



A revision of the genus *Leontodon* (Asteraceae) in the Azores based on morphological and molecular evidence

MÓNICA MOURA¹, LUÍS SILVA¹, ELISABETE F. DIAS¹, HANNO SCHAEFER² & MARK CARINE³

¹CIBIO Research Center in Biodiversity and Genetic Resources, CIBIO-Azores, Department of Biology, University of the Azores, Portugal.
E-mail: moura@uac.pt

²Plant Biodiversity Research, Technische Universität München, D-85354 Freising, Germany.

³Department of Life Sciences, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK.

Abstract

Two endemic species of *Leontodon* are currently recognized in the Azores archipelago: *Leontodon filii* and *L. rigens*. However, there has been confusion regarding the application of these names and field observations and herbarium studies suggested three morphotypes in the islands. Here, we present a taxonomic revision of the Azorean endemic *Leontodon* species using morphological characters and new molecular data from the ITS region and from three chloroplast regions: *trnQ*, *trnV* and *matK*. Fifty-one quantitative and qualitative morphological characters were examined that revealed consistent differences between specimens from the western, central and eastern subarchipelagos (where, on the latter, *Leontodon* is restricted to São Miguel). Molecular analysis revealed two well defined monophyletic groups, one comprising accessions from São Miguel and the second comprising accessions from the western group, while central group accessions were in an unresolved polytomy. Both analyses also indicated the occurrence of hybridization with *L. saxatilis*, a widespread non-endemic species. Taken together, molecular and morphological data suggest the reinstatement of a third Azorean *Leontodon* taxon endemic to the western group. A key to the *Leontodon* of the Azores and descriptions of the endemic taxa are provided.

Key words: *Leontodon hochstetteri*, Asteraceae, phylogeny, morphology, island endemic

Introduction

The genus *Leontodon* Linnaeus (1753: 798) subg. *Leontodon* Widder (1931: 146) comprises c. 40 species with a distribution centred in the Mediterranean area and extending into North Europe and South West Asia (Hand *et al.* 2013). A molecular phylogenetic study by Samuel *et al.* (2006) confirmed that the European and Anatolian-Caucasean *L. hispidus* Linnaeus (1753:799) group (Meusel and Jäger 1992), and *L. kulczinskii* Popov & Chrshanovski (1949: 299), from the East Carpathians, belong to section *Leontodon* Widder (1975: 26), which is morphologically characterized by single capitula on simple leafless stems. However, this section is also considered to include the Azorean endemic *Leontodon* species, with multiple capitula on bracteate stems (Paiva & Ormonde 1972, 1974; Lack 1981). The *Leontodon* species currently listed as endemic to the Azores archipelago (Silva *et al.* 2010) are *L. filii* (Hochst. ex Seub. 1844: 34) Paiva & Ormonde (1972: 447), and *L. rigens* (Dryand. in Aiton 1789: 127) Paiva & Ormonde (1972: 448). These species were previously considered to belong to *Crepis* Linnaeus (1753: 805), *Microderis* DC. (1838: 127) and *Picris* Linnaeus (1753: 792), until Paiva & Ormonde (1972; 1974) placed both species in *Leontodon*, with the degree of floral stem ramification and the number of capitula the key discriminating traits between the two taxa. The first molecular phylogenetic analysis including Azorean *Leontodon* was conducted by Samuel *et al.* (2006) who confirmed the inclusion of *L. rigens* in section *Leontodon*. *Leontodon filii* was not included in that study.

The two Azorean *Leontodon* species have been historically listed as co-habiting the same locations on several of the Azorean islands, with the exception of Corvo, where only *L. rigens* was recorded, and Graciosa and Santa Maria, where both species were considered as absent (Azores Biodiversity Portal 2008). In the most recent checklist for the Azorean vascular flora (Silva *et al.* 2010), *L. filii* was listed as present in Pico, São Jorge, and Terceira, but doubtful in Faial and São Miguel islands, while *L. rigens* was considered to occur in São Miguel and doubtful in Pico and Terceira. *Leontodon* populations on Flores and Corvo were not listed as *L. rigens*, because the authors had come to the

conclusion that they belong to a third distinct morphotype. Furthermore, historical herbarium specimens also pointed to a third endemic species, *Microderis umbellata* Hochst. ex Seub. (1844: 33), collected in Flores during an 1838 botanical excursion to the Azores by Karl Hochstetter (Seubert & Hochstetter 1843), and considered by the collector as specific to that island.

Besides *L. rigens* and *L. filii*, Paiva & Ormonde (1972; 1974) also cited a third *Leontodon* species for the Azores, namely the cosmopolitan *L. saxatilis* Lamarck (1778: 115) subsp. *saxatilis* (= *L. saxatilis* subsp. *rothi* Maire 1934: 833 in Jahandiez *et al.* 1934), listed in Silva *et al.* (2010) as occurring in all Azorean islands, under the synonym of *L. saxatilis* subsp. *longirostris* (Finch & P. D. Sell 1975: 247–248 in Heywood 1975) P. Silva (Bacelar *et al.* 1987: 155). A recent archipelago-wide population genetics study (Dias *et al.* 2014) using microsatellite data, retrieved two main genetic groups but also detected complex substructures within populations from Flores and Corvo (treated as *L. rigens* in that study).

Considering the conflicting evidence from historical accounts, field observations and molecular population genetics data, we aim to clarify the taxonomy and phylogenetic relationships of the Azorean *Leontodon*, using morphological data in conjunction with sequence data from the nuclear ribosomal internal transcribed spacer (ITS) region and the chloroplast regions *matK*, *trnQ* and *trnV*, specifically addressing the following questions: 1) How many endemic *Leontodon* taxa exist in the Azores? 2) How are they related phylogenetically? 3) What are their distributions across the archipelago?

Material and Methods

Study site:—The Azores archipelago, located in the North Atlantic Ocean, comprises nine islands of volcanic origin which span over 615 km, and are generally divided into three island groups, western (Corvo and Flores), central (Terceira, Graciosa, São Jorge, Pico and Faial) and eastern group (São Miguel and Santa Maria). The archipelago is situated 942 km northwest of Madeira, 1,435 km west from mainland Portugal and 3,380 km east from North America on a WNW-ESE axis between 37–40°N and 25–31°W (Fig. 1). The archipelago is relatively young, with the oldest island being Santa Maria (5–6 Myr, Ávila *et al.* 2012) and the youngest Pico (0.25 Myr, França *et al.* 2003).

Plant sampling:—Sampling was conducted archipelago wide, covering the three groups of islands. One to two representative voucher specimens per population were collected, pressed, mounted and stored at AZB. Depending on leaf size, one or two leaves per individual were collected and immediately stored in a zip-lock bag with silica gel. After being completely dry the leaves were vacuum sealed in plastic bags, indexed and stored in folders. The locations of all vouchers were geo-referenced and a sampling map generated with this data using Quantum GIS Desktop 2.0.1-Dufour (Fig. 1).

DNA extraction, PCR and sequencing:—DNA was extracted using the modified CTAB protocol outlined by Carine *et al.* (2004). All amplification reactions were performed in 25 µL containing 10 µmol/L (1 µL) of the respective primers, and approximately 35 ng of purified DNA (1 µL). The ITS region was amplified for 54 accessions using the protocol of Carine *et al.* (2004). Three chloroplast (cp) regions were amplified for 24 accessions using the protocol of Carine *et al.* (2007) and the primers of Shaw *et al.* (2007) for the regions *trnQ* and *trnV*, and of Schaefer *et al.* (2011a) for *matK*. Sequencing was done by STABVida (Portugal) and at the Natural History Museum Sequencing Facility (London).

Alignments and phylogenetic analyses:—Sequence data were assembled, edited and aligned using Geneious ver. 5.6.6 (Biomatters) and the Geneious alignment algorithm. The alignments were then inspected and manually optimized in Geneious. Accessions of *Leontodon* spp. available in GenBank were included in the analysis (see appendix for accession numbers). Phylogenetic analysis of the combined data set (ITS and cp regions) followed the same methodology as used for each individual data set, with *Reichardia tingitana* (Linnaeus 1753: 791) Roth (1787: 35) used as outgroup in the combined analysis and *L. saxatilis* in the ITS and cp data analysis. Maximum parsimony (MP) analysis were conducted in PAUP* ver. 4.0b10 (Swofford 2003). The analysis used 100 heuristic searches, random stepwise addition, and TBR branch swapping. A strict consensus tree was calculated. Branch support values were assessed by bootstrap analysis, using 1,000 bootstrap replicates each comprising 100 heuristic searches, random stepwise addition and NNI branch swapping. jModeltest ver. 2.1.3 (Darriba *et al.* 2012) was used to determine the best-fitting model of sequence evolution based on the Akaike Information Criterion (AIC). A Maximum Likelihood analysis (ML) was conducted using RAxML-HPC2 ver. 7.4.4 (Stamatakis *et al.* 2008) on the CIPRES Science Gateway (Miller *et al.* 2010) with 1000 bootstraps and a partitioned dataset for the combined matrix. New sequences were submitted to GenBank and accession numbers are listed in the appendix.

Morphological data:—The morphological characters screened were selected based on descriptions found in Seubert & Hochstetter (1843), Seubert (1844), Paiva & Ormonde (1974), Lack (1981), Franco (1984) and Hind (2005). Quantitative characters used pertained to the stem (7), leaf (11), petiole (3), synflorescence (14), capitulum (20), flower (19) and fruit (8). Additionally, we screened for qualitative differences regarding the leaf shape, type and abundance of trichomes (leaves, synflorescence and capitula), architecture of the flowering stems, occurrence of paleae, and type of achenes and pappus setae. A morphometric dataset for Azorean samples was assembled with herbarium specimens available at AZB. In total, 16 specimens from São Miguel, 35 from the central group and 18 from the western group were examined. For each specimen, three measures (replicates) for each quantitative trait were taken.

The occurrence of hybrids was investigated using leaf characters and possible changes in the structure of the achenes. The leaf length:width ratio was measured in 14 putative hybrid specimens from AZB, MO, BM, K and LY, 25 specimens of *L. saxatilis* from AZ, K, LISE, LY, and MO, and in the Azorean endemic collections deposited at AZB. Another 13 western group accessions, 31 São Miguel accessions, 51 central group accessions, 43 putative hybrids, and 32 specimens of *L. saxatilis* stored at AZ, BM, BR, FI, G, K, LISE, LY, M, MANCH, MO, P, TUB, WAG, were also observed and evaluated qualitatively.

The quantitative morphological matrix, including hybrid leaf ratio data, was analysed with PASW Statistics 18 (SPSS Inc.) using a MANOVA followed by Tukey HSD test. A multivariate approach was also used to evaluate taxon differentiation globally, namely a discriminant analysis including those traits which had shown significant differences between at least two groups of accessions. In order to increase chart readability, the scores of each variable were multiplied by 15 for both canonical functions.

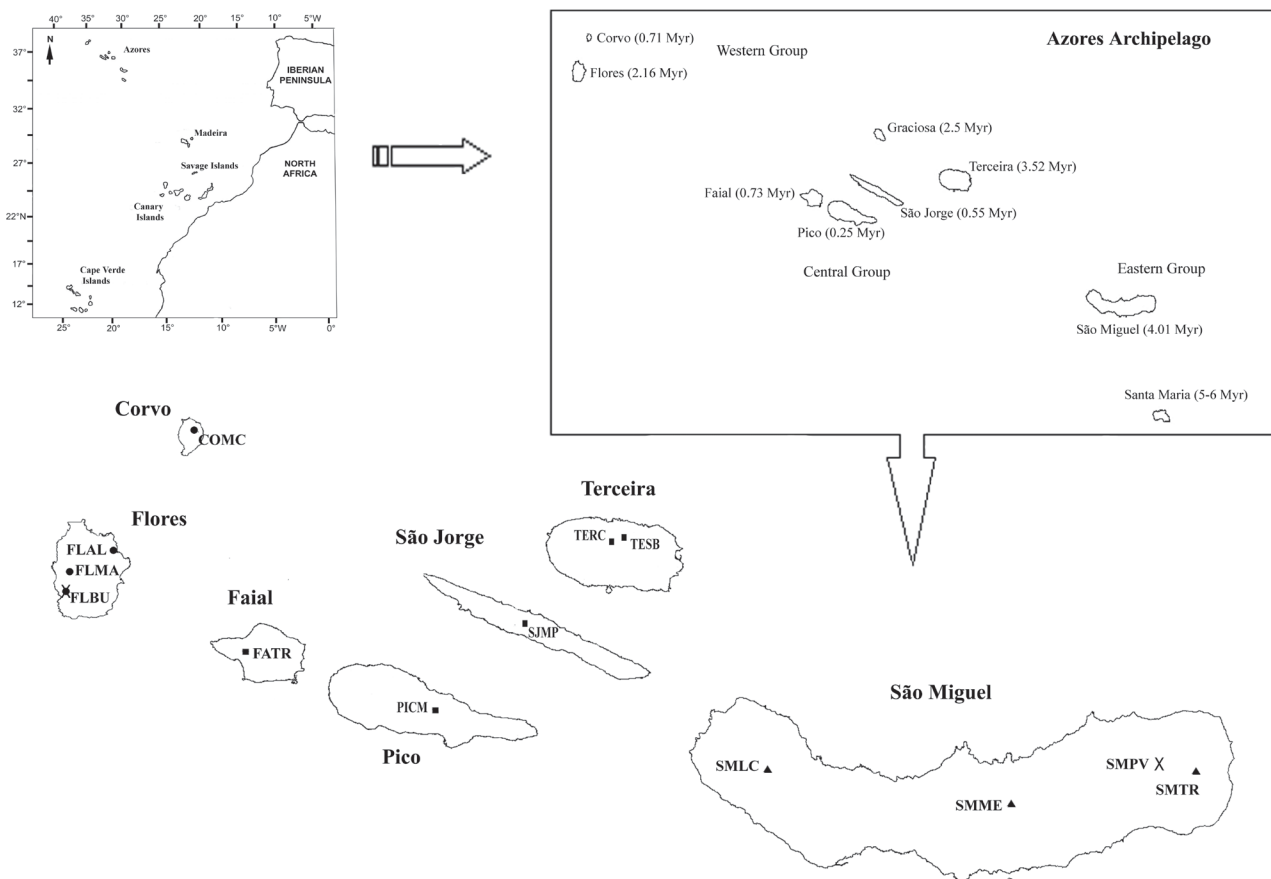


FIGURE 1. Map of the Azores archipelago with the sites of the sampled individuals, estimations of the islands geological ages, and the location of the Azores relative to other land masses. São Miguel populations are represented by triangles, central group populations by squares and western group populations by circles. Crosses represent the locations of putative hybrids. Adapted from Dias *et al.* (2014).

Results

Phylogenetic analyses:—The ITS alignment comprised 29 ingroup accessions and three outgroup accessions, and had

a length of 881 bp. The cp alignment was composed of 24 ingroup accessions and five outgroup accessions, and had a length of 2299 bp. Matrix cells scored as gaps or missing data corresponded to 5.4 % of the ITS matrix and to 26.9 % of the cp data matrix.

For the ITS region, MP analyses resulted in 85 best trees, 107 steps long, a consistency index (CI) of 0.901 and a retention (RI) index of 0.939 (Fig. 2A). MP analyses of the cp data resulted in 194 best trees, 32 steps long, with a CI of 1.000 and a RI of 1.000 (Fig. 2B). The best fitting model selected by AIC was GTR+I. Since addition of the invariable site parameter “I” is not advised for RAxML as it is already incorporated in the standard algorithm (Stamatakis *et al.* 2008), the analysis were conducted without this parameter. Separate analysis of both cp and ITS datasets produced similar results and thus combined analyses were also performed including also all sequences obtained by Samuel *et al.* (2006) for the genus *Leontodon* stored at GenBank. The combined MP analyses recovered 180 best trees, 550 steps long, with a CI of 0.758 and a RI of 0.916 (Fig. 3).

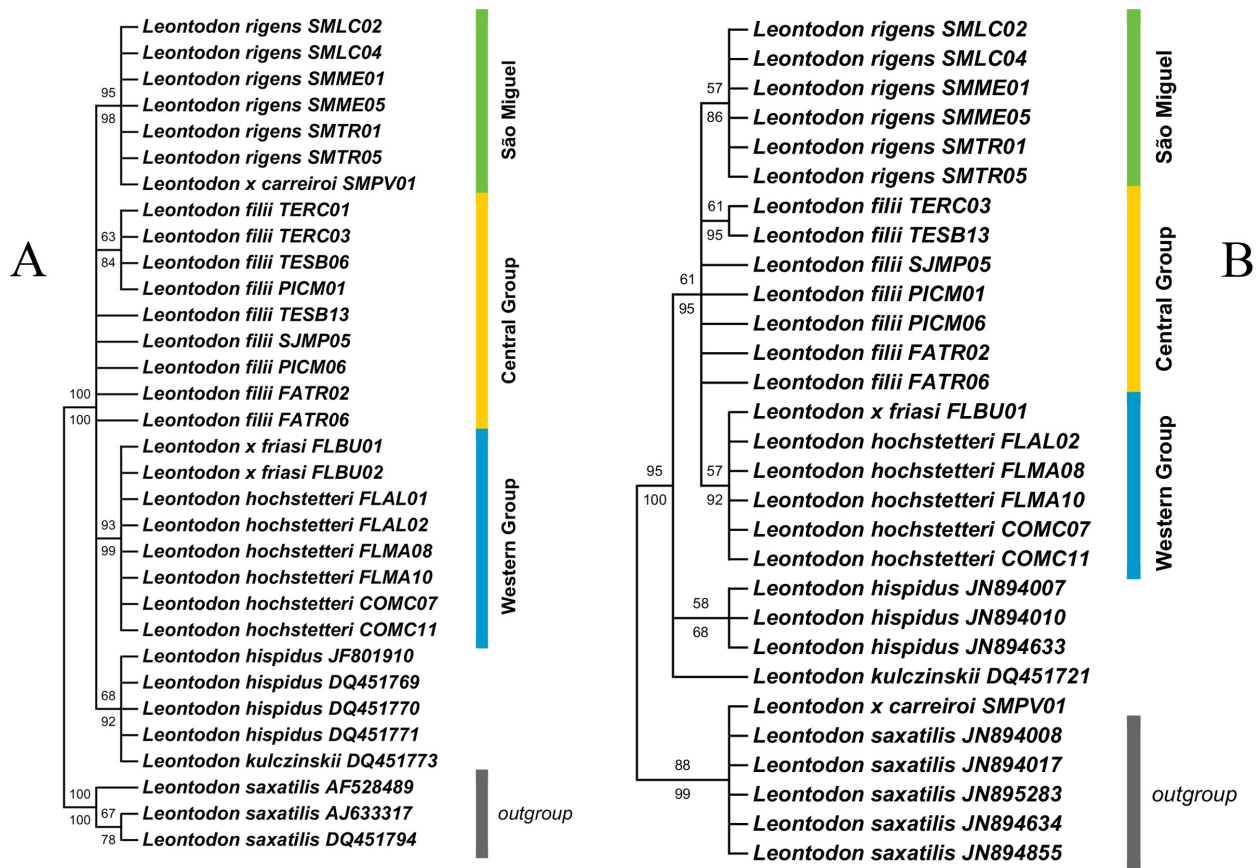


FIGURE 2. Maximum parsimony 50% majority-rule consensus tree obtained from nuclear ITS sequence data (A) and from the combined chloroplast sequence data (B). Values above branches show MP bootstrap support; values below are the corresponding ML bootstrap support. Only values above 50% in at least one of the analysis criteria are shown.

The nuclear and chloroplast analysis of section *Leontodon* (Fig. 2A and 2B) as well as the combined analysis for the genus *Leontodon* (Fig. 3) returned similar MP and ML trees with two highly supported clades (84–100% bootstrap in the combined tree) grouping separately the São Miguel and western group accessions. A subset of the central group accessions formed a third clade in the nuclear and cp analysis of section *Leontodon*. Relationships between the three groups of Azorean accessions were poorly resolved and, in the ITS tree, the *L. hispidus*-*L. kulczinskii* clade formed an unresolved polytomy with the Azorean taxa.

Two accessions of putative *L. filii* sampled on Flores (FLBU01 and 2) turned out to be genetically identical to all *L. rigens* accessions from Flores and Corvo. The accession of *L. filii* sampled in São Miguel (SMPV01) clustered differently in the nuclear and chloroplast trees, grouping with the remaining São Miguel accessions in the ITS tree (Fig. 2A), and with the *L. saxatilis* accessions in the cp tree (2B).

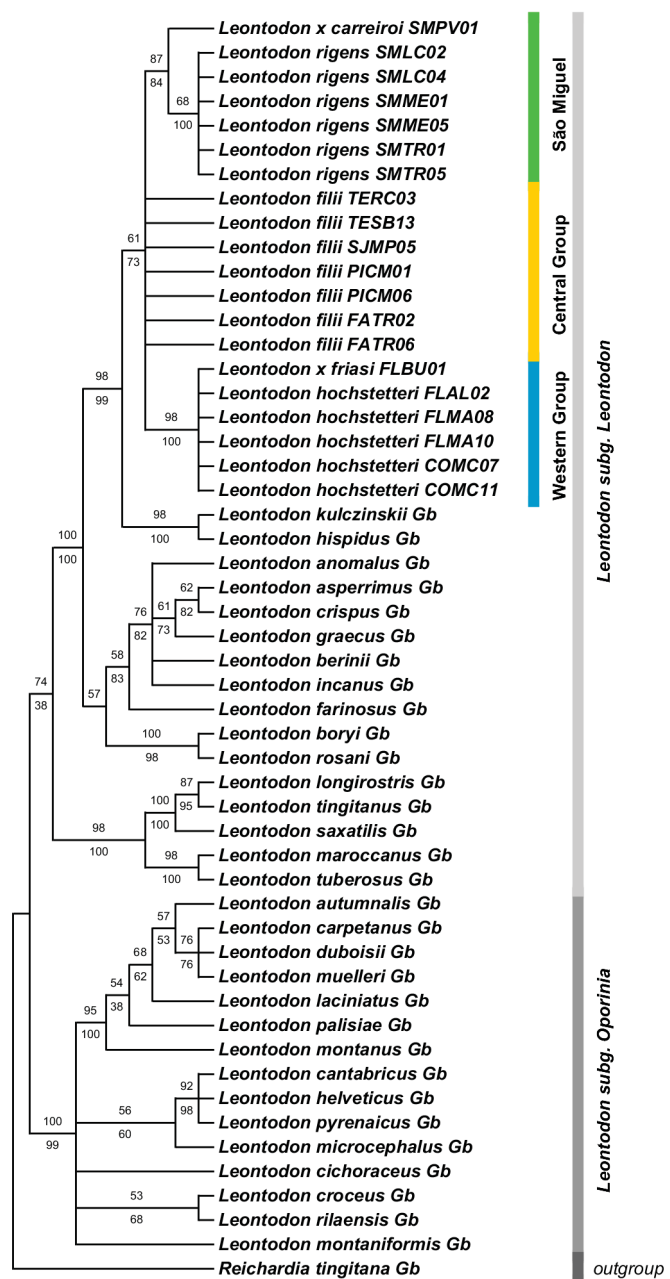


FIGURE 3. Maximum parsimony 50% majority-rule consensus tree obtained from combined nuclear and chloroplast data. Values above branches show MP bootstrap support; values below are the corresponding ML bootstrap support. Only values above 50% in at least one of the analysis criteria are shown.

Morphological data:—The MANOVA and Tukey HSD test (Table 1) revealed that, for the vast majority of the traits analysed, the central group accessions were significantly different from specimens of the western group and São Miguel. Furthermore, significant differences between accessions from the three groups of islands were found in the number of synflorescence ramifications and pappus length. São Miguel accessions were significantly taller, while achenes (length and width) were significantly smaller in the western group (Table 1).

Results of the discriminant analysis based on quantitative synflorescence, flower, and fruit traits for *Leontodon* endemic taxa in the Azores islands grouped accessions into three clusters, according to their geographical location within the archipelago, with the exception of the putative *L. filii* specimens sampled on São Miguel and Flores, which clustered with the central group accessions (Fig. 4). The first two canonical analysis functions explained 67.7% (function 1) and 32.3% (function 2) of the total variance, respectively.

TABLE 1. Average variability in quantitative characters found between specimens of *Leontodon rigens* and *L. filii* from the western, and central group and São Miguel.

Characters	Western						Central						São Miguel						ANOVA		Post-hoc Group
	N	Mean	SD	SE	N	Mean	SD	SE	N	Mean	SD	SE	N	Mean	SD	SE	df	F	p		
Plant height	18	33.72	11.09	2.61	31	36.79	7.10	1.28	15	45.38	8.79	2.27	2	61	7.76	0.0010			a a b		
Leaf number	18	2.83	3.09	0.73	32	3.97	2.69	0.48	16	5.88	3.32	0.83	2	63	4.54	0.0143			a ab b		
Leaf length	18	15.20	5.67	1.34	32	12.34	5.40	0.95	16	17.92	9.62	2.41	2	63	3.84	0.0267			ab a b		
Leaf width	17	7.81	4.50	1.09	32	5.44	2.43	0.43	16	7.10	1.77	0.44	2	62	3.97	0.0239			b a ab		
Lamina length	18	5.18	5.71	1.35	32	3.19	2.58	0.46	16	4.99	5.32	1.33	2	63	1.60	0.2106			NS		
Petiole length	18	7.64	3.52	0.83	32	9.87	4.75	0.84	16	8.15	3.14	0.79	2	63	2.02	0.1412			NS		
Petiole width	18	1.44	0.94	0.22	32	0.67	0.26	0.05	16	1.20	0.70	0.17	2	63	9.96	0.0002			b a b		
Synflorescence ramifications	18	2.89	0.76	0.18	32	1.59	0.87	0.15	16	4.44	1.26	0.32	2	63	48.60	0.0000			b a c		
Pedicel	18	1.20	0.51	0.12	28	5.42	3.67	0.69	16	3.58	1.01	0.25	2	59	15.08	0.0000			a b b		
Pedicel bract length	17	3.98	0.92	0.22	32	4.20	0.95	0.17	16	3.80	0.75	0.19	2	62	1.14	0.3269			NS		
Pedicel bract width	17	0.21	0.27	0.07	32	0.14	0.24	0.04	16	0.17	0.19	0.05	2	62	0.50	0.6065			NS		
Capitula number	18	58.00	34.50	8.13	32	6.13	4.15	0.73	16	59.00	25.36	6.34	2	63	46.78	0.0000			b a b		
Capitulum flowers	18	43.44	11.21	2.64	32	81.47	20.20	3.57	15	37.33	7.96	2.06	2	62	54.13	0.0000			a b a		
Capitulum diameter	18	1.09	0.27	0.06	32	2.30	0.72	0.13	15	1.37	0.23	0.06	2	62	33.89	0.0000			a b a		
External bract length	18	2.77	0.46	0.11	31	3.81	0.73	0.13	16	2.55	0.33	0.08	2	62	31.49	0.0000			a b a		
External bract width	18	0.49	0.12	0.03	31	0.56	0.10	0.02	16	0.43	0.06	0.02	2	62	10.15	0.0002			ab b a		
Internal bract length	18	7.18	1.38	0.33	31	11.29	1.55	0.28	16	7.64	1.12	0.28	2	62	62.34	0.0000			a b a		
Internal bract width	18	0.77	0.17	0.04	31	1.10	0.21	0.04	16	0.87	0.21	0.05	2	62	16.97	0.0000			a b a		
Corolla length	18	9.03	1.45	0.34	29	13.26	2.79	0.52	15	9.99	1.12	0.29	2	59	24.95	0.0000			a b a		
Corolla tube length	18	2.61	0.48	0.11	29	3.94	0.86	0.16	15	3.00	0.39	0.10	2	59	23.69	0.0000			a b a		
Ligule width	18	1.36	1.15	0.27	29	1.02	0.29	0.05	15	0.79	0.15	0.04	2	59	3.28	0.0446			b ab a		
Anther length	18	3.59	0.41	0.10	29	4.48	0.60	0.11	15	3.77	0.53	0.14	2	59	18.11	0.0000			a b a		
Style length	18	5.05	0.51	0.12	29	5.95	0.89	0.16	15	5.22	0.62	0.16	2	59	10.00	0.0002			a b a		
Style width	18	0.30	0.09	0.02	29	0.33	0.07	0.01	15	0.23	0.07	0.02	2	59	8.31	0.0007			b a b		
Style arm length	18	1.15	0.28	0.07	30	1.14	0.35	0.06	15	0.95	0.27	0.07	2	60	2.27	0.1118			NS		
Achene length	18	1.18	0.48	0.11	31	2.99	2.14	0.38	16	3.20	1.55	0.39	2	62	8.10	0.0007			a b b		
Achene width	18	0.30	0.07	0.02	31	0.43	0.12	0.02	16	0.39	0.17	0.04	2	62	6.31	0.0032			a b b		
Pappus length	18	5.26	0.74	0.17	31	7.24	0.84	0.15	16	5.91	0.46	0.11	2	62	45.04	0.0000			a c b		

The qualitative characters screened revealed that the specimens from the three groups of islands can be distinguished by the shape of the synflorescence, while other characters are not significantly different. Leaves are generally more densely pubescent on both surfaces in the central group, while in São Miguel and western group plants, the lower surface is often more densely covered than the upper surface. Trichomes are more often found in the upper portion of the synflorescence and on the phyllaries in central group plants than in the rest of the archipelago; moreover, 2-4-fid trichomes are also more commonly found in the central group, while in the remaining islands single or 2-fid trichomes are more frequent. The synflorescence ranges from very lax in the central group with a few branches and a somewhat lower level of apical ramification, to more densely ramified both in São Miguel and the western group. The relatively smaller pedicels in the western group and an extreme level of apical ramification make the synflorescence much denser than in São Miguel. Another important difference is the presence of paleae in the capitula of western group and São Miguel plants that are absent in those from the central group. A slight difference might also be found in the pappus setae, which are generally more clearly plumose in central group plants than in the other islands, where the pappus setae are more often subplumose, with setae rachis coarsely barbellate.

The morphology of putative *L. filii* specimens sampled on São Miguel and Flores follows the structure of central group plants with the exception of leaf shape which is lanceolate to oblanceolate (the leaf length:width ratio was largest in those specimens) and the leaf margin which is generally dentate instead of serrate. Dimorphic achenes were also found: pappus setae are generally plumose or subplumose but some of the achenes located at the margin the capitulum show a pappus of scales or scales with a few hairs. More rarely, in São Miguel, some of the specimens showed paleaceous capitula.

A ANOVA applied to the leaf length:width ratio resulted in three significantly different groups of accessions ($F = 12.39$; $df = 6$; $P < 0.0001$), with *L. saxatilis* showing the highest ratio (12.39; group a), the putative *L. filii* specimens collected for this study in São Miguel (SMPV; 7.82) and Flores (FLBU; 7.17), together with putative *L. filii* herbarium specimens from São Miguel (5.99), showed an intermediate ratio (group b), and the endemic taxa (group c), the lowest, with 2.45 for the eastern accessions, 2.30 for the central and 2.08 for the western accessions.

Discussion

Taxon circumscription and distribution of Azorean *Leontodon*:—Considering both morphological and molecular results, two well defined groups stand out, one composed of accessions from São Miguel and the other by accessions from the western group (Flores and Corvo). Previous revisions (Paiva and Ormonde 1972, 1974; Lack 1981) grouped these populations under the name *L. rigens*, however our results indicate that they merit recognition as different species, namely *L. rigens* (endemic to São Miguel) and *L. hochstetteri* (a necessary new name for the plants endemic to Flores and Corvo).

Central group accessions are referable to a third endemic Azorean species, namely *Leontodon filii*. This taxon formed the least distinct of the Azorean *Leontodon* based on the molecular analysis results although notably Terceira accessions clustered together with low (61–63%; MP) to high (84–95%; ML) support in the nuclear and cp trees, highlighting the distinctiveness of plants from the island, a pattern also found in other angiosperm groups (Schaefer *et al.* 2011b; Silva *et al.* 2011). In the discriminant morphological analysis, the central group accessions formed a separate group, and the ANOVA indicated that the central group accessions were significantly different for most of the analysed traits. Further distinctiveness was observed in morphological qualitative traits, which clearly separated all *L. filii* accessions from those belonging to *L. rigens* and *L. hochstetteri*. Particularly, the presence of paleae in the capitula of *L. rigens* and *L. hochstetteri* is an interesting difference since capitula in *Leontodon* species in general are not paleaceous (Tutin *et al.* 1976). Considering all morphological and molecular evidence gathered we thus conclude that *L. filii* should be recognized as a distinct species.

Leontodon filii has been reported from São Miguel by various authors (see Lack 1981). In the extensive sampling conducted archipelago-wide for the population genetics study of Dias *et al.* (2014), only two specimens with an *L. filii* phenotype were found in São Miguel at “Pico da Vara” mountain. We included one of these specimens, SMPV01, in our molecular analysis, which grouped with *L. saxatilis* in the cp tree, but shared the *L. rigens* ribotype. Although having a *L. filii* type synflorescence, leaves of the Pico da Vara specimens were lanceolate to oblanceolate with larger length:width ratios than in *L. filii* from the central group islands. Furthermore, the margins are coarsely dentate. Both of these traits are characteristic of *L. saxatilis*. When we measured historic specimens of putative *L. filii* (collected mostly by Bruno Tavares Carreiro and Thomas Hunt in São Miguel), similar ratios and margins were observed.

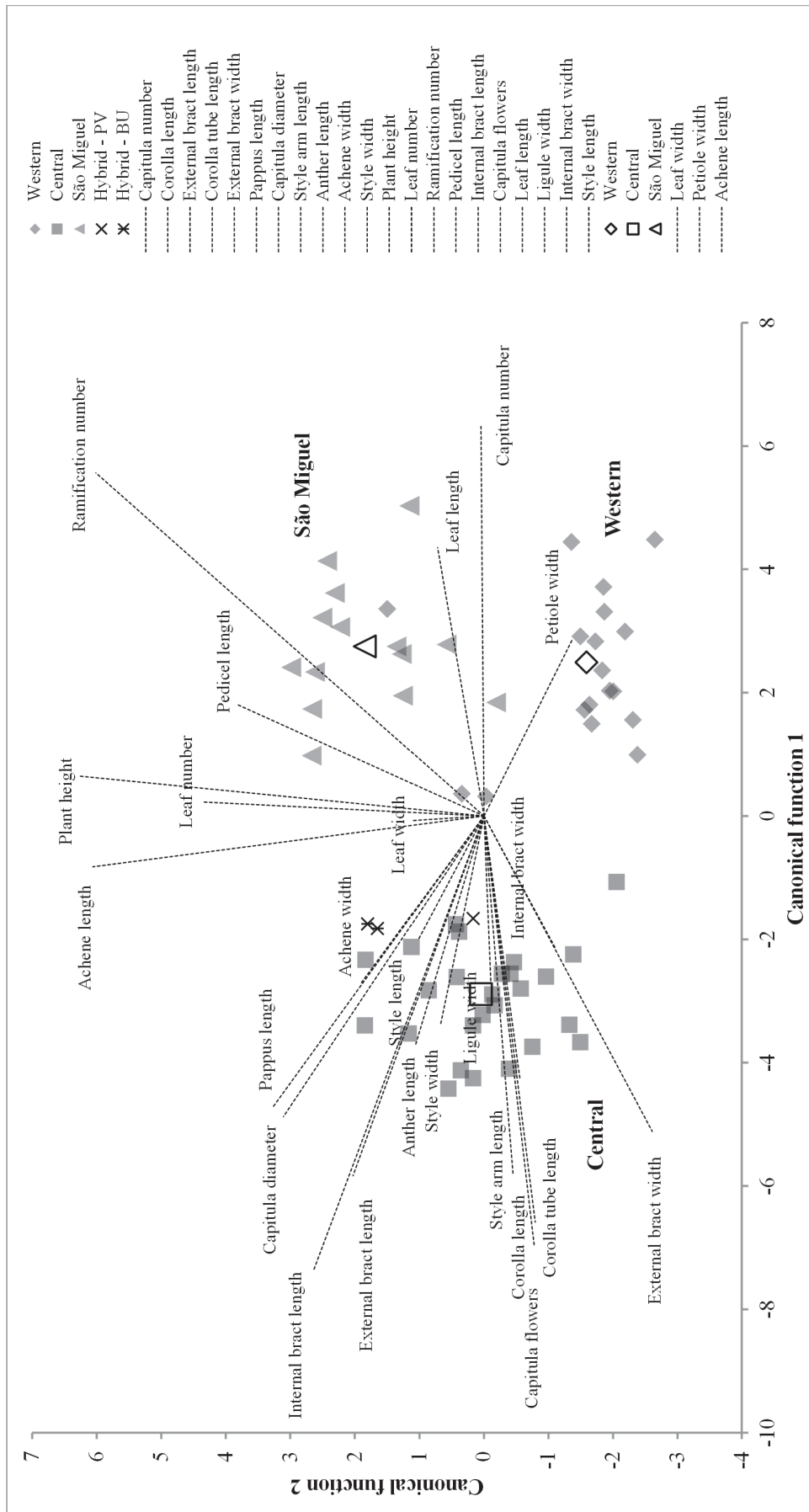


FIGURE 4. Analysis of characters by groups of islands. Biplot resulting from a discriminant analysis, representing individuals and variables based on two canonical functions. Scores of all variables were multiplied by 15 to increase plot legibility.



FIGURE 5. Field photographs of: A) *Leontodon hochstetteri*, Flores Island (J. Martins); B) *Leontodon filii*, Terceira Island (H. Schaefer); C) *Leontodon rigens*, São Miguel Island (M. Moura); and D) *Leontodon* × *carreiroi* (= *L. saxatilis* × *L. rigens*), São Miguel Island (H. Schaefer).

Considering that the leaf of *L. saxatilis* is long and oblanceolate with coarsely dentate margins it is thus possible that a hybrid expression of leaf characters may have resulted in narrower leaves than those of *L. rigens* and in a leaf margin similar to that of *L. saxatilis*. This combination of characters suggests a hybrid origin for the plants in question. Specimens from Flores resembling central group *L. filii* were genetically identical to *L. hochstetteri* but displayed a similar leaf shape to the Pico da Vara hybrid specimens, suggesting a possible hybrid origin for those plants also.

Putative hybrids on both Flores and São Miguel consistently show dimorphic achenes; a situation probably inherited from *L. saxatilis* and previously described in *Leontodon* × *vegetus* Finch & P. D. Sell in Sell & Murrell (2006: 531), a hybrid lineage between *L. saxatilis* and *L. hispidus*. In a few cases, we have also found putative hybrids from São Miguel Island, with the above mentioned differences in leaf shape, and also with paleae in the capitula. Thus, the morphologies arising from such hybridization events might be varied.

It is noteworthy that Gandoger (1918) described two new species of *Thrincia* Roth (1797: 97) for the Azores, namely, *T. subglabra* Gandoger (1918: 53–54) and *T. carreiroi* Gandoger (1918: 53), with types collected from Lagoa, São Miguel, and one subspecies (*T. nudicaulis* Lowe (1831: 28) subsp. *azorica* Gandoger (1888: 334)), with the type collected in Faial Island. Later, the Azorean *Thrincia* designated by Gandoger was considered by Paiva & Ormonde (1974) as belonging to *L. filii*. Our revision of the Carreiro material on which Gandoger based *T. subglabra* and *T. carreiroi*, grouped them with the *L. saxatilis* hybrids molecularly identified in this study, due to similar leaf shapes and larger length:width leaf ratios, and to the presence of dimorphic achenes. Based on leaf morphology, *T. nudicaulis* subsp. *azorica*, seems to belong to *L. filii*.

In summary, our study indicates the occurrence of three endemic *Leontodon* taxa, namely *L. rigens* in São Miguel, *L. filii* in the central group, and *L. hochstetteri* in the western group (Fig. 5A–C). Furthermore, our molecular and morphological results provide evidence of hybridization between *L. rigens* and *L. saxatilis* in São Miguel (Fig. 5D), and between *L. hochstetteri* and *L. saxatilis* in Flores.

Relationships and speciation patterns of the Azorean *Leontodon*:—Our molecular data did not permit direct inferences on the relationships between the three Azorean taxa, although they do confirm their placement in section *Leontodon* (Samuel *et al.* 2006) as a monophyletic group. A close relationship with the *L. hispidus*-*L. kulczinskii* clade was also confirmed. Dias *et al.* (2014), in a population study with SSR, highlighted the higher number of alleles in populations from São Miguel as an indication that initial colonization took place in that island, with a later dispersal from east to west within the archipelago. Our results do not conflict with this hypothesis as both *L. rigens* and *L. hochstetteri* show high levels of specific differentiation, which might reflect a comparatively ancient colonization event, resulting in the evolution of *L. rigens* by anagenetic speciation and a later appearance of a distinct western form due to the founder effect within the archipelago. The closeness of those two species, revealed by the SSR data (Dias *et al.* 2014) and by our morphometric discriminant analysis, further supports the notion of an initial anagenetic event leading to an increase in capitula numbers, a feature confined to the Azorean species within section *Leontodon*, with its highest expression in *L. hochstetteri*. However, although having a significantly higher number of capitula, *L. rigens* and *L. hochstetteri* both display a significantly lower number of flowers per capitulum and smaller capitula size, as well as a smaller corolla, which could indicate the possibility of self-compatibility. In contrast, *L. filii* has larger and more attractive flowers, which might indicate self-incompatibility (Ortiz *et al.* 2006).

Whilst morphologically the most distinctive of the three Azorean species, the *L. filii* accessions did not group together in our genetic analysis. High levels of phenotypic distinctiveness coupled with weak molecular resolution suggestive of recent speciation, has been described for other Azorean taxa, namely the endemic *Platanthera* orchids (Bateman *et al.* 2014) and has been referred to as a ‘genetic divergence lag’ (Bateman *et al.* 2012). The hypothesis that *L. filii* resulted from a later speciation event in one of the oldest islands of the central group followed by dispersal to the remaining islands of the group and the establishment as the dominant form in those islands was suggested by Dias *et al.* (2014) when discussing the within-archipelago population genetic structure obtained for the Azorean *Leontodon*.

Implications for conservation:—The finding that there are three local endemic *Leontodon* species in the Azores, including a single island endemic in São Miguel, underscores the conservation guidelines already suggested by Dias *et al.* (2014), which included the need to avoid ad-hoc translocation of diaspores or plants between different parts of the archipelago. Confirmation of the occurrence of hybrids in this study, previously suggested by Dias *et al.* (2014), also strengthens their recommendation of molecular screening of populations before use as diaspore sources for conservation measures. Furthermore, population size estimates and management plans need to be adapted to account for three instead of two species.



FIGURE 6. Holotype of *Leontodon x friasi* (= *L. saxatilis x L. hochstetteri*) (AZB).

Taxonomic Treatment

Below, we provide a key to all *Leontodon* taxa in the Azores and descriptions of the endemic taxa, including two new notho-species described here. In order to clarify misidentifications of Azorean *Leontodon* in herbaria, we also include an extensive list of examined sheets.

Key

1. - Flowering stipes ramified into a dense corymbose or umbellate panicle 2
- Flowering stipes not ramified or ramified into a lax panicle 3
2. - Panicle corymbose with pedicels (1.2–) 3.6 (–7.0) cm long *Leontodon rigens*
- Panicle umbellate with pedicels (0.3–) 1.2 (–3.6) cm long *Leontodon hochstetteri*
3. - Synflorescence a lax panicle; capitula without paleae; achenes isomorphic; leaves elliptic to ovate, or obovate *Leontodon filii*
- Synflorescence a lax panicle or flowering stipes not ramified; capitula sometimes paleaceous; achenes mostly dimorphic; leaves lanceolate, oblanceolate or oblong 4
4. - Flowering stipes not ramified; capitula borne singly; corollas greyish yellow on the outer faces; capitula without paleae *Leontodon saxatilis*
- Flowering stipes mostly ramified, sometimes not ramified; capitula borne in clusters or singly; corollas yellow on the outer faces; capitula sometimes paleaceous *Leontodon* × *carreiroi* / *Leontodon* × *friasi* *

* *Leontodon* × *carreiroi* naturally occurs in São Miguel, sympatric with *Leontodon rigens*; *Leontodon* × *friasi* naturally occurs in Flores, sympatric with *Leontodon hochstetteri*.

Leontodon hochstetteri M. Moura & L. Silva *nom. nov.*

≡ *Microderis umbellata* Hochstetter ex Seubert (1844: 33).

Holotype:—AZORES. “in dumetis montis ‘Pic de Pico’ supra Villa Magdalena”: 1838, C. Hochstetter *s.n.* (TUB!, isotype: P!).

– *Picris hochstetteri* C. H. Schultz Bipontinus *nom. non rite public.*

Acaulous rosetiform rhizomatous perennial herb; white latex present. Rootstock usually stout, sometimes a long napiform root. Leaves few to several (1–11), petiolate; petiole (2.0–) 7.6 (–20.3) cm long × (0.4–) 1.4 (–4.0) cm wide, grooved, often narrowly winged; petiole trichomes often simple; leaf (7.3–) 15.2 (–34.8) cm long × (2.5–) 7.8 (–19.2) cm wide; elliptic to ovate or obovate, attenuate at base onto apex of petiole; usually sparsely pubescent above and densely pubescent beneath, hairs about 1 mm long or longer and attenuate, apices simple and straight, curved or appearing almost uncinatate or often bifid; venation pinnate, usually paler than lamina, midrib prominent beneath, with many hairs, grooved above; margins flat to coarsely undulate, serrate, coarsely serrate or sometimes deeply lobed at base, lobes simple or sometimes bifid; lamina apices acute, obtuse or rounded. One or two flowering stipes up to (17–) 34 (–60) cm tall; ramification generally initially dichotomous at the middle, with 2–5 proximal ramifications and with multiple distal ramifications; dense umbellate panicle, barely aphyllous, stipe striate, moderately hispid pubescent at the base but almost glabrous at peduncles and pedicels, usually with one leaf-like bract beneath main branches and scale-like bracteoles beneath upper branches; stipe trichomes simple to bifid; pedicels (0.3–) 1.2 (–3.6) cm long, usually thickening below involucre, bracteolate, bracteoles scale like, (1–) 4 (–12) mm long; the pedicel bracteoles sometimes also found at the base of the capitulum forming an incomplete, unequal calyculus around 2–3 mm long. Capitula ligulate, (0.4–) 1.1 (–2.5) cm in diameter, (12–) 58 (–134) per synflorescence; involucre cylindrical in bud and scarcely widening in flower at apex, base becoming slightly inflated postanthesis and in fruit; phyllaries biseriate, external bracts (1.0–) 2.8 (–5.4), internal bracts (3.1–) 7.2 (11.0) mm long × (0.3–) 0.8 (2.2) mm wide, margins glabrous below and sparsely ciliate towards apex, tissue papillate and usually blackish; receptacle flat, paleaceous, paleae c. 3.9–9.8 mm long × 0.1–0.7 mm wide, linear, usually dark, apices attenuate/long-acute, sparsely to moderately ciliate, cilia long uniseriate and eglandular. Florets (21–) 43 (–56) ligulate, hermaphrodite, fertile, corollas yellow to orange but becoming brown postanthesis, eventually deciduous; corolla tube (0.8–) 2.6 (–5.1) mm long, glabrous, pale yellow, ligule (5.6–) 9.0 (17.2) mm long × (0.4–) 1.4 (–5.1) mm wide, glabrous inside, sparsely pubescent outside just above sinus with eglandular hairs, ligule apex with five distinct teeth, teeth apices thickened, glabrous; anther cylinder yellow (2.3–) 3.6 (–5.2) mm long, apical anther appendages obtuse to broadly rounded, slightly longer than wide, basal anther appendages sagittate; styles (2.5–) 5.0 (–6.7) mm long, style arms (0.8–) 1.2 (–1.6) mm long, ascending or divergent,

very short pubescent outside throughout. Achenes (0.4-) 1.2 (-3.2) mm long × (0.1-) 0.3 (-0.6) mm wide, narrowly fusiform, narrowing slightly upwards to a distinct apical callus, body striate, lightly rugose across striae; pappus setae (3.1-) 5.3 (-7.3) mm long, setae at first coarsely scabrid, and about as long as corolla tube, maturing to plumose or subplumose, with setae rachis coarsely barbellate. Molecularly differs from all other Azorean *Leontodon* in 5 positions of the ITS region, in the motifs CCGCTGGCG (C replaced by **T**), GTCAAGCTG (G replaced by **A**), CTGTTGCGG (C replaced by **T**), CCCTCAGC (C replaced by **T**) and GTTTGAGGA (T/C replaced by **G**); in one position of the *matK* region, in the motif AAGAGAGCC (A replaced by **G**); and in a deletion in the *trnV* region, in the motif TTTT-AGTT (T deletion).

Notes:—Seubert & Hochstetter (1843) used the name *Microderis umbellata* to refer to this taxon, the type of which, collected by Karl Hochstetter, is at TUB. The name cannot be used due to the existence of *L. umbellatum* Schrank (1789: 334). Another Karl Hochstetter specimen is at P and was labelled “*Picris hochstetteri* C. H. Schultz Bip. 29/360” by C. H. Schultz-Bipontinus. There is no evidence of this name ever being validly published and the replacement name *L. hochstetteri* is proposed here. Although the types of *Microderis umbellata* are labelled as collected at Pico, we believe this was a labelling error because the species is mentioned twice in Seubert & Hochstetter (1843) as specific to Flores Island. The holotype at TUB matches the drawing and protologue in Seubert (1844).

Distribution:—*Leontodon hochstetteri* is known only from the islands of Flores and Corvo.

Habitat:—Steep slopes, ravines, craters, rocks, coastal cliffs and waterfalls. From almost sea level up to above 900 m. More frequent above 300 m. In the margin and in the openings of native forest (*Laurus azorica*, *Juniperus brevifolia*) and woodland (*Juniperus brevifolia*). In Corvo it is rare due to strong grazing pressure by feral goats and sheep, but survives inside the island’s central crater “Caldeirão” in rock outcrops covered by low stature native vegetation and in the steep coastal cliffs of the western and northern part of the island.

Phenology:—All three Azorean endemic *Leontodon* species have similar flowering times, starting from the end of June until November; flowering specimens have been observed during the month of December, in years with mild winter conditions. Overlapping phenological states are common during the summer months with a mix of vegetative, flowering and fruiting plants in the same population. Within the populations screened for the present study and that of Dias *et al.* (2014), we observed that neighbouring plants with similar size do not flower synchronously and only ca. 60% of a population’s individuals develop flowers yearly.

Conservation Status:—The number of endemic *Leontodon* individuals estimated by Schaefer (2005) for Flores was 4,000–5,000. However, *L. hochstetteri* is rare in Corvo, where <1,000 individuals are estimated to survive in inaccessible places. On Flores it is strongly grazed by rabbits, wherever they can reach it; on Corvo rabbits are so far absent but the presence of grazing cattle inside the Caldeirão crater and rim (considered as a Biosphere Reserve in 2007 by UNESCO) as well as feral goats and sheep, which can enter the island cliffs, constitutes a severe threat to the survival of *L. hochstetteri* as well as to several other Azorean endangered endemic plants, and should thus be regulated. According to the IUCN classification, and based on the estimated number of plants, *L. hochstetteri* would be considered as Vulnerable (V) B1ab(i,ii,iii)+2ab(i,ii,iii); C2a(i).

Leontodon filii (Hochstetter ex Seubert) Paiva & Ormonde (1973: 447)

≡ *Microderis filii* Hochstetter ex Seubert (1844: 34) ≡ *Picris filii* (Hochstetter ex Seubert) Bentham & Hooker f. (1873: 512).

Lectotype designated by Lack 1981:—AZORES. “In praeruptis humidis montis Pico alt. 3000–4000”: July 1838, C. Hochstetter 97 (TUB!, isoelectotypes: BM! FI-W! G! K! P! TUB! W!).

– *Thrinicia nudicaulis* subsp. *azorica* Gandoger (1918: 54).

Holotype:—AZORES. Faial: Caldeira, 24 July 1878, Thiébaud 812 (LY!).

Acaulous rosetiform rhizomatous perennial herb; white latex present. Rootstock usually stout, woody, sometimes a long napiform root. Leaves few to several (1–10), petiolate; petiole (3.0-) 9.9 (-23.8) cm long × (0.2-) 0.7 (-1.8) cm wide, grooved, often narrowly winged; petiole trichomes often 2–3-fid; leaf (4.0-) 12.3 (-34.5) cm long × (1.1-) 5.4 (-11.7) cm wide; elliptic to ovate, or obovate, attenuate at base onto apex of petiole; usually densely pubescent above and beneath, hairs about 1 mm long or longer and attenuate, curved or appearing almost uncinatate, apices more often 2–3-fid up to 4-fid; venation pinnate, usually paler than lamina, midrib prominent beneath with many hairs, usually grooved above; margins flat to coarsely undulate, serrate, coarsely serrate or sometimes deeply lobed at base, lobes simple or sometimes bifid, lamina apices acute or acuminate. Two to three flowering stipes up to (20-) 37 (-52) cm tall; erect rarely ascending; ramification generally initially dichotomous at the base, with 1–4 proximal ramifications; lax panicle, usually aphyllous, internodes long, stipe striate, densely pubescent at base, peduncles and pedicels, usually

with scale-like bracteoles beneath upper branches; stipe trichomes usually 2–3-fid up to 4-fid; pedicels (0.4-) 6.2 (-32.2) cm long, usually thickening below involucre, bracteolate, bracteoles scale like, (2-) 4 (-10) mm long, also with hairs, narrow triangular, entire; the pedicel bracteoles often also found at the base of the capitulum forming a more or less incomplete, unequal calyculus around 2–4 mm long. Capitula ligulate, (0.5-) 2.2 (-4.4) cm in diameter, (1-) 6 (-17) per synflorescence; involucre cylindrical in bud and scarcely widening in flower at apex, base becoming slightly inflated postanthesis and in fruit; phyllaries biseriate, triangular to oblong, external bracts (0.9-) 3.8 (-7.7) mm long, internal bracts (6.7-) 11.3 (18.6) mm long × (0.1-) 1.1 (2.1) mm wide, margins glabrous below and sparsely ciliate towards apex, tissue papillate and usually blackish; bract trichomes usually 2-fid; receptacle flat, alveolated, ciliated. Florets (33-) 82 (-122) ligulate, hermaphrodite, fertile, corollas yellow to orange but becoming brown postanthesis, eventually deciduous; corolla tube (1.0-) 3.9 (-7.3) mm long, yellow, ligule (7.3-) 13.3 (-26.5) mm long × (0.1-) 1.1 (-2.1) mm wide, glabrous inside, sparsely pubescent outside just above sinus with eglandular hairs, ligule apex with five distinct teeth, teeth apices thickened, glabrous; anther cylinder yellow (2.3-) 4.5 (-7.1) mm long, apical anther appendages acute to obtuse, slightly longer than wide, basal anther appendages sagittate; styles (3.5-) 6.0 (12.5) mm long; style arms (0.1-) 1.2 (-3.2) mm long, ascending or divergent, very short pubescent outside throughout. Achenes pale brown, (0.6-) 3.0 (-9.2) mm long × (0.1-) 0.4 (-1.1) mm wide, narrowly fusiform, narrowing slightly upwards to a distinct apical callus, body striate, lightly rugose across striae; pappus setae (4.4-) 7.2 (-12.6) mm long, plumose. The ITS region differs from all other Azorean *Leontodon* in the motif GTTT TAGGA (C/G replaced by T).

Notes:—The lectotype of *L. filii* is at TUB and was designated by Lack (1981) based on the protologue and drawing depicted in *Flora Azorica* (Seubert 1844). The sheet has a typed label indicating that it was collected by Karl Hochstetter in Pico mountain. However, a second sheet, with a smaller specimen, also illustrated in Seubert (1844) as representing “*Microderis filii*”, bears what appears to be an original label handwritten by Karl Hochstetter, indicating that the species occurs on the islands of Terceira, Pico, Faial (central group) and Flores (western group). In Seubert & Hochstetter (1843), although *L. filii* is listed, there is no reference to its distribution within the archipelago and only *L. hochstetteri* is mentioned as specific to Flores. In our sampling of Flores, two specimens showed a typical *L. filii* phenotype, however, in the molecular analysis turned out to belong to *L. hochstetteri* and they are considered here to be *L. hochstetteri* × *L. saxatilis* hybrids (see below). It is unclear whether Hochstetter also encountered hybrids in Flores; we have not seen specimens to support this idea.

Distribution:—*Leontodon filii* is distributed to the islands of Terceira, São Jorge, Pico and Faial.

Habitat:—From almost sea level up to 1450 m. More frequent above 500 m. In wet habitats, with a more or less continuous water supply. Steep slopes, ravines and craters, rarely near coastal waterfalls. In open grassland and around lakes, especially on rather protruding hummocks. In crevices on vertical cliffs and on dense humus layers or *Sphagnum* spp. carpet on slopes in ravines and craters. In forests dominated by *Juniperus brevifolia* and *Erica azorica*, also associated with *Festuca francoi*.

Phenology:—See *L. hochstetteri*.

Conservation Status:—Although being the most widespread of the three Azorean *Leontodon* species, the estimated population numbers are 5,000–10,000 individuals (Schaefer 2005) and it was previously classified as rare (Schaefer 2003), a top priority species for conservation (Silva *et al.* 2009) and Endangered [B2ab (i, ii, iii); Corvelo 2010]. *Leontodon filii* 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 and transformation of natural vegetation into pastures. Thus, according to the IUCN classification, and based on the estimated number of plants, *L. filii* would be considered as Vulnerable (V) B1ab(i,ii,iii)+2ab(i,ii,iii); C2a(i).

Leontodon rigens (Dryander in Aiton) Paiva & Ormonde (1973: 448)

≡ *Crepis rigens* Dryander in Aiton (1789: 127) ≡ *Microderis rigens* (Dryander in Aiton) DC (1838: 128) ≡ *Picris rigens* (Dryander in Aiton) Benth & Hooker f. (1873: 512) ≡ *Hieracioides rigens* (Aiton) Kuntze (1891: 346).

Holotype:—AZORES. “Nat. of the Azores, Mr. Francis Masson. Introd. 1778” (BM!).

– *Hypochaeris strigosa* Solander ex Lowe (1868: 537) *nom. non rite public.*

Acaulous rosetiform rhizomatous perennial herb; white latex present. Rootstock usually stout, woody, sometimes a long napiform root. Leaves few to several (1–14), petiolate. Petiole (1-) 8 (-17) cm long × (0.2-) 1.2 (-3.5) cm wide, grooved, often narrowly winged; petiole trichomes often simple. Leaf (5-) 18 (50) cm long × (3-) 7 (-12) cm wide; elliptic to ovate, sometimes lanceolate or almost obovate, attenuate at base onto apex of petiole; usually sparsely to densely pubescent above and densely pubescent beneath, hairs about 1 mm long or longer and attenuate, apices simple

and straight, curved or appearing almost uncinatate or often bifid; venation pinnate, usually paler than lamina, midrib prominent beneath with many hairs, grooved above; margins flat to coarsely undulate, serrate, coarsely serrate, tooth acuminate, or sometimes deeply lobed at base, lobes simple or sometimes bifid; lamina apices acute, obtuse or rounded. One or two flowering stipes up to (32-) 45 (-69) cm tall, erect; ramification generally initially dichotomous at the base, with 2–7 proximal ramifications and with multiple distal ramifications; corymbose panicle, barely aphyllous, stipe striate, moderately hispid pubescent at the base but almost glabrous at peduncles and pedicels, usually with one leaf-like bract beneath each main branch and scale-like bracteoles beneath upper branches; stipe trichomes simple to bifid; pedicels (1.2-) 3.6 (-7.0) cm long, usually thickening below involucre, bracteolate, bracteoles scale like, (1.5-) 3 (-8.2) mm long, narrow triangular entire; the pedicel bracteoles sometimes also found at the base of the capitulum forming an incomplete, unequal calyculus around 2–3 mm long. Capitula ligulate, (0.6-) 1.4 (-2.4) cm in diameter, (14-) 59 (-114) per synflorescence; involucre cylindrical in bud and scarcely widening in flower at apex, base becoming slightly inflated postanthesis and in fruit; phyllaries biseriate, external bracts (0.9-) 2.6 (-4.6) mm long, internal bracts (3.99-) 7.7 (-11.4) mm long × (0.3-) 0.9 (-1.9) mm wide, margins glabrous below and sparsely ciliate towards apex, tissue papillate and usually blackish; receptacle flat, paleaceous, paleae 4.4–14.0 mm long × 0.1–0.7 mm wide, linear, usually with dark margins, apices attenuate/long-acute, sparsely to moderately ciliate, cilia long uniseriate and eglandular. Florets (26-) 37 (-56) ligulate, hermaphrodite, fertile, corollas yellow to orange, but becoming pale brown postanthesis, eventually deciduous; corolla tube (1.2-) 3.0 (-5.8) mm long, glabrous, pale yellow, ligule (5.6-) 10.0 (-19.1) mm long × (0.3-) 0.8 (-1.6) mm wide, glabrous inside, sparsely pubescent outside just above sinus with eglandular hairs, ligule apex with five distinct teeth, teeth apices thickened, glabrous; anther cylinder yellow (1.4-) 3.8 (-9.0) mm long, apical anther appendages obtuse to broadly rounded, slightly longer than wide, basal anther appendages sagittate; styles (3.2-) 5.2 (-11.5) mm long, style arms (0.2-) 1.0 (-2.4) mm long, ascending or divergent, very short pubescent outside throughout. Achenes pale brown, (0.6-) 3.2 (-6.3) mm long × (0.1-) 0.4 (-1.1) mm wide, narrowly fusiform, narrowing slightly upwards to a distinct apical callus, body striate, lightly rugose across striae; pappus setae (3.6-) 5.9 (-8.0) mm long, setae at first coarsely scabrid, and about as long as corolla tube, maturing to plumose or subplumose, with setae rachis coarsely barbellate. Molecularly differs from all other Azorean *Leontodon* in 4 positions of the ITS region, in the motifs GATG**T**GGAG (G replaced by **T**), CCCT**G**CCGG (C replaced by **G**), TAG**G**AAAGC (G replaced by **A**) and G**T**TT**C**AGGA (T/G replaced by **C**); and in one position of the *trnQ* region, in the motif ACA**A**AAAA (T replaced by **A**).

Distribution:—*Leontodon rigens* is an endemic of São Miguel Island.

Habitat:—Generally not below 300 m. In moist habitats on steep slopes, roadsides, in the margins or in the openings of the native scrubland (*Calluna vulgaris*) and of the native forest (*Laurus azorica*, *Ilex perado* subsp. *azorica*, *Juniperus brevifolia*). Also in open grassland, on cuttings through sandy deposits and on cliffs. In crevices on vertical cliffs and on dense humus layers or *Sphagnum* spp. carpet on slopes in ravines and craters, also associated with *Festuca francoi* or *Deschampsia foliosa*.

Phenology:—See *L. hochstetteri*.

Conservation Status:—Previous attempts to classify *L. rigens* according to IUCN criteria led Corvelo (2010) to list it as Endangered [B2ab (i, ii, iii)]. It was also considered a top priority species by Silva *et al.* (2009). However, these estimations also included the western *Leontodon* species. Population numbers were estimated by Schaefer (2005) (as “*Leontodon spec. nov. ined.*”) to be <1,000. During the extensive sampling conducted for this study and by Dias *et al.* (2014), 14 populations of *L. rigens* were identified in fragmented native vegetation patches in the central part and the eastern and western extremes of São Miguel, with an estimated total number of <4,000 individuals. In several of these locations (e.g. Lagoa do Fogo and Sete Cidades waterbasin locations), goats can be found grazing, although the areas are part of the São Miguel Natural Park. Furthermore, wild rabbits are also known to feed on the plants. Thus, according to the IUCN classification, and based on the estimated number of plants, *L. rigens* would be considered as Vulnerable (V) B1ab(i,ii,iii)+2ab(i,ii,iii); C2a(i).

Leontodon saxatilis × *Leontodon hochstetteri* = *Leontodon* × *friasi* M. Moura & L. Silva *nothosp. nov.*

Holotype:—AZORES. Flores: Burreiro, 18 July 2010, Silva LF-FLBU-001 (AZB1349!, isotype: BM!).

– *Leontodon filii* sensu Paiva & Ormonde (1973: 447) *pro parte quoad plantarum ex Flores*.

Acaulous rosettiformal rhizomatous perennial herb; white latex present. Rootstock usually stout, woody, sometimes a long napiform root. Leaves few to several (9–10), petiolate; petiole 6–14 cm long × 0.3–0.9 cm wide, grooved, often narrowly winged; petiole trichomes often 2-fid, less frequently simple or 3-fid; lamina 7–15 cm long × 1.1–3.5

cm wide; lanceolate to oblanceolate, attenuate at base onto apex of petiole; usually densely pubescent above and densely pubescent beneath, hairs about 1 mm long or longer and attenuate, curved or appearing almost uncinata, apices more often 2-fid up to 3-fid; venation pinnate, usually paler than lamina, midrib prominent beneath with many hairs, usually grooved above; margins flat to coarsely undulate, coarsely dentate, lamina apices acute or acuminate, sometimes almost round. Two to three flowering stipes up 34–38 cm tall; erect or ascending; ramification generally absent or dichotomous, with 2 ramifications; internodes very long, stipe striate, more densely pubescent at base, scarcely pubescent or almost glabrous at peduncles and pedicels, usually with scale-like bracteoles beneath capitula; stipe trichomes usually 2-fid up to 3-fid; pedicels 8–32 cm long, usually thickening below involucre, bracteolate, bracteoles scale like, linear, entire 2–5 mm long, also with hairs; the pedicel bracteoles sometimes also found at the base of the capitulum forming an incomplete, unequal calyculus around 2–3 mm long. Capitula ligulate, 1.8–3.0 cm in diameter, 4 per synflorescence; involucre cylindrical in bud and scarcely widening in flower at apex, base becoming slightly inflated postanthesis and in fruit; phyllaries biseriate, triangular to oblong, external bracts 1.8–4.6 mm long, internal bracts 8.5–11.2 mm long \times 0.3–1.5 mm wide, margins glabrous below and sparsely ciliate towards apex, tissue papillate and usually blackish; bract trichomes usually 1 to 2-fid. Florets 55–73 ligulate, hermaphrodite, corollas yellow to orange but becoming brown post-anthesis, eventually deciduous; corolla tube 1.8–3.4 mm long, yellow, ligule 7.3–11.3 mm long \times 0.4–1.0 mm wide, glabrous inside, sparsely to densely pubescent outside just above sinus and also above that area with eglandular hairs, ligule apex with five distinct teeth, teeth apices thickened, glabrous; anther cylinder yellow 2.5–4.9 mm long, apical anther appendages acute to obtuse; styles 3.5–5.7 mm long; style arms 0.5–1.3 mm long, very short pubescent outside throughout. Achenes pale brown, 3.9–8.1 mm long \times 0.3–0.6 mm wide, narrowly fusiform, narrowing slightly upwards to a distinct apical callus, body striate, lightly rugose across striae; pappus setae 5–8 mm long, plumose or subplumose; some of the achenes in the margin with a pappus of scales or scales and a few hairs.

Note:—The name *Leontodon* \times *friasi* is here proposed in honour of Professor António Manuel de Frias Martins, Azorean naturalist, malacologist and evolutionary biologist. Professor “Frias”, as generally known by his colleagues and students, is one of the pioneers in the diffusion of the knowledge about Azorean biodiversity.

Distribution:—So far known only from Burreiro in Flores; but may also occur more widely on the island and on Corvo where the two parental species also co-occur.

Habitat and abundance:—Found on a road margin. Apparently rare. No existing herbarium specimens were found during this study.

Leontodon saxatilis* \times *Leontodon rigens* = *Leontodon* \times *carreiroi* (Gandoger) M. Moura & L. Silva *nothosp.* & *comb. nov.

= *Thrinchia carreiroi* Gandoger (1918: 53).

Lectotype designated by Lack 1981:—AZORES. São Miguel: Lagoa, Janelas do Inferno, August 1903, *Carreiro 902B* (LY!, isolecotypes: LY!, AZ1768-1772!).

= *Thrinchia subglabra* Gandoger (1918: 53–54).

Holotype:—AZORES. São Miguel: Lagoa, Janelas do Inferno, August 1903, *Carreiro 980* (LY!, isotypes: AZ1764-1765!).

– *Leontodon filii sensu* Paiva & Ormonde (1973: 447) *pro parte quoad plantarum ex São Miguel*.

Acaulous rosetiform rhizomatous perennial herb; white latex present. Rootstock usually stout, woody, sometimes a long napiform root. Leaves few to several (5–7), petiolate; petiole 4–10 cm long \times 0.3–0.8 cm wide, grooved, often narrowly winged; petiole trichomes often 2-fid, less frequently simple or 3-fid; lamina 4–17 cm long \times 1.6–5 cm wide; lanceolate to oblanceolate, attenuate at base onto apex of petiole; usually sparsely pubescent above and densely pubescent beneath, hairs about 1 mm long or longer and attenuate, curved or appearing almost uncinata, apices more often 2-fid up to 3-fid; venation pinnate, usually paler than lamina, midrib prominent beneath with many hairs, usually grooved above; margins flat to coarsely undulate, coarsely dentate, rarely serrated, lamina apices acute or acuminate. Two to three flowering stipes up 44 cm tall; erect or ascending; some or all the stipes not ramified; ramification generally absent or initially dichotomous at the base, with 2 proximal ramifications; very lax panicle, with a leaf-like bract at the main branches, internodes very long, stipe striate, densely pubescent at base, less pubescent or almost glabrous at peduncles and pedicels, usually with scale-like bracteoles beneath capitula; stipe trichomes usually 2-fid up to 3-fid; pedicels (3-) 6–36 cm long, or longer if there is only the peduncle, usually thickening below involucre, bracteolate, bracteoles scale like, linear, entire 3–5 mm long; the pedicel bracteoles sometimes also found at the base of the capitulum forming an incomplete, unequal calyculus around 2–3 mm long. Capitula ligulate, 0.7–2.5 cm in

diameter, 5 per synflorescence; involucre cylindrical in bud and scarcely widening in flower at apex, base becoming slightly inflated postanthesis and in fruit; phyllaries biseriate, triangular to oblong, external bracts 1–3 mm long, internal bracts 8–10 mm long \times 0.5–1 mm wide, margins glabrous below and sparsely ciliate towards apex, tissue papillate and usually blackish; bract trichomes usually 1 to 2-fid. Florets 33–58 ligulate, hermaphrodite, corollas yellow to orange but becoming brown postanthesis, eventually deciduous; corolla tube 2–4 mm long, yellow, ligule 9–15 mm long \times 0.5–0.9 mm wide, glabrous inside, sparsely to densely pubescent outside just above sinus and also above that area with eglandular hairs, ligule apex with five distinct teeth, teeth apices thickened, glabrous; anther cylinder yellow 4 mm long, apical anther appendages acute to obtuse; styles 4–5 mm long; style arms 0.3–0.9 mm long, very short pubescent outside throughout. In some plants the capitula are paleaceous, paleae 9–11.5 mm long \times 0.14–0.21 mm wide, linear, usually with dark margins, apices attenuate/long-acute, sparsely to moderately ciliate, cilia long uniseriate and eglandular. Achenes pale brown, 0.9–1.4 mm long \times 0.1–0.3 mm wide, narrowly fusiform, narrowing slightly upwards to a distinct apical callus, body striate, lightly rugose across striae; pappus setae 5–10 mm long, plumose or subplumose; some of the achenes in the margin with a pappus of scales or scales and a few hairs.

Distribution:—Known from Lagoa, Sete Cidades and Nordeste in São Miguel.

Habitat and abundance:—Found on a roadside slope. Apparently rare although several herbarium specimens exist from the 19th and early 20th centuries.

Specimens Examined

Leontodon hochstetteri:—AZORES. Flores: Borda da Lagoa Seca, 4 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLLS-001* (AZB301!); Borda da Lagoa Seca, 4 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLLS-003* (AZB303!); Borda da Lagoa Seca, 4 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLLS-004* (AZB304!); Borda da Lagoa Seca, 4 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLLS-005* (AZB305!); Borda da Lagoa Seca, 4 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLLS-006* (AZB306!); Borda da Lagoa Seca, 4 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLLS-007* (AZB307!); Borda da Lagoa Seca, 4 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLLS-008* (AZB308!); Borda da Lagoa Seca, 4 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLLS-009* (AZB309!); Estrada do Morro Alto, 5 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLMA-001* (AZB314!); Estrada do Morro Alto, 5 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLMA-002* (AZB315!); Estrada do Morro Alto, 5 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLMA-003* (AZB316!); Estrada do Morro Alto, 5 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LR-FLMA-004* (AZB317!); Alto da Fajãzinha, 22 September 1971, *Gonçalves 3720* (BM!); *s. loc.*, 27 July 1894, *Trelease 487* (BM!, K!); Ribeira da Cruz, 27 July 1894, *Trelease 487* (AZ111!, MO5421227!); *s. loc.*, July 1842, *Watson 183* (K1867 (2 specimens)!, MANCH (2 specimens)!). Corvo: Fonte das Poças, 8 June 1971, *Gonçalves 2577* (BM!); Road from Caldeira (1 km from rim) towards Corvo village, 12 August 1985, *Parry 124* (BM!). Doubtful location [see notes for *L. hochstetteri* in the Taxonomic Treatment section]: [Pico, on the way from Vila Madalena to Pico mountain], July 1838, *Hochstetter s. n.* (TUB3367!); [At the foot of Pico mountain], *Hochstetter s. n.* (P00417745!).

Leontodon filii:—AZORES. Terceira: Furna do Enxofre, 9 July 1894, *Trelease 489* (AZ1732!, K!, MO5421231!); Caldeira de Santa Bárbara, 19 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-TESB-013* (AZB1002!); Rocha do Chambre, 19 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-TERC-011* (AZB987!); Rocha do Chambre, 19 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-TERC-008* (AZB984!); Rocha do Chambre, 19 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-TERC-007* (AZB983!); Descida para a Rocha do Chambre, 19 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-TERC-003* (AZB979!); Descida para a Rocha do Chambre, 19 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-TERC-002* (AZB978!); Descida para a Rocha do Chambre, 19 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-TERC-001* (AZB977!); São Miguel Arcanjo, 9 August 1971, *Gonçalves 3397* (BM!); Bagacina, 12 July 1971, *Gonçalves 3268* (BM!); Algar do Carvão, *Ormonde 852* (LISE75870!); Pico da Bagacina, estrada Angra-Pico da Bagacina, 25 August 1966, *Ormonde 150* (LISE75869!). São Jorge: Ribeira da Areia e Lagoa do Brenho, 07/08, *Carreiro 978B* (AZ1727-1729 (3 specimens)!); Línguas de Fogo, 07/03, *Carreiro 978* (AZ1730-1731!); Norte Pequeno, 07/08, *Carreiro 478A* (AZ1724-1726 (3 specimens)!); Pico do Areeiro, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJPA-001* (AZB794!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-001* (AZB780!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-002* (AZB781!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-003* (AZB782!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-004* (AZB783!);

Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-005* (AZB784!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-006* (AZB785!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-007* (AZB786!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-008* (AZB787!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-009* (AZB788!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-010* (AZB789!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-011* (AZB790!); Morro Pelado, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-014* (AZB793!); Pico da Esperança, 15 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-SJPE-001* (AZB812!); Chão das Lagoinhas, 5 September 1971, *Goncalves 3494* (BM!); São Jorge, July 1903, *Carreiro 978* (feuille n° 1) (LY!); São Jorge, July 1903, *Carreiro 978* (feuille n° 2) (LY!); *s. loc.*, July 1908, *Carreiro 978B* (MO5421229!). Pico: Caldeirão da Ribeirinha, 14 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PIRB-002* (AZB1051!); Caldeirão da Ribeirinha, 14 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PIRB-002* (AZB1052!); Cabeço dos Mistérios, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PICM-003* (AZB614!); Cabeço dos Mistérios, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PICM-002* (AZB613!); Cabeço dos Mistérios, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PICM-006* (AZB617!); Cabeço dos Mistérios, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PICM-004* (AZB615!); Cabeço dos Mistérios, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PICM-001* (AZB612!); Cabeço dos Mistérios, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PICM-007* (AZB618!); Ribeira Funda, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PIRF-001* (AZB619!); Ribeira Funda, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PIRF-007* (AZB625!); Ribeira Funda, 13-07-2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PIRF-002* (AZB620!); Ribeira Funda, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PIRF-005* (AZB623!); Ribeira Funda, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PIRF-003* (AZB621!); Ribeira Funda, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PIRF-004* (AZB622!); Ribeira Funda, 13 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-PIRF-006* (AZB624!); *s. loc.*, July 1838, *Hochstetter 97* (BM!, FI108353!, K000252019!, M0030715!, MO4675235!, P00417737- P00417739 (3 specimens)!, TUB3366 (2 specimens)!, WAG0003536!); *s. loc.*, July 1838, *Hochstetter s. n.* (BR532950!, G00300311-G00300314 (4 specimens)!); São Roque do Pico, near Lagoa do Capitão, 15 June 1964, *Dansereau, Pinto da Silva, Rainha 689* (LISE70537!). Faial: Parque de Estacionamento da Caldeira, 12 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-FAEC-001* (AZB570!); Parque de Estacionamento da Caldeira, 12 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-FAEC-002* (AZB571!); Cabeço do Trinta, 11 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-FATR-007* (AZB565!); Cabeço do Trinta, 11 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-FATR-005* (AZB563!); Cabeço do Trinta, 11 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-FATR-006* (AZB564!); Cabeço do Trinta, 11 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-FATR-004* (AZB562!); Cabeço do Trinta, 11 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-FATR-002* (AZB560!); Cabeço do Trinta, 11 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-FATR-003* (AZB561!); Cabeço do Trinta, 11 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-FATR-008* (AZB566!); Cabeço do Trinta, 11 July 2008, *Maciel, Martins, Moreira, Carine, Rumsey LF-FATR-009* (AZB567!); Cedros, Levada, 10 October 1963, *Goncalves 751* (BM!); Along path leading down crater, 27 August 1985, *Parry 221* (BM!); *s. loc.*, *B. do Castello de Paiva 862* (K!); Above Cedros, 1961, *Pickering 700* (K (2 specimens)!); Cedros, near Caldeira, 5 October 1961, *Goncalves s.n.* (K!); Cedros near Cancela, 8 June 1964, *Dansereau, Pinto da Silva, Rainha 467* (LISE70332!); Caldeira, valley to NW of Pedra do Altar, 10 June 1964, *Dansereau, Pinto da Silva, Rainha 514* (LISE70373!); Caldeira, 24 July 1878, *Thiébaud 812* (LY!); *s. loc.*, 26 July 1894, *Brown 158* (MO5421230!). Uncertain island [see notes for *L. filii* in the Taxonomic Treatment section]: *s. loc.*, 1868, *Drouet s. n.* (BM (2 specimens)!); “Faial (?)”, *s. loc.*, September 1842, *Watson s. n.* (MANCH!); “Terceira, Faial, Pico, Flores”, *s. loc.*, July 1838, *Hochstetter 97* (TUB3366!).

Leontodon rigens:—AZORES. São Miguel: Pico do Carvão, August 1898, *Carreiro 363* (AZ1713!); Sete Cidades, August 1908, *Carreiro s. n.* (AZ1714!); Lagoa, Janelas do Inferno, August 1903, *Carreiro s. n.* (AZ1715!); Lombadas, August 1897, *Carreiro s. n.* (AZ1716!); Bretanha, August 1899, *Carreiro s. n.* (AZ1717!); Lagoa, Junqueiras, September 1904, *Carreiro s. n.* (AZ1718-1719!); Lagoa, Janelas do Inferno, August 1903, *Carreiro s. n.* (AZ1720!); Sete Cidades, August 1900, *Carreiro s. n.* (AZ1721!); Pico do Carvão, August 1898, *Carreiro 363* (AZ1722!); Feteiras, Abril 1891, *Carreiro s. n.* (AZ1723!); Road to Outeiro da Lomba, 31 July 2010, *Dias, L.B. Silva LR-SMOL-001* (AZB1378!); Road to Pico da Cruz, 31 July 2010, *Dias, L.B. Silva LR-SMPI-001* (AZB1379!); Lagoa do Canário, 31 July 2010, *Dias, L.B. Silva LR-SMLC-006* (AZB1380!); Road to Lagoa do Canário, 31 July 2010, *Dias, L.B. Silva LR-SMEC-001* (AZB1382!); Caldeira do Alferes, 7 August 2010, *Dias, L.B. Silva LR-SMAL-001* (AZB1386!); Lomba do Pico, 7 August 2010, *Dias, L.B. Silva LR-SMLP-001* (AZB1387!); Lagoas Empadadas, 8 August 2010, *Dias, L.B. Silva LR-SMEM-001* (AZB1388!); Pico do Carvão, 21 August 2010, *Dias, L.B. Silva LR-SMPR-001* (AZB1397!); Vista do Rei, 21 August

2010, *Dias, L.B. Silva LR-SMVR-001* (AZB1396!); Planalto dos Graminhais, 17 September 2010, *Dias, L.B. Silva LR-SMPG-001* (AZB1407!); Planalto dos Graminhais, 17 September 2010, *Dias, L.B. Silva LR-SMPG-027* (AZB1408!); Planalto dos Graminhais, 17 September 2010, *Dias, L.B. Silva LR-SMPG-030* (AZB1409!); Planalto dos Graminhais, 17 September 2010, *Dias, L.B. Silva LR-SMPG-039* (AZB1410!); Planalto dos Graminhais, 17 September 2010, *Dias, L.B. Silva LR-SMPG-042* (AZB1411!); Tronqueira, 17 September 2010, *Dias, L.B. Silva LR-SMTR-006* (AZB1412!); Monte Escuro, 18 September 2010, *Dias, L.B. Silva LR-SMME-006* (AZB1413!); Lombadas, 18 September 2010, *Dias, L.B. Silva LR-SMLO-001* (AZB1414!); Tronqueira, 9 September 2010, *Dias, L.B. Silva LR-SMTR-064* (AZB1443!); Pico Bartolomeu, 9 September 2010, *Dias, L.B. Silva LR-SMPB-001* (AZB1444!); Lagoa do Fogo, 19 September 2010, *Dias, L.B. Silva LR-SMLF-044* (AZB1447!); Lagoa do Fogo, 23 September 2010, *Dias, L.B. Silva LR-SMLF-020* (AZB1448!); Lagoa do Fogo, 23 September 2010, *Dias, L.B. Silva LR-SMLF-038* (AZB1449!); Lagoa do Areeiro, 24 September 2010, *Dias, L.B. Silva LR-SMLA-003* (AZB1450!); Lagoa do Canário, 13 September, 2008, *Moura LR-SMLC-002* (AZB1079!); Lagoa do Canário, 31 July 2010, *Dias, L.B. Silva LR-SMLC-005* (AZB1382!); Monte Escuro, 13 September 2008, *Moura LR-SMME-004* (AZB1086!); Monte Escuro, 13 September 2008, *Moura LR-SMME-003* (AZB1085!); Monte Escuro, 13, September 2008, *Moura LR-SMME-001* (AZB1083!); Monte Escuro, 13 September 2008, *Moura LR-SMME-005* (AZB1087!); Tronqueira, 14 September 2008, *Moura LR-SMTR-003* (AZB1090!); Lagoa do Canário, 13 September 2008, *Moura LR-SMLC-006* (AZB1562!); Lagoa do Canário, 13 September 2008, *Moura LR-SMLC-005* (AZB1082!); Lagoa do Canário, 13 September 2008, *Moura LR-SMLC-003* (AZB1080!); Lagoa do Canário, 13 September 2008, *Moura LR-SMLC-001* (AZB1078!); Lagoas Empadadas, 7 August 2010, *Dias, L.B. Silva s. n.* (AZB1387!); Lagoa do Canário, 31 July 2010, *Dias, L.B. Silva LR-SMLC-021* (AZB1381!); Road to Pico da Cruz, 31 July 2010, *Dias, L.B. Silva LR-SMPI-001* (AZB1379!); Road to Outeiro da Lomba, 31 July 2010, *Dias, L.B. Silva LR-SMOL-001* (AZB1378!); Muro das 9 Janelas, 27 July 1968, *Botelho Gonçalves 2441* (BM!); Roadside between Furnas and Nordeste, August 1956, *Pickering 140, sheet 1* (BM!); Seara, Sete Cidades, 30 July 1970, *Dolman 372* (BM!); Lagoa do Fogo, 20 July 1987, *Wieringa 161* (K!); between Furnas and Nordeste, 12 September 1954, *Pickering s. n.* (K!); *s. loc.*, 1847, *Hunt s. n.* (K!, MANCH (2 specimens!)); *s. loc.*, 1865, *Godman s. n.* (K!); *s. loc.*, 1844, *Hunt s. n.* (MANCH!); *s. loc.*, *s. d.*, *Hunt s. n.* (MANCH!); Lagoa do Fogo, 20 July 1987, *Wieringa s. n.* (MO5049847!); Pico do Carvão, 22 August 1894, *Trelease 488* (MO5421228!). Uncertain island: Cultivated at Kew from Azorean material (“said in Hort. Kew to be from the Azores”), *s. d.*, *s. col. s. n.* (BM!); *s. loc.*, 1847, *Hunt 153* (BM!); *s. loc.*, August 1956, *Pickering 140, sheet 2* (BM!); *s. loc.*, *s. d.*, *Hunt s. n.* (K (2 specimens!)).

Leontodon* × *friasi:—AZORES. Flores: Burreiro, 18 July 2010, *Silva LF-FLBU-001* (AZB1349!); Burreiro, 18 July 2010, *Silva LF-FLBU-002* (BM!).

Leontodon* × *carreiroi:—AZORES. São Miguel: Sete Cidades, Cumeeira, August 1900, *Carreiro 902* (AZ1794–1795 (2 specimens!); LY!, MO5421237!); Sete Cidades, Grota do Cerrado das Freiras, September 1903, *Carreiro 902A* (AZ6638–6640, AZ1792–1793 (5 specimens!); LY (2 specimens!)); Lagoa, Junqueiras, September 1904, *Carreiro s. n.* (AZ1761–1762 (2 specimens!)); Lagoa, Janelas do Inferno, August 1903, *Carreiro 980* (AZ1764–1765 (2 specimens!); LY!); Lagoa, Janelas do Inferno, August 1903, *Carreiro s. n.* (AZ1766–1767 (2 specimens!)); Lagoa, Janelas do Inferno, August 1903, *Carreiro 902B* (AZ1768–1772 (5 specimens!); LY (2 specimens!)); Nordeste, Pico da Vara, 14 October 2010, *Dias LF-SMPV-001* (AZB1445!); Nordeste, Pico da Vara, 14 October 2010, *Dias LF-SMPV-002* (AZB1446!); *s. loc.*, 1845, *Hunt s. n.* (FI108353!, K (4 specimens!); MANCH (5 specimens!); OXF!, P02664559–02664560 (2 specimens!); Lagoa, August 1903, *Carreiro s. n.* (LY!); Sete Cidades, 30 August 1894, *Trelease 491* (MO2682472!); Sete Cidades, September 1903, *Carreiro s. n.* (OXF!); *s. loc.*, 1847, *Hunt 175* (OXF!). Uncertain island: *s. loc.*, *s. d.*, *Hunt s. n.* (K!).

Leontodon saxatilis:—AZORES. Santa Maria: *s. loc.*, 25 June 1896, *Trelease 499B* (AZ1774!); *s. loc.*, 30 June 1896, *Trelease 499C* (MO5421238!). São Miguel: Lagoa, Janelas do Inferno, August 1903, *Carreiro 831A* (AZ1783–1784 (2 specimens!); LY (3 specimens!)); Caldeiras, August 1902, *Carreiro 943* (AZ1780–1782 (3 specimens!); LY (4 specimens!)); Caldeiras, June 1899, *Carreiro 831* (AZ1785–1786 (2 specimens!)); Muro das Nove Janelas, May 1891, *Carreiro s. n.* (1787 AZ!); Rocha, March 1895, *Carreiro 103* (AZ1788–1789 (2 specimens!)); Muro do Carvão, March 1895, *Carreiro 185* (AZ1790–1791!); *s. loc.*, 1846, *Hunt 175* (K000252013!); *s. loc.*, 1845, *Hunt “175?”* (K!); *s. loc.*, 1845, *Hunt 175* (K!); *s. loc.*, 1847, *Hunt “175*”* (K!); *s. loc.*, 1865, *Godman s. n.* (K000252009 (2 specimens!); K000252016 !); Pico da Cruz, November 1881, *Arruda Furtado s. n.* (K!); Calhetas, *s. d.*, *Ormonde 825* (LISE75867 (2 specimens!)); Muro do Carvão, March 1895, *Carreiro s. n.* (LY (3 specimens!)); Rocha, March 1895, *Carreiro s. n.* (LY!); Serra Gorda, 21 August 1894, *Trelease 499* (MO5421240!). Terceira: *s. loc.*, 1862, *B. do Castello de Paiva s. n.* (K00252014!); Caminho de Cima, 1 April 1899, *Sampaio s. n.* (AZ1777!); Furna do Enxofre, *s. d.*, *Ormonde 736* (LISE75868 (3 specimens!)); *s. loc.*, 27 June 1894, *Trelease 502* (MO5421242!). Graciosa: *s. loc.*, July 1903, *Carreiro 831C* (AZ1778!); Folga, 18 August 1894, *Trelease 500* (AZ1775!, MO5421241!). São Jorge: Línguas de Fogo, July

1903, *Carreiro 831B* (AZ1776!, AZ1779!, LY (2 specimens!)); *s. loc.*, July 1908, *Carreiro s. n.* (AZ1775!); Calheta, 23 June 1894, *Trelease 490* (MO5421243!). Pico: Candelária, near porto de Ana Clara, 6 June 1864, *Dansereau, Pinto da Silva & Rainha 418* (LISE70286 (2 specimens!)). Faial: Lugar dos Quinhões, Feteira, 4 June 1947, *R. Silva 17* (LISE21317 (2 specimens!)); *s. loc.*, 17 July 1894, *Brown 159* (MO5421239!). Flores: Lajes, Boca da Baleia, 6 August 1963, *Botelho Gonçalves 1401* (LISE68256!).

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Appendix

List of taxa used in the molecular analysis, voucher information, and GenBank accession numbers. All samples of *L. hochstetteri*, *L. filii*, *L. rigens* and hybrid specimens are stored at the DNA Bank of Azorean Flora, which is part of AZB.

Leontodon hochstetteri:—Flores (Estrada do Morro Alto) Maciel, Martins, Moreira, Carine, Rumsey LR-FLMA-008 (ITS KM589258, *trnQ* KM589301, *trnV* KM589318, *matK* KM589347); Flores (Estrada do Morro Alto) Maciel, Martins, Moreira, Carine, Rumsey LR-FLMA-010 (ITS KM589276, *trnQ* KM589287, *trnV* KM589324, *matK* KM589336); Flores (Alagoa) Maciel, Martins, Moreira, Carine, Rumsey LR-FLAL-001 (ITS KM589256); Flores (Alagoa) Maciel, Martins, Moreira, Carine, Rumsey LR-FLAL-002 (ITS KM589272, *trnQ* KM589282, *trnV* KM589325, *matK* KM589328); Corvo (Caldeirão, Ponta do Marco road) Maciel, Martins, Moreira, Carine, Rumsey LR-COMC-007 (ITS KM589267, *trnQ* KM589303, *trnV* KM589306, *matK* KM589338); Corvo (Caldeirão, Ponta do Marco road) Maciel, Martins, Moreira, Carine, Rumsey LR-COMC-011 (ITS KM589274, *trnQ* KM589285, *trnV* KM589307, *matK* KM589341).

Leontodon filii:—Terceira (Rocha do Chambre) Maciel, Martins, Moreira, Carine, Rumsey LF-TERC-001 (ITS KM589277); Terceira (Rocha do Chambre) Maciel, Martins, Moreira, Carine, Rumsey LF-TERC-003 (ITS KM589273, *trnQ* KM589281, *trnV* KM589322, *matK* KM589329); Terceira (Caldeira de Santa Bárbara) Maciel, Martins, Moreira, Carine, Rumsey LF-TEB-006 (ITS KM589259); Terceira (Caldeira de Santa Bárbara) Maciel, Martins, Moreira, Carine, Rumsey LF-TEB-013 (ITS KM589260, *trnQ* KM589295, *trnV* KM589310, *matK* KM589333); São Jorge (Morro Pelado) Maciel, Martins, Moreira, Carine, Rumsey LF-SJMP-005 (ITS KM589268, *trnQ* KM589298, *trnV* KM589312, *matK* KM589344); Pico (Cabeço dos Mistérios) Maciel, Martins, Moreira, Carine, Rumsey LF-PICM-001 (ITS KM589279, *trnQ* KM589300, *trnV* KM589304, *matK* KM589332); Pico (Cabeço dos Mistérios) Maciel, Martins,

Moreira, Carine, Rumsey LF-PICM-006 (ITS KM589269, *trnQ* KM589283, *trnV* KM589321, *matK* KM589335); Faial (Cabeço do Trinta) Maciel, Martins, Moreira, Carine, Rumsey LF-FATR-002 (ITS KM589271, *trnQ* KM589293, *trnV* KM589309, *matK* KM589340); Faial (Cabeço do Trinta) Maciel, Martins, Moreira, Carine, Rumsey LF-FATR-006 (ITS KM589264, *trnQ* KM589284, *trnV* KM589311, *matK* KM589346).

Leontodon rigens:—São Miguel (Lagoa do Canário) Dias, L.B. Silva LR-SMLC-002 (ITS KM589261, *trnQ* KM589297, *trnV* KM589323, *matK* KM589330); São Miguel (Lagoa do Canário) Dias, L.B. Silva LR-SMLC-004 (ITS KM589266, *trnQ* KM589292, *trnV* KM589319, *matK* KM589337); São Miguel (Monte Escuro) Dias, L.B. Silva LR-SMME-001 (ITS KM589265, *trnQ* KM589291, *trnV* KM589313, *matK* KM589343); São Miguel (Monte Escuro) Dias, L.B. Silva LR-SMME-005 (ITS KM589275, *trnQ* KM589302, *trnV* KM589317, *matK* KM589339); São Miguel (Tronqueira) Moura, Dias, L.B. Silva LR-SMTR-001 (ITS KM589278, *trnQ* KM589294, *trnV* KM589315, *matK* KM589345); São Miguel (Tronqueira) Moura, Dias, L.B. Silva LR-SMTR-005 (ITS KM589263, *trnQ* KM589288, *trnV* KM589308, *matK* KM589334).

Leontodon* × *friasi:—Flores (Burreiro), Silva LF-FLBU-001 (ITS KM589257, *trnQ* KM589289, *trnV* KM589320, *matK* KM589342); Flores (Burreiro), Silva LR-FLBU-002 (ITS KM589270).

Leontodon* × *carreiroi:—São Miguel (Pico da Vara) Dias LR-SMPV-001 (ITS KM589262, *trnQ* KM589296, *trnV* KM589316, *matK* KM589331).

GenBank accessions:—*Leontodon hispidus* L. – Stuessy 15537 (ITS DQ451769). *Leontodon hispidus* L. – Hörandl *et al.* 5389 (ITS DQ451770, *matK* DQ451707). *Leontodon hispidus* L. – Hörandl 1495 (ITS DQ451771). *Leontodon kulczinskii* Popov & Chrshan. – Dobner & Zidorn 98-00113 (ITS DQ451773, *matK* DQ451721). *Leontodon saxatilis* Lam. – Stuessy *et al.* 15453B (ITS AF528489, *matK* DQ451725). *Leontodon saxatilis* Lam. – Hörandl & Hadacek 7076 (ITS DQ451794). *Leontodon anomalus* Ball – Schrott & Gutermann 17067 (ITS DQ451753, *matK* DQ451691). *Leontodon asperrimus* (Willd.) Ball – Schneeweiß *et al.* 8182 (ITS DQ451754, *matK* DQ451692). *Leontodon crispus* Vill. – Gutermann 35682 (ITS AF528488, *matK* AF528430). *Leontodon graecus* Boiss. & Heldr. – Tremetsberger *s. n.* (ITS DQ451765, *matK* DQ451702). *Leontodon berinii* Reichb. – Kuhns & Zidorn 970624h (ITS DQ451756, *matK* DQ451696). *Leontodon incanus* Schrank – Gutermann 37630 (ITS DQ451772, *matK* DQ451709). *Leontodon farinosus* Merino & Pau – Alamillo *et al. s. n.* (ITS DQ451764, *matK* DQ451701). *Leontodon boryi* Boiss. – Rico *s. n.* (ITS DQ451757, *matK* DQ451695). *Leontodon rosani* Ten. – Spitaler & Zidorn CZ-20040413B-1 (ITS DQ451792, *matK* DQ451729). *Leontodon longirostris* (Finch & P.D. Sell) – Gutermann 37111 (ITS DQ451777, *matK* DQ451710). *Leontodon tingitanus* (Boiss. & Reut.) Ball – Gutermann 37432 (ITS DQ45179, *matK* DQ451727). *Leontodon maroccanus* (Pers.) Ball – Spitaler & Zidorn CZ-20030421B-1 (ITS DQ451778, *matK* DQ451715). *Leontodon tuberosus* L. – Tremetsberger *s. n.* (ITS AF528487, *matK* DQ451728). *Leontodon autumnalis* L. – Stuessy 15541 (ITS AF528486, *matK* DQ451694). *Leontodon carpetanus* Lange – Ladero & Gonzalez-Iglesias *s. n.* (ITS DQ451759, *matK* DQ451699). *Leontodon duboisii* Sennen – Bosc *s. n.* (ITS DQ451763, *matK* DQ451700). *Leontodon muelleri* (Sch. Bip.) Fiori – Ortiz & Tremetsberger 7/04 (ITS DQ451783, *matK* DQ451716). *Leontodon laciniatus* (Bertol.) Widder – Ehrendorfer *s. n.* (ITS DQ451774). *Leontodon palisiae* Izuzq. – Guerra 1412 (ITS DQ451787, *matK* DQ451718). *Leontodon montanus* Lam. Hörandl 1498 (ITS DQ451782, *matK* DQ451713). *Leontodon cantabricus* Widder – Alamillo *et al. s. n.* (ITS DQ451758, *matK* DQ451720). *Leontodon helveticus* Mérat – Hörandl 1494 (ITS DQ451766, *matK* DQ451704). *Leontodon pyrenaicus* Gouan – Schneeweiß & Schönschwetter 8829 (ITS DQ451788, *matK* DQ451719). *Leontodon microcephalus* Boiss. – Rico *s. n.* (*matK* DQ451711). *Leontodon cichoriaceus* Boiss. – Gutermann 35155 (ITS DQ451760, *matK* DQ451698). *Leontodon croceus* Haenke – Hörandl 2695 (ITS DQ451762, *matK* DQ451697). *Leontodon rilaensis* Hayek – Dobner & Zidorn 98-00084 (ITS DQ451791, *matK* DQ451722). *Leontodon montaniformis* Widder – Hörandl *et al.* 4615 (ITS DQ451780, *matK* DQ451714). *Reichardia tingitana* (L.) Roth – GAT-bg44 (ITS AJ633303). *Reichardia tingitana* (L.) Roth – KEW 223-70-02 090 (*matK* DQ507979).