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Article

Appearances Can Be Deceptive: Morphological, Phylogenetic, and Nomenclatural Delineation of Two Newly Named African Species Related to *Frankenia pulverulenta* (Frankeniaceae)

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Abstract: *Frankenia* is a morphologically complex genus with some species exhibiting few diagnostic characters and significant morphological variability. This led to misidentification or synonymisation of many names, based on one or a few diagnostic traits. This phenomenon affects the annual sea-heath, *F. pulverulenta*, a Eurasian-Mediterranean herb that has become subcosmopolitan, in which several entities were included due to shared features, namely the annual lifespan or the flattened leaves. However, this fact also extends to shrubby species, such as the Madeiran *F. cespitosa*. Here, integrative taxonomic studies were undertaken, encompassing detailed morphological descriptions of macro- and microcharacters, along with molecular phylogenetic analyses of both nuclear ribosomal (ITS1-5.8S-ITS2 region) and plastid (*matK* gene) DNA sequence data, and biogeographic data. The research resulted in the most complete phylogenetic trees of *Frankenia* to date, leading to the reinstatement of two African species broadly differing from *F. pulverulenta*. Firstly, *F. florida* L.Chevall., a name applied to a species occurring in the Saharan regions of Algeria, Morocco, Mali and Mauritania, is often accepted as a variety or subspecies of the annual sea-heath. In contrast, *F. densa* Pohnert, a species endemic to Namibia and northern South Africa, is synonymised with *F. pulverulenta*. However, since those two names were later homonyms of two Chilean and Australian plants, they were deemed illegitimate upon publication. Consequently, two new names are proposed for them: *F. sahariensis* and *F. dinteri*, respectively. The substantiation of both entities as independent species is provided by data on morphology, distribution, ecology and molecular phylogenetics, which demonstrate their distinctiveness from *F. pulverulenta*. Nomenclatural synonymy and types are also presented for all concerned names, including the designation of two new lectotypes.

Keywords: African flora; *Frankenia*; Frankeniaceae; ITS; *matK*; new names; nomenclature; phylogenetic analyses; taxonomy

1. Introduction

The genus *Frankenia* L. is the sole member currently recognised within Frankeniaceae Desv., *nom. cons.*, when expanded to include *Anthobryum* Phil., *Beatsonia* Roxb., *Hypericopsis* Boiss. and *Niederleinia* Hieron. [1–4], and references therein. So broadly treated about 80–90 species are often accepted that are distributed in temperate or tropical regions, commonly in Mediterranean-type areas around the world, but with ca. 40 species found in Australia [5,6]. Most members of *Frankenia* exhibit a woody or suffruticose habit, erect to prostrate, sometimes densely pulvinate or with subspinescent branches, but some others are prostrate to ascendant annual herbs [7,8]. With very few exceptions, most species usually grow on saline soils, including coastal and inland salt marshes and gypsum- or calcium-rich outcrops [9], often enduring semi-arid to arid climates that mostly show prevalent winter rainfall

[10]. One such exception is the South African narrow endemic *F. fruticosa* J.C.Manning & Helme, which occurs on quartz soils [11]. Because most taxa grow under strongly stressing conditions, many endemics are found which are restricted to small areas or archipelagos [12], whereas others such as the annual sea-heath, *F. pulverulenta* L., have become subcosmopolitan [13,14]. These peculiar lifestyles have led to acquisition of specialised structures, such as salt-secreting multicellular glands that often generate whitish salt crusts on leaves and stems [8]. This characteristic is shared with representatives of some related families in Caryophyllales, such as Plumbaginaceae Juss., *nom. cons.*, or Tamaricaceae Link, *nom. cons.* [15], though in each case they exhibit distinct structural features [16].

From a taxonomic perspective, the first comprehensive treatment of the genus was undertaken by Niedenzu [7], who accepted *Frankenia*, *Anthobryum*, *Beatsonia*, *Hypericopsis* and *Niederleinia* as distinct genera. Just a few years later, Summerhayes [5] published a revision of the Australian taxa and described most of the species currently accepted. More recently, Whalen [17] conducted a taxonomic study on the American Frankeniaceae, where a detailed morphological revision was presented along with a discussion on the status of the South American genera *Anthobryum* and *Niederleinia*, which she synonymised to *Frankenia*. Consequently, though being a good starting point for a treatment of the whole genus, Niedenzu's [7] account is incomplete and requires a thorough update. Among the partial monographs, different authors have presented taxonomic arrangements for the genus in large regions of Eurasia and Africa. After the revisions for Flora of the USSR [18], Flora europaea [19] and Flora iranica [20], with some additions by Lomonosova [21], up to seven species plus twelve infraspecific taxa (subspecies, varieties, and forms) are widely accepted.

For Africa, the revision of the Moroccan taxa by Nègre [22] stands out, in which the author studied in detail the circumscription and synonymy of taxa previously summarised by Jahandiez and Maire [23] and Emberger and Maire [24] for Morocco and neighbouring areas. He accepted there four species plus fourteen subspecific and varietal taxa. More recently, Crespo et al. [12] have clarified the circumscription of some neglected names concerning southern African plants and have recognised seven species, most of them endemics often misidentified with other widespread relatives. However, the diverse taxonomic criteria adopted within the last decades by authors dealing with *Frankenia* in diverse territories have generated quite heterogeneous treatments that much difficult a global understanding of the genus for most taxonomists.

Furthermore, molecular studies including species of *Frankenia* are also scarce. In a work focused on relationships between Frankeniaceae and Tamaricaceae based on nrDNA sequences, Gaskin et al. [3] included eight *Frankenia* species from North America, Australia, and Eurasia, such as the outstanding *F. persica* (Boiss.) Jaub. & Spach (≡ *Hypericopsis persica* Boiss.). The most recent phylogenetic studies on the genus were published by Crespo et al. [12], who presented a preliminary tree based on ITS sequences including 16 species from Eurasia and Africa, which served as a basis to recover or describe some neglected species from South Africa often misidentified with *F. pulverulenta*.

Very few species in this genus are annual or biennial. In particular, the annual sea-heath, *Frankenia pulverulenta*, is a Eurasian-Mediterranean ephemeral herb that today is broadly distributed around the world [14], occurring in saline soils disturbed by human activities [13–17]. According to Crespo et al. [12], it is typically a prostrate plant with many-branched, non-rooting stems, densely and minutely pubescent on one side; leaves flat, broadly obovate-cuneate, subconcolorous, glabrous on the adaxial surface and variably hairy on the abaxial surface, rounded and emarginate at the apex and cuneate at the base; flowers pentamerous, small, axillary, and solitary, scattered; calyx up to 5 mm long; corolla up to 5 mm, pinkish; capsule 3-carpelar; placentas 3, with 12–20 ovules each; seeds numerous, small (up to 0.5–0.7 mm long), ellipsoid, monosulcate, with testa weakly and irregularly ornamented, very sparsely covered with small-sized papillae (4–17 µm), homogeneous (conical-obtuse) in shape.

Recent investigations conducted in southern Africa, through both fieldwork and herbarium studies [12], revealed the existence of peculiar populations showing some superficial resemblance to *F. pulverulenta*, mostly on account of their flattened roundish to broadly ovate-oblong leaves. However, those authors demonstrated that several distinct biological entities had been overlooked

under that designation within the last decades. On the one hand, the name *F. nodiflora* Lam., often synonymised to *F. pulverulenta*, was restored for littoral populations of creeping prostrate shrublets, with concolorous glabrous leaves and dense glomerular inflorescences, occurring in saltmarshes and salt pans of Cape Flats (Western Cape Province). On the other, *F. nummularia* M.B.Crespo, M.Á.Alonso, Mart.-Azorín, J.L.Villar & Mucina was newly described for populations of creeping prostrate shrublets, with discolored glabrous leaves and loosely dichasial, usually widely branched inflorescences, from inland salt-pans and saline river beds in the southwestern part of the Karoo Region (Northern and Western Cape Provinces). These had usually been misidentified as the annual sea-heath, *F. pulverulenta*.

Similar research on other African populations of annual or short-lived perennial plants usually related to *F. pulverulenta* also unveiled surprising data. Firstly, populations of a North African plant, occurring in saline substrates of the western Sahara regions, were described as *F. florida* L.Chevall., a later homonym of the Chilean *F. florida* Phil. and hence an illegitimate name according to the *Shenzhen Code* (hereafter ICN, [25]). That North African name has often been treated as *F. pulverulenta* var. *florida* Maire or subsp. *florida* (Maire) Maire [4,26], or also as merely a synonym of the annual sea-heath. Secondly, populations of a remarkable species growing on saline soils of inland Namibia were described as *F. densa* Pohnert, a later homonym of the Australian *F. densa* Summerh., which is hence illegitimate and unavailable for use. However, despite several characteristics allow separation from the morphologically close *F. pulverulenta*, Pohnert's name is currently reduced to synonymy of the latter [4].

In the present contribution, as part of our ongoing integrative taxonomic studies on the genus *Frankenia*, the position and phylogenetic relationships of both *F. florida* L.Chevall. and *F. densa* Pohnert are studied. Morphological, distributional, ecological, and molecular phylogenetic data are shown that support recognition of both entities as independent species, not related to *F. pulverulenta*, for which the new names *F. sahariensis* and *F. dinteri* are respectively proposed. Nomenclatural synonyms and types are also reported for all concerned names, including designation of two new lectotypes.

2. Materials and Methods

2.1. Morphological and Habitat Studies

Detailed morphological observations were conducted on both living plants from wild populations and dried herbarium specimens sourced from the herbaria ABH, BM, BOL, G-DC, K, LINN, MA, MPU, NBG, P, and W (acronyms according to Thiers [27]), using an OLYMPUS SZX7 binocular microscope. Digital sheets from the herbaria GH, GZU, HBG, JE, LY, M, MO, PRE, RSA, US, WAG, and Z were reviewed as well. A list of the herbarium material examined, including nomenclatural types, is reported for each species, with barcode numbers are provided after each herbarium acronym when available.

Scanning Electron Microscope (SEM) micrographs of seeds were captured using a JEOL JSM-IT500HR operating at 15 kV. No special treatment was needed for the material before observation. A minimum of 10 mature seeds from different individuals of each studied species (Table 1) were carefully examined. The samples were affixed to metallic stubs and coated with 10 nm of platinum in a QUORUM Q150T ES Plus sputter coater. Measurements on the SEM micrographs were conducted using ImageJ v.1.8.0 [28].

The authors of the taxa cited follow the guidelines of IPNI [29]. Nomenclatural issues accord with the *Shenzhen Code* (ICN; [25]). For the new species from southern Africa, orthography of geographical names and grid-number system follow Leistner and Morris [30], and the grid-number system accord with the National Geospatial Information [31]. The geographic coding of the collection sites (e.g., 2816BB or -BB, always linked to 4-digit code) refers to the centre point for a 15' latitude × 15' longitude sub-tile as defined by the South African topographical map sheet referencing system [31]. This system is broadly known as 'quarter degree square' (QDS) grid, since each topographic

map sheet is considered a tile (coded, for instance, as 2816), divided into four sub-tiles (coded, for instance, as -BB).

The bioclimatic and biogeographic classification of southern Africa is based on Mucina and Rutherford [32]. For North African species, the biogeographical characterisations of Quézel [33] and Takhtajan [34] were also considered. Distribution maps were created using cartography tools from Google Earth.

Table 1. Seed samples of *Frankenia* for SEM studies, with provenance and herbarium vouchers.

Taxon	Locality	Herbarium voucher
<i>F. sahariensis</i>	Mauritania: Iouik	P-05038748
<i>F. dinteri</i>	South Africa: Klipfontein	ABH-76891
<i>F. pulverulenta</i>	Spain: Alicante, Orxeta	ABH-7952

2.2. Molecular analyses

Silica gel-dried materials and herbarium vouchers were utilised for total DNA extraction following a modified 2× cetyltrimethylammonium bromide (CTAB) protocol [35]. When herbarium material was unavailable for sampling, silica-gel dried material from wild populations (one sample per population) of each taxon was used, since the phylogenetic trees remained unchanged after addition of new samples from the same population. Total DNA was then purified using MOBIO minicolumns and typically stored in 0.1× TE buffer [10 mM Tris-HCl, 1 mM ethylenediaminetetraacetic acid (EDTA), pH 8.0]. The internal transcribed spacer (ITS) region (comprising the ITS1 spacer, the 5.8S gene, and the ITS2 spacer) of nuclear ribosomal DNA (nrDNA) was amplified using the ITS5 and ITS4 primers [36], while the Maturase K (*matK*) gene of plastid DNA (cpDNA) was amplified using the XF (TAATTTACGATCAATTCAATTTC) and 5R (GTTCTAGCACAAAGAAAGTCG) primers [37]. Amplifications were conducted in a total reaction volume of 25.5 µl, which included 12.5 µl of DreamTaq PCR Master Mix (2×), 10 µl of distilled water (Thermo Scientific, Waltham, MA, USA), 0.5 µl of 0.4% bovine serum albumin (BSA), 0.5 µl of dimethyl sulfoxide (DMSO), 0.5 µl of each primer (10 pmol/µl), and 1 µl of template DNA, all processed on a 9700 GeneAmp thermocycler (Applied Biosystems). The PCR program for ITS involved an initial step of 2 min at 95 °C, followed by 35 cycles of 95 °C for 1 min, 53 °C for 1 min, and 72 °C for 2 min, concluding with a final extension at 72 °C for 5 min. The PCR program for *matK* included an initial step of 2 min at 94 °C, followed by 32 cycles of 94 °C for 1 min, 53 °C for 1 min, and 72 °C for 1 min and 30 seconds, finishing with a final extension at 72 °C for 4 min.

Sequencer 4.1 (Gene Codes Corp., Ann Arbor, MI, USA) was utilised to assemble complementary strands and verify software base-calling. Sequence alignment was conducted using MUSCLE [38] within MEGA X v.10.2.6 [39], supplemented by minor manual adjustments to create the final aligned matrix. The analyses incorporated fifty-six samples representing twenty species of *Frankenia*, encompassing the primary Eurasian and African groups within the genus, and including *Myricaria germanica* L., *Reaumuria alternifolia* (Labill.) Britten, *R. songarica* (Pall.) Maxim., and *Tamarix gallica* L. as outgroups.

Two datasets were constructed: One for the ITS region (including 54 *Frankenia* sequences plus 4 outgroup sequences, totalling 720 positions), and another for the *matK* gene (comprising 38 *Frankenia* sequences plus 3 outgroup sequences, with a total of 829 positions). Specifically for this study, a total of 38 *matK* plus 28 ITS sequences were generated (Table 2), while the remaining ones were sourced from various plant databases according to GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) availability (see [12]). As a result, only a few accessions in the ITS and *matK* datasets originate from different plant sources. Accessions listed in GenBank as “*Reaumuria hypericoides* Willd.” are represented in our trees as *R. alternifolia*, given that the former name is a superfluous synonym of the latter and, as such, has priority. Likewise, the ITS accession OR183467, previously filed as “*Frankenia hirsuta* L.” (voucher ABH-45933!), indeed corresponds to the closely related species *F. salsuginea* Adıgüzel & Aytaç (Table 2).

Phylogenetic analyses of both the ITS region and the *matK* gene were conducted using Maximum Parsimony (MP), Maximum Likelihood (ML), and Neighbour Joining (NJ) methods. The MP analysis was performed using both PAUP with heuristic search options based on the Nearest Neighbour Interchange (NNI) strategy, and MEGA with heuristic search options applying the Subtree-Pruning-Rerooting (SPR) method with search level 1 [40] for comparative results, with 10,000 replicates. ML [41] and NJ [42] analyses were also executed in MEGA, alongside the selection of the optimal model of DNA substitutions for each method using the Akaike Information Criterion (AIC, [43]); the models with the lowest Bayesian Information Criterion (BIC) scores were deemed most suitable for describing the substitution patterns in the ML and NJ analyses. Additionally, jModelTest 2.1.10 [44] was utilised to identify the best model of DNA substitutions for the Bayesian Inference (BI) analyses, again applying the AIC. Phylogenetic reconstructions for Maximum Likelihood (ML) and evolutionary distances for the Neighbor-Joining (NJ) method were estimated using the Kimura 2-parameter (K2) model [45] for the ITS matrix. This model allowed for some sites to be evolutionarily invariable, with 26.46% of sites fitting this criterion (+I). In contrast, the *matK* matrix utilised the Tamura 3-parameter (T92) model [46], coupled with a discrete Gamma distribution ($G = 1.0742$) to model rate variation among sites. For these analyses, all sites in the matrices were considered. To ensure comparability, ambiguous positions were removed for each sequence pair using the pairwise deletion option. This removal did not result in significant differences in the obtained phylogenies, although it affected support percentages for a few branches. Support for all methods was assessed using bootstrapping [47] with 10,000 replicates, retaining only 10 trees per replicate. Clades with bootstrap percentage (BP) values of 50–74% were considered weakly supported, 75–89% moderately supported, and 90–100% strongly supported.

Furthermore, Bayesian inference (BI) analyses were conducted using MrBayes 3.2 [48], where the Markov Chain Monte Carlo (MCMC) algorithm was executed for 10 million generations, with samples taken every 1000 generations. Two independent runs were carried out. The analyses employed the General Time Reversible (GTR) + proportion of invariant sites (I) + Gamma distribution (G) model, as suggested by the results from jModelTest based on the Akaike Information Criterion (AIC). The initial 25% of generations were excluded (burninfrac = 0.25), and the remaining trees were utilised to compile a posterior probability (PP) distribution through a 50% majority-rule consensus. Clade support was again evaluated using Bootstrap analysis [47], with 10,000 replicates while retaining only 10 trees per replicate. Clades with $PP \geq 0.95$ were regarded as strongly supported.

Table 2. List of outgroups and *Frankenia* accessions used for the phylogenetic analyses, with data on provenance and source plus Genbank codes of the ITS and *matK* accessions utilised.

Taxon	Provenance (herbarium voucher)	Source	ITS	Source	<i>matK</i>
<i>Tamarix gallica</i> L.	France: Saintes Maries de la Mer (ABH-57865)	Villar et al. [49]	MH626294	–	–
	Italy: Sardinia	Meimberg et al. [50]	–	–	AF204861
<i>Myricaria germanica</i> L.	Kazakhstan: Zajsanskaya depression (LE)	Zhang et al. [51]	KJ808607	–	–
	China: Unspecified (CPG-11863)	Chen et al. [52]	–	–	KX526795
<i>Reaumuria alternifolia</i> (Labill.) Britten ¹	Azerbaijan: Caucasus (MW)	Zhang et al. [53]	KJ729627	–	–
<i>Reaumuria songarica</i> (Pall.) Maxim.	China: Xinjiang (M)	Zhang et al. [51]	OQ617495	–	–
	China: Xinjiang (TURP)	Song et al. [54]	–	–	MT918094
<i>Frankenia anneliseae</i> M.B.Crespo & al.	South Africa: Klipfontein (ABH-76891)	Crespo et al. [12]	OR183455	–	–
	South Africa: Skoverfontein (ABH-83196)	Crespo et al. [12]	OR183456	This paper	PV258653
	South Africa: Klipfontein (ABH-76872)	–	–	This paper	PV258654
	Spain: Huelva, Lepe, El Terrón (ABH-83544)	This paper	PV241633	This paper	PV258655

<i>F. boissieri</i> Reut. ex	Portugal: Algarve, Vale de Parra (ABH-73553)	This paper	PV241634	–	–
<i>F. cespitosa</i> Lowe	Portugal: Madeira Is., Porto Santo, Morenos (MA-902612)	This paper	PV241635	–	–
	Spain: Canary Is., Las Palmas de Gran Canaria, Isleta (ABH-83612)	Crespo et al. [12]	OR183458	This paper	PV258656
<i>F. capitata</i> Webb & Berthel.	Spain: Canary Is., Lanzarote, Teguise (ABH-83884)	This paper	PV241636	–	–
	Spain: Canary Is., Lanzarote, Yaiza (ABH-83881)	This paper	PV241637	This paper	PV258658
	Spain: Canary Is., Lanzarote, Yaiza (ABH-83880)	–	–	This paper	PV258657
<i>F. composita</i> Pau & Font Quer	Morocco: Al Hoceïma, Cala Iris (ABH-81590)	Crespo et al. [12]	OR183459	This paper	PV258659
	Spain: Murcia, El Carmolí (ABH-84195)	This paper	PV241638	This paper	PV258660
	Spain: Alicante, Santa Pola (ABH-79956)	Crespo et al. [12]	OR183462	This paper	PV258663
	Morocco: Nador, Punta Charrana (ABH-54294)	Crespo et al. [12]	OR183461	This paper	PV258662
<i>F. corymbosa</i> Desf.	Morocco: Al-Hoceïma (ABH-54526)	Crespo et al. [12]	OR183460	–	–
	Spain: Murcia, Cabo Cope (ABH-83531)	Crespo et al. [12]	OR183463	This paper	PV258661
	Namibia: Goageb (ABH-76804)	This paper	PV241642	This paper	PV258666
<i>F. dinteri</i> M.Á.Alonso & al., nom. nov.	South Africa: Onseepkans (ABH-83234)	This paper	PV241639	This paper	PV258667
	South Africa: Daberas Farm (ABH-83264)	This paper	PV241640	This paper	PV258665
	South Africa: Augrabies (ABH-83265)	This paper	PV241641	This paper	PV258664
	Spain: Canary Isl., Tenerife (ABH-79975)	Crespo et al. [12]	OR183464	This paper	PV258668
	Spain: Canary Isl., Tenerife, Güímar (ABH-83613)	Crespo et al. [12]	OR183465	–	–
<i>F. ericifolia</i> C.Sm. ex DC., nom. cons. prop.	Spain: Canary Isl., Tenerife, Granadilla de Abona (ABH-83873)	This paper	PV241646	This paper	PV258669
	Spain: Canary Isl., Tenerife, Malpaso, IA3069 (MA)	This paper	PV241643	This paper	PV258670
	Spain: Canary Isl., Lanzarote, Caleta del Mojón Blanco (ABH-83889)	This paper	PV241644	This paper	PV258671
	Spain: Canary Isl., Lanzarote, Risco de Famara (ABH-83893)	This paper	PV241645	This paper	PV258672
<i>F. fruticosa</i> J.C.Mannig & Helme	South Africa: Moedverloren (ABH-76898)	Crespo et al. [12]	OR183466	–	–
<i>F. hirsuta</i> L.	Italy: Puglia, Bari (ABH-84234)	This paper	PV241648	This paper	PV258673
	Cyprus: Akamas (MA-526424)	This paper	PV241647	–	–
	Morocco: Sidi Ifni to Oued Noun (MA-	Crespo et al.	OR183468	This	PV258674
<i>F. ifniensis</i> Caball.	Morocco: El Farsia (MA-712824)	This paper	PV241649	–	–
	Morocco: Gelmim (MA-902279)	This paper	PV241650	–	–
	Libya: Cyrenaica, Jbel Akhdar (MA-	This paper	PV241652	–	–
<i>F. laevis</i> L.	France: Aude, Étang de La Palme (ABH-	Crespo et al.	OR183469	This	PV258676
	Spain: Mallorca, Conejera (ABH-57810)	This paper	PV241651	This	PV258675
<i>F. nummularia</i>	South Africa: Kookfontein River (ABH- ²⁰⁰⁰)	Crespo et al. ²⁰⁰⁰	OR183471	–	–
M.B.Crespo & al.	South Africa: Tankwa Karoo (ABH- ²⁰⁰⁰)	Crespo et al. ²⁰⁰⁰	OR183472	This	PV258677
<i>F. pseudoericifolia</i> Rivas Mart. & al.	Portugal: Cape Verde, São Antão (MA-0906845)	Crespo et al. [12]	OR183473	–	–
	South Africa: Redelinghuis (ABH-77205)	Crespo et al.	OR183474	–	–

	South Africa: Skoverfontein (ABH-83195)	This paper	PV241657	–	–
	Spain: Teruel, Alcañiz (ABH-73564)	Crespo et al.	OR183475	–	–
	Spain: Alicante, Cabo de las Huertas (ABH-74763)	This paper	PV241653	This paper	PV258678
	Spain: Albacete, Fuentealbilla (ABH-40820)	This paper	PV241654	–	–
<i>F. pulverulenta</i> L.	Morocco: Melga-el-Ouidane (ABH-59986)	This paper	PV241655	This paper	PV258679
	Spain: Canary Isl., Tenerife, Puerto de la Cruz (ABH-79974)	Crespo et al. [12]	OR183477	This paper	PV258680
	Italy: Puglia, Torre Specchiola (ABH-84244)	This paper	PV241656	This paper	PV258681
	Spain: Alicante, Cabo de las Huertas (ABH-41853)	Crespo et al. [12]	OR183476	–	–
<i>F. repens</i> (P.J.Bergius)	South Africa: S of Hondeklipbaai (ABH-76862)	Crespo et al. [12]	OR183479	–	–
Fourc.	South Africa: Velddrift (ABH-76849)	–	–	This paper	PV258682
	South Africa: S of Groenrivier (ABH-76868)	Crespo et al. [12]	OR183478	This paper	PV258683
<i>F. sahariensis</i>	Morocco: Guelmim to Tan Tan (MA-786164)	This paper	PV241658	This paper	PV258684
M.Á.Alonso & al., nom. nov.	Morocco: Sidi Ifni (MA-913227)	This paper	PV241659	This paper	PV258685
<i>F. salsuginea</i> Adığuzel & Aytaç ²	Turkyie: Tuz Gölü, salty lagoon (ABH-45022)	Crespo et al. [12]	OR183467	This paper	PV258687
	Turkyie: Dörtyol (MA-561567)	This paper	PV241660	This paper	PV258686
<i>F. thymifolia</i> Desf.	Algeria: Bougrob, Chott Cherguí (ABH-1402)	Crespo et al.	OR183481	This paper	PV258688
	Spain: Zaragoza: Bujaraloz (ABH-75454)	Crespo et al. [12]	OR183480	This paper	PV258689
<i>F. velutina</i> Brouss. ex DC	Morocco: Essaouira (ABH-79929)	Crespo et al. [12]	OR183482	This paper	PV258690

¹Filed in GenBank as the synonym name *R. hypericoides* Willd. (nom. illeg.); ² Filed in GenBank as *F. hirsuta* (see Crespo et al. [12]).

3. Results

3.1. Taxonomic treatment and description of new taxa

3.1.1. *Frankenia sahariensis* M.Á.Alonso, M.B.Crespo, Abad-Brotos, Mart.-Azorín & J.L.Villar, nom. nov.

- = *Frankenia florida* L.Chevall. in Bull. Herb. Boissier ser. 2, 3(9): 768. 1903 [replaced synonym], *nom. illeg.* [non Phil. in Anales Univ. Chile 41: 676. 1872] = *F. pulverulenta* var. *florida* Maire in Bull. Soc. Hist. Nat. Afrique N. 27: 210. 1936 = *F. pulverulenta* subsp. *florida* (Maire) Maire, Cat. Pl. Maroc 4: 1071. 1941. *Type*: ALGERIA. [El Menia Province:] El Goléa [currently, El Menia], in arenosis salsis. April 1902, L. Chevallier 404 (**lectotype, designated here**: P-06618528!, Figure 1; isolectotypes: P-05145114!, P-06618529!, P-06618525!, MPU-007119!, MPU-007120!, US-00679979 [digital image!], GZU-000269792 [digital image!], JE-00003246, JE-00003247 [digital image!], LY-0084391 [digital image!], WAG-0249595 [digital image!], MO-357730 [digital image!]).
- = *F. intermedia* var. *annua* Caball. in Trab. Mus. Ci. Nat., Ser. Bot. 30: 30. 1935. *Type*: MOROCCO. [Western Sahara]: In collibus arenosis insolatis prope Sidi-Ifni, 13 June 1934, A. Caballero (**lectotype, designated here**: MA-78660!; isolectotype: MPU-300233!).
- *F. pulverulenta* subsp. *floribunda* sensu Quézel & Santa, Nouv. Fl. Algérie: 685. 1963 [sphalm.]. *Note*: The subspecific epithet, “*floribunda*”, is most likely a mistaken desinence for “*florida*”, not a formally proposed name.

Description: Herbs annual or short-lived perennial, weakly lignified at base, loosely branched, tap-rooted, and mostly glabrous to sparsely puberulous. Stems non-rooting, usually prostrate to decumbent, 5–30 cm long, often with divaricate branches, with internodes up to 2.5 cm long; young branchlets yellowish to reddish, mostly with scattered whitish depositions, glabrous or shortly and

densely puberulous, with minute curled or hooked trichomes (0.1–0.2 mm long) only on one side and near the nodes. *Leaves* opposite, patent to erect-patent, green or sometimes reddish, and mostly with scattered glands bearing whitish depositions; *petiole* 0.5–0.8 × 0.2–0.3 mm, flattened, and tapering distally; *sheath* extending along petiole margins to blade, loosely ciliate to subglabrous, with (2–)4–5 pairs of lateral cilia, unequal in length (0.2–0.5 mm long), whitish, cylindric to flattened, and obtuse or acute at the apex; *leaf blade* (1.8–)2.5–4 × 0.5–0.7 mm, triangular-ovate to oblong-ovate, mostly subfalcate upwards, with obtuse apex and cordate to rounded base, often strongly revolute on margins or flattened in the lower third, somewhat fleshy and glaucescent, concolorous or sometimes slightly paler abaxially, glabrous on the upper side, loosely hairy beneath with short straight trichomes 0.1–0.2 mm long; *midrib* notably thickened, tapering slightly towards the apex, continuous with the petiole and raised abaxially, and extending for most of the blade length. *Flowers* pentamerous, perfect, sessile, solitary on dichotomies or borne in axillary or terminal dichasial groups, usually condensed and glomerular; *floral bracts* 2, leaf-like but smaller, 2–2.5 × 0.5–0.7 mm, erect to erect-patent, connate at base and shortly covering the calyx base for ca. 0.5 mm, about half the calyx length; *bracteoles* 2, bract-like but smaller, 0.5–1.5 × 0.4–0.6 mm, alternating with bracts, erect, strongly revolute on margins, about half the calyx length, with petiole ca. 0.5 mm long, adnate to the calyx base. *Calyx* 2.5–4.2 × 0.6–1 mm, tubular at anthesis to gradually fusiform later, often twisted, straight, indurate, sessile, reddish or rarely yellowish, prominently 5-ribbed, entirely glabrous or densely papillate (with a heterogeneous whitish indumentum of long flattened papillae 0.2–0.3 mm long, globose-claviform papillae ca. 0.1 mm long, and minute globose vesicles), only between the glabrous thickened ribs, and sometimes with scattered whitish depositions; *teeth* 5, 0.5–1 mm long, erect, triangular, acute, cucullate, shortly mucronate at apex (mucro ca. 0.1–0.2 mm long), narrowly membranous and shortly papillate on margins. *Petals* 5, 4–6 × 1–1.5 mm, long exceeding the calyx, obovate-cuneate, pinkish-mauve but whitish below, slightly overlapping laterally, exceeding about half to two-thirds the length of calyx; *claw* 2–2.5 × 0.3–0.4 mm, narrowly cuneate, tapering to blade, yellowish, and partly hidden into the calyx tube; *ligule* 1.5–2 × 0.2–0.3 mm, narrowly oblanceolate, longitudinally adnate to the claw, the free apex ca. 0.2–0.4 mm long, ovate-oblong, obtuse to subacute, and entire; *blade* 2.3–3.5 × 1–1.5 mm, broadly obovate-cuneate, rounded at apex, irregularly erose-denticulate. *Stamens* 6, in two unequal whorls, overtopping ca. 1.5 mm the calyx teeth at anthesis; filaments 3.5–5.5 mm long, whitish, expanded ca. 0.5 mm wide in the lower part but gradually tapering and filiform in the distal part; *anthers* 0.6–0.8 mm long, yellowish, ellipsoid, versatile. *Ovary* ca. 1.5 mm long, ellipsoid, subtrigonous, 3-carpelar; *placentas* 3, parietal-basal, extending up to the lower half to two-thirds of carpel wall length, with ventral traces moderately to profusely branched; *ovules* 9–12 per placenta, attached along most of the placenta by erect funiculi ca. 0.1 mm long. *Style* 3–4 mm long, terete, whitish, with 3 *stylar branches* filiform, 0.5–0.8 mm long, whitish. *Capsule* 1.4–2 × 0.8–1 mm, ovoid-ellipsoid, subtrigonous, hidden in the calyx tube, early dehiscent. *Seeds* 24–30 per capsule, 0.5–0.8 × 0.2–0.3 mm, sulcate on one side, ellipsoid, brown, darker at the funicular part, and developing rapidly even before the flower has completely withered; *testa* thin, not mucilaginous, with a surface weakly and irregularly ornamented with a subrectangular-reticulate pattern, finely striate, covered with small-sized papillae 8–17 μ m long, homogeneous in shape, globose to conical-obtuse, sessile, more densely disposed on the distal part.



Figure 1. Lectotype of *Frankenia sahariensis* from El Goléa (currently El Menia), Algeria, L. Chevallier 404 (P-06618528). Scale bar = 1 cm (on the small upper label). © Muséum National d'Histoire Naturelle, herbarium collections, Paris (reproduced with permission).

Etymology: The specific epithet (*sahariensis*, *-e*) refers to the Sahara Desert, the native area of the species. The name replaces the illegitimate “*F. florida* L.Chevall.”, a later homonym of the Chilean “*F. florida* Phil.” (see below). The type of the former was collected in 1902 and distributed by Louis P.D. Chevallier with number 404 of his exsiccata *Plantae Saharae Algeriensis*.

Phenology: Flowering in early January–early June (occasionally in August–September), fruiting in February–Juny (occasionally in September–October).

Habitat and distribution: *Frankenia sahariensis* is found in mostly sandy soils, in subsaline depressions often along ravines and wadies, from 0–1300 m elevation. It is endemic to the western parts of the Sahara Desert [55], south to the High Atlas Range, spreading from the Atlantic coast of northern Mauritania and southern Morocco to central and eastern Algeria and northwestern Mali (Figure 2). Biogeographically, and according to the current data, it is endemic to the western parts of the Saharan province of the Saharo-Arabian region of Takhtajan [34]. In this vast territory, *F. sahariensis* occurs in halophilous vegetation types within the Oceanic Saharan, Western Saharan, Northwestern Saharan, and Steppe-Northern African domains of Quézel [33].

Nomenclatural remarks: Chevallier [56] first described this remarkable plant after his collections near El Goléa (currently El Menia), in the Saharan region of southern Algeria. It was named “*F. florida*”, most probably due to the outstanding showy flowers it exhibits at anthesis. However, the earlier homonym *F. florida* Phil. had already been used for a Chilean congener [57], a fact that made Chevallier’s name illegitimate (Art. 53.1 of the ICN) and unavailable for use. Nonetheless, since the Saharan plant somewhat resembles *F. pulverulenta* (see below), it has often been subordinated to the latter at different infraspecific ranks. First, Maire [58] accepted it as a variety, and indirectly validated the name *F. pulverulenta* var. *florida* Maire (Art. 58.1 of the ICN). Later, this basionym was treated by Maire [24] at subspecies rank, a currently broadly accepted combination (see [4,59]). Nonetheless, when treated at specific rank no previous valid names are available for the Saharan plant, and therefore a replacing name, *F. sahariensis* nom. nov. (Art. 6.11 of the ICN), is proposed here for the illegitimate *F. florida* L.Chevall.

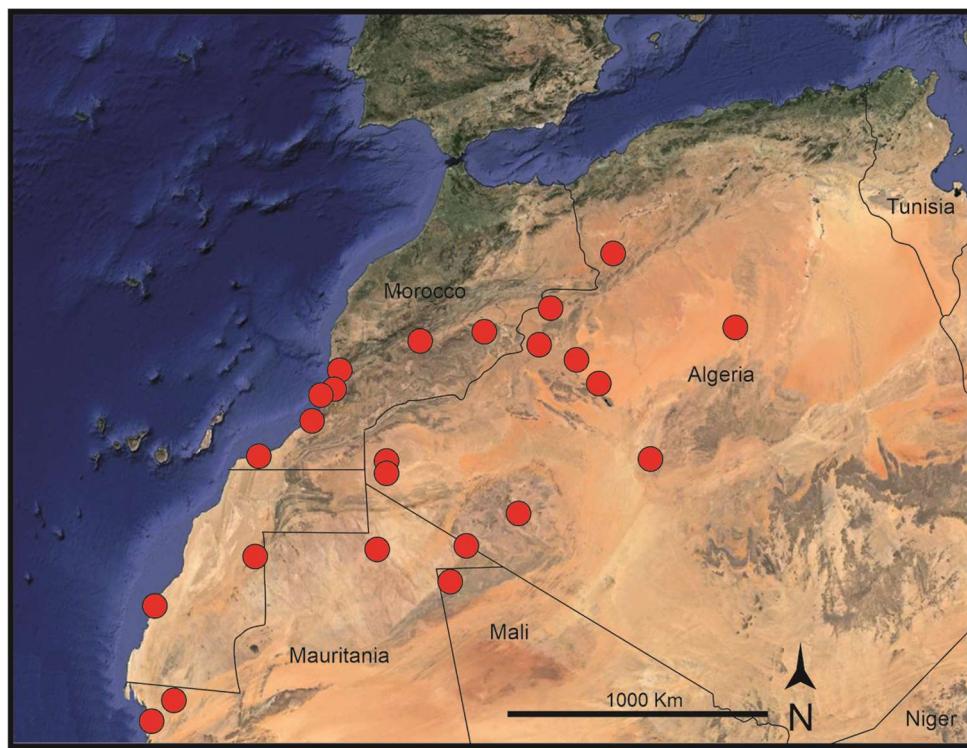


Figure 2. *Frankenia sahariensis*. Distribution map of the studied material.

Other studied material: ALGERIA (DZA). **Béni Abbès Province:** Sahara, Moyenne vallée de la Saoura, June 1941, Volkonsky (MPU-300246!). Sahara: Embouchure de la Saoura, May 1926, Balachowsky (MPU-300247!). **Djanet Province:** Sahara Central, Tassili N’Ajjer, lieux humides à Ahrème, en aval d’Ihérir, 7 January 1966, ? (P-05145224!). **El Menia Province:** Loc d’El Goléa [currently, El Menia], vases salées, April 1954, P. Quézel (MPU-300243!). **Naâma Province:** Sfissifa, 3

June 1887, *A. Bousquet* (MPU-048475!). Aïn-Sefra, 21 April 1888, *E. Bonnet & P. Maury* (P-06801050!). **Tindouf Province:** Sahara Occidentale: Oued Jehach entre Tindouf et l'Oued Drâa, lieux sableux, printemps 1938, *Ollivier 187* (MPU-048470!). Sahara Occidentale, Tindouf, assez abondant, March 1928, *Dr. Estival* (MPU-048483!). Sahara Occidentale, Region de Chenachane, Chenachane, ? 1923, *Dr. Tripeau* (MPU-300238!). Sahara Occidentale, Nkheila, jardin, 29 March 1995, *Monod 19676* (P-05038753!). Ibidem, zone d'épandage, *Monod 19678* (P-05038755!). Ibidem, *Monod 19679* (P-05038747!). Sahara Occidentale, Entre Nkheila et Rabouni, 30 March 1995, *Monod 19703* (P-05038750!). MALI. **Tombouctou Region:** El Mzereb (El Hank), dans un terrain sale, 20 April 1954, *J. Sougy 392* (P-00799803!). MAURITANIA. **Dakhlet Nouadhibou Province:** Ténaloul (Ten Alloui), sebkhas du littoral, 22 April 1938, *Murat 2390* (P-05038740!, MPU-300262!). Iouik [Iwik], côte de Mauritania, 9 April 1982, *Th. Monod 18336* (P-05038748!). **Tiris Zemmour Province:** Soudan Français, Chegga-Guelta, 3 January 19[38], [O. de] *Puygaudeau* (P-05038749!). Sahara Occidental, Falaise du Hank, ravin d'Aïn-Chegga, Janvier 1939, *Dr. Rolland 106* (MPU-048484!). MOROCCO. **Dakhla-Oued Ed Dahab Region:** Dakhla, río de Oro, 28 May 1977, *Th. Monod 16192* (P-05144446!). **Drâa-Tafilalet Region:** Daoura, dans une dava, sur la Hammada de la Daoura, 2 hours vers la vallée vers Hachi-Chamba, 9 April ?, *Dr. Le Carbout* (MPU-300240!). Daoura, dans la vallée de la Daoura vers Achi-Chamba, 17 May ?, *Dr. Le Carbout* (MPU-300241!). Entre Ouarzazate et Skoura, 25 March 1932, *F. Peltier* (MPU-048495!). Drâa: graviers de l'Oued Imini à Ouarzazate, 14 February 1936, *Gattefossé* (MPU-967102!). **Guelmim-Oued Noun Region:** Oued Noun, *Ollivier 14* (MPU-300264). In aridis subsalsis inter Labyar et Notfia, 1 April 1937, *R. Maire* (MPU-300242!). Anti-Altas, Goulimine (Guelmin), 23–28 August 1936, *M. Langueron* (MPU-300234!). Prov. Guelmin 53 km from Guelmin on road to Tan-Tan, near café, 7 February 2007, *S. Jury & T.M. Upson 20492* (MA-786164!). Prov. Guelmim 14 km WSW von Guelmim an der Straße (P41) Nach Tan-Tan, ca. 200 m, 28°56'N 10°08'W, 15 April 1997, *D. Podlech 53647* (W-0365982!, RSA-0548173 [digital image!]). Entre Goulimine (Guelmin) et El Aioun du Drâa, 6 September 1941, *J. de Lepiney, Ch. Runge & Ch. Sauvage 2035* (MPU-759265!). **Laâyoune-Sakia El Hamra Region:** Sahara Occidental: El Aaiun (Seguia el-Hamra), *Izik* [Mision d'Études de la Biologie des Acridiens 2482] (MPU-300239!). Sahara Occidentale: Zemmour [Gueltat-Zemmour], dans les regis près de la Guelta, March-April 1934, *Luthereau* (MPU-300237!). **Souss-Massa Region:** In planitie at septentr. urbis Tiznit, 13 April 1934, *R. Maire & E. Wilczek* (MPU-300236!). Prov. Tiznit, beach West of Gourizime, near the road from Tiznit to Sidi-Ifni, 20 m, 29°37'N 10°02'W, 14 April 1997, *D. Podlech 53623* (W-0365981!). Prov. Tiznit, Oued Massa ca. 40 km Tiznit, 50 m, 3 April 1994, *A. Tribsch* (W-0365983!). Souss-Massa-Drâa, Tiznit, Ifni Mesti, sur del puerto de Sidi Ifni, 24 March 2015, *D. Gutiérrez* et al. *DG503* (MA-00913227!). Prov. Agadir, 10 km NW Agadir, at the coast, 120 m, 30°29'26"N 9°40'17"W, 19 June 1996, *A. Achhal* et al. 96-0511 (W-0365985!). In depressis subsalsis ad Tigert, prope Herculis Promontorium (Cap Ghir), 4 April 1937, *R. Maire* (MPU-300235!). Sud-Ouest du Maroc, Imeoghguemmi [sic], ? 1875, *Mardochée* (MPU-750398!). In arvis prope Tasila, ad ostium fluminis Massa, 3 April 1937, *R. Maire* (MPU-300251!). In arenosis ditionis Tazeroualt, in faucibus Sidi-el-Ghiat, 400 m, 12 Abril 1934, *R. Maire & E. Wilczek* (MPU-300263!).

3.1.2. *Frankenia dinteri* M.Á.Alonso, M.B.Crespo, Abad-Brotos, Mart.-Azorín & J.L.Villar, nom. nov.

= *Frankenia densa* Pohnert in Mitt. Bot. Staatssamml. München 1(9-10): 447. 1954. [replaced synonym], *nom. illeg.* [non Summerh. in J. Linn. Soc., Bot. 48: 373 (1930)]. **Type** (see Pohnert 1954: 448): NAMIBIA. [Otjozondjupa Region:] Grootfontein-Süd, 22 November 1934, *K. Dinter 8059* (holotype: M-0104483 [digital image!], available at <https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.m0104483>); isotypes: M-0104484 [digital image!], PRE-0293175-0 [digital image!], PRE-526699-0 [digital image!] HBG-516900 [digital image!], BOL-136934!, K!). Paratypes: NAMIBIA. [Karas Region:] Bethanien [Bethany], 24 December 1934, *K. Dinter 8270* (BOL-136934!, HBG-516901 [digital image!], K!). Figure 3.

Description: Herbs annual or short-lived perennial, often robust and weakly lignified at base, profusely and densely branched, tap-rooted, mostly glabrous to sparsely puberulous. Stems non-rooting, usually erect to ascendant, 5–30 cm long, often with divaricate branches, with internodes up

to 2.5 cm long; *young branchlets* yellowish-brown to reddish, mostly with scattered whitish depositions, glabrous or shortly and loosely puberulous, with minute curled to hooked trichomes (0.1–0.2 mm long), only on one side. *Leaves* opposite, patent to erect-patent, green or sometimes reddish, and mostly with scattered glands bearing whitish depositions; *petiole* 0.8–1.2 × 0.5–0.6 mm, flattened, and tapering distally, sometimes reddish; *sheath* extending along petiole margins to blade, ciliate with 4–6 pairs of lateral cilia, unequal in length (up to 0.4–0.5 mm long), whitish, cylindric to flattened, and obtuse or acute at apex; *leaf blade* (2.5–)3–4.5(–6) × 0.5–2 mm, narrowly elliptic to oblong, mostly subfalcate upwards, with obtuse apex and ± rounded base, often strongly revolute on margins or flattened in the lower third, somewhat fleshy and glaucescent, concolorous or occasionally somewhat paler abaxially, glabrous on the upper side with scattered whitish depositions and waxes, and glabrous or loosely hairy beneath with scattered short straight trichomes 0.1–0.2 mm long; *midrib* narrow, linear, tapering slightly towards apex, continuous with petiole below, somewhat raised abaxially, and extending for most of the blade length. *Flowers* pentamerous, perfect, sessile, often crowded in dense axillary or terminal dichasial groups, usually densely condensed and glomerular, many-flowered; *floral bracts* 2, leaf-like, 3–4 × 0.6–0.7 mm, erect to erect-patent, connate at base and shortly covering the calyx base for ca. 0.5 mm, about equalling or slightly exceeding the calyx length; *bracteoles* 2, bract-like but smaller, 1–2 × 0.4–1 mm, alternating with bracts, erect, strongly revolute on margins, about half to two-thirds the calyx length, with petiole ca. 1 mm long, adnate to calyx base. *Calyx* 3.3–4.7 × 0.6–1 mm, tubular at the anthesis to gradually fusiform later, non-twisted, straight, indurate, often reddish, prominently 5-ribbed, entirely glabrous or loosely puberulous (with a homogeneous whitish indumentum of minute straight papillae ca. 0.1 mm long) between the thickened glabrous ribs, often with scattered whitish depositions; *teeth* 5, ca. 0.5 mm long, erect, triangular, acute, cucullate, shortly mucronate at apex (mucro ca. 0.4 mm long), narrowly membranous and shortly papillate on margins. *Petals* 5, 3.5–5 × 0.5–0.8 mm, exceeding the calyx, obovate-cuneate, pinkish-mauve but whitish below, often broadly overlapping laterally, exceeding about one-third to half the calyx length; *claw* 2–2.5 × 0.3–0.4 mm, narrowly cuneate, tapering to blade, yellowish, and entirely hidden into the calyx tube; *ligule* 2–2.5 × 0.4–0.5 mm, narrowly lanceolate, longitudinally adnate to the claw, the free apex ca. 1 × 0.5 mm, ovate-oblong, broader than the claw at base, obtuse to subacute, and entire; *blade* 2–2.5 × 0.5–0.8 mm, obovate, rounded at apex, irregularly erose-denticulate. *Stamens* 6, in two unequal whorls, hidden in calyx teeth at anthesis; filaments 2.3–2.5 mm long, whitish, expanded ca. 0.5 mm wide in the lower part but gradually tapering and filiform in the distal part; *anthers* 0.6–0.8 mm long, yellowish, ellipsoid, versatile. *Ovary* ca. 2 mm long, elliptic-ovoid, subtrigonous, 3-carpelar; *placentas* 3, parietal-basal, extending up to the lower half to two thirds of carpel wall length, with ventral traces moderately to profusely branched; *ovules* 10–12 per placenta, attached along most of the placenta by erect funiculi ca. 0.1 mm long. *Style* 1.7–2 mm long, terete, whitish, with 3 *stylar branches* filiform, 0.5–0.6 mm long, whitish. *Capsule* 3–4.5 × 1.4–2 mm, ovoid-ellipsoid, subtrigonous, hidden in the calyx tube, early dehiscent. *Seeds* 25–30 per capsule, 0.5–0.6 × 0.2–0.3 mm, sulcate on one side, ellipsoid, light brown, darker at the funicular part, and developing rapidly even before the flower has completely withered; *testa* thin, not mucilaginous, with a surface weakly and irregularly ornamented with a subrectangular-reticulate pattern, finely striate, covered with scattered small-sized papillae 7–12 µm long, homogeneous in shape, conical-obtuse, sessile, more densely disposed on the distal part.

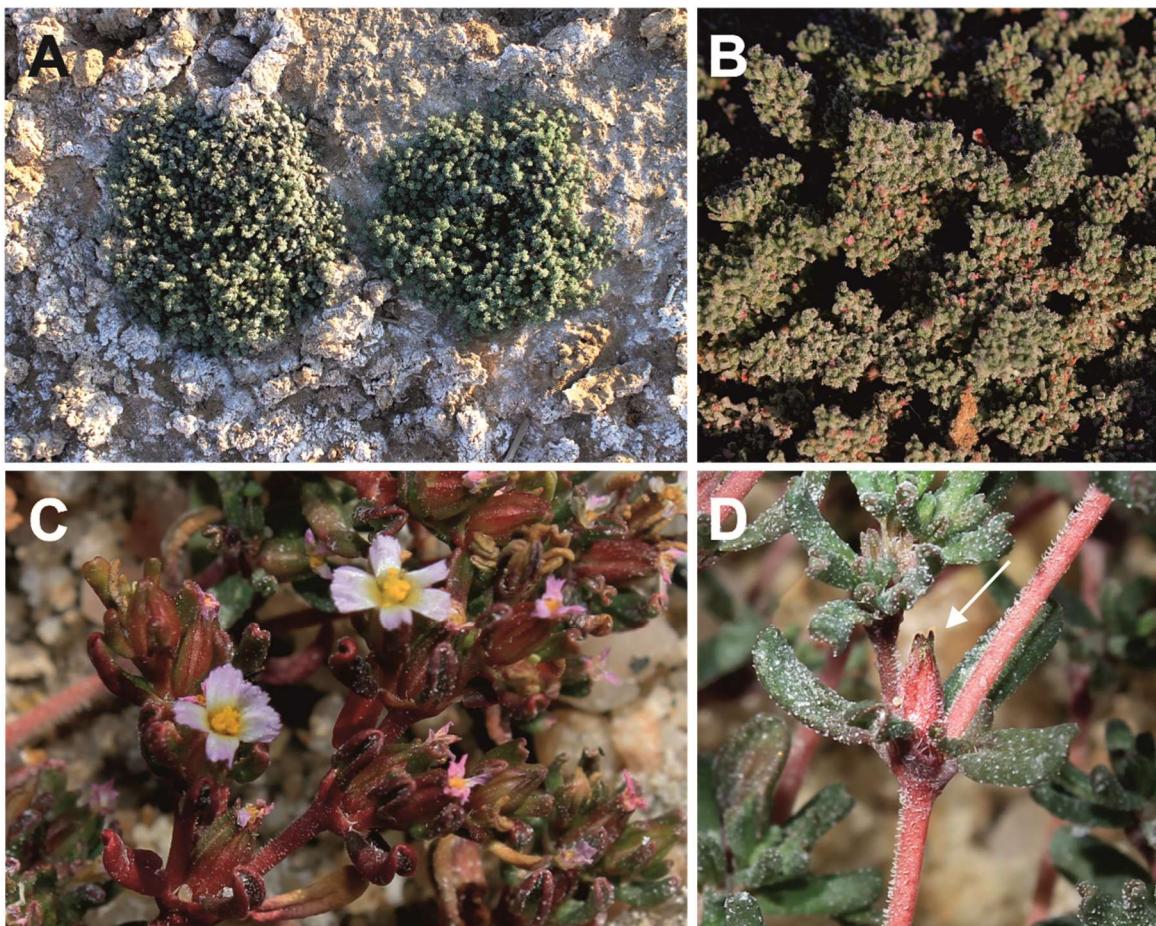


Figure 3. *Frankenia dinteri*. (A) Habit in habitat; (B) Detail of many-flowered inflorescences; (C) Flowering branchlets at anthesis; (D) Detail of calyx after anthesis, with acuminate teeth (arrow). Photographs by Mario Martínez-Azorín: (A, B) Goageb, Namibia; (C, D) Onseepkans, South Africa.

Eponymy: The specific epithet honours Moritz Kurt Dinter (1868–1945), a renowned German botanist who extensively collected plants in south-western Africa, mostly in Namibia, and particularly he gathered in 1934 the specimens upon which Pohnert [60] first described his “*Frankenia densa*”, an illegitimate later homonym of the Australian *F. densa* Summerh. (see below).

Phenology: Flowering in late April–early October (occasionally in November–January), fruiting in May–November (occasionally in December–February).

Habitat and distribution: *Frankenia dinteri* occurs on saline, sandy to clayish soils in wetlands, ravines, or close to lagoons, at elevations of 300–1225 m. The known distribution of the new species extends from Grootfontein (Otjozondjupa Region, Northern Namibia), the type locality, to Goageb (Karas Region, southern Namibia), but spreads southwards into northwestern South Africa to Salt River, north of Vanrhynsdorp (Western Cape Province) and far eastwards to Bloemhof (North West Province) (Figure 4). Biogeographically, and according to the current data, it is endemic to the Namib, Namaland, and Karroo Provinces of the Karoo-Namib Region (sensu Takhtajan [34]). In that large territory, *F. dinteri* is found in halophilous vegetation-types occurring in the Nama-Karoo (NK), Succulent Karoo (SK), Desert (D), and Savanna (SV) Biomes [32].

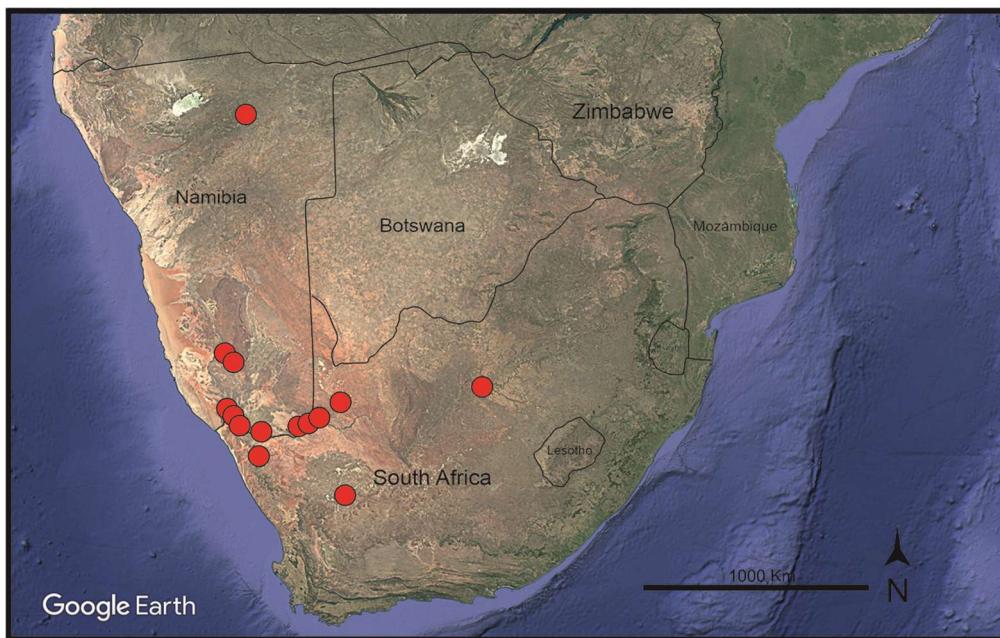


Figure 4. *Frankenia dinteri*. Distribution map of the studied material.

Nomenclatural remarks: This outstanding southern African sea-heath was first described by Pohnert [60] as “*Frankenia densa*” from materials collected in inland Namibia which included robust, profusely branched plants with many-flowered and densely crowded inflorescences. However, the name *F. densa* had already been published by Summerhayes [34] for a sea-heath from central and southern Australia, which made Pohnert’s name illegitimate (Art. 53.1 of the ICN). Apparently, no valid name exists at specific rank for the southern African plant, and hence a replacing name, *F. dinteri* nom. nov. (Art. 6.11 of the ICN), is proposed here for the illegitimate *F. densa* Pohnert.

Other studied material: NAMIBIA. **Karas Region:** Goageb, near bridge on B4 along dry river bed, 26°44'54"S 17°13'13"E, 922 m elevation, 10 August 2016, M. Mart.-Azorín et al. (ABH-76804!). Warmbad, im rivierbett, 22 May 1972, W. Giess & M. Müller 12120 (WAG-0249597 [digital image!]). Seeheim, 17 November 1922, K. Dinter 4214 (GH-02434737 [digital image!]). Reg. Gross-Namaland, Ganas, 12 December 1884, H. Schinz 267 (Z-000067508 [digital image!]). Southwest Africa: Kahanstal, 2 December 1934, K. Dinter 8154 (BOL!, K!). SOUTH AFRICA. **Northern Cape Province:** 2816 (Oranjemund): Sendelingsdrif, stagnant pool along Orange River near Octa Mine (-BB), 25 August 1982, W. Metelerkamp 400 (BOL!); Little Namaqualand: Alties River bed, 1 December 1910, N.S. Pillans 5381 (BOL!); Little Namaqualand: Dry sand near stream Kuboos (-BD), October 1926, N.S. Pillans 5409 (BOL!); Little Namaqualand: Mouth of Orange River (-CB), on dry mud, lagoon, October 1926, N.S. Pillans 5576 (BOL!); Little Namaqualand: Mouth of Orange River (-CB), sandy banks, October 1926, N.S. Pillans 5583 (BOL!); Namaqualand, Richtersveld Nat. Park, S. Avenants Grove, January 1995, G. & W. Williamson 5590 (NBG-153968!). 2818 (Warmbad) Regionis occidentalis: Henkries, Orange River (-CC), 30 November 1897, M. Schlechter 22 (BOL!). 2819 (Ariamsvlei): Daberas Farm (-BD), 28°29'32"S 19°56'38"E, 573 m, 23 August 2022, M. Mart.-Azorín, M.B. Crespo, M.Á. Alonso, J.L. Villar & M. Pinter (ABH-83264!); Onseepkans, near Orange River (-CD), 28°46'37"S 19°15'47"E, 359 m, 21 August 2022, M. Mart.-Azorín, M.B. Crespo, M.Á. Alonso, J.L. Villar & M. Pinter (ABH-83234!); Kenhardt Distr.: Farm Skroef, bank of Orange River (-DA), 26 September 1987, E.V. Hoepen 1887 (BOL!, PRE!). 2820 (Kakamas): Augrabies, (falls) near Park (-CB), 28°39'02"S 20°21'55"E, 616 m, 23 August 2022 M. Mart.-Azorín, M.B. Crespo, M.Á. Alonso, J.L. Villar & M. Pinter (ABH-83265!). 2917 (Springbok): Namabeep, dry river bed (-DB), 26 March 1964, D.S. Hardy 1682 (K!). 3020 (Brandvlei): Between Brandvlei and Williston, Karreekop farm, sandy plains with scattered rocks (-DC), 30°58'59"S 20°39'18"E, 987 m, 24 August 2022, M. Mart.-Azorín, M.B. Crespo, M.Á. Alonso, J.L. Villar & M. Pinter (ABH-83275!). **North West Province:** 2725 (Bloemhof): [Between Christiana and Bloemhof], Vaal River Salt works, saltpan

(-CB), 27°44'S 25°20'E, 29 April 1973, B. Straschil (W-0365984). **Western Cape Province:** 3118 (Vanrhynsdorp): 18 miles N of Vanrhynsdorp, Salt River, 22 January 1930, C.E. Moss 17983 (BM!).

3.2. Phylogenetic relationships

The aligned ITS dataset was 720 bp, 249 of which (34.58%) were potentially parsimony informative. The phylogenetic relationships of taxa are shown in Figure 5 as recovered in our ML tree. The percentage of trees in which the associated taxa clustered together (after 10,000 bootstrap replicates) in the ML analysis are shown above branches, while PP values from the BI analysis are shown below branches. Trees obtained with MP and NJ methods (Figure S1A,B) yielded similar topologies to the ML tree. In the MP analysis, eight most parsimonious trees were obtained with a tree length (TL) of 581 steps, a consistency index (CI) of 0.796, and a retention index (RI) of 0.913.

The general topology of the obtained ITS tree (Figure 5) is almost identical to that reported by Crespo et al. [12], which was based on a more reduced set of species and samples, though it also yields a strongly monophyletic genus *Frankenia* (99BP, 1.00PP), when compared with outgroups of the sister family Tamaricaceae (*Tamarix*, *Myricaria*, and *Reaumuria*). The addition of samples of *F. sahariensis* and *F. dinteri*, as well as other congeners from Eurasia and Africa (including Macaronesia), revealed new internal relationships (both within and between clades).

On the one hand, a strongly supported (95BP, 1.00PP) broad aggregate is found that comprises three unresolved major lineages (clades A+B+C) matching those of Crespo et al. [12]. Firstly, Clade A is composed in the ML analysis by two groups of taxa. The first group encompasses all samples of *F. dinteri* from Namibia and South Africa, forming a strongly supported (99BP, 1.00PP) clade that is weakly supported (53BP) as sister of the remaining groups within Clade A, but is placed in the BI analysis in an unresolved position together with the broad aggregate of clades [A+[B+C]]. The second group is formed by a well-supported (70BP, 1.00PP) broad lineage including the South African samples of the strongly supported (96BP, 1.00PP) “*F. repens* group” (sensu Crespo et al. [12]) with *F. anneliseae* M.B.Crespo & al., *F. repens* (P.J.Bergius) Fourc. and *F. nummularia* M.B.Crespo & al., to which clades of two North African-Iberian species, *F. boissieri* Reuter and *F. thymifolia* Desf., are strongly supported successive sisters. Secondly, samples of the SW Mediterranean *F. corymbosa* Desf. (Clade C) are arranged in a strongly supported (99BP, 1.00PP) compact group, which is nested only in the BI analysis as a weakly supported (0.74PP) sister to Clade B. Thirdly, Clade B is formed by two major, moderately supported lineages. On one side, Subclade B1 (75BP, 0.78PP) mostly comprises members of the major Macaronesian archipelagos (i.e., the Madeiran *F. cespitosa* Lowe, the Canarian “*F. ericifolia* group”, and the Cape Verdean *F. pseudoericifolia* Rivas Mart. & al.) plus two western Saharan species (i.e., *F. ifiniensis* and the newly named *F. sahariensis*), which are arranged into three unresolved lineages. In one of those lineages, all samples of “*F. ericifolia* group” are strongly supported (93BP, 0.99PP) as sister to *F. sahariensis* samples. On the other side, Subclade B2 (99BP, 1.00PP) merges an apparently heterogeneous aggregate of species with western Mediterranean-Atlantic (*F. laevis*), North African-Atlantic (*F. composita* and *F. velutina* Brouss. ex DC.), or currently subcosmopolitan (*F. pulverulenta*) distributions. Among them, all samples of *F. pulverulenta* form in the ML analysis a weakly supported (53BP) clade.

On the other hand, the “*F. hirsuta* group” (sensu Crespo et al. [12]) consolidates as Clade D, a strongly supported (99BP, 1.00PP) group formed by all samples of *F. hirsuta* s.str. (E Mediterranean) plus *F. salsuginea* (central Anatolia), which is sister to the aggregate of clades A-C with a strong support (95BP, 1.00PP).

Finally, the South African narrow endemic *F. fruticosa* remains as sister (59BP, 0.99PP) to all other studied members of *Frankenia*.

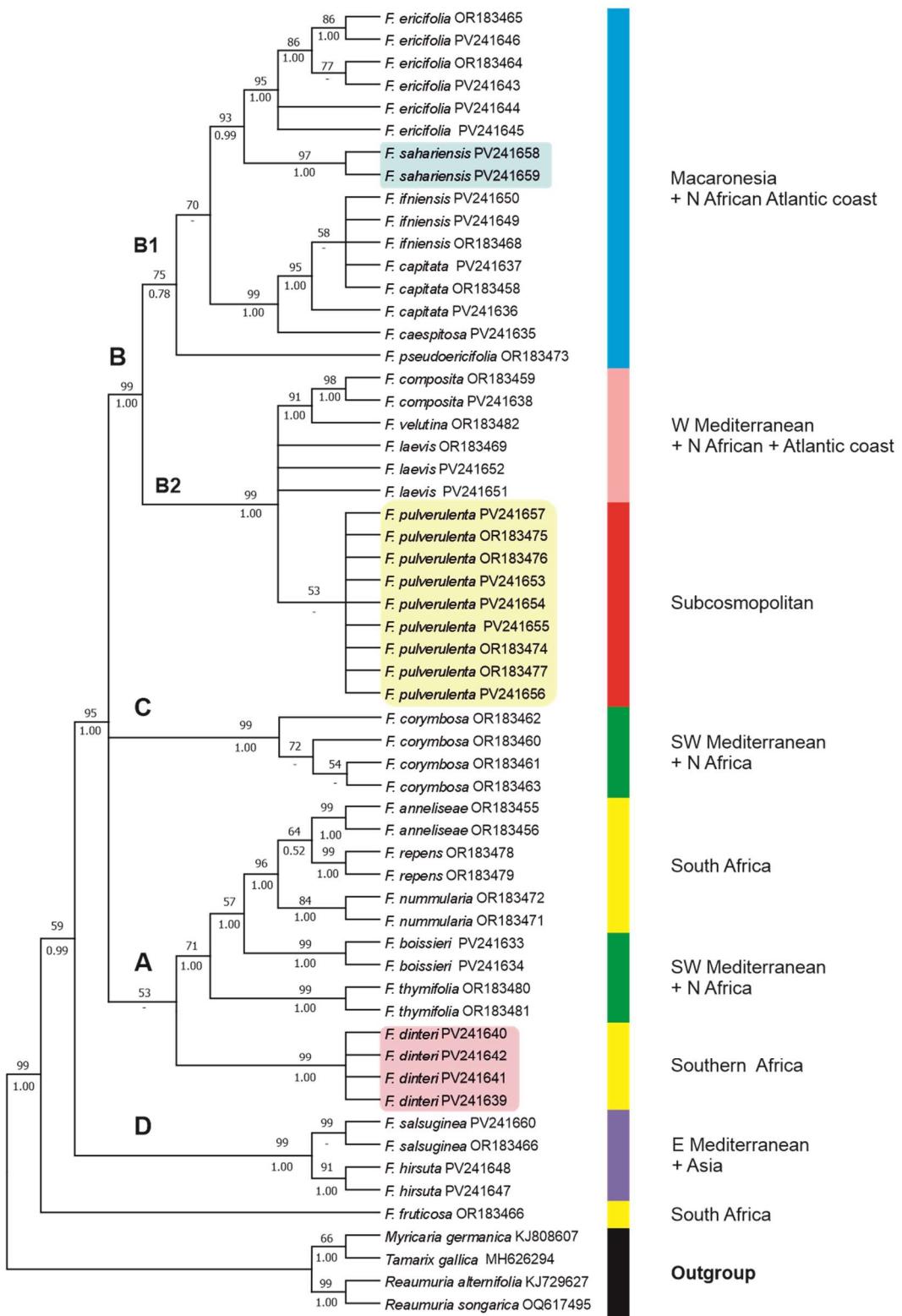


Figure 5. Maximum Likelihood (ML) phylogenetic tree of *Frankenia* accessions from ITS nrDNA sequences as obtained with MEGA. The three main clades recovered in the analyses are marked A–D on the tree, following Crespo et al. [12], plus two additional subclades (B1 and B2). Samples of *F. sahariensis*, *F. pulverulenta* and *F. dinteri* are highlighted in their corresponding clades or subclades for easier comparison of their relative position. Numbers above branches indicate the bootstrap percentage (BP) values after 10,000 replicates from the ML analysis, whereas numbers below branches indicate the posterior probabilities (PP) from the Bayesian Inference analysis. GenBank codes are shown after each taxon/accession name.

The aligned *matK* dataset was 829 bp, 124 of which (14.95%) were potentially parsimony informative. The phylogenetic relationships of taxa are shown in Figure 6 as recovered in our ML tree. As said before, the percentage of trees in which the associated taxa clustered together (after 10,000 bootstrap replicates) in the ML analysis are shown above branches, whereas PP values from the BI analysis are shown below branches. Trees obtained with MP and NJ methods (Figure S1C,D) yielded similar topologies to ML tree. In the MP analysis, nine most parsimonious trees were obtained with a tree length (TL) of 226 steps, a consistency index (CI) of 0.848, and a retention index (RI) of 0.929.

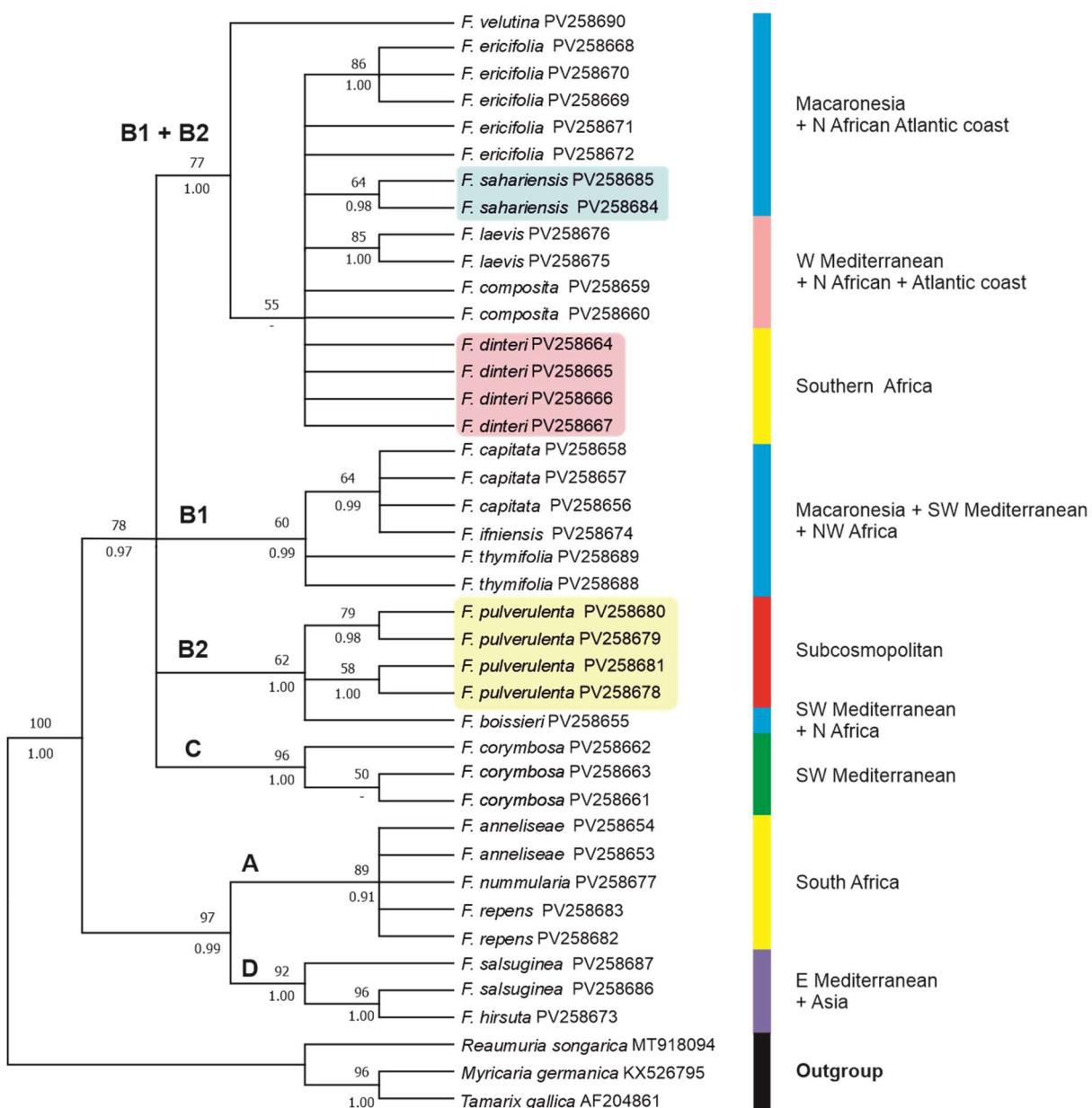


Figure 6. Maximum Likelihood (ML) phylogenetic trees of *Frankenia* accessions from *matK* cpDNA sequences as obtained with MEGA. The four main clades and subclades recovered in the analyses are marked A–D on the tree, paralleling the ITS tree. Similarly, accessions of *F. sahariensis*, *F. dinteri* and *F. pulverulenta* are highlighted to easily compare their relative positions. Numbers above branches indicate the bootstrap percentage (BP) values after 10,000 replicates from the ML analysis, whereas numbers below branches indicate the posterior probabilities (PP) from the Bayesian Inference analysis. GenBank codes are shown after each taxon/accession name.

In the obtained *matK* tree (Figure 6), *Frankenia* is also recovered as a strongly monophyletic (100BP, 1.00PP) clade, with two main lineages corresponding to clades [[A+D]+[B+C]] of the ITS tree, though displaying a different scenario of interspecific relationships. The recovered main clades are partly coincident with those shown in the ITS tree, and their codes are retained in the *matK* tree for parallelism. However, some of those major clades show lower internal resolution than in the ITS tree. No useful sequences were generated for the South African *F. fruticosa*.

On the one hand, the first lineage is strongly supported (97BP, 0.99PP) and encompasses Clade A (89BP, 0.91PP), with the South African members of the “*F. repens* group” not fully resolved internally, plus Clade D (92BP, 1.00PP), with the “*F. hirsuta* group” including the eastern Mediterranean (*F. hirsuta*) and Anatolian (*F. salsuginosa*).

On the other hand, clades B+C form a lineage that is sister to Clade A+D (78BP, 0.97PP) and is fully unresolved internally. Firstly, a heterogeneous moderately supported (77BP, 1.00PP) aggregate (Clade B1+B2) is found that merges species from Clades A, B1, and B2 of the ITS tree. In this group, the northwestern African coastal species *F. velutina* is found, only in the ML analysis, as weakly supported (55BP) sister of the remaining members. Provenances of those members are diverse, such as *F. ericifolia* (Canary Islands), *F. sahariensis* (western Sahara Desert), *F. laevis* and *F. composita* (Mediterranean basin and Atlantic coasts of Northern Africa and Europe), and *F. dinteri* (southern Africa). Although internal relationships among those taxa are not well resolved, three subclades arise in Clade B1+B2 that respectively include all samples of *F. sahariensis* (64BP, 98PP), all samples of *F. laevis* (85BP, 1.00PP), and some samples of *F. ericifolia* (86BP, 1.00PP). Samples of *F. dinteri*, which formed in the ITS tree a strongly supported lineage in Clade A, are unresolved along with members of Clades B1 and B2. Secondly, the Canarian *F. capitata*, the western Saharan *F. ifniensis* Caball., and the SW Mediterranean and N African *F. thymifolia*, constitute Clade B1 (64BP, 0.99PP), whose internal relationships are not well resolved. However, an internally unresolved subclade with *F. capitata* plus *F. ifniensis* is found in both analyses conducted that is sister (59BP, 0.96PP) to samples of *F. thymifolia* that in contrast nested with members of Clade A in the ITS tree. Thirdly, Clade B2 shows a moderate support (62BP, 1.00PP) and encompasses all samples of *F. pulverulenta* (Eurasian-Mediterranean species that became subcosmopolitan) plus the sample of *F. boissieri* (SW Mediterranean and African-Atlantic species), without full internal resolution. In contrast, the BI analysis recovered all samples of *F. pulverulenta* in a strongly supported (1.00PP) clade. Members of Clade B2 were included in the homonymous one in the ITS tree, excepting *F. boissieri* that was recovered in the ITS analysis as member of Clade A. Finally, the SW Mediterranean *F. corymbosa* is nested in a strongly supported (96BP, 1.00PP) distinct Clade C, which only in the BI analysis is recovered as sister (0.75PP) to the former aggregate.

4. Discussion

The findings presented here are largely consistent with those reported by Crespo et al. [12] and form part of a broader study evaluating the generic and specific relationships within Frankeniaceae, with a particular focus on the Eurasian and African taxa.

Both obtained ITS and *matK* trees (Figures 5 and 6) represent the most comprehensive phylogenetic trees of *Frankenia* to date. While still incomplete, they provide a solid foundation for a preliminary phylogenetic survey on the genus in Eurasia and Africa, which will be expanded in the coming years. When combined with morphological data and field observations, these molecular trees provide a clear picture, allowing for a more accurate interpretation of certain African taxa that are often synonymised or subordinated to the annual sea-heath, *F. pulverulenta* (Table 3). This is exemplified by the two species that have been newly named here, *F. sahariensis* and *F. dinteri*, which are the principal focus of the present work.

Table 3. Comparison of morphological characters of the newly named African species, *Frankenia sahariensis* and *F. dinteri*, to the annual sea-heath *F. pulverulenta*.

<i>F. sahariensis</i>	<i>F. dinteri</i>	<i>F. pulverulenta</i>
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General habit	Annual or perennial herbaceous and weakly lignified at base	Annual or perennial herbaceous and weakly lignified at base	Annual or rarely short-lived perennial
Stem features	Prostrate to decumbent, non-rooting	Erect to ascendant, non-rooting	Prostrate to ascending, non-rooting
Branchlet indumentum	± densely puberulous on one side and near nodes	± densely pubescent on one side	± densely pubescent on one side
Branch trichomes: types and length (mm)	minute, ca. 0.1–0.2, curled or hooked	minute, ca. 0.1–0.2, curled or hooked	minute, ca. 0.1–0.2, curled
Petiole length × width (mm)	0.5–0.8 × 0.2–0.3,	0.8–1.2 × 0.5–0.6	0.5–1.5 × 0.2–0.3
Petiole sheath	(2–)4–5 pairs of cilia	4–6 pairs of cilia	2–6 pairs of cilia
Sheath cilia length (mm) and colour	0.2–0.5 mm, unequal, whitish	0.4–0.5 mm, unequal, whitish	0.3–0.6, unequal, whitish
Leaf blade length × width (mm)	(1.8–)2.5–4 × 0.5–0.7	(2.5–)3–4.5 (6) × 0.5–2	2–5 × 1.5–3
Leaf blade outline and colour	Triangular-ovate to oblong-ovate, ± concolorous, midrib notably thickened	Elliptic to oblong, ± concolorous, midrib narrow, not thickened	Obovate-cuneate, ± concolorous, midrib narrow, not thickened
Leaf blade shape and margins	Obtuse apex and cordate to rounded base; often strongly revolute on margins or flattened in the lower third	Obtuse apex and rounded base; often strongly revolute on margins or flattened in the lower third	Rounded, slightly emarginate apex and cuneate base; flattened or slightly revolute on margins
Leaf blade indumentum	Glabrous on the upper side, glabrous to loosely hairy beneath with scattered short straight trichomes 0.1–0.2 mm long	Glabrous on the upper side, and glabrous to loosely hairy beneath with scattered short straight trichomes 0.1–0.2 mm long	Glabrous on the upper side, ± densely pubescent beneath with scattered short straight trichomes 0.1–0.2 mm long
Inflorescence	Flowers often in axillary or terminal dichasial groups, usually condensed and glomerular	Flowers in dense axillary or terminal dichasial groups, usually densely condensed and glomerular	Flowers solitary and scattered along branch dichotomies in loose groups
Bracteole length × width (mm)	0.5–1.5 × 0.4–0.6, about half the calyx length	1–2 × 0.4–1 mm, about half the calyx length	2.5–4, as long as or longer than calyx
Calyx length × width (mm), shape and torsion	2–4 × 0.6–1, fusiform-tubular to fusiform, often twisted	3–4.7 × 0.6–1, fusiform-tubular to fusiform, non-twisted	2.5–4(–5) × 0.8–1.5, fusiform-tubular to fusiform, non-twisted
Calyx indument (appearance and length)	Entirely glabrous or densely papillate between the glabrous ribs, with heterogeneous trichomes (flattened papillae 0.2–0.3 mm, globose-claviform papillae ca. 0.1 mm, and minute globose vesicles)	Entirely glabrous or puberulous between the glabrous ribs, with homogeneous papillae ca. 0.1 mm long	Entirely glabrous or puberulous between the glabrous ribs, with homogeneous papillae up to 0.2 mm
Calyx teeth length (mm) and shape	0.5–1, acute, mucronate (mucro ca. 0.1–0.2 mm), cucullate	ca. 0.5, acute, long mucronate (mucro ca. 0.4 mm), cucullate.	0.4–0.8, acute to mucronate (mucro ca. 0.1 mm), cucullate
Petal size (mm) and blade colour	5–6 × 1–1.5, pinkish-mauve but whitish below	4–4.5 × 0.5–0.8 pinkish-mauve but whitish below	3.5–5 × 0.6–0.9, whitish-pink to pinkish-mauve, whitish below
Petal blade size (mm), and shape	2.3–3.5 × 1–1.5, obovate-cuneate, rounded and erose-denticulate at apex	2–2.5 × 0.5–0.8, obovate, rounded to truncate and irregularly erose-denticulate at apex	2–2.5 × 0.5–0.8, narrowly cuneate to obovate, truncate and erose-denticulate at apex
Petal claw (mm)	2–2.5 × 0.3–0.4, narrowly cuneate	2–2.5 × 0.3–0.4, narrowly cuneate	2–2.5 × 0.3–0.5, cuneate
Petal ligule (mm)	2–2.5 × 0.3–0.4 mm, free apex ca. 0.2–0.4 × 0.2–0.3 mm, ovate-ovate-oblong, obtuse to subacute, entire	2–2.5 × 0.4–0.5, free apex ca. 1 × 0.5 mm, ovate-oblong, obtuse to subacute, entire	1–2 × 0.2–0.3, free apex ca. 0.4 mm, triangular, acute, entire
Stamen filament length (mm) and morphology	3.5–5.5, expanded ca. 0.5 mm in the lower part, but tapering and filiform in the distal part	2.3–2.5, expanded ca. 0.5 mm in the lower half, but tapering and filiform in the distal part	4–6, expanded ca. 0.2 mm in the lower half, but tapering and filiform in the distal part
Anther length (mm), shape and colour	0.6–0.8, ellipsoid, yellowish	0.6–0.8, ellipsoid, yellowish	0.2–0.4, oblong-ellipsoid, yellowish
Ovules per placenta	9–12	10–12	12–20
Capsule size (mm)	1.4–2 × 0.8–1	3–4.5 × 1.4–2	2–3 × 0.5–1
Seed number and size (mm)	24–30, 0.4–0.5 × 0.2–0.25	25–30, 0.5–0.6 × 0.2–0.3	up to 45, 0.5–0.7 × 0.2–0.3
Testa papillae length (μm)	10–14	7–12	4–17

Papillae morphology and distribution	Homogeneous, globose to conical-obtuse, denser on distal part	Homogeneous, conical-obtuse, denser on distal part	Homogeneous, conical-obtuse, denser on distal part
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Frankenia pulverulenta is native to Eurasia (including the Mediterranean basin) and has become Subcosmopolitan after introduction worldwide [14]. The species is currently distributed in temperate and subtropical regions, ranging from sea level to nearly 2000 m elevation, which thrives in both very cold regions and hot deserts. According to the taxonomy currently adopted in some general databases (e.g. [4,26,59]), it is the only annual species in the genus, which occurs mostly in regions with low precipitation worldwide and grows optimally in soils with a certain concentration of salts (i.e., chlorides, sulphates, or nitrogen compounds), often in frequented and disturbed areas [61]. For that reason, it is usually regarded as a halo-nitrophilous or gypsum-loving herb [8], with a high degree of morphological plasticity. This lifestyle might be connected to the broad variation it apparently exhibits in terms of body size and indumentum [62]. In addition to its annual cycle, *F. pulverulenta* shows distinctive morphological characteristics that facilitate identification, including nearly flattened leaves that are cuneate at the base and notched at the apex, solitary scattered flowers, and capsules containing numerous small seeds (Table 3). That presumed morphological polymorphism has led some authors to synonymise *F. pulverulenta* to other congeners with broad, flattened leaves but strongly differing on many other respects. Recently, Crespo et al. [12] have studied two South African species, *F. nodiflora* and *F. nummularia*, long mistaken within the broadly circumscribed *F. pulverulenta*, which widely parallel the present case.

On the one hand, samples of *F. sahariensis* collected in the western Saharan regions are nested far apart from those of the typical *F. pulverulenta* in all analyses conducted. The position in the ITS tree (Figure 5) of *F. sahariensis* as a strongly supported sister of the Canarian *F. ericifolia* clade is consistent with the geographic distribution of both species, occurring about the same latitude in the Atlantic regions of NW Africa and the eastern Canary Islands, not far from each other. In contrast, the *matK* tree (Figure 6) yields both latter species in a wide clade with poor internal resolution, which also comprises several morphologically diverse species. Among them, only samples of *F. sahariensis*, *F. laevis* and partly *F. ericifolia* nest individually in well supported clades, whereas positions of the remaining (*F. composita*, *F. velutina*, and *F. dinteri*) are not resolved. All those entities exhibit morphological differences that allow easy distinction at different taxonomic ranks [22]. Conversely, all samples of *F. pulverulenta* (coming from diverse distant places, such as the Mediterranean basin, the Canary Islands, and South Africa) are found together in a heterogeneous weakly supported clade in the ITS tree, which is close to *F. laevis*, *F. velutina* and *F. composita*, a group of perennial mostly Atlantic and southwestern Mediterranean taxa sometimes accepted at subspecific rank in a broadly circumscribed *F. laevis* [22,26]. Furthermore, in the *matK* tree *F. pulverulenta* nests together with *F. boissieri*, but without full internal resolution. Nevertheless, all those phylogenetic relationships are apparently not correlated to sound morphological patterns and can be best interpreted on biogeographical grounds, as discussed below.

In the protologue of *F. sahariensis* (as *F. florida* L.Chevall., *non* Phil.), Chevallier [56] (1903) related his new species to the highly variable subcosmopolitan *F. pulverulenta*. In fact, it is often subordinated to the latter as a variety [58] or subspecies [24]. However, sound morphological characteristics allow confident distinction of both species (Table 3):

- i) blade of leaves triangular-ovate to oblong-ovate, with cordate to rounded base and a prominent thickened midrib on the underside of blade in *F. sahariensis* vs. broadly obovate blade with cuneate base and thin midrib not remarkably prominent in *F. pulverulenta*;
- ii) calyx indument heterogeneous, with flattened trichomes between ribs intermingled with small globose-claviform trichomes and minute papillae in *F. sahariensis* vs. calyx with homogeneous indument of small curled trichomes also present on the underside of leaves in *F. pulverulenta*;
- iii) petals much exceeding about half to two-thirds the calyx length (vs. petals exceeding only about one-third to half the calyx length in *F. pulverulenta*); and
- iv) seeds morphologically close in both species (Figure 7), though less abundant in *F. sahariensis* (24–30 per capsule) than in *F. pulverulenta* (up to 45 per capsule).

All these features make individuals of *F. sahariensis* quite distinctive during anthesis in the field. Both species exhibit significant overlap in their distributions and co-occur at least in the coastal areas, such as the Ifni region of western Sahara. From this area, Caballero [63] described *F. intermedia* var. *annua* Caball. (MA-78660!), which is now considered a synonym of *F. sahariensis*, as well as *F. pulverulenta* var. *grandifolia* Caball. (MA-78705!), a plant with larger leaves and longer petioles that is indistinguishable from and should be synonymised to the typical *F. pulverulenta*, as suggested by Maire [24] and Nègre [22].

Chevallier [56] also noted the annual or short-lived perennial habit of *F. sahariensis* (as *F. florida*), stressing its resemblance to *F. laevis* and *F. intermedia* (*F. laevis* var. *intermedia* (DC.) Bonnet), two entities predominantly occurring along the Mediterranean and Atlantic coasts of Europe and North Africa [19]. However, both latter taxa are woody perennial, shrubby species with prostrate to ascendant stems with denser indumentum all around; leaves are strongly revolute, not cordate at base, often densely pubescent to tomentose beneath [22]; and the calyx indument in both species is always lacking globose-claviform trichomes between ribs. Furthermore, calyx ribs in *F. intermedia* exhibit long cilia [64]. Morphological relationships are weaker to other relatives occurring in northwestern Africa, such as *F. velutina*, *F. boissieri* or *F. composita* (see Nègre [22]). Nevertheless, some connections can be argued with the Canarian *F. ericifolia*, based on the shared prostrate habit, leaves sometimes flattened and geographical proximity, which might support the phylogenetic closeness unveiled by the obtained trees (Figures 5 and 6). Despite those similarities, *F. ericifolia* differs significantly from *F. sahariensis* by its shrubby woody habit, the mostly revolute leaves covered with short hairs all over, never cordate at the base, with a weaker non-thickened midrib; and the homogeneous calyx indument with short conical trichomes. For all those reasons, *F. sahariensis* can be readily distinguished from *F. pulverulenta* and other relatives, therefore deserving recognition at species rank as previously suggested by Ozenda [55, as *F. florida* L.Chevall.].

On the other hand, all samples of *F. dinteri* collected from a substantial territory encompassing southern Namibia and northwestern South Africa are distinctly separated from those of the typical *F. pulverulenta* in all analyses conducted. Regarding the ITS tree (Figure 5), *F. dinteri* forms a strongly supported group in Clade A that is weakly related to the remaining South African studied species of the "*F. repens* group". In contrast, the *matK* tree (Figure 6) recovers all samples of *F. dinteri* not coalescent into a single clade but rather dispersed across Clade D, in which several subshrub species with diverse origins (*F. sahariensis*, *F. laevis*, *F. ericifolia*, *F. composita*, and *F. velutina*) nest together without complete internal resolution. Once again, phylogenetic relationships of *F. dinteri* appear to respond best to biogeographical patterns than to morphology (see below).

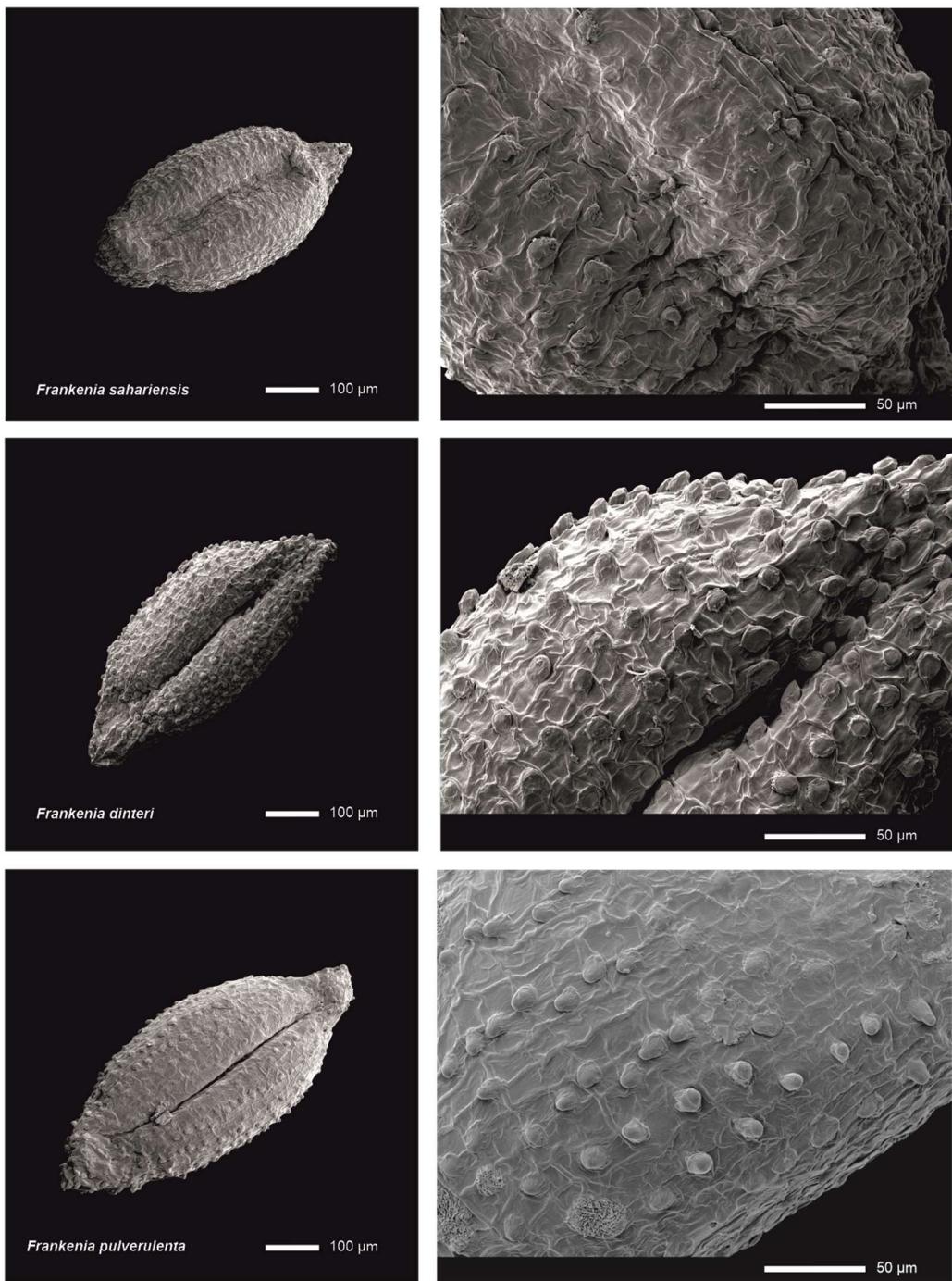


Figure 7. Seed morphology (left) and testa details (right) of: (A, B) *Frankenia sahariensis* (P-05038748); (C, D) *F. dinteri* (ABH-76891); (E, F) *F. pulverulenta* (ABH-7952). Scale bars = 100 µm (A, C, E), 50 µm (B, D, F).

In the protologue of *F. dinteri*, Pohnert [60, as *F. densa*] hypothesised that his newly described species exhibited a close resemblance to *F. laevis*, although also displayed intermediate characteristics with *F. pulverulenta*. However, *F. laevis* is not known to occur in sub-Saharan Africa, and shows quite different morphological features, such as the prostrate shrubby stems (vs. annual herbaceous or slightly suffrutescent at base in *F. dinteri*) with leaves non-fleshy, strongly revolute and densely pubescent to tomentose beneath (vs. leaves fleshy, often flattened at base and glabrous to subglabrous beneath in *F. dinteri*); flowers axillary and scattered along branches (vs. flowers often densely crowded in terminal cymes in *F. dinteri*); and bracteoles about equalling the calyx length (vs. bracteoles about half the calyx length in *F. dinteri*). Furthermore, the original description also presented *F. densa* as a shrublet, though a detailed observation demonstrated that it is a robust annual

or short-living perennial herb, only superficially resembling *F. pulverulenta*. On that basis, both names were likely synonymised by Obermeyer [62], a treatment which was adopted by subsequent authors so far (cf. [65,66]). However, sound morphological differences exist apart from the habit that allow easy separation (Table 3) of both latter entities:

- i) flowers often densely crowded in many-flowered cymes in *F. dinteri* vs. axillary, solitary or in lax cymes in *F. pulverulenta*) (Figure 3A,B);
- ii) floral bracts about half to two-thirds the calyx length vs. equalling to slightly exceeding the calyx length in *F. pulverulenta*;
- iii) bracteoles 1–2 mm long vs. 2.5–4 mm in *F. pulverulenta* (Figure 3C,D);
- iv) calyx teeth mucro ca. 0.4 mm long vs. ca. 0.1 mm in *F. pulverulenta* (Figure 3D);
- v) anthers 0.6–0.8 mm long vs. 0.2–0.4 mm long;
- vi) capsule 3–4.5 mm long vs. 2–3 mm in *F. pulverulenta* (Table 3); and
- vii) seeds morphologically close in both species (Figure 7), though less abundant in *F. dinteri* (25–30 per capsule) than in *F. pulverulenta* (up to 45 per capsule).

As mentioned before, and according to our data, both species overlap their distributions and are sympatric at least in the south of its distribution area (i.e. the Karro region of South Africa). However, the morphological patterns separating both entities remain invariable and warrant confident distinction, which is congruent with their remote position in all our trees (Figures 5 and 6). Resemblances to other congeners are weak and probably due to convergence.

Finally, in this context it is worth mentioning the case of *F. cespitosa* Lowe, a name that is sometimes synonymised with *F. pulverulenta* [4] or also with *F. laevis* L. [26]. *Frankenia cespitosa* was harvested in the islands of Madeira (at Ponta S. Lourenço) and Porto Santo, both from the Archipelago of Madeira (Portugal), and was described by Lowe [67] as a morphologically close relative of *F. ericifolia* and *F. corymbosa*. A thorough examination of the original material (K!, BM!, P!) reveals that the Madeiran *F. cespitosa* is unmistakably a woody perennial species, with leaves linear, strongly revolute and densely covered with whitish salt crusts (as observed on the stems), flowers in dense terminal crowded inflorescences, and calyx strongly twisted, among other features. All these characters separate the Madeiran plant from both *F. pulverulenta* and *F. laevis*, the latter producing leaves lacking extensive salt crusts, flowers axillary and solitary along branchlets, and calyx untwisted. In contrast, the morphological features of *F. cespitosa* closely resemble those of certain species from Macaronesia and northwestern Africa, as suggested in the protologue. In fact, the obtained ITS tree confirms such inferred morphological connections, placing the Madeiran *F. cespitosa* far apart from *F. laevis*, as a strongly supported sister to an unresolved clade comprising *F. capitata* Webb & Berthel. (Canary Islands) plus *F. ifniensis* Caball. (Atlantic coast of northwestern Africa), occasionally treated as *F. corymbosa* var. *ifniensis* (Caball.) Maire, with which it shares its gross morphology as well. Furthermore, they all are connected to the *F. ericifolia*-*F. sahariensis* clade (Canary Islands-northwestern Africa) plus *F. pseudoericifolia* (Cape Verde Archipelago), highlighting also biogeographical relationships between Macaronesia and northwestern Africa. Unfortunately, no *matK* data were obtained to date that illustrate about the position of *F. cespitosa* in the plastid phylogeny.

5. Conclusions

As currently circumscribed, many species of *Frankenia* are accepted in such a broad sense that they encompass various biological entities superficially similar but quite diverse when studied in detail. Although appearances can be deceptive, the application of integrative taxonomy, combining morphological, phylogenetic, ecological and distributional data, reveals the existence of distinct biological entities that need to be identified in due measure and that should be accepted in proper taxonomic ranks.

According to the morphological and molecular phylogenetic data obtained in the present work, *F. sahariensis* and *F. dinteri* show differences enough to be accepted as specifically distinct from *F. pulverulenta* and other Eurasian and African members of the genus. Further research is going on to

generate sequences of new plastid regions that will contribute to complete the picture on phylogenetic relationships of Eurasian and African aggregates of *Frankenia*.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org. Figure S1: Phylogenetic trees of *Frankenia* accessions after: **(A)** Maximum Parsimony (MP) analysis of ITS nuclear sequences; **(B)** Neighbour Joining (NJ) analysis of ITS nuclear sequences; **(C)** Maximum Parsimony (MP) analysis of *matK* plastid sequences; **(D)** Neighbour Joining (NJ) analysis of *matK* plastid sequence.

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Data Availability Statement: DNA sequences generated in the present research are available at GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). Other information related to this study will be provided discretionally upon request to the corresponding author.

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