016).

According to our previous findings (Borges Silva & al., 2016), most *Tolpis* populations in the Azorean archipelago displayed inbreeding coefficient (F_{is}) values that may indicate the occurrence of inbreeding in small populations. One of the probable causes, as previously discussed, is habitat alteration due to direct (e.g., land use changes) or indirect human intervention (i.e., introductions of invasive plants and animals).

Translocation of some individuals of Azorean *Tolpis succulenta* (sensu lato) species (e.g., populations from São Miguel, Santa Maria and Graciosa Islands) should consider the genetic structure demonstrated in this study to avoid genetic erosion from hybridization with specimens of different genetic groups. It is essential to avoid ad-hoc translocations of diaspores or plants between different islands within the Azores archipelago (e.g., seeds or plantlets from São Miguel should not be introduced into Flores or Corvo, and diaspores collected in the Central group should not be introduced into either the Western or the Eastern groups), similar to others endemic species, e.g., *Leontodon* (Moura & al., 2013; 2015; Dias & al., 2014).

The maintenance of ex situ seed collections may also be an important conservation strategy to preserve the unique gene pools of the most differentiated populations (Moreira & al., 2009; Martins & al., 2011; Moura & al., 2013, 2015). However, seed sampling should be done with great care across the entire population area to ensure that all genotypes are equally represented in the collection (Moura & al., 2013, 2015; Dias & al., 2014). In such cases, a genetic rescue program could be implemented through an ex situ seed propagation protocol, using seeds from each population, followed by the reintroduction of plantlets into their original populations. Ex situ propagation should be carried out under controlled laboratory conditions rather than in open-air nurseries or gardens to prevent contamination with local populations (Moura & al., 2013, 2015; Dias & al., 2014; Silva & al., 2015).

In addition to government-imposed restrictions on inter-population mixing, other management actions should be taken (Moura & al., 2013, 2015; Dias & al., 2014), similar to those currently implemented in the Canary Islands for endangered species. These measures include information campaigns and training for roadside workers operating in natural areas (Martín Esquivel, 2005), and most importantly, the establishment of in situ protection measures by preserving the species' natural habitats (Moura & al., 2013, 2015; Dias & al., 2014).

In conclusion, this study contributed to generate data fundamental to implementing an appropriate conservation plan for Azorean and Madeiran endemic *Tolpis* by documenting morphologic variability patterns and detecting populations in critical need of protection.

■ AUTHOR CONTRIBUTIONS

LBS and MM conceived and designed the research. LBS and LS performed the statistical analyses. LBS, MM, LS, MMS, RBE, DJC, and MEM collected materials. LBS carried out the measurements of morphometric characters, including supervising students in the laboratory. LBS, MM and GR, performed the taxonomic treatment. LBS wrote the manuscript with input from all authors. All authors contributed to the interpretation of results and approved the final version of the manuscript.

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Appendix 1. List of 137 *Tolpis* sampling locations in the Azores and Madeira archipelagos, with island and taxon attribution.

Species name	Archipelago	Island(s)	No. of populations
<i>Tolpis azorica</i>	Azores	Faial, Pico, São Jorge and Terceira	41
<i>Tolpis azorica</i>	Azores	São Miguel	29
<i>Tolpis azorica</i>	Azores	Corvo and Flores	11
<i>Tolpis macrorrhiza</i>	Madeira	Madeira	12
<i>Tolpis succulenta</i>	Azores	Graciosa	3
<i>Tolpis succulenta</i>	Azores	Santa Maria	4
<i>Tolpis succulenta</i>	Azores	São Miguel	10
<i>Tolpis succulenta</i>	Azores	Faial, São Jorge and Terceira	3
<i>Tolpis succulenta</i>	Azores	Corvo and Flores	2
<i>Tolpis succulenta</i>	Madeira	Madeira	14
<i>Tolpis succulenta</i>	Madeira	Porto Santo	8

Geographic distribution maps of these populations are provided in Fig. 1 (Azores) and Fig. 2 (Madeira).

Appendix 2. Voucher specimens for *Tolpis azorica* examined in this study.

Taxon name; political subdivision; locality (when known), collection date (if applicable), collector(s) and number (herbarium code).

Tolpis azorica (Nutt.) P. Silva. **Portugal, Azores, Pico Island:** Cabeço do Caveiro, 7 Jul 2009, Moura, Silva TA-PICA-001 (AZB1232); Cabeço do Caveiro, 7 Jul 2009, Moura, Silva TA-PICA-002 (AZB1233); Pico da Urze, 10 Jul 2009, Moura, Silva TA-PIPU-001 (AZB1239); Pico da Urze, 10 Jul 2009, Moura, Silva TA-PIPU-002 (AZB1240); Pico da Urze, 4 Sep 2017, Nogueira TA-PIPU-013 (AZB2887); Cabeço do Mistério, 11 Jul 2009, Moura, Silva TA-PICM-001 (AZB1241); Cabeço do Mistério, 08 Jul 2009, Moura, Silva TA-PICM-002 (AZB1242); Cabeço do Mistério, 4 Sep 2017, Nogueira TA-PICM-011 (AZB2882); Cabeço do Mistério, 4 Sep 2017, Nogueira TA-PICM-012 (AZB2883); Cabeço do Mistério, 4 Sep 2017, Nogueira TA-PICM-013 (AZB2884); Perto Caldeirão da Ribeirinha, 6 Jul 2010, Moura, Dias TA-PIRB-001 (AZB1298); Perto Caldeirão da Ribeirinha, 4 Sep 2017, Nogueira TA-PIRB-016 (AZB2879); Perto Caldeirão da Ribeirinha, 4 Sep 2017, Nogueira TA-PIRB-017 (AZB2880); Perto Caldeirão da Ribeirinha, 4 Sep 2017, Nogueira TA-PIRB-018 (AZB2881); Cabeço do Leitão, 6 Jul 2010, Moura TA-PICL-001 (AZB1299); Lagoa do Peixinho, 6 Jul 2010, Moura, Dias TA-PILP-001 (AZB1300); Cabeço da Cruz, 7 Jul 2010, Moura TA-PICC-001 (AZB1303); Cabeço Raso, 7 Jul 2010, Moura, Dias TA-PICR-001 (AZB1304); Cabeço Redondo, 9 Jul 2010, Moura, Dias TA-PIRE-001 (AZB1305); Cabeço Redondo, 4 Sep 2017, Nogueira TA-PIRE-011 (AZB2870); Cabeço Redondo, 4 Sep 2017, Nogueira TA-PIRE-012 (AZB2871); Cabeço Redondo, 4 Sep 2017, Nogueira TA-PIRE-013 (AZB2872); Montanha, Baldia de S, Mateus, 8 Jul 2010, Moura TA-PIBM-001 (AZB1306); Transversal, perto de Torrinhãs, 9 Jul 2010, Moura, Dias TA-PITT-001 (AZB1307); Transversal, perto de Torrinhãs, 4 Sep 2017, Nogueira TA-PITT-011 (AZB2873); Transversal, perto de Torrinhãs, 4 Sep 2017, Nogueira TA-PITT-012 (AZB2374); Transversal, perto de Torrinhãs, 4 Sep 2017, Nogueira TA-PITT-013 (AZB2375); Lomba do Capitão, 10 Jul 2010, Moura, Dias TA-PILO-001 (AZB1310); Curral Queimado, 08 Jul 2010, Moura, Dias TA-PICQ-001 (AZB1492); Grotões, 09 Aug 1971, Gonçalves 3388 (BM000033313); Caneco António da Casta, on west side of peak of O. Pico, 25 Aug 1985, Parry 187 (BM000033314); High up, 30 Aug 1970, Brooke, 312 (BM000033326); Baldio das Fontainhas - altitude de 700 m, 25 Jul 1962, Gonçalves 596 (LISI-AZO 22002/1999); Lagoa do Caiado, 24 Jul 2012, Vitek s.n. (W 2013-0000079); Pico, 1842, Watson 608256 (MANCH); Lagoa do Caiado, 24 Jul 2012, Vitek s.n. (W 2013-0000080); s. loc., 18 Jul 1838, Hochstetter 3365 (TUB 011219); s. loc., 18 Jul 1838, Hochstetter s.n. (TUB011219); **Terceira Island:** Algar do Carvão, 26 Jul 2009, Silva TA-TEAC-001 (AZB1256); Algar do Carvão, 26 Jul 2009, Silva TA-TEAC-002 (AZB1257); Pico do Gaspar, 27 Sep 2010, Moura, Carine, Runsey, Jones TA-TEPG-001 (AZB1424); Rocha do Chambre, 27 Sep 2010, Moura, Carine, Runsey, Jones TA-TERC-003 (AZB1425); Cancela do Estaleiro, 29 Sep 2010, Moura TA-TECE-001 (AZB1429); Pico do Negrão, 29 Sep 2010, Moura TA-TEPN-001 (AZB1431); Caldeira de Aqualva, 30 Sep 2010, Moura TA-TECA-001 (AZB1434); Quinta da Madalena, 30 Sep 2010, Moura TA-TEQM-009 (AZB1435); Caldeira de Santa Bárbara, 26 Jul 2009, Silva TA-TESB-001 (AZB1258); Caldeira de Santa Bárbara, 26 Jul 2009, Silva TA-TESB-002 (AZB1259); Caldeira de Santa Bárbara, 26 Sep 2010, Carine, Runsey, Jones TA-TESB-011 (AZB1423); Caldeira de Santa Bárbara, exterior, 28 Sep 2010, Moura TA-TESB-031 (AZB1426); Caldeira de Santa Bárbara, exterior, 28 Sep 2010, Moura TA-TESB-034 (AZB1427); Caldeira de Santa Bárbara, exterior, 28 Sep 2010, Moura TA-TESB-041 (AZB1428); Serra do Labaçal, Moldes, 29 Sep, Moura TA-TESL-001 (AZB1432); Altares Angra, 13 Sep 1984, Gonçalves s.n. (AZU1275); Altares Angra, 13 Sep 1984, Gonçalves s.n. (AZU7477); s. loc., 1868, Drouet s.n. (BM000024266); Angra, 01 Aug 1978, Abreu s.n. (COI000794630); Biscoito da Ferraria, 03 Jul, Paiva 353 (LISE70248); Vila Praia da Vitória - altitude de 570 m, 10 Jul 1971, Gonçalves 3173 (LISI-AZO 31990/1999); s. loc., 30 Jun 1937, Palhinha, Sobrinho s.n. (LISU45230); **Faial Island:** Alto do Guarda-Sol, 28 Jul 2010, Silva TA-FAGS-001 (AZB1361); Alto do Chão, 27 Jul 2010, Silva TA-FAAC-001 (AZB1363); Caldeira, 27 Jul 2010, Silva TA-FACA-001 (AZB1364); Cabeço dos Trinta, 28 Jul 2010, Silva TA-FATR-001 (AZB1365); Estrada para a Caldeira a partir dos Falmengos, 10 Oct 1998, Schäfer s.n. (AZU1134); Salão, 16 Oct 1999, Schäfer s.n. (AZU1144); Caldeira slope inside crater, along path leading from rim to base of crater, 24 Aug 1985, Parry 185 (BM000033315); Caldeira outerslope, near the road nearly over, 29 Oct 1970, Brooke 11408 (BM000033330); Alto do Cavouco, 8 Aug 1962, Gonçalves 616 (BM000033332); Near top of crater (Caldeira), Aug 1956, s. coll., 139 (BM000033334); Caldeira, s.d., Nuttall s.n. (BM000033338); Forest road between Cabeço Verde and Cabeço dos Trinta, 07 Nov 2008, Maciel, Martin, Moreira, Moura, Carine, Runsey, Fraga U. Açores-NHM 81 (BM013856233); Path down from car park at SE end of Caldeira (Canto dos Baquinhos), 07 Dec 2008, Maciel, Martins, Moreira, Moura, Carine, Rumsey, Fraga U. Açores-NHM 86 (BM013856234); Horta, Jardim, 28 Jun 1991, Constância 198 (COI00091652); Faial, s.d., Anon, 608257 (MANCH); Faial, s.d., Anon, 608280 (MANCH); Caldeira - altitude de 500 m, 5 Aug 1972, Gonçalves 4599 (LISI-AZO 34117/1999); Alto do Cavouco, 8 Aug 1962, Gonçalves 616 (LISI-AZO 22025/1999); Caldeira, 02 Aug 1938, Cunha, Sobrinho s.n. (LISU45163); Caldeira, 02 Aug 1938, Cunha, Sobrinho s.n. (LISU45164); Canada dos Alaminhos, 02 Aug 1938, Cunha, Sobrinho s.n. (LISU45165); Canada dos Alaminhos, 02 Aug 1938, Cunha, Sobrinho s.n. (LISU45166); Canada dos Alaminhos, 02 Aug 1938, Cunha, Sobrinho s.n. (LISU45168); Caldeira, 04 Jul 2008, Gutte 134/2008 (LZ 203902); Caldeira, 01 Aug 1972, Lüpnitz s.n. (MJG 033046); Caldeira, 01 Aug 1972, Lüpnitz s.n. (MJG 033047); Caldeira, 01 Aug 1972, Lüpnitz s.n. (MJG 033048); Caldeira, 01 Aug 1972, Lüpnitz s.n. (MJG 033049); s. loc., 02 Aug 1937, s. coll., s.n. (MNHN-P-P02664416); s. loc., 25 Jul 1894, Brown 156 (MO5480446); Caldeira, 17 Sep 1975, Gonçalves s.n. (W 1988-0011094); **São Jorge Island:** Caminho da Fajã João Dias, 28 Sep 2010, Sardos, Carine, Runsey, Jones TA-SJJD-001 (AZB1453); Subida para o Pico da Esperança, 29 Sep 2010, Sardos, Carine, Runsey, Jones TA-SJSE-010 (AZB1456); Pico Verde, 29 Sep 2010, Sardos, Carine, Runsey, Jones TA-SJPV-001 (AZB1460); Pico da Esperança,

Appendix 2. Continued.

29 Sep 2010, *Sardos, Carine, Runsey, Jones TA-SJPE-001* (AZB1462); Terreirão, 29 Sep 2010, *Sardos, Carine, Runsey, Jones TA-SJTE-001* (AZB1468); Terreirão, 29 Sep 2010, *Sardos, Carine, Runsey, Jones TA-SJTE-002* (AZB1469); Terreirão, 29 Sep 2010, *Sardos, Carine, Runsey, Jones TA-SJTE-003* (AZB1470); Caminho da Fajã do Santo Cristo, 30 Sep 2010, *Sardos, Carine, Runsey, Jones TA-SJFS-001* (AZB1471); Caminho da Fajã do Santo Cristo, 30 Sep 2010, *Sardos, Carine, Runsey, Jones TA-SJFS-010* (AZB1472); Unmetalled road immediately south of Morro Pelado, 05 Jul 2008, *Maciel, Martins, Moreira, Moura, Carine, Rumsey, Fraga U. Açores-NHM 126* (BM013856353); Ribodos dos Vumes, 04 Sep 1971, *Gonçalves 3456* (BM000033324); Calheta, Ribeira dos Vimes, 4 Sep 1971, *Gonçalves 3456* (LISI-AZO-32382/1999); Velas, 8 Aug 1983, *Gonçalves 6781* (LISI-AZO 42816/1999); Grotas do Pico da Serra, 22 Aug 1938, *Cunha, Sobrinho s.n.* (LISU45160); Grotas do Pico da Serra, 22 Aug 1938, *Cunha, Sobrinho s.n.* (LISU45161); Grotas do Pico da Serra, 22 Aug 1938, *Cunha, Sobrinho s.n.* (LISU45162).

Appendix 3. Voucher specimens for *Tolpis graciosensis* examined in this study.

Taxon name: political subdivision: locality (when known), collection date (if applicable), collector(s) and number (herbarium code).

Tolpis graciosensis Borges Silva & M. Moura, sp. nov. **Portugal, Azores, Graciosa Island:** Beira Mar da Luz da Baía do Filipe, 12 Jul 2010, *Moura, Dias TS-GRBL-001* (AZB1314); Ilhéu da Praia, 13 Jul 2010, *Moura, Dias TS-GRIP-001* (AZB1315); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-016* (AZB4278); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-017* (AZB4279); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-018* (AZB4280); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-019* (AZB4281); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-020* (AZB4282); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-021* (AZB4283); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-022* (AZB4284); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-023* (AZB4285); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-024* (AZB4286); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-025* (AZB4287); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-026* (AZB4288); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-027* (AZB4289); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-028* (AZB4290); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-029* (AZB4291); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-030* (AZB4292); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-031* (AZB4293); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-032* (AZB4294); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-033* (AZB4295); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-034* (AZB4296); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-035* (AZB4297); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-036* (AZB4298); Beira-mar da Luz, Baía do Filipe, 26 Jun 2019, *Crawford TS-GRBL-037* (AZB4299); Santa Cruz, Quitadouro, 26 Jun 2019, *Crawford TS-GRSQ-001* (AZB4300); Santa Cruz, Quitadouro, 26 Jun 2019, *Crawford TS-GRSQ-002* (AZB4301); Santa Cruz, Quitadouro, 26 Jun 2019, *Crawford TS-GRSQ-003* (AZB4302); Santa Cruz, Quitadouro, 26 Jun 2019, *Crawford TS-GRSQ-004* (AZB4303); 26 Jun 2019, *Crawford TS-GRSQ-005* (AZB4304); Santa Cruz, Quitadouro, 26 Jun 2019, *Crawford TS-GRSQ-006* (AZB4305); Santa Cruz, Quitadouro, 26 Jun 2019, *Crawford TS-GRSQ-007* (AZB4306); Santa Cruz, Quitadouro, 26 Jun 2019, *Crawford TS-GRSQ-008* (AZB4307); Santa Cruz, Quitadouro, 26 Jun 2019, *Crawford TS-GRSQ-009* (AZB4308); Santa Cruz, Quitadouro, 26 Jun 2019, *Crawford TS-GRSQ-010* (AZB4309); Santa Cruz, Quitadouro, 26 Jun 2019, *Crawford TS-GRSQ-011* (AZB4310); Santa Cruz, 08 Sep 1971, *Gonçalves 3076* (BM013856306).

Appendix 4. Voucher specimens for *Tolpis macrorhiza* examined in this study.

Taxon name; political subdivision: locality (when known), collection date (if applicable), collector(s) and number (herbarium code).

Tolpis macrorrhiza (Banks ex Hook.) DC. **Portugal, Madeira Island:** Encumeada descida para o Chão dos Louros, 9 Dec 2010, *Sequeira TM-MDCL-003* (AZB1969); Encumeada, descida para o Chão dos Louros, 9 Dec 2010, *Sequeira TM-MDCL-004* (AZB1970); Encumeada descida para o Chão dos Louros, 28 May 2014, *Sequeira TM-MDCL-009* (AZB2151); Levada do Caldeirão Verde, 11 Aug 2011, *Sequeira, Ferreira TM-MDCV-001* (AZB2072); Encumeada início da levada do Folhadal, 23 Aug 2012, *Sequeira, Sequeira, Sequeira TM-MDLI-002* (AZB2103); Encumeada, início da levada do Folhadal, 23 Aug 2014, *Sequeira, Sequeira, Sequeira TM-MDLI-004* (AZB2105); Levada do Folhadal saída do túnel, 23 Apr 2011, *Sequeira, Sequeira, Sequeira TM-MDLO-001* (AZB2071); Estrada Poiso para o Ribeiro Frio, 13 Dec 2010, *Sequeira TM-MDPR-002* (AZB1973); Estrada Poiso para o Ribeiro Frio, 13 Dec 2010, *Sequeira TM-MDPR-004* (AZB1974); Descida do Poiso para o Ribeiro Frio, 17 Aug 2011, *Sequeira TM-MDPR-009* (AZB2036); Pico Areeiro, 03 Jul 2013, *Sequeira TM-MDEP-002* (AZB2288); Pico Areeiro, 03 Jul 2013, *Sequeira TM-MDEP-003* (AZB2140); Paúl da Serra, 03 Jul 2013, *Sequeira TM-MDSE-001* (AZB2141); Levada do Folhadal, 28 May 2014, *Sequeira TM-MDLI-006* (AZB2143); Rabaçal, levado do Alecrim, 31 Jul 2012, *Sequeira TM-MDLA-002* (AZB2145); Rabaçal, levado do Alecrim, 31 Jul 2012, *Sequeira TM-MDLA-003* (AZB2146); Rabaçal, levado do Alecrim, 31 Jul 2012, *Sequeira TM-MDLA-004* (AZB2147); Terreiro da Luta, 28 May 2014, *Sequeira TM-MDTL-001* (AZB2289); Terreiro da Luta, 28 May 2014, *Sequeira TM-MDTL-002* (AZB2290); Terreiro da Luta, 28 May 2014, *Sequeira TM-MDTL-003* (AZB2291); Levada do Folhadal, 28 May 2014, *Sequeira TM-MDLO-004* (AZB2148).

Appendix 5. Voucher specimens for *Tolpis mariensis* examined in this study.

Taxon name: political subdivision: locality (when known), collection date (if applicable), collector(s) and number (herbarium code).

Tolpis mariensis Borges Silva & M.Moura. sp. nov. **Portugal, Azores, Santa Maria Island:** Vila do Porto, costa junto ao Aeroporto, 9 Aug 1996, *Barcelos s.n.* (AZU5137); Vila do Porto, costa junto ao Aeroporto, 9 Aug 1996, *Barcelos s.n.* (AZU5142); Cruz, este do Santo Espírito, 31 Aug 2001, *Schäfer s.n.* (AZU1168); Anjos, 02 Jul 2009, *Moura, Silva TS-MAAN-002* (AZB1195); Maia, 02 Jul 2009, *Moura, Silva TS-MAMA-009* (AZB1196); Maia, 02 Jul 2009, *Moura, Silva TS-MAMA-010* (AZB1197); Pico Alto, 04 Jul 2009, *Moura, Silva TS-MAPA-001* (AZB1208); Pico Alto, 04 Jul 2009, *Moura, Silva TS-MAPA-002* (AZB1209); Pico Alto, 04 Jul 2009, *Moura, Silva TS-MAPA-011* (AZB1260); Pico Alto, 04 Jul 2009, *Moura, Silva TS-MAPA-012* (AZB1261); Pico Alto, 04 Jul 2009, *Moura, Silva TS-MAPA-013* (AZB1262); Pico Alto, 04 Jul 2009, *Moura, Silva TS-MAPA-014* (AZB1263); São Lourenço, 02 Jul 2009, *Moura, Silva TS-MASL-004* (AZB1198); São Lourenço, 02 Jul 2009 *Moura, Silva TS-MASL-005* (AZB1199); Pico Alto, high on the mountain but not on summit, 28 Jun 1970, *Brooke 11,628* (BM000033328); Chaminé N Malbusca, 20 May 2001, *Schäfer s.n.* (BM000039894); São Pedro, 31 Jan 1972, *Gonçalves 3752* (BM013856271); s. loc., 01 Jun 1903, *Carreiro 829C* (COI00079459); s. loc., Jun 1899, *Carreiro 829* (COI00079460); s. loc., Jun 1899, *Carreiro 829A* (COI00079461); s. loc. 01 Aug 1999, *Carreiro 829B* (COI000794641); Estrada do Calhau da Roupá, Vila do Porto, 05 May 1973, *Pombo 181* (COI00079466); Monte das Flores, on way to cré, 22 May, *Pinto da Silva 266* (LISE70165); Monte das Flores, on way to cré, 22 May, *Pinto da Silva 266* (LISE70165A); Almagreira, Ponte dos Agriões, 20 May, *Pinto da Silva 320* (LISE); Almagreira, above Ponte dos Agriões, 01 Jul, *Pinto da Silva 904A* (LISE70709); Pico Alto - altitude de 550 m, 23 Apr 1972, *Gonçalves 3873* (LISI-AZO 32822/1999); Anjos, abundante entre as rochas, 30 Jun 1937, *Palhinha, Sobrinho s.n.* (LISU45176); s. loc., Jun 1899, *Carreiro s.n.* (LY); s. loc., 01 Jul 1903, *Carreiro 829C* (LY); s. loc., 01 Jul 1899, *Carreiro s.n.* (LY); s. loc., 01 Jul

Appendix 5. Continued.

1899, *Carreiro s.n.* (LY); s. loc., 01 Jun 1999, *Carreiro 829* (LY0010214); s. loc., Jun 1899, *Carreiro 829B* (LY0010227); s. loc., Jun 1899, *Carreiro s.n.* (LY0010241); s. loc., Jun 1899, *Carreiro s.n.* (LY0010242); s. loc., 01 Jul 1903, *Carreiro 829C* (LY0010243); Anjos, 10 Jul 2008, *Gutte 168/2008* (LZ 203921); s. loc., 23 Jul 1896, *Treleave 481B* (MO126616); s. loc., 1899, *Treleave 481C* (MO126617); s. loc., Jun 1899, *Treleave 481D* (MO126618); s. loc., Jun 1899, *Carreiro 829C* (MO2525370); s. loc., 26 Aug 1894, *Carreiro 829A* (MO2525374); s. loc., 23 Jul 1894, *Carreiro 829* (MO2525376); s. loc., 20 Jul 1894, *Carreiro 829B* (MO5483325), Santa Maria, Jun 1899, Anon, *s.n.* (OXF980520).

Appendix 6. Voucher specimens for *Tolpis maritima* examined in this study.

Taxon name; political subdivision: locality (when known), collection date (if applicable), collector(s) and number (herbarium code).

Tolpis maritima Borges Silva & M.Moura, sp. nov. **Portugal, Azores, São Miguel Island:** Poço Azul da Achadinha, 23 Sep 2017, *Borges Silva TS-SMAZ-001* (AZB2903); Poço Azul da Achadinha, 23 Sep 2017, *Borges Silva TS-SMAZ-002* (AZB2904); Poço Azul da Achadinha 23 Sep 2017, *Borges Silva TS-SMAZ-003* (AZB2905); Zona Balnear da Boca da Ribeira da Vila do Nordeste, 23 Sep 2017, *Borges Silva TS-SMBR-001* (AZB2919); Zona Balnear da Boca da Ribeira da Vila do Nordeste, 23 Sep 2017, *Borges Silva TS-SMBR-002* (AZB2920); Zona Balnear da Boca da Ribeira da Vila do Nordeste, 23 Sep 2017, *Borges Silva TS-SMBR-003* (AZB2921); Zona Balnear da Boca da Ribeira da Vila do Nordeste, 23 Sep 2017, *Borges Silva TS-SMBR-004* (AZB2922); Zona Balnear da Boca da Ribeira da Vila do Nordeste, 23 Sep 2017, *Borges Silva TS-SMBR-005* (AZB2923); Praia do Lombo Gordo, 11 May 2010, *Moura, Sardos TS-SMLG-001* (AZB1328); Praia do Lombo Gordo, 23 Sep 2017, *Borges Silva TS-SMLG-020* (AZB2906); Praia do Lombo Gordo, 23 Sep 2017, *Borges Silva TS-SMLG-021* (AZB2907); Praia do Lombo Gordo, 23 Sep 2017, *Borges Silva TS-SMLG-022* (AZB2908); Praia do Lombo Gordo, 23 Sep 2017, *Borges Silva TS-SMLG-023* (AZB2909); Praia do Lombo Gordo, 23 Sep 2017, *Borges Silva TS-SMLG-024* (AZB2910); Porto da Ajuda da Bretanha, 23 Aug 2010, *Borges Silva TS-SMPA-021* (AZB1398); Porto da Ajuda da Bretanha, 23 Aug 2010, *Borges Silva TS-SMPA-022* (AZB1399); Porto da Ajuda da Bretanha, 23 Aug 2010, *Borges Silva TS-SMPA-023* (AZB1400); Porto da Ajuda da Bretanha, 23 Aug 2010, *Borges Silva TS-SMPA-024* (AZB1401); Porto da Ajuda da Bretanha, 14 Nov 2016, *Borges Silva TS-SMPA-025* (AZB2349); Porto da Ajuda da Bretanha, 14 Nov 2016, *Borges Silva TS-SMPA-026* (AZB2350); Porto da Ajuda da Bretanha, 14 Nov 2016, *Borges Silva TS-SMPA-027* (AZB2353); Porto Velho das Capelas, 6 Jul 2010, *Moura, Sardos, Borges Silva TS-SMPC-001* (AZB1491); Porto Velho das Capelas, 27 Jul 2010, *Moura, Sardos, Borges Silva TS-SMPC-018* (AZB1327); Porto Velho das Capelas, 14 Nov 2016, *Borges Silva TS-SMPC-051* (AZB2351); Porto Velho das Capelas, 14 Nov 2016, *Borges Silva TS-SMPC-052* (AZB2352); Parque do Pelado de endêmicas da Lomba da Fazenda, 23 Sep 2017, *Borges Silva TS-SMPE-001* (AZB2911); Parque do Pelado de endêmicas da Lomba da Fazenda, 23 Sep 2017, *Borges Silva TS-SMPE-002* (AZB2912); Parque do Pelado de endêmicas da Lomba da Fazenda, 26 Aug 2017, *Borges Silva TS-SMPE-003* (AZB2913); Parque do Pelado de endêmicas da Lomba da Fazenda, 26 Aug 2017, *Borges Silva TS-SMPE-004* (AZB2914); Parque do Pelado de endêmicas da Lomba da Fazenda, 26 Aug 2017, *Borges Silva TS-SMPE-005* (AZB2915); Parque do Pelado de endêmicas da Lomba da Fazenda, 26 Aug 2017, *Borges Silva TS-SMPE-006* (AZB2916); Parque do Pelado de endêmicas da Lomba da Fazenda, 26 Aug 2017, *Borges Silva TS-SMPE-007* (AZB2917); Parque do Pelado de endêmicas da Lomba da Fazenda, 26 Aug 2017, *Borges Silva TS-SMPE-008* (AZB2918); Salga Salto da Farinha, 23 Sep 2017, *Borges Silva TS-SMSF-001* (AZB2894); Salga Salto da Farinha, 23 Sep 2017, *Borges Silva TS-SMSF-002* (AZB2895); Salga Salto da Farinha, 23 Sep 2017, *Borges Silva TS-SMSF-003* (AZB2896); Salga Salto da Farinha, 23 Sep 2017, *Borges Silva TS-SMSF-004* (AZB2897); Salga Salto da Farinha, 23 Sep 2017, *Borges Silva TS-SMSF-005* (AZB2898); Salga Salto da Farinha, 26 Aug 2017, *Borges Silva TS-SMSF-006* (AZB2899); Salga Salto da Farinha, 26 Aug 2017, *Borges Silva TS-SMSF-007* (AZB2900); Salga Salto da Farinha, 26 Aug 2017, *Borges Silva TS-SMSF-008* (AZB2901); Salga Salto da Farinha, 26 Aug 2017, *Borges Silva TS-SMSF-009* (AZB2902); Praia da Viola da Lomba da Maia, 23 Sep 2017, *Borges Silva TS-SMVM-001* (AZB2891); Praia da Viola da Lomba da Maia, 23 Sep 2017, *Borges Silva TS-SMVM-002* (AZB2892); Praia da Viola da Lomba da Maia, 23 Sep 2017, *Borges Silva TS-SMVM-003* (AZB2893); s. loc., 1846, *Hunt s.n.* (BM000033336); Beach south of Ponta da Madrugada, 07 Mar 2008, *Maciel & al. U. Açores-NHM 11* (BM013856291); s. loc., 1777, *Masson s.n.* (BM013856299); Capelas, Aug 1956, *s. coll.*, 39 (BM013856303); Capelas, Aug 1956, *s. coll.*, 47 (BM013856304); Relva, 01 Jul 1904, *Carreiro 829E* (COI00079462); s. loc., 01 Aug 1908, *Carreiro 829F* (COI00079463); Mosteiros, 01 Aug 1900, *Carreiro 901A* (COI000794636); Mosteiros, Aug 1900, *s. coll.*, 901 (COI00079642); Ribeira Grande, Ponta do Cintrão, 23 Jul 1964, *Dansereau & al. 808* (COI00079465); Mosteiros, 1900, *Gandoger 901* (LY); Praia, 01 Jun 1903, *Carreiro 360A* (LY0010221); Praia, 01 Sep 1903, *Carreiro s.n.* (LY0010224); Relva, 01 Jul 1904, *Carreiro 829E* (LY0010225); Mosteiros 01 Aug 1900, *Carreiro 901* (LY0010239); Lagoa das Furnas, May 1895, *Treleave 474* (MO126625); Ribeira Grande, *Carreiro 361* (MO2525359); Praia, Aug 1903, *Carreiro 360A*, (MO2525363); Praia, Aug 1903, *Carreiro 360A*, (MO2525365); Praia, Aug 1903, *Carreiro 360H*, (MO2525366); Relva, Jul 1904, *Carreiro 829e*, (MO2525375); Mosteiros, Aug 1900, *Carreiro 901A*, (MO2525372); Mosteiros, Aug 1900, *Carreiro 901* (MO2525373).

Appendix 7. Voucher specimens for *Tolpis maritimoccidentalis* examined in this study.

Taxon name; political subdivision: locality (when known), collection date (if applicable), collector(s) and number (herbarium code).

Tolpis maritimoccidentalis Borges Silva & M.Moura, sp. nov. **Portugal, Azores, Corvo Island:** s.loc., 12 Aug 1894, *Treleave 477* (AZ1688); Vila, 20 Jul 1972, *Gonçalves 4172* (BM00001172022); Vila, 09 Jun 1971, *Gonçalves 2663* (BM013856302); Vila - altitude de 10 m, 9 Jun 1971, *Gonçalves 2663* (LISI-AZO 31599/1999); s. loc., 12 Aug 1894, *Treleave 476* (MO126626); s. loc., 1 Jul 1896, *Treleave 477* (MO126631); s. loc., 13 Jul 1894, *Treleave 476* (MO126636); **Flores Island:** Santa Cruz, 12 Aug 1894, *Treleave 479* (AZ168); Cais do Porto - altitude de 3 m, 27 Jul 1964, *Gonçalves 1747* (LISI-AZO 24209/1999); Fazenda de S. Cruz on a flat grassy bank near a river, 27 Jul 1967, *Pryor 121* (BM000033321); Santa Cruz, Vila, 30 Jun 1972, *Gonçalves 4239* (BM013856305); Cais do Porto, 27 Jul 1964, *Gonçalves s.n.* (LISI-AZO 24209/1999); Santa Cruz, 12 Aug 1894, *Treleave 478* (MO126627); Santa Cruz, 12 Aug 1894, *Treleave 479* (MO126629); Ponta Delgada, 12 Aug 1894, *Treleave 480* (MO126632); s. loc., 26 Jul 1894, *Treleave 481* (MO126628).

Appendix 8. Voucher specimens for *Tolpis maritimocentralis* examined in this study.

Taxon name; political subdivision: locality (when known), collection date (if applicable), collector(s) and number (herbarium code).

Tolpis maritimocentralis Borges Silva & M.Moura, sp. nov. **Portugal, Azores, Terceira Island:** Monte Brasil, Jun 1903, *Carreiro 829B* (AZ1672); Monte Brasil, 17 Jun 2021, *Elias TS-TEMB-001* (AZB4277); s. loc., 01 Jun 1903, *Carreiro 829D* (COI00079464); Angra do Heroísmo, 7 Jul 1971, *Gonçalves 2901* (LISI-AZO31861/1999); s. loc., 01 Jun 1903, *Carreiro, 829D* (LY0010244); s. loc., Jun 1903, *Carreiro 829D* (MO2525375); **São Jorge Island:** Velas, Caminho da Fajã do Norte Pequeno, 8 Aug 1983, *Gonçalves 6781* (LISI42816); **Faial Island:** Horta, 05 Aug 1972, *Gonçalves 4526* (BM013856301); s. loc., Jun 1838, *Hochstetter 93* (BM013856308); Horta, 1842, *Watson 1790* (EMU608255); Horta muralha do forte, 4 Sep 1965, *Gonçalves 1995* (LISI-AZO 24955/1999); s. loc., Jul, *Drouet s.n.* (LY0015133); s. loc., Jun 1838, *Hochstetter 93* (MNHN-P-P02664758); s. loc., Jun 1838, *Hochstetter 93* (MNHN-P-P02664759); s. loc., Jun 1838, *Hochstetter 93* (MNHN-P-P02664760); s. loc., 29 Jul 1894, *Brown 157* (MO25253779).

Appendix 9. Voucher information for *Tolpis micraelensis* examined in this study.

Taxon name; political subdivision: locality (when known), collection date (if applicable), collector(s) and number (herbarium code).

Tolpis micraelensis Borges Silva & M. Moura sp. nov. **Portugal, Azores, São Miguel Island:** Lombadas, Aug 1897, *Carreiro s.n.* (AZ1648); Lombadas, Aug 1897, *Carreiro s.n.* (AZ1649); Sete Cidades, Aug 1900, *Carreiro 3* (AZ1650); Salto do Cavalo, Sep 1905, *Carreiro 828F* (AZ1654); Tronqueira do Nordeste, Sep 1905, *Carreiro s.n.* (AZ1657); Espigão do Barreiros, Aug 1905, *Carreiro 828g* (AZ1658); Lagoa, Janela do Inferno, Aug 1906, *Carreiro 12* (AZ1659); Lagoa, Janela do Inferno, Aug 1906, *Carreiro 13* (AZ1660); Sete Cidades, Aug 1900, *Carreiro 17* (AZ1664); Pico do Carvão, Aug 1898, *Carreiro 360* (AZ1665-1666 (2 specimens)); Caminho da Praia da Lagoa do Fogo, Aug 1903, *Carreiro 360A* (AZ1669-1670 (2 specimens)); Lagoa do Caldeirão Grande, 6 Sep 2010, *Borges Silva TA-SMCG-011* (AZB1402); Sete Cidades, Caldeira do Alferes, 7 Aug, 2010, *Borges Silva, Dias TA-SMAL-001* (AZB1389); Criação, 21 Aug 2010, *Borges Silva, Dias TA-SMCR-001* (AZB1395); Lagoa Empadadas, 8 Aug 2010, *Borges Silva, Dias TA-SMEM-001* (AZB1391); Sete Cidades, Estaleiros, 7 Aug 2010, *Borges Silva, Dias TA-SMES-001* (AZB1390); Lagoa do Areeiro, 24 Oct 2010, *Borges Silva, Dias TA-SMLA-001* (AZB1451); Lagoa do Canário, 27 Apr 2010, *Moura TA-SMLC-001* (AZB1321); Lagoa do Canário, 31 Jul 2010, *Borges Silva, Dias TA-SMLC-024* (AZB1384); Lagoa do Canário, 31 Jul 2010, *Borges Silva, Dias TA-SMLC-076* (AZB1385); Lagoa das Éguas Norte e Sul, 11 Sep 2010, *Borges Silva TA-SMLE-006* (AZB1403); Lagoa das Éguas Norte e Sul, 11 Sep 2010, *Borges Silva TA-SMLE-018* (AZB1404); Lagoa das Éguas Norte e Sul, 11 Sep 2010, *Borges Silva TA-SMLE-023* (AZB1405); Lagoa das Éguas Norte e Sul, 11 Sep 2010, *Borges Silva TA-SMLE-024* (AZB1406); Lagoa do Fogo, interior da Caldeira, 18 May 2010, *Moura TA-SMLF-100* (AZB1324); Lagoa do Fogo, interior da Caldeira, 18 May 2010, *Moura TA-SMLF-107* (AZB1325); Lombadas, 18 Sep 2010, *Borges Silva, Dias TA-SMLO-013* (AZB1317); Monte Escuro, 18 Sep 2010, *Borges Silva, Dias TA-SMME-001* (AZB1422); Pico Bartolomeu, 9 Oct 2010, *Borges Silva, Dias TA-SMPB-021* (AZB1442); Pico Bartolomeu, 11 May 2010, *Moura, Sardos TA-SMPB-001* (AZB1319); Pico Bartolomeu, 11 May 2010, *Moura, Sardos TA-SMPB-002* (AZB1320); Planalto dos Graminhais, 17 Sep 2010, *Moura, Borges Silva, Dias TA-SMPG-001* (AZB1420); Planalto dos Graminhais, 17 Sep 2010, *Moura, Borges Silva, Dias TA-SMPG-005* (AZB1421); Caminho do Pico Da Cruz, 31 Jul 2010, *Borges Silva, Dias TA-SMPI-001* (AZB1383); Pico do Carvão, 21 Aug 2010, *Borges Silva, Dias TA-SMPR-001* (AZB1392); Pico do Carvão, 21 Aug 2010, *Borges Silva, Dias TA-SMPR-002* (AZB1393); Tronqueira, 1 Jun 2010, *Moura TA-SMTR-006* (AZB1326); Tronqueira, 11 May 2010, *Moura, Sardos TA-SMTR-058* (AZB1318); Tronqueira, Miradouro, 17 Sep 2010, *Moura, Borges Silva, Dias TA-SMTR-063* (AZB1416); Tronqueira, Miradouro, 17 Sep 2010, *Moura, Borges Silva, Dias TA-SMTR-061* (AZB1415); Tronqueira, Miradouro, 17 Sep 2010, *Moura, Borges Silva, Dias TA-SMTR-068* (AZB1417); Tronqueira, Miradouro, 17 Sep 2010, *Moura, Borges Silva, Dias TA-SMTR-096* (AZB1419); Vista do Rei, 21 Aug 2010, *Borges Silva, Dias TA-SMVR-001* (AZB1394); s. loc., 1846, *Hunt s.n.* (BM000033317); Roadside between Furnas and Nordeste, Aug, s. coll., 138 (BM000033319); Pico da Vara, near Tronqueira, ca. 6 km along Nordeste to Povoação Road, 25 Jul 1985, *Parry s.n.* (BM000033322); Caldeira das Sete cidades, North Rim, Hedgegrow, 30 Jul 1970, *Dolman 383* (BM000033323); s. loc., 1845, *Hunt s.n.* (BM000033329); Vista do Rei, 27 Jul 1968, *Gonçalves 2449* (BM000033333); s. loc., 1846, *Hunt s.n.* (BM013856232); Lagoa, 01 Aug 1903, *Carreiro 828B* (COI000794622); Furnas, 14 Sep 1972, *Carreiro 828F* (COI000794623); Furnas, Jul 1891, *Carreiro s.n.* (COI000794624); Caldeiras, 01 Aug 1999, *Carreiro 828* (COI000794625); Água de Pau, 01 Aug 1905, *Carreiro 828E* (COI000794626); Lagoa, 01 Aug 1905, *Carreiro 828D* (COI000794628); Lagoa, 01 Aug 1905, *Carreiro 828C* (COI000794629); Muro das 9 janelas, Jul 1879, *Carreiro s.n.* (COI000794635); Pico do Carvão, Aug 1898, *Carreiro 369* (COI000794637); Praia, 01 Aug 1903, *Carreiro 360A* (COI000794638); Praia, 01 Aug 1903, *Carreiro 360A* (COI000794639); Praia, 01 Aug 1903, *Carreiro 828A* (COI000794640); Pico da Cruz, 26 Jul 1958, *Cymbion s.n.* (LISI-AZO 20016/1999); Vista do Rei - altitude de 500 m, 27 Jul 1968, *Botelho, Gonçalves 2448* (LISI-AZO 27470/1999); Pedra do Galego, próximo das Furnas no talude das estradas, 30 Jun 1937, *Palhinha, Sobrinho s.n.* (LISU45167); Pedra do Galego, próximo das Furnas no talude das estradas, 30 Jun 1937, *Palhinha, Sobrinho s.n.* (LISU45170); s. loc., Jul 1847, *Welwitsch 177* (LISU45171); s. loc., Jul 1847, *Welwitsch s.n.* (LISU45172); Sete Cidades, 08 Sep 1938, *Cunha, Sobrinho s.n.* (LISU45177); Tronqueira do Nordeste, 13 Sep 1938, *Cunha, Sobrinho s.n.* (LISU45178); Sete Cidades, 08 Sep 1938, *Cunha, Sobrinho s.n.* (LISU45179); s. loc., 07 Aug 1907, *Hunt 184* (LY0010209); Caldeiras, 08 Feb 1898, *Carreiro s.n.* (LY0010210); Pico do Carvão, 08 Feb 1898, *Carreiro 360* (LY0010212); Praia, 01 Aug 1903, *Carreiro 828A* (LY0010223); Água de Pau, 01 Aug 1905, *Gandoger 828E* (LY0010226); Caldeiras, 01 Sep 1899, *Carreiro 828* (LY0010229); Furnas, 01 Aug 1905, *Gandoger 828F* (LY0010230); Furnas, 01 Jul 1899, *Gandoger s.n.* (LY0010231); Lagoa, 1 Aug 1905, *Gandoger 828C* (LY0010232); Pico do Carvão, Aug 1898, *Carreiro s.n.* (LY0010236); s. loc., s. d., *Hunt 608258* (MANCH); s. loc., s. d., *Hunt 608259* (MANCH); s. loc., s. d., *Hunt, 608260* (MANCH); s. loc., 1845, *Hunt, 608261* (MANCH); s. loc., s. d., *Hunt, 608262* (MANCH); s. loc., s. d., *Hunt, 608265* (MANCH); s. loc., 1846, *Hunt s.n.* (MNHN-P-P02664413); s. loc., 1846, *Hunt s.n.* (MNHN-P-P02664414); s. loc., 1846, *Hunt 182* (MNHN-P-P02664415); s. loc., 1846, *Hunt 182* (MNHN-P-P02664417); s. loc., 1846, *Hunt 182* (MNHN-P-P02664680); s. loc., 1846, *Hunt 182* (MNHN-P-P02664681); s. loc., 1846, *Hunt 182* (MNHN-P-P04418254); Serra Gorda, 22 Aug 1894, *Treleave 468* (MO126620); Sete Cidades, 31 Aug 1894, *Treleave 469* (MO126621); Pico do Carvão, 1899, *Treleave s.n.* (MO126622); Pico do Carvão, 25 Aug 1894, *Treleave 467* (MO126623); Graminhais, Sep 1905, *Treleave 466* (MO126624); Pico do Carvão, 15 Jul 1894, *Carreiro 360* (MO2525360); Água do Pau, Aug 1903, *Carreiro 828E* (MO2525367); Furnas, Aug 1899, *Carreiro 828F* (MO2525368); Praia, Aug 1903, *Carreiro 828A* (MO2525369); Caldeiras, Aug 1905, *Carreiro 828* (MO2525377); Lagoa, s. loc., *Carreiro 828B* (MO2525378); São Miguel, s. d., *Hochstetter s.n.* (OXF 98039T); São Miguel s. d., *Hochstetter s.n.* (OXF 98040L); Lagoa do Fogo, s. d., Anon. s.n. (OXF98051N); s. loc., 18 Jan 1905, s. coll., s.n. (PH00024819); Tronqueira, 2014, *Stieglitz 2015/16* (WU0123194); Tronqueira, Sep 2014, *Stieglitz s.n.* (WU0151301).

Appendix 10. Voucher specimens for *Tolpis occidentalis* examined in this study.

Taxon name; political subdivision: locality (when known), collection date (if applicable), collector(s) and number (herbarium code).

Tolpis occidentalis Borges Silva & M. Moura sp. nov. **Portugal, Azores, Corvo Island:** Caminho Ponta do Marco do Caldeirão, 24 Jul 2010, *Silva TA-COMC-011* (AZB1373); Cumieira oeste do Caldeirão, 1 Aug 2017, *Pipa TA-COCO-001* (AZB2888); Cumieira oeste do Caldeirão, 1 Aug 2017, *Pipa TA-COCO-002* (AZB2889); Cumieira oeste do Caldeirão, 1 Aug 2017, *Pipa TA-COCO-003* (AZB2890); Fonte das Poças, 08 Jun 1971, *Gonçalves 2576* (BM000033331); Cliff face at north end of Caldeirão, 07 Sep 2008, *Maciel, Martins, Moreira, Moura, Carine, Rumsey, Fraga NHM 76* (BM013856231); Estado Farol, 18 Oct 1971, *Gonçalves 3674* (BM000033327); Farol, 18 Oct 1971, *Gonçalves 3691* (BM000033337); Fonte das Poças, 8 Jun 1971, *Gonçalves 2576* (LISI-AZO 31528/1999); Caldeira, 22 Aug 1894, *Treleave 473* (MO126619); **Flores Island:** Ponte, 9 Aug 1894, *Treleave 441* (AZ1671); Estrada do Morro Alto, 24 Sep 2007, *Moura, Maciel TA-FLMA-001* (AZB235); Estrada do Morro Alto, 24 Sep 2007, *Moura, Maciel TA-FLMA-002* (AZB236); Cidrão, 24 Sep 2007, *Moura, Maciel TA-FLCI-001* (AZB237); Cidrão, 24 Sep 2007, *Moura, Maciel TA-FLCI-002* (AZB238); Cidrão, 24 Sep 2007, *Moura, Maciel TA-FLCI-003* (AZB239); Cidrão, 24 Sep 2007, *Moura, Maciel TA-FLCI-004* (AZB240); Cidrão, 24 Sep 2007, *Moura, Maciel TA-FLCI-005* (AZB241); Ribeira da Badanela, 20 Jul 2010, *Silva, TA-FLRB-001* (AZB1353); Pico dos Sete Pés, 20 Jul 2010, *Silva s.n.* (AZB1354-b); s. loc., Jun - Aug 1967, *Pryor s.n.* (BM000024265); Lagoa Branca, track leading to Morro Alto, 08 Aug 1985, *Parry 75* (BM000033325); Ribeira do Cascalho, 1 Aug 1965, *Gonçalves 1995* (BM000033335); Ribeira do Cascalho, 1 Aug 1965, *Gonçalves 1955* (LISI24835); s. loc., 2 Aug 1894, *Treleave 465* (MO126613); Fajazinha, 1 Aug 1894, *Treleave 464* (MO126614); Ponte, 9 Aug 1894, *Treleave 463* (MO126615).

Appendix 11. Voucher specimens for *Tolpis succulenta* examined in this study.

Taxon name; political subdivision: locality (when known), collection date (if applicable), collector(s) and number (herbarium code).

Tolpis succulenta (Aiton) Lowe. **Portugal, Madeira, Porto Santo Island:** Pedreira pico de Ana Ferreira, 27 Nov 2011, *Jardim TS-PSAF-001* (AZB); Pedreira pico de Ana Ferreira, 27 Nov 2011, *Jardim TS-PSAF-002* (AZB); Pedreira pico de Ana Ferreira, 27 Nov 2011, *Jardim TS-PSAF-003* (AZB); Pico Castelo, 27 Nov 2011, *Jardim TS-PSPC-001* (AZB2038); Pico Castelo, 27 Nov 2011, *Jardim TS-PSPC-002* (AZB2039); Pico Castelo, 27 Nov 2011, *Jardim TS-PSPC-003* (AZB2040); Rocha de N. Sra. entrada da Pedreira, 30 Mar 2012, *Sequeira, Pupo, Jardim TS-PSRS-001* (AZB2100); Rocha de N. Sra. entrada da Pedreira, 30 Mar 2012, *Sequeira, Pupo, Jardim TS-PSRS-002* (AZB2101); Serra de Fora, 11 Mar 2011, *Jardim TS-PSSF-001* (AZB2041); Serra de Fora, 11 Mar 2011, *Jardim TS-PSSF-002* (AZB2042); Serra de Fora, 11 Mar 2011, *Jardim TS-PSSF-003* (AZB2043); Ilhéu de Ferro, 23 May 2014, *Jardim TS-PSFI-001* (AZB2120); Ilhéu de Ferro, 23 May 2014, *Jardim TS-PSFI-002* (AZB2121); Ilhéu de Ferro, 23 May 2014, *Jardim TS-PSFI-003* (AZB2122); Pico Facho, 30 Apr 2013, *Jardim TS-PSPF-001* (AZB2124); Pico Facho, 30 Apr 2013, *Jardim TS-PSPF-002* (AZB2126); Pico Facho, 30 Apr 2013, *Jardim TS-PSPF-005* (AZB2128); Pico Facho, 30 Apr 2013, *Jardim TS-PSPF-006* (AZB2286); Ilhéu Cal, 16 May 2014, *Jardim TS-PSIC-001* (AZB2130); Ilhéu Cal, 16 May 2014, *Jardim TS-PSIC-002* (AZB2131); Ilhéu Cal, 16 May 2014, *Jardim TS-PSIC-003* (AZB2132); Fonte da Areia, 15 May 2014, *Jardim TS-PSFR-001* (AZB2133); Fonte da Areia, 15 May 2014, *Jardim TS-PSFR-002* (AZB2134); Ilhéu de Baixo, Cliff overlooking grande by old houses, 11 Apr 1986, *Press, Short 1183* (BM013856315); Vila Baleira, along the beach towards Porta Arriga, 18 Apr 1986, *Press, Short 1373* (BM013856316); s. loc., 1828, *Lowe s.n.* (BM013856319), **Madeira Island:** Terreiro da Luta, 17 Aug 2011, *Sequeira TS-MDTL-001* (AZB2037); Terreiro da Luta, 13 Dec 2010, *Sequeira TS-MDTL-002* (AZB1956); Terreiro da Luta estrada para a Camacha, 13 Dec 2011, *Sequeira TS-MDTL-003* (AZB); Porto da Cruz junto à praia, 11 Jun 2011, *Sequeira TS-MDCR-001* (AZB2063); Porto da Cruz junto à praia, 11 Jun 2011, *Sequeira TS-MDCR-002* (AZB2064); Porto da Cruz junto à praia, 11 Jun 2011, *Sequeira TS-MDCR-003* (AZB2065); Estrada pico Areiro circa Poço da Neve, 17 Aug 2011, *Sequeira TS-MDEP-001* (AZB2078); Estrada pico Areiro circa Poço da Neve, 17 Aug 2011, *Sequeira TS-MDEP-003* (AZB2080); Estrada pico Areiro circa Poço da Neve, 17 Aug 2011, *Sequeira TS-MDEP-006* (AZB2083); Encumeada-Ribeira Brava estrada junto à pousada, 09 Dec 2010, *Sequeira TS-MDER-005* (AZB1955); Praia Formosa, 11 Jun 2011, *Sequeira TS-MDFO-002* (AZB2051); Praia Formosa, 11 Jun 2011, *Sequeira TS-MDFO-003* (AZB2052); Praia Formosa, 11 Jun 2011, *Sequeira TS-MDFO-005* (AZB2054); Maroços perto do túnel para o Porto da Cruz, 11 Jun 2011, *Sequeira TS-MDMA-003* (AZB2062); Estrada do Monte para St. António Funchal, 13 Dec 2010, *Sequeira TS-MDMS-002* (AZB1958); Paúl do Mar, 07 Apr 2013, *Sequeira, Pupo TS-MDPL-001* (AZB2033); Paúl do Mar, 07 Apr 2013, *Sequeira, Pupo TS-MDPL-002* (AZB2034); Paúl do Mar, 07 Apr 2013, *Sequeira, Pupo TS-MDPL-004* (AZB2035); Porto Moniz, junto ao mar, 31 Dec 2010, *Sequeira TS-MDPM-012* (AZB1962); Porto Moniz junto ao mar, 21 Jun 2011, *Sequeira, Pupo TS-MDPM-015* (AZB2086); Porto Moniz junto ao mar, 21 Jun 2011, *Sequeira, Pupo TS-MDPM-016* (AZB2087); Porto Novo, 11 Jun 2011, *Sequeira TS-MDPN-001* (AZB2055); Porto Novo, 11 Jun 2011, *Sequeira TS-MDPN-002* (AZB2056); Porto Novo, 11 Jun 2011, *Sequeira TS-MDPN-003* (AZB2057); Porto Novo, 11 Jun 2011, *Sequeira TS-MDPN-004* (AZB2058); Ponta do Sol, 22 Jan 2011, *Sequeira TS-MDP0-004* (AZB1967); Ponta do Sol, 22 Jan 2011, *Sequeira TS-MDP0-011* (AZB1968); Canhas estrada para a Ponta do Sol, 20 Nov 2010, *Sequeira TS-MDPS-001* (AZB1952); Canhas estrada para a Ponta do Sol, 20 Nov 2010, *Sequeira TS-MDPS-002* (AZB1953); Ribeira Brava miradouro, 10 Jan 2011, *Sequeira TS-MDRB-004* (AZB1964); Ribeira Brava miradouro, 10 Jan 2011, *Sequeira TS-MDRB-005* (AZB1965); Ribeira do Inferno estrada Seixal, 21 Jun 2011, *Sequeira, Pupo TS-MDRI-001* (AZB2068); Ribeira do Inferno estrada Seixal, 21 Jun 2011, *Sequeira, Pupo TS-MDRI-003* (AZB2070); Vereda dos Prazeres, 28 May 2014, *Sequeira TS-MDVP-001* (AZB2136); Vereda dos Prazeres, 28 May 2014, *Sequeira TS-MDVP-002* (AZB2150); Vereda dos Prazeres, 28 May 2014, *Sequeira TS-MDVP-003* (AZB2162); Ponta do Sol, 28 May 2014, *Sequeira TS-MDP0-012* (AZB2155); Road Curral das Freiras - Eira do Serrado, 13 Jun 1997, *Nordt, Parolly 97-39* (B100066692); s. loc., s. d. *Sloane s.n.* (BM000589002); Summit of Pico do Arieiro, 23 Apr 2855, *Lowe 69* (BM0000083834); Porto da Cruz, 26 May 1864, *Lowe 681* (BM0000083836); Ponta Delgada, 6 Jun 1850, *Lowe 660* (BM0000083837); s. loc., 1776, *Masson s.n.* (BM000829784); s. loc., 1777, *Masson s.n.* (BM000829785); s. loc., 1777, *Masson s.n.* (BM000829786); 1 km west of Pico do Facho, towards Machico, 02 Aug 1981, *Hampshire 117* (BM001172029); Prazeres, 26 Oct 1984, *Short 174* (BM001172030); West Funchal, levada between São Martinho and Quebradas, 16 Aug 1981, *Hampshire 236* (BM001172031); Near Funchal, 14 May 1895, *Anon, s.n.* (BM001172032); Santa, steep North side of Ribeira do Tristão Jorge, 22 Jun 1985, *Press 1035* (BM001172033); Jardim do Mar, 26 Oct 1984, *Short 161* (BM001172034); Between Camacha and Vale do Paraíso on EN102, 23 Oct 1981, *Hampshire 414* (BM001172035); São Vicente, north coast road, 500 m west of village, 30 Aug 1981, *Hampshire 605* (BM013856270); Porto Moniz, Sea cliffs east of village along N, coast road, 22 Oct 1984, *Short 88* (BM013856272); South side of tunnel at Ribeira do Inferno, 12 Nov 1980, *Short, Hampshire 10* (BM013856273); s. loc., 1857, *s. coll., s.n.* (BM013856274); Curral das Freiras, Aug 1869, *s. coll., s.n.* (BM013856275); Ilhéu dos Embarcadores, 1865-1866, *s. coll., 159* (BM013856276); Curral das Freiras, 1837, *Shuttleworth s.n.* (BM013856277); s. loc., Aug 1861, *s. coll., s.n.* (BM013856278); s. loc., s. d., *s. coll., s.n.* (BM013856279); s. loc., Aug 1838, *Hochstetter 92* (BM013856280); Below Poiso (above Funchal), 09 Sep 1984, *Davis 70385* (BM013856281); Funchal, beyond the bridge over the Ribeiro Seco, 19 Jun 1864, *Lowe 415* (BM013856282); Pico Grande, Jul 1847, *Lowe 415* (BM013856283); Porto da Cruz, 13 Jun 1864, *Lowe 681* (BM013856284); Porto da Cruz, 12 Jun 1864, *Lowe 681* (BM013856285); Ponta Delgada, Aug 1855, *Lowe 660* (BM013856286); Ponta de São Lourenço, 25 Jun 1838, *Lowe 415* (BM013856287); Ponta de São Lourenço, 25 Jun 1838, *Lowe, 685* (BM013856288); Porto da Cruz, 26 May 1864, *Lowe 660* (BM013856289); Between Fajã da Nogueira and Cruzinha, 21 Aug 1981, *Hampshire 387* (BM013856290); Cabo Girão, 25 Nov 1989, *Chilton, Turland 27* (BM013856292); Porto Moniz, 25 Nov 1989, *Chilton, Turland 66* (BM013856293); Serra d'Água, just north of village along road to São Vicente, Vertical rock-face by roadside, 15 Aug 1984, *Press, Short 66* (BM013856294); Ribeira da Janela to Seixal on EN101, 17 Jun 1985, *Press 963* (BM013856295); Santa Cruz, 17 Jun 1980, *Graham s.n.* (BM013856296); Ribeira da Janela to Seixal on EN101, 17 Jun 1985, *Press 964* (BM013856297); Between Ribeira da Janela and Seixal, 26 Nov 1989, *Chilton, Turland 75* (BM013856298); Curral das Freiras, Jul 1839, *Anon, s.n.* (BM013856310); Above Funchal, 1892, *Murray s.n.* (BM013856311); Funchal, 13 Jun 1895, *Murray s.n.* (BM013856312); Baía de Abra, 06 Mar 1986, *J.F.M. Cannon 5039* (BM013856313); Levada de Santa Luzia, May 1992, *Anon, s.n.* (BM013856314); Porto Moniz, side of road (EN101), near village, 30 Aug 1981, *Hampshire 584* (BM013856317); Along track leading eastwards from Serra de Água - Encumeada road to above Jardim da Serra, 24 Oct 1984, *Short 131* (BM013856318); Pico do Facho, May 1828, *Lowe s.n.* (BM013856320); s. loc., s. d., *s. coll., s.n.* (BM013856321); Porto Moniz, between 4.7 - 6.7 km from village, 27 Mar 1984, *Press, Short 380* (BM013856322); Between São Vicente and Seixal, Sep 1892, *Murray s.n.* (BM013856323); Jardim da Serra, 1866, *Madon s.n.* (BM013856324); East of Caniço, Portinho, 11 Aug 1981, *Hampshire 179* (BM013856325); Near Poiso, 15 Aug 1970, *Franquinho 11* (BM013856326); Levada above Fajã da Nogueira, 21 Aug 1981, *Hampshire s.n.* (BM013856327); Between Machico and Caniçal, 28 Apr 1924, *Lamreles 32* (BM013856328); Hills above Porto Moniz, 07 Aug 2003, *Veldkamp 8809* (BM013856329); Forest above Jamboto, 08 Aug 2003, *Veldkamp 8811* (BM013856330); Between Funchal and Camara de Lobos, Aug 1853, *F.M.J. Welwitsch 3624* (BM013856352); Machico, 19 Jul 1975, *Duvigneaud 75M508 BIS* (BR00000006150747); Porto da Cruz, 29 Jul 1975, *Duvigneaud 75M725* (BR00000006150754); Machico, 19 Jul 1975, *Duvigneaud 75M508* (BR00000006150761); Curral das Freiras, 13 Jul 1977, *Jacques 10734* (BR00000006402648); Funchal, 20 May 1997, *Bouharmont 27508* (BR0000022308696); Levada do Norte, Encumeada, 22 May 1997, *Bouharmont 27549* (BR0000022308719); P. S. Vicente, Caniçal, 23 May 1997, *Bouharmont 27586* (BR0000022308726); Santa, North side of Ribeira do Tristão Jorge, 22 Jun 1985, *Press 1035* (BR0000022308733); Ponta de São Lourenço, 23 May 1997, *Évrard 12399* (BR0000022308740); Funchal, 07 Jun 1900, *Bornmüller 853* (BR0000022308757); Funchal, 01 Jul 1900, *Bornmüller 854* (BR0000022308764); Machico, 02 Aug 1981, *Hampshire 117* (BR0000022308771); São João, 05 Jun 1827, *Holl s.n.* (BR0000022308788); Ponta Delgada, 27 Jul 1900, *Bornmüller 850* (BR0000022308795); s. loc., s. d., *s.n.* (BW14724); Ilhéu dos Embarcadores, 1865-1866, *Mandon 159* (COI00039775); Jardim da Serra, 1865-1866, *Mandon 158* (COI00039776); s. loc., s. d., *s. coll., s.n.* (G00458357); s. loc., 1832, *Lowe 660* (G00458358); s. loc., 1832, *Lowe 32* (G00458396); Porto da Cruz, Serrado, 09 Aug 1867, *s. coll., s.n.* (GH00013128); s. loc., s. d., *Kamphövener 101* (IFAN14591); Machico, 1941, *Carv s.n.* (LISE8223); Vale da Lapa, Nov 1941, *Carvalho s.n.* (LISI); Vale da Lapa, Nov 1941, *Carvalho s.n.* (LISI); Vale da Lapa, Nov 1941, *Carvalho s.n.* (LISI); Ri-beiro Frio, Nov 1941, *Carvalho s.n.* (LISI); Ribeiro Frio, Nov 1941, *Carvalho s.n.* (LISI); Machico, Nov 1941, *Carvalho s.n.* (LISI); Entre o Pico Ruivo e

Appendix 11. Continued.

Encumeada Alta, Nov 1941, *Carvalho s.n.* (LISI); Encumeada Alta, Nov 1941, *Carvalho s.n.* (LISI); Caniçal, saída do túnel para Machico, 07 Nov 2001, *Mezneres, Ferreira 623* (LISI 35/2002); s. loc., 21 Dec 1900, *s. coll., s.n.* (LY0010213); Pico do Arieiro, 11 Oct 1998, *Gutte 521/98* (LZ 160301); Funchal, 08 Oct 1998, *Gutte 459/98* (LZ 160360); Encumeada, 13 Oct 1998, *Gutte 603/98* (LZ 160432); Ilhéu do Desembarcadouro, 1865-1866, *Cosson s.n.* (MNHN-P-P02664418); Ilhéu do Desembarcadouro, 1865-1866, *Cosson s.n.* (MNHN-P-P02664420); Ilhéu do Desembarcadouro, 1865-1866, *Cosson s.n.* (MNHN-P-P02664421); Ilhéu do Desembarcadouro, 1865-1866, *Cosson s.n.* (MNHN-P-P02664422); Ilhéu do Desembarcadouro, 1865-1866, *Cosson s.n.* (MNHN-P-P02664423); Ilhéu do Desembarcadouro, 1865-1866, *Cosson s.n.* (MNHN-P-P02664424); Ilhéu do Desembarcadouro, 1865-1866, *Cosson s.n.* (MNHN-P-P02664425); s. loc., 1853-1860, *Welwitsch 3624* (MNHN-P-P02664661); s. loc., 1878, *Schultz s.n.* (MNHN-P-P02664757); Porto da Cruz, 13 Jun 1864, *Lowe 681* (MNHN-P-P02664761); St. Anna, 14 Jun 1827, *Holl s.n.* (MNHN-P-P02664763); s. loc., 1842, *Webb s.n.* (MNHN-P-P02664764); s. loc., s. d., *Webb s.n.* (MNHN-P-P02664765); s. loc., s. d., *s. coll., s.n.* (MNHN-P-P02664766); s. loc., s. d., *Bornmüller s.n.* (MNHN-P-P02664767); Funchal, 07 Apr 1900, *Bornmüller 853* (MNHN-P-P02664768); Funchal, 07 Apr 1900, *Bornmüller 853* (MNHN-P-P02664769); Ponta Delgada, 27 Jul 1900, *Bornmüller 850* (MNHN-P-P02664770); Calheta, 16 Jun 1900, *Bornmüller 852* (MNHN-P-P02664771); Ponta Delgada, 27 Jul 1900, *Bornmüller 850* (MNHN-P-P02664772); Ponta Delgada, 27 Jul 1900, *Bornmüller 850* (MNHN-P-P02664773); Ponta Delgada, 27 Jul 1900, *Bornmüller 849* (MNHN-P-P02664774); Ponta Delgada, 27 Jul 1900, *Bornmüller 849* (MNHN-P-P02664775); Curral das Freiras, 23 Jul 1900, *Bornmüller 855* (MNHN-P-P02664776); s. loc., 1847, *Pourret s.n.* (MNHN-P-P02664777); s. loc., s. d., *Poiret s.n.* (MNHN-P-P02833587); s. loc., 1857, *Mason s.n.* (MNHN-P-P02833590); Jardim da Serra, 1865-1866, *Cosson s.n.* (MNHN-P-P02833591); s. loc., 1833, *s. coll., s.n.* (MNHN-P-P02833592); s. loc., 19 Jul 1868, *Delacour s.n.* (MNHN-P-P03278474); Ilhéu do Desembarcadouro, 1865-1866, *Cosson s.n.* (MNHN-P-P03278504); s. loc., s. d., *Masson s.n.* (S-G-1704); s. loc., s. d., *Masson s.n.* (S-G-1715); Funchal, Aug 1858, *Hochsteter 92* (TUB); Porto Moniz, 02 Apr 2011, "*L. Median; M. Sequeira*" LM5254 (W 2014-0002419).