BORN IN THE MEDITERRANEAN: COMPREHENSIVE TAXONOMIC REVISION OF *BISCUTELLA* SER. *BISCUTELLA* (BRASSICACEAE) BASED ON MORPHOLOGICAL AND PHYLOGENETIC DATA[1,2]

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ABSTRACT

Biscutella L. ser. *Biscutella* (= *Biscutella* ser. *Lyratae* Malin.) comprises mostly annual or short-lived perennial plants occurring in the Mediterranean basin and the Middle East, which exhibit some diagnostic floral features. Taxa in the series have considerable morphological plasticity, which is not well correlated with clear geographic or ecologic patterns. Traditional taxonomic accounts have focused on a number of vegetative and floral characters that have proved to be highly variable, a fact that contributed to taxonomic inflation mostly in northern Africa. A detailed study and re-evaluation of morphological characters, together with recent phylogenetic data based on concatenation of two plastid and one nuclear region sequence data, yielded the basis for a taxonomic reappraisal of the series. In this respect, a new comprehensive integrative taxonomic arrangement for *Biscutella* ser. *Biscutella* is presented in which 10 taxa are accepted, namely seven species and three additional varieties. The name *B. eriocarpa* DC. is reinterpreted and suggested to include the highest morphological variation found in northern Morocco. Its treatment here accepts two varieties, one of which is described as new (*B. eriocarpa* var. *riphaea* A. Vicente, M. Á. Alonso & M. B. Crespo). In addition, the circumscriptions of several species, such as *B. boetica* Boiss. & Reut., *B. didyma* L., *B. lyrata* L., and *B. maritima* Ten., are revisited. Nomenclatural types, synonymy, brief descriptions, cytogenetic data, conservation status, distribution maps, and identification keys are included for the accepted taxa, with seven lectotypes and one epitype being designated here.

Key words: *Biscutella*, Cruciferae, integrative taxonomy, Mediterranean endemics, Mediterranean flora, nomenclature, northern Africa.

The genus *Biscutella* L. (Brassicaceae Burnett nom. cons., or Cruciferae Juss. nom. cons.) includes annual herbs or dwarf shrubs distributed through Europe, northern Africa, and Southwest Asia, and comprises about 45 to 53 species according to more recent studies (Warwick & Al-Shehbaz, 2006; Marhold, 2011; Al-Shehbaz, 2012). Two sections morphologically well differentiated are commonly recognized (Grau & Klingenberg, 1993; Guinea & Heywood, 1993): *Biscutella* sect. *Biscutella* and *Biscutella* sect. *Jondraba* (Medik.) DC. (≡ *Jondraba* Medik.). *Biscutella* ser. *Biscutella* (= *Biscutella* ser. *Lyratae* Malin.) includes the type of the genus and comprises mostly annual or short-lived perennial plants, with petals gradually tapering at base and lateral intrastaminal nectaries (Malinowski, 1911; Olowokudejo, 1986; Guinea & Heywood, 1993), and it is mainly distributed in northern Africa, Southwest Asia, and western Europe.

Biscutella is the type of tribe Biscutelleae, which also includes other morphologically divergent genera such as *Heldreichia* Boiss., *Lunaria* L., *Megadenia* Maxim., and *Ricotia* L. (Özüdoğru et al., 2015, 2017). *Biscutella* is notorious for its taxonomic complexity, due to the wide variation of vegetative features, with broad interspecific morphological plasticity found in many taxa, and the relative uniformity of flower and fruit characters (Olowokudejo, 1986; Guinea & Heywood, 1993). Consequently, many contrasting taxonomic treatments are

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[2] M. Á. A. and M. B. C. designed the study. A. V. performed most of the laboratory analyses. A. V. and M. B. C. conducted the analyses. M. Á. A. and M. B. C. wrote the major part of the manuscript and prepared the illustrations. All authors participated in the field work, collected plant material, and greatly contributed and provided comments on the first drafts.

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available, according to the criteria adopted and sources used by the different authors (see Candolle, 1811; Jordan, 1864; Malinowski, 1911; Machatschki-Laurich, 1926; Guinea, 1964; Appel & Al-Shehbaz, 2003; Marhold, 2011; Al-Shehbaz, 2012; The Plant List, 2013). This variation is nevertheless unequally distributed.

Taxa of *Biscutella* ser. *Biscutella* are widespread in the Mediterranean basin and Southwest Asia (Malinowski, 1911; Machatschki-Laurich, 1926; Maire, 1967; Hedge, 1968, 1984; Olowokudejo, 1986; Guinea & Heywood, 1993). Relative morphological homogeneity can be observed in the central-eastern Mediterranean basin to Southwest Asia where *B. didyma* L. is mostly distributed, whereas the highest morphological plasticity and diversity occurs in northern Africa (Vicente et al., 2016a, 2019a).

In recent works, the *Biscutella didyma* group tends to be treated in a very broad sense, many of the species historically accepted being considered as synonyms of *B. didyma* in several regional floras (see Quézel & Santa, 1963; Maire, 1967; Hedge, 1968, 1984; Pottier-Alapetite, 1979; Guinea & Heywood, 1993; Fennane, 1999). Some of these taxa remain included at infraspecific ranks in many floras to describe the wide variation on fruit features found in the group. First, plants with glabrous fruits are very often treated as *B. didyma* var. *leiocarpa* (DC.) Halácsy (Zohari, 1966; Meikle, 1977). Furthermore, *B. ciliata* DC. var. *applanata* Mach.-Laur. has been commonly applied to plants with flattened silicles (Hedge, 1968, 1984), which appears to be the commonest form in the Middle East.

In addition, *Biscutella depressa* Willd. is a taxon described from Egypt by Willdenow (1809), comprising small-sized plants with silicle margins remarkably swollen, whose morphological features have been considered consistent enough by some authors to treat this taxon at specific (Machatschki-Laurich, 1926) or infraspecific (Guinea, 1964; Boulos, 1999) ranks.

Recently, two subspecies of *Biscutella didyma* (subspecies *didyma* and subspecies *apula* Nyman) have been recognized by Raffaelli (1991). These comprise two extremes of variation of the species in the central Mediterranean basin. The name *B. didyma* subsp. *didyma* (= *B. columnae* Ten.) was applied to plants with leaves crowded in a basal rosette and bract-like stem leaves, bearing short and dense fruiting racemes. Conversely, the name *B. didyma* subsp. *apula* (= *B. ciliata*) remained for plants exhibiting many leaves alternate on stems, lacking a dense rosette and producing dense fruiting racemes, usually looser in the basal part. In the same work, that author described *B. morisiana* Raffaelli from Sardinia to refer to an entity morphologically close to *B. didyma* subsp. *didyma* but distinguished by a supposedly peculiar type of silicle. Finally, *B. didyma* subsp. *dunensis* Chrtek & B. Slavík has recently been described (Chrtek & Slavík, 1981) from sand dunes of Cyprus, based on the small plant size and an apparently constant type of silicle.

The wide morphological variation found in *Biscutella* ser. *Biscutella* in northern Africa has received very different taxonomic treatments. On the one hand, Battandier (1888) included nine taxa to cover all the variability found in the series, and Maire (1967) recognized up to 30 infraspecific taxa in the series in his *Flore de l'Afrique du Nord*, producing the most comprehensive analytic approach applied to the group thus far. Both arrangements are mainly based on fruit size and indumentum, and other highly variable characters such as leaf morphology or flower color and scent, a fact that contributed to more confusion regarding the genus taxonomy. On the other hand, recent treatments of *Biscutella* in floras of North African countries (Quézel & Santa, 1963; Jafri, 1977; Boulos, 1999; Fennane, 1999; Grau, 2002; Le Floc'h et al., 2010) usually follow synthetic approaches in which only one to three taxa are accepted.

In general terms, the name *Biscutella lyrata* L. (= *B. microcarpa* DC.) has been traditionally applied to southern Iberian annual plants with basal lyrate leaves, small silicles, and usually filiform fruiting pedicels, and many floras have included or at least considered as probable the presence of this species under different ranks in northern Africa (see Desfontaines, 1798; Battandier & Trabut, 1902; Guinea & Heywood, 1964, 1993; Maire, 1967; Pottier-Alapetite, 1979; Le Floc'h et al., 2010). Nevertheless, two decades ago some authors stated that *B. lyrata* should be disregarded in northern Morocco, on the basis of the absence of winged staminal filaments in the Moroccan plants (Grau, 1999). This fact was recently confirmed on studies focused on the genus including molecular analyses (Vicente et al., 2016a, 2019a) in which close phylogenetic relationship was discarded between the true Spanish *B. lyrata* and the North African entities. In addition, these authors (Vicente et al., 2016a, 2017) have recently attributed some lyrate-leaved Algerian and Tunisian plants to different taxa, such as *B. raphanifolia* Poir. var. *algeriensis* (Jord.) A. Vicente, M. Á. Alonso & M. B. Crespo or *B. maritima* Ten., the presence of the latter being previously stated by Raffaelli and Ricceri (1989) in northwestern Tunisia. Similarly, populations from Gharb region (northwestern Morocco) morphologically related to and sometimes identified with *B. maritima* have been recently described as a new species, *B. pseudolyrata* A. Vicente, M. Á. Alonso & M. B. Crespo, which grows in peculiar, deep red sandy soils of Neogenic-Quaternary origin.

Morphological plasticity of *Biscutella* ser. *Biscutella* found mostly in Morocco and Algeria, which Maire (1967) arranged in 30 infraspecific taxa within *B. didyma*, has been attributed in recent floras to the

variability of both *B. didyma* s.l. and *B. microcarpa* (Fennane, 1999) or *B. boetica* Boiss. & Reut. (Grau, 2002). Finally, *B. eriocarpa* DC., an African entity described by Candolle (1811) from a single incomplete specimen collected by Broussonet from an unspecified site between southern Spain and Mogador, has often been considered a synonym of *B. didyma* (Guinea & Heywood, 1993; The Plant List, 2013) or *B. boetica* (Grau, 2002), its real identity remaining enigmatic to date as first suggested by Manton (1932).

The aims of the present work are: (1) to re-evaluate the morphological data traditionally used for taxonomic purposes in light of recent molecular phylogenies of *Biscutella* ser. *Biscutella*; (2) to review the circumscription, taxonomic status, and nomenclature of the accepted taxa by combining both morphological and phylogenetic data; and (3) to build a new comprehensive integrative taxonomic arrangement of the series to better understand this often confusing group of Mediterranean taxa.

Materials and Methods

morphological studies

Fresh material of all recognized taxa in *Biscutella* ser. *Biscutella* collected during field work in Spain, Morocco, Algeria, Italy (including Sicily and Sardinia), Turkey, and Tunisia, as well as herbarium specimens conserved at ABH, B, BC, BCN, CAI, COA, COFC, COI, EGE, FI, G, GDA, GZU, HAL, JE, K, MA, MPU, P, RNG, SALA, SEV, VAL, and VLA (acronyms according to Thiers, 2020) were used for morphological and molecular studies. The principal Mediterranean and Southwest Asian floras were consulted for taxonomic identification (Battandier, 1888; Quézel & Santa, 1963; Maire, 1967; Hedge, 1968, 1984; Pottier-Alapetite, 1979; Pignatti, 1982, Grau & Klingenberg, 1993; Guinea & Heywood, 1993; Boulos, 1999; Fennane, 1999). Over 800 herbarium vouchers were visually examined, and both qualitative and quantitative analyses were conducted on over 600 of those specimens (see Appendix 1 for selected material). The characters observed or measured were selected from those traditionally used in the literature on the genus (Poiret, 1789; Jordan, 1864; Malinowski, 1911; Guinea, 1964; Maire, 1967), along with those considered relevant according to our observations (see Table 1).

In general terms, measurements were made over mature plants, bearing both flowers and well-developed fruiting inflorescences. Fruit and seed measurements were taken only from mature silicles. All size intervals shown in the morphological descriptions correspond to "length × width." Six distinct types of fruit indumentum were defined in order to establish a proper arrangement, based on previous studies of Olowokudejo (1985) and Raffaelli (1991) (Table 2), albeit intermediate stages were frequently observed. According to Vicente et al. (2019a), pedicel mean length was calculated by measuring the first five basal fruits of the panicle terminal branches, and raceme density was obtained by calculating the number of fruits on the first 3–5 cm of the terminal branches, depending on the raceme length. The beginning of the inflorescence was considered to be just before the first stem branch, as far as there were no well-developed leaves above it; otherwise, the beginning was considered to be just after the last well-developed leaf. The leaf and fruit indumentum as well as nectaries and pollen grains were examined under a Scanning Electron Microscope (SEM) JEOL JSM-840 (JEOL, Ltd., Tokyo, Japan), operating at 1.5 kV. No special treatment was required prior to observation. Regarding pollen features, measurements from over 15 specimens of *Biscutella* ser. *Biscutella* were undertaken on acetolized grains. Samples were glued directly on metallic stubs, and then coated with about 30 nm gold in a Balzers SCD004 sputter coater (Oerlikon Balzers, Balzers, Liechtenstein). The ImageJ software (Rasband, 1997–2017) was utilized for measuring on SEM micrographs. The proposed conservation status for each accepted taxon was achieved according to the Red List categories and criteria of the IUCN (2012). Author names of taxa accord with IPNI (2020). Nomenclatural issues follow the *Shenzhen Code* (ICN, Turland et al., 2018).

phylogenetic studies

A comprehensive phylogeny of *Biscutella* ser. *Biscutella* was constructed showing the relationships of the accepted taxa in the series (see Alonso et al., 2020). The data matrix included 45 samples of *Biscutella* with *Lepidium draba* L. (≡ *Cardaria draba* (L.) Desv.) and *Megadenia speluncarum* Vorob., Vorosch. & Gorovoj (sensu Artyukova et al., 2014) as outgroups (see Appendix 2). All specimens sampled for molecular work were also included in the morphological analyses. For each sampled taxon, nucleotide sequences of one nuclear ribosomal DNA (nrDNA) region (internal transcribed spacers [ITS] ITS1-ITS2 plus 5.8S gene) and two chloroplast DNA (cpDNA) regions (*rpl32-trnL* and *trnV* intron) were obtained. Three different data sets were produced, corresponding respectively to: (1) the concatenated plastid (two regions) data matrix; (2) the nuclear (ITS) data matrix; and (3) the concatenated molecular (plastid plus nuclear) sequence data matrix. Phylogenetic reconstruction for maximum likelihood (ML) was estimated using the 3-parameter method of Tamura (1992) with a Gamma distribution (*G*) for all matrices. Furthermore, a Bayesian inference (BI) analysis

Table 1. Most valuable morphological characters defining taxa in *Biscutella* L. ser. *Biscutella*.

Character	*B. boetica*	*B. didyma* var. *didyma*	*B. didyma* var. *ciliata*	*B. eriocarpa* var. *eriocarpa*	*B. eriocarpa* var. *riphaea*	*B. lyrata*	*B. maritima*	*B. pseudolyrata*	*B. raphanifolia* var. *raphanifolia*	*B. raphanifolia* var. *algeriensis*
Stem length (cm)	20–60(–70)	(7–)15–50	(7–)15–50(–60)	13–37	(10–)20–50(–65)	15–45	15–85(–120)	25–45(–60)	30–100	23–40
Stem indumentum	hirsute at base	hirsute at base	hirsute at base	glabrescent to hirsute at base	hirsute at base	glabrescent	hirsute at base	glabrescent to hirsute at base	hirsute to lanate at base	hirsute at base
Leaf indumentum	hirsute	hirsute	hirsute	hirsute	hirsute	glabrescent, scarcely hirsute	hirsute	hirsute	hirsute to lanate	hirsute
Basal leaf shape	oblanceolate (dentate to pinnatipartite)	oblanceolate (dentate to pinnatisect)	oblanceolate (dentate to pinnatisect)	dentate to pinnatipartite-pinnatisect	pinnatipartite-pinnatisect	lyrate-pinnatipartite	lyrate-spatulate (oblanceolate)	lyrate to oblanceolate	lyrate-pinnatipartite	lyrate-pinnatipartite
Basal leaf size (cm)	up to 11 × 3.5	up to 8 × 2.5	up to 7 × 2	up to 7 × 2.5	up to 13 × 4.5	9 × 3	up to 14(–20) × 4.5(–6)	up to 12 × 3	up to 20 × 6	up to 8.5 × 3.5
Cauline leaves	1 to 5 (rarely absent)	absent (occasionally 1)	present	0 to 1(to 3)	1 to 8	1 to 5 (rarely absent)	absent (occasionally 1 to 3 at base)	absent (occasionally 1 to 2)	present	present (occasionally absent)
Cauline leaves insertion	attenuate-semiamplexicaul	attenuate	attenuate	attenuate to semiamplexicaul	attenuate to amplexicaul	attenuate	attenuate-semiamplexicaul	attenuate	amplexicaul to auriculate	amplexicaul to attenuate
Inflorescence branching pattern	B–C(C+)	B–C+	B–C+	(A)B–C	(A)B–C(C+)	A–C(C+)	B–C+	A–C(C+)	D	D
Number of terminal racemes per branch	2 to 8(to 15)	1 to 8(to 15)	1 to 8(to 11)	1 to 8	2 to 8(to 13)	1 to 8	2 to 8(to 15)	1 to 8	8 to 20(to 30)	8 to 20(to 30)
Raceme length/stem length ratio	0.25–0.5(–0.6)	0.06–0.25	0.09–0.30	0.10–0.33(–0.4)	0.15–0.4	0.21–0.5	0.10–0.35	0.19–0.42	0.05–0.16	0.10–0.25
Pedicel insertion	non-unilateral, patent to erect-patent (unilateral)	non-unilateral erect (to erect-patent)	non-unilateral erect (to erect-patent)	unilateral or non-unilateral, patent to erect-patent	unilateral or non-unilateral erect to erect-patent	patent to erect-patent	non-unilateral, patent to erect-patent	non-unilateral, erect-patent	non-unilateral, erect-patent	non-unilateral, erect-patent
Pedicel length (first 5 basal fruit mean) (mm)	6.5–9(–10)	2–6	2.2–8	(3.5–)4.7–9	4.5–8.5(–10)	5–9	(5.5–)7–12	6.5–11	5.3–11	5.4–10.4
Sepal length (mm)	1.5–2.5	1.3–2.5	1.3–2.5	1.5–2.5	1.5–2.6	1.3–2	(1.5–)2–3	1.8–3	1.8–3	1.4–2.6
Petal length (mm)	2.5–5	(2–)2.5–4.5	2.1–5	2.5–5	2.3–4.8	2–4	(3.5–)4–6.5	2.8–5(–6)	3–6	2.9–5(–6)
Staminal filament	not winged	not winged	not winged	not winged	not winged	broadly membranous wing	not winged	not winged	not winged	not winged
Median nectary length (mm)	0.2–0.4	inconspicuous or up to 0.2	inconspicuous or up to 0.2	up to 0.25	up to 0.25	up to 0.4	(0.4–)0.5–0.7(–0.8)	0.4–0.6	inconspicuous or up to 0.4	inconspicuous or up to 0.4
Raceme density (fruits/cm) [mean value]	1 to 3(to 4) [2.3]	5 to 9 [7.0]	3 to 9 [5.8]	(3 to)4 to 10 [6.5]	3 to 8 [5.3]	1 to 3(to 4) [2.5]	(1 to)2 to 5(to 6) [3.7]	1 to 3(to 4) [2.3]	(1 to)2 to 5 [3.4]	2 to 5 [3.2]
Fruit width (mm)	(4.5–)5–10	(6–)7–13.5	7–13.5	5–10	5.5–10(–13)	4–6	(6–)7–13	6.5–12	(8.2–)9–15	4.5–9(–11)
Style length (mm)	1.8–3(–3.8)	1.5–2.5	1.8–3	1.5–2.5	1.5–3	1–2(–2.5)	2–3.5	(1.6–)1.9–2.9	2.6–4.5(–5)	2–3
Style length/fruit width ratio	(0.28–)0.3–0.45	0.18–0.23	0.19–0.25	0.22–0.35	0.22–0.40	0.30–0.40	(0.23–)0.25–0.37	(0.18–)0.22–0.33	0.27–0.40	0.28–0.45
Fruit indumentum type	S2–S3, S6	S1–S6	S1–S6	S1–S3, S6	S2–S3, S6	S1, S4–S6	S1–S6	S1–S6	S6(S1–S5)	S2 (mostly), S1–S6

Table 2. Different models of fruit indumentum in *Biscutella* L. ser. *Biscutella*, as considered in the morphological study.

Indumentum type	Trichome distribution pattern
S1	Surface and margins totally covered by clavate trichomes, with or without tiny conical trichomes
S2	Surface covered with tiny conical hairs together with clavate hairs on margin and center, where they are longer
S3	Clavate trichomes distributed only on margin, generally lacking tiny conical indumentum
S4	Clavate trichomes only present on the central part, with or without tiny conical indumentum
S5	Surface only covered with tiny conical indumentum, lacking clavate trichomes
S6	Entirely glabrous silicles

was conducted with MrBayes 3.2 (Ronquist et al., 2012). For details on material used, analyses performed, and GenBank accession numbers, see Alonso et al. (2020).

Results

Morphological results

Basal and cauline leaves

In general terms, all the studied groups presented a basal rosette of petiolate leaves, showing different densities (from three to more than 20 leaves). Leaf shape usually does not remain a constant character in some cases, since individuals with different leaf morphology can be occasionally found in most taxa (Fig. 1). Nevertheless, several general patterns are observed. On the one hand, *Biscutella boetica* and *B. didyma* and most western Moroccan entities, hereinafter *B. eriocarpa* var. *eriocarpa*, generally exhibit oblanceolate and regularly dentate leaves, but occurrence of individuals with pinnatifid or pinnatisect leaves is also common in the distribution area of the latter, and even in a single population. These will be henceforth referred to as *B. eriocarpa* var. *riphaea* A. Vicente, M. Á. Alonso & M. B. Crespo (Fig. 1A), and are common in the eastern distribution of the species. On the other hand, *B. lyrata*, *B. maritima*, *B. pseudolyrata*, and *B. raphanifolia* (s.l.) usually exhibit lyrate leaves, with relatively regular lateral lobes and mostly exhibiting a broad, rounded and relatively entire terminal lobe (Fig. 1B–D). Some Tunisian and Algerian specimens of *B. maritima* (e.g., MA-724301, MA-746967) tend to show spatulate leaves after reduction of most of the lateral lobes in the regular lyrate ones. In addition, some deviant specimens of both *B. maritima* from Constantine (Fig. 1C7) and *B. pseudolyrata* from Kenitra and Rabat (Fig. 1B7) produced mostly oblanceolate leaves with long petioles (e.g., P-04657216, P-04657219, P-04743559, P-04745864). Most of the Moroccan populations belonging to *Biscutella* ser. *Biscutella*, usually identified as "*B. lyrata*," presented pinnatipartite to pinnatisect leaves, mostly lacking a broad and subentire terminal lobe.

Cauline leaves are sessile and their size decreases upward, the uppermost being always bract-like. The typical *Biscutella lyrata*, *B. pseudolyrata*, and *B. maritima* generally lack well-developed cauline leaves. Among the Moroccan population often erroneously identified as "*B. lyrata*" two clear patterns can be observed. *Biscutella eriocarpa* var. *eriocarpa* mostly lacks cauline leaves, whereas *B. eriocarpa* var. *riphaea* exhibit several well-developed leaves on the basal half of the stem. However, both varieties occur together in the same geographic area and even the same population. Insertion of well-developed cauline leaves in *Biscutella* ser. *Biscutella* ranged from attenuate to amplexicaul and while some tendencies can be found, leaf insertion constitutes a rather inconstant character. Nonetheless, individuals of *B. raphanifolia* usually bear amplexicaul or semiamplexicaul caulinar leaves.

Indumentum is a constant character for all taxa in the series, albeit density can vary between individuals (cf. Olowokudejo, 1985; Raffaelli, 1991). In most cases, plants are hirsute, with an indumentum of short (ca. 1 mm long) trichomes. These are placed on the leaf surface and more densely arranged on veins, in which they tend to be more rigid and thickened at base. Some specimens of *Biscutella raphanifolia* var. *raphanifolia* present, together with those typical hirsute trichomes, other soft and flexuous trichomes often reaching 1.5 mm long that give the leaves a villous aspect.

Inflorescence

The 11 types of inflorescence presented by Olowokudejo (1992) are here reduced to four (Fig. 2), according to the wide range of variation observed. Type A corresponds to plants presenting a simple raceme, whereas type B consists of a simple panicle. Types C and D exhibit inflorescences with compound (many-branched) panicle, where the complexity of the branching pattern tends to decrease from the base to top. The branching pattern in type C consists of a double panicle, presenting dyads in, at least, 30% of the lateral branches. The inflorescences in type D consist of a profusely branched panicle, with at least 30% (but commonly overpassing 50%) of the lateral branches

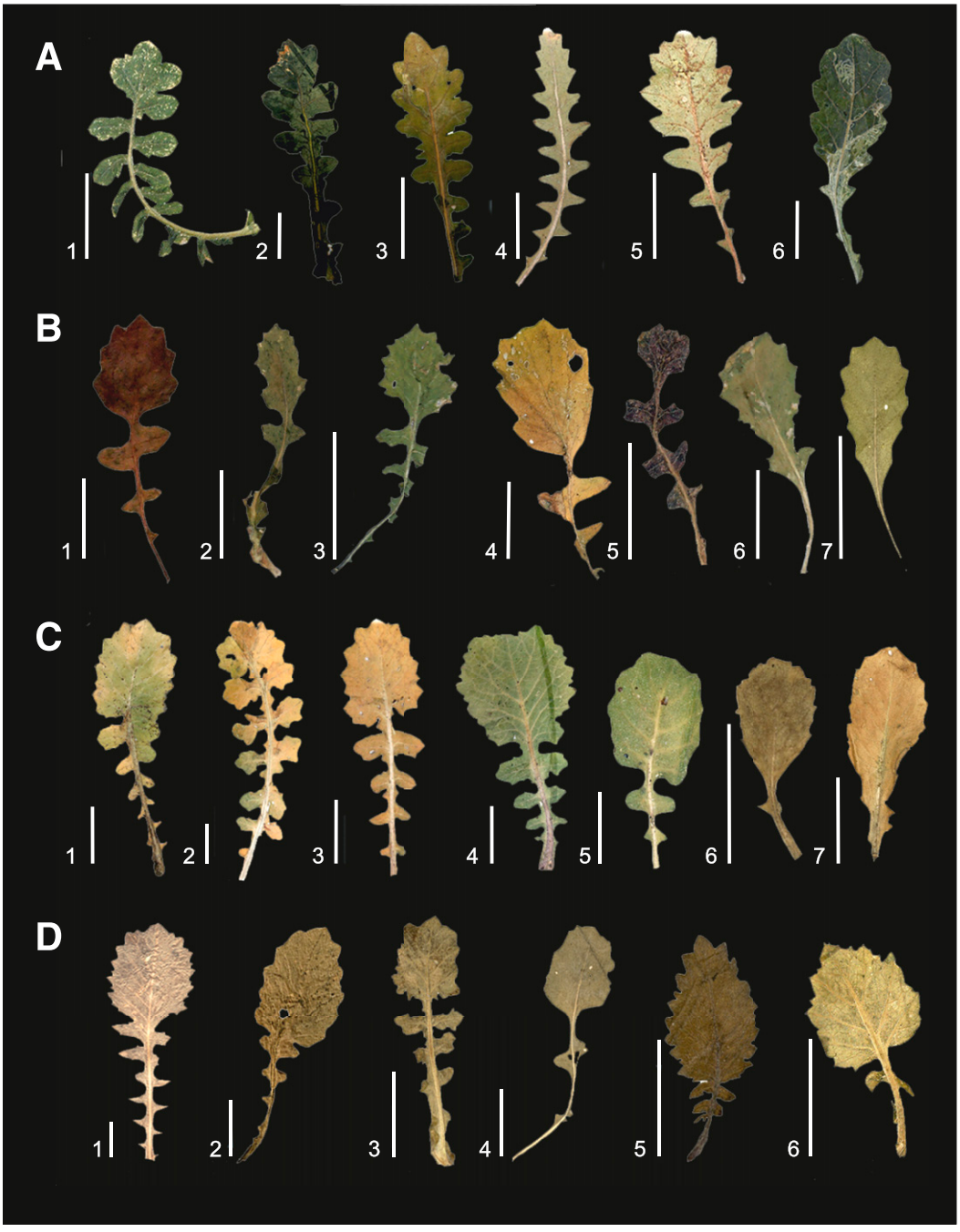

Figure 1. Leaf variation found in some North African taxa of *Biscutella* L. ser. *Biscutella* with lyrate to sublyrate leaves. —A. *Biscutella eriocarpa* DC. s.l. (1. ABH-68371, 2. ABH-68337, 3. ABH-68353, 4. ABH-59292, 5. ABH-68339, 6. ABH-68354). —B. *Biscutella pseudolyrata* A. Vicente, M. Á. Alonso & M. B. Crespo (1. MA-44485, 2. ABH-74993, 3. ABH-74995, 4. ABH-75002, 5. ABH-72445, 6. ABH-74995, 7. P-04657219). —C. *Biscutella maritima* Ten. (1. ABH-70573, 2. ABH-70558, 3. ABH-70576, 4. ABH-70519, 5. ABH-70574, 6. P-05438830, 7. P-05325933). —D. *Biscutella raphanifolia* Poir. s.l. (1. P-00166955, 2. MPU-003730, 3. P-05438159, 4. P-05438188, 5. P-05438658, 6. ABH-72641). Scale bars = 2 cm.

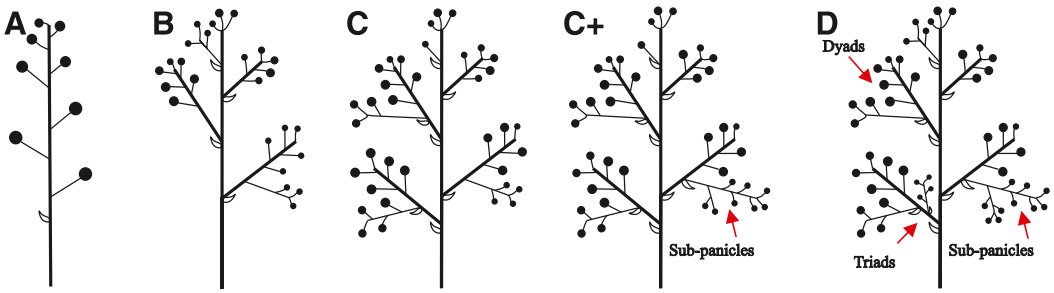

Figure 2. Inflorescence types found in taxa of *Biscutella* L. ser. *Biscutella*. —A. Simple raceme. —B. Simple panicle, sometimes with dyads. —C. Double panicle (with dyads and occasionally some triads or sub-panicles, up to eight terminal racemes in total). —D. Profusely branched panicle (with dyads, triads, and sub-panicles, more than eight terminal racemes in total).

showing dyads, triads, and/or sub-panicles (Fig. 2) with more than eight terminal racemes.

Most *Biscutella raphanifolia* specimens (including both varieties) produced the profusely branched panicles of type D, which characterize that species (Vicente et al., 2016a). Consequently, the terminal racemes in those individuals tend to be shorter but vey numerous (eight to 30 per stem). Branching patterns were variable from B to C in the remaining groups. However, larger plants occasionally exhibited a wider but loose panicle of type C including scarce few-flowered sub-panicles, albeit with up to eight terminal racemes (hereafter type C+).

Fruit density and raceme length

Fruit density and raceme length are related characters with relatively high taxonomic value. Plants belonging to the *Biscutella didyma* group usually produce strongly condensed racemes (with the ratio raceme length/stem length usually less than 0.2) and high fruit density, although a certain range of variation exists within this group. In most cases, representatives of *B. didyma* var. *didyma* produce short and very dense fruiting racemes, whereas those of *B. didyma* var. *ciliata* (DC.) Vis. produce racemes sometimes longer and looser in the basal part, though many intermediate cases occur. In contrast, *B. boetica* specimens usually produce elongated racemes in fruit, often reaching half of the total stem length, with density of lower silicles never exceeding three fruits/cm (mean value: 2.3). Of African taxa, *B. eriocarpa* bears dense inflorescences, with three to 10 fruits/cm (mean value: $\geq$ 5.3), the length of which can be quite variable, whereas *B. pseudolyrata* usually bears loose racemes with one to three(to four) fruits/cm (mean value 2.3).

As said before, *Biscutella raphanifolia* specimens present short and dense inflorescences derived from its peculiar branching pattern. Finally, *B. lyrata* exhibits a relatively low raceme density with one to three(to four) fruits/cm (mean value: 2.5) and an elongated fruiting inflorescence (0.21–0.5, relation raceme length/stem length) with filiform pedicels, whereas *B. maritima* exhibits a wide range of fruit density with (one to)two to five(to six) fruits/cm (mean value: 3.7) and an intermediate raceme elongation with stouter pedicels. Those results are congruent with data reported by Raffaelli (1985a).

Pedicel length and insertion

Biscutella boetica and *B. maritima* generally show patent pedicels, which may be related to their elongation (pedicel mean length 6.5–9(10) mm and (5.5)7–11 mm respectively). On the other hand, *B. didyma* is characterized by short pedicels, barely exceeding 6 mm long in most individuals with erect to erect-patent insertion, albeit some specimens occasionally bear pedicels up to 10 mm long. *Biscutella pseudolyrata* generally presents long (6.5–11 pedicel mean length) and erect-patent pedicels, while *B. raphanifolia*, *B. eriocarpa*, and *B. lyrata* produce pedicels of intermediate length.

Most specimens belonging to *Biscutella eriocarpa* var. *eriocarpa* and *B. eriocarpa* var. *riphaea* show a remarkably unilateral fruiting inflorescence and, in general terms, when presenting non-unilateral inflorescences, pedicel insertion tends to be erect or erect-patent. Apart from these two taxa, most individuals of the remaining species in *Biscutella* ser. *Biscutella* show non-unilateral inflorescences, though some unilateral or almost unilateral racemes were exceptionally observed in some specimens of both *B. raphanifolia* or *B. boetica*.

Fruit indumentum and margin

Two types of indumentum are found in *Biscutella* ser. *Biscutella*: either clavate trichomes showing a wide range of length variation, from nearly sessile to clearly elongated up to 300 μm, or recurved and tiny conical hairs more or less densely arranged.

Indumentum is very variable in all studied taxa (Table 2), which usually presented most of the established types and any kind of intermediate forms. Exceptionally, the type S2 is clearly predominant in *Biscutella boetica*, although other types such as S3 and S6 can also be found. To a lesser extent, that trend is also observed in *B. eriocarpa* var. *riphaea*, whereas var. *eriocarpa* shows broader indumentum variation.

Some tendency to a reduction of trichome density was observed in *B. didyma*, in which silicles type S6 and S3 were especially common, with a lower indumentum density. Most individuals of *B. raphanifolia* var. *raphanifolia* show glabrous silicles, as indicated in the protologue, while variety *algeriensis* exhibits a wider variation (see Vicente et al., 2016a).

The specimens from Sardinia belonging to *Biscutella morisiana* (here treated in synonymy of *B. didyma* var. *didyma*) generally show the indumentum type described by Raffaelli (1991), namely type S3 or S2 with the claviform trichomes very laxly distributed on the central part, but a certain range of variation is also found including silicles lacking conical trichomes. Finally, specimens with entirely glabrous silicles, traditionally identified as *B. leiocarpa* DC., were found throughout the series distribution.

The margin of the silicles shows in many cases different grades of widening but, although some trends can be observed in some groups, this character was usually quite variable. In most of the *Biscutella didyma* individuals from Egypt and Libya (usually identified as *B. depressa*) the silicle margin exhibits an extremely remarkable swelling, not found in the rest of the specimens. In fact, plants with entirely flattened silicles were found throughout the whole distribution of the series.

Fruit size

Silicles on *Biscutella lyrata* never exceed 6 mm wide, this being one of its differential characters. Some specimens of other taxa bearing silicles up to 6 mm wide were very occasionally found in northern Morocco, often corresponding to small, poorly developed plants. Conversely, the broadest silicles are found in *B. raphanifolia* var. *raphanifolia* (8.2–15 mm), *B. maritima* (6–13 mm), and *B. didyma* (6–13.5 mm). In the latter, plants from the Middle East tend to produce larger fruits than specimens from the western Mediterranean, but again silicles of all sizes are commonly found in both distribution ranges. In general terms, the Tunisian plants of *B. maritima* show smaller size in all fruit features than the Italian ones.

Style length

Biscutella raphanifolia var. *raphanifolia* produces styles 2.6–4.5(–5) mm, longer than in the remaining members of the series, which usually do not exceed 3 mm long. However, when comparing style length/fruit width ratio, more relevant data are revealed. Thus, *B. didyma* shows the smallest ratio, shorter than 0.23 in most cases. Furthermore, *B. boetica*, *B. raphanifolia*, and *B. lyrata* show longer styles in relation to the silicle size (ratio up to 0.4–0.45), and taxa such as *B. eriocarpa* var. *eriocarpa* and *B. pseudolyrata* present slightly lower ratios (from 0.22 to 0.32–0.35).

Stamen filament morphology

The presence of a clear broad membranous wing in the filaments of median stamens was observed exclusively in Spanish plants belonging to *Biscutella lyrata*, and therefore is a diagnostic character for the species. The remaining members of the series always exhibit stamen filaments that are filiform and unwinged, apparently without significant differences in length and shape among taxa.

Nectary morphology

All taxa in *Biscutella* ser. *Biscutella* present four nectary glands: two median nectaries, located at base of the median staminal filaments (extrastaminal), and two lateral nectaries placed at base of the lateral filaments (intrastaminal) (Fig. 3). Thus, the lateral nectaries partially surround the staminal filaments, producing a semi-circular or curved shape (Fig. 3D).

Although the lateral nectaries tend to be inconspicuous or shortly elongated in most cases, the median ones show a wide range of length variation, which remains constant in some groups. *Biscutella didyma* always presents median nectaries that are inconspicuous or slightly elongated, up to 0.2 mm long (Fig. 3A), whereas the remaining taxa usually present longer ones. The median nectaries are consistently elongated in all *B. maritima* individuals, reaching (0.4)0.5–0.7(0.8) mm long and with a regular cylindrical shape (Fig. 3B), a character constant and exclusive of the species. Similarly, *B. pseudolyrata* (Fig. 3C) also exhibits elongated nectaries 0.4–0.6 mm, but clavate in shape. The rest of the taxa show variable nectaries up to 0.4 mm long, although *B. eriocarpa* individuals usually present shorter nectaries, up to 0.25 mm long (Fig. 3D).

Pollen morphology

Pollen grains in *Biscutella* are tricolpate, isopolar, with radial symmetry, elliptical in equatorial view and circular and lobed in polar view, with reticulate surface (Díez, 1987). Despite the small number (15) of samples studied, some patterns could be observed on the pollen size. The six samples belonging to the eastern and central Mediterranean taxa, *B. didyma* and *B. maritima*, presented longer polar axis/length (36.7–43.7 μm), whereas the remaining nine samples of western Mediterranean taxa, *B. boetica*, *B. eriocarpa* var. *riphaea*, *B. lyrata*, *B. pseudolyrata*, and *B. raphanifolia* var. *algeriensis*, presented shorter polar axis/length (25.3–35 μm).

Seed morphology

Members of *Biscutella* show characteristic seeds with a prominent and accumbent radicle (pleurorhizal type as defined by Candolle, 1824), which occupies

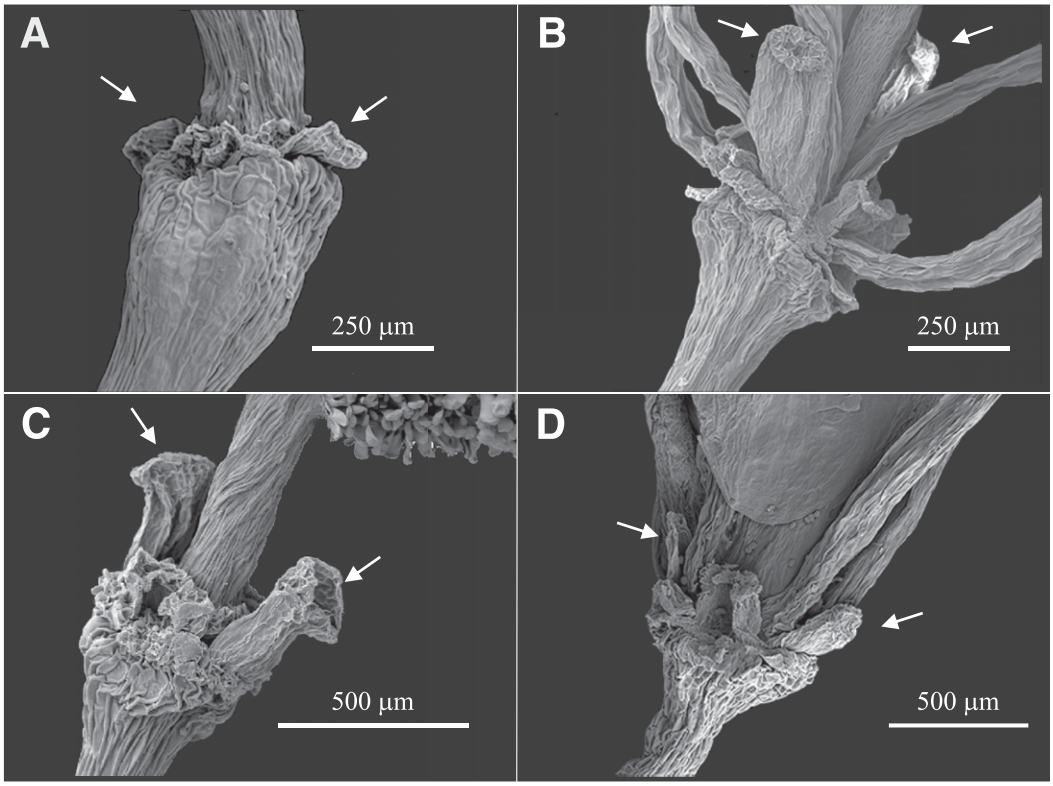

Figure 3. Variation of median nectaries (marked with arrows) in *Biscutella* L. ser. *Biscutella*. —A. *Biscutella didyma* L. (ABH-70569). —B. *Biscutella maritima* Ten. (ABH-70574). —C. *Biscutella pseudolyrata* A. Vicente, M. Á. Alonso & M. B. Crespo (ABH-74993). —D. *Biscutella eriocarpa* DC. var. *eriocarpa* (ABH-69882).

about half the length of the seed. In *Biscutella* ser. *Biscutella*, seeds are uniform in shape and color. They can be defined as orbicular in the sense of Murley (1951) and Vaughan and Whitehouse (1971), i.e., lenticular, strongly flattened, with a rounded to broadly elliptical outline. The color is often pale brown to yellow-orangish or olive-greenish. Variations in both features are equally found within most taxa in the series. The testa surface is smooth, lacking any outstanding structure, although sometimes it appears somewhat wrinkled, slightly alveolate or ridged, and minutely papillate on edges (cf. Černohorský, 1947; Vaughan & Whitehouse, 1971). These variations are also found in most representatives of the series and are not diagnostic for any particular taxon.

It is worth mentioning that all members in *Biscutella* ser. *Biscutella* exhibit seeds with very similar sizes, ranging from 1.1 to 2.5 mm long, which widely overlap among the different taxa. Seed size is not always correlated with the fruit size, since often seeds are notably smaller than their corresponding mericarp, excepting *B. lyrata* whose seeds almost entirely fill the mericarp. However, some tendencies exist deserving further comments. The largest seeds are usually found in the eastern and central Mediterranean taxa *B. didyma* var. *didyma* (1.8–2.4 mm) and *B. maritima* (2–2.5 mm), whereas the smallest correspond to the southern Spain taxon *B. lyrata* (1.2–1.6 mm). Other taxa exhibit a wide range of seed measurements overlapping with most of their relatives, such as the western Mediterranean *B. boetica* (1.3–2.3 mm), *B. eriocarpa* s.l. (1.1–2.1 mm), or *B. pseudolyrata* (1.4–2.1 mm), and the eastern Mediterranean *B. didyma* var. *ciliata* (1.5–2.2 mm). All of these facts make seed features not particularly relevant for taxon discrimination.

Phylogenetic results

The simplified ML consensus tree of the concatenated molecular matrix (2254 positions, highest log likelihood = –6518.31) is shown in Figure 4, in which bootstrap (BS) percentages and Bayesian posterior probability (PP) values are placed above branches (respectively, from the ML and BI analyses).

Biscutella ser. *Biscutella* is formed by six major clades (Clades A–F). The basal one (Clade A) corresponds to the taxon of southern Spain *B. lyrata* (100% BS, 1.00 PP), strongly supported (99% BS, 1.00 PP) as sister to the remaining taxa in the series. The central-

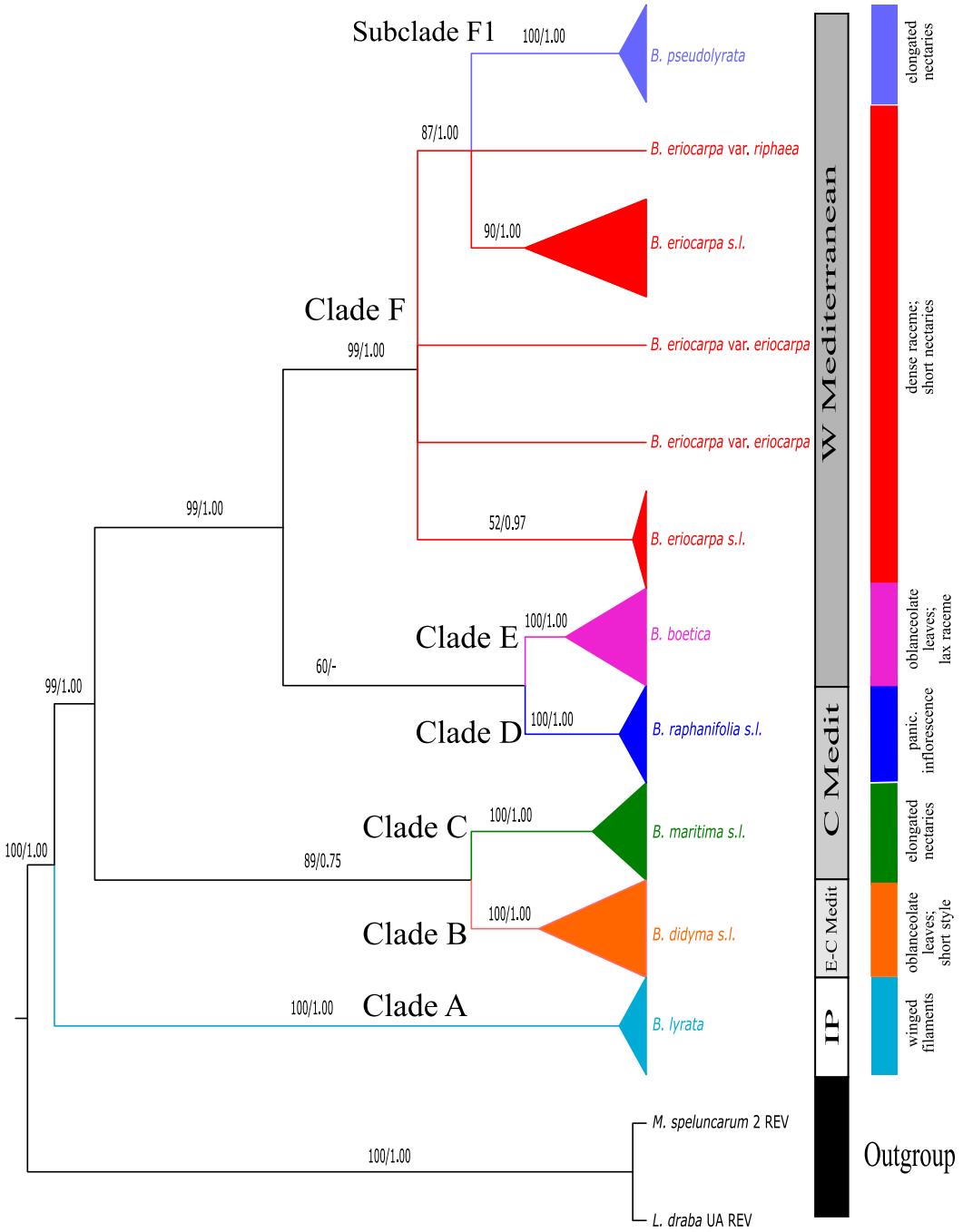

Figure 4. Condensed maximum likelihood (ML) phylogenetic tree of *Biscutella* L. ser. *Biscutella* (after Alonso et al., 2020), estimated from concatenated cpDNA (*rpl*32-*trnL* and *trnV*) and nrDNA (ITS) sequences (final dataset of 47 nucleotide sequences, with a total of 2254 positions). Bootstrap (BS) percentage and Bayesian posterior probability (PP) are shown above branches.

eastern Mediterranean *B. didyma* s.l. (Clade B; 100% BS, 1.00 PP) and the central Mediterranean *B. maritima* (Clade C; 100% BS, 1.00 PP) are moderately sister groups (89% BP, 75 PP). The latter two are strongly supported (99% BS, 1.00 PP) as sister to a weakly supported (60% BP, – PP) clade including the North African *B. raphanifolia* (Clade D; 100% BS, 1.00 PP) and the southwestern Mediterranean *B. boetica* (Clade E; 100% BS, 1.00 PP). The latter pair is sister to the "*B. eriocarpa*–*B. pseudolyrata* clade" with strong support

(Clade F; 99% BS, 1.00 PP), a group in which internal relationships are not fully resolved, albeit *B. pseudolyrata* forms a strongly supported group (Subclade F1; 99% BS, 1.00 PP) along with most samples of *B. eriocarpa* s.l. For additional information and more detailed data see Alonso et al. (2020).

Discussion

Characters traditionally used to discriminate among taxa in *Biscutella* ser. *Biscutella* (cf. Cosson, 1887; Maire, 1967; Pottier-Alapetite, 1979; Pignatti, 1982; Grau & Klingenberg, 1993; Fennane, 1999) have revealed highly variable and not always diagnostic for taxonomy. Among the characters measured (Table 1), only 11 (namely the stem length, basal leaf shape, presence of cauline leaves, inflorescence branching pattern, raceme length and density, pedicel length and insertion, median nectary length, style length, and presence of winged staminal filaments) were considered informative enough for taxonomical purposes, but a combination of characters is needed to properly define most taxa (see below section 5). Despite the different patterns of polar axis/length found in pollen grains of *Biscutella* ser. *Biscutella*, this character was not considered at this point due to the scarce number of samples analyzed. Further studies comprising more individuals of all taxa accepted in the series are needed to determine the real value of this character. Similarly, seed features were not discriminant. Only some trends concerning the seed size were observed, but they were discarded due to the extensive overlapping found among taxa.

As recently shown by Vicente et al. (2016a, 2017, 2019a) and Alonso et al. (2020), a new arrangement for the entire series (including a more satisfactory delimitation of taxa) is achieved which is more consistent with the observed morphological and molecular variation (see Alonso et al., 2020). The new taxonomic arrangement accepts seven monophyletic groups including 10 taxa (seven species plus three varieties) that are easily defined by a syndrome of morphological characters.

Firstly, *Biscutella lyrata* (Clade A) is a species with quite constant morphology. It is well characterized by its winged staminal filaments, which, as remarked by Grau (1999), is a feature absent in all the African taxa with rosulate, lyrate leaves (as well as in the rest of the known members of the genus). This fact, together with the outstanding molecular results, undoubtedly discount the presence of *B. lyrata* in northern Africa, it being exclusive to Cádiz Province in southern Spain (see Vicente et al., 2019a). In addition, the chromosome number $2n = 12$ [$n = 6$] (Manton, 1937; Olowokudejo & Heywood, 1984; Santa Bárbara et al., 1994; all three as "*B. microcarpa*"), unique in the whole genus, together with the basal and isolated position of the strongly supported clade of *B. lyrata* (Clade A; 100% BS, 1.00 PP) in the phylogenetic trees, suggest this species to be ancestral within *Biscutella* ser. *Biscutella* with the chromosome basic number $x = 6$ being the probable result of dysploidy in the early evolution of the series (the remaining sections and series are $x = 8, 9$) (see Alonso et al., 2020). Similar patterns of genome evolution have recently been reported by Mandáková et al. (2018) in the related *Ricotia*, a genus in which descendant dysploidy played an important role in cladogenesis.

Specimens belonging to *Biscutella didyma* group form a strongly supported clade in all trees (Clade B), in which inner subclades do not match a clear geographical pattern. This group is widespread through the central and eastern Mediterranean basin and Southwest Asia, though lacking from the western Mediterranean basin and northwest Africa (Morocco and Algeria). Some morphological variations were observed, with two clear extremes: (1) plants with a dense basal rosette, showing several well-developed cauline leaves and often some elongation in the basal part of the fruiting raceme (*B. didyma* s. str.), and (2) plants usually lacking a well-defined basal rosette, mostly with bract-like cauline leaves and dense corymbose fruiting racemes (sometimes named *B. apula* L. or *B. ciliata*). Although a predominance of the second group existed in Corsica, the Balkan Peninsula, and the Middle East, a huge morphological variability was found throughout the entire range of the species, both morphotypes growing together in close locations (e.g., Corsica, Bastia: P-053844423, P-05384419) and even in a single population (e.g., Bastia: P-05404870, P-05362152; Sardinia: Siniscola, Mt. Albo, ABH-70560; Sardinia, Jerzu: ABH-70569; Puglia: Crispiano to State, pr. gravine Amastuola: ABH-73578; Turkey, Muğla, Datça: ABH-76352; Greece, Rhodes: P-05362266; Santorini: GZU-00318723; Crete: GZU-0054594). A combination of morphological and phylogenetic results (not shown) do not support a clear ecological or geographical separation between both morphotypes that might justify acceptance at subspecific rank (e.g., *B. didyma* subsp. *didyma* and *B. didyma* subsp. *apula*) as proposed by Raffaelli (1991). Conversely, they are treated here at varietal rank (e.g., *B. didyma* var. *didyma* and *B. didyma* var. *ciliata*, respectively) as extremes of variation with intermediate forms, sometimes difficult to assign. All chromosome counts for *B. didyma* yielded $2n = 16$ [$n = 8$] (Manton, 1937 as "*B. ciliata*"; Al-Shehbaz & Al-Omar, 1982; Olowokudejo & Heywood, 1984; Raffaelli & Fiorini, 1986).

Similarly, plants from Sardinia morphologically close to *Biscutella didyma* s.l. were described as *B. morisiana* by Raffaelli (1991), based on apparently exclusive fruit features. However, according to our field and herbarium observations, fruit indumentum in the Sardinian

populations is variable and not exclusive, and consequently it does not seem a character consistent enough to separate a distinct species. Our observations are well supported by the phylogenetic results in which the Sardinian samples are embedded among other members of *B. didyma* without any geographical pattern (cf. Alonso et al., 2020), and consequently *B. morisiana* is here better treated as a mere morphological variation of *B. didyma*. Similarly, both glabrous and flat silicles are characters found in many populations throughout the Mediterranean basin, not being consistent enough to define any taxa as traditionally occurred with *B. leiocarpa* and *B. ciliata* var. *applanata*, respectively. Regarding *B. depressa*, it is an outstanding member of the "*didyma*" lineage (Clade B), morphologically easy to recognize and occupying a well-delimited distribution area from Cyrenaica (eastern Libya) to the Nile river delta (Egypt), for which counts of $2n = 16$ [$n = 8$] chromosomes have been reported (see Manton, 1932; Olowokudejo & Heywood, 1984 as *B. didyma*). The presence of strongly swollen fruit margins is said to be a diagnostic character of these plants, but occasionally it is also found in other representatives of the lineage, such as those described as *B. didyma* subsp. *dunensis* from Cyprus (see Chrtek & Slavík, 1981) or even in some populations of *B. boetica* and *B. didyma* s.l. Furthermore, the small plant size of *B. depressa* highlighted by Machatschki-Laurich (1926) is a rather constant character in the Egyptian populations, whereas some plants found in Libya often reach 30–40 cm tall. Its distribution and the outstanding swollen margins of silicle point to the existence of some geographical or ecological isolation, perhaps caused by their proximity to the Sahara and Sinai deserts. For all those reasons, the varietal rank within *B. didyma* has been suggested for this entity (El Hadidi et al., 1988), but further studies, including phylogenetic analyses, are needed to provide a definitive taxonomic assignment.

The second central Mediterranean lineage corresponds to *Biscutella maritima*, a well-characterized species from Italy, Sicily, northern Tunisia, and eastern Algeria, which constitutes a strongly supported lineage (Clade C). This species is easy to identify based on a unique combination of morphological characters, such as the lyrate basal leaves, the absence of well-developed cauline leaves, the generally long and patent pedicels, and perhaps most importantly the presence of highly elongated (up to 0.8 mm) median nectaries, which constitutes an exclusive character in the genus, only being similar in some *B. pseudolyrata* specimens (northwestern Morocco). Despite the geographical variation observed, such as smaller size and broad leaf shape plasticity in North African individuals, that constant combination of characters allows undoubted identification of *B. maritima*. This central Mediterranean species shows $2n = 16$ [$n = 8$] chromosomes (Manton, 1932 as "*B. lyrata*"; Larsen & Laegaard, 1971 as "*B. radicata*"; Olowokudejo & Heywood, 1984 as "*B. lyrata*"; Fiorini & Raffaelli, 1990 as "*B. lyrata* subsp. *laxiflora*"). Further work is still needed to better clarify its phylogenetic connections to other members of the series.

One of the most interesting results of our analyses concerns the western Mediterranean members of the series, namely "*Biscutella didyma* pro parte maxima" sensu Maire (1967) and Fennane (1999), which form a strongly supported group (Clades D–F) in the ML tree. Most North African endemics such as *B. eriocarpa*, *B. raphanifolia*, and *B. pseudolyrata*, together with the Iberian-Moroccan endemic *B. boetica*, are found in that group. As pointed out by Grau (1999 as "*B. boetica* sensu lato") and Vicente et al. (2019b), northern Africa is the center of diversity for that aggregate on account of the broad morphological variation displayed by most of its members in its whole distribution area.

First, *Biscutella raphanifolia* s.l. (Clade D) is exclusive to the northern areas of Algeria and Tunisia (cf. Raffaelli, 1985a; Vicente et al., 2016a). Plants belonging to that species showed lyrate leaves, lacked highly elongated median nectaries and produced inflorescences in profusely branched panicles (type D). Two extremes of variation can be recognized at varietal rank (Vicente et al., 2016a): (1) stem long and stout (to 100 cm tall), somewhat fruticose at base with several well-developed cauline leaves, and silicles usually glabrous and large; and (2) stem short and slender (up to 40 cm tall), herbaceous at base, lacking well-developed cauline leaves, and silicles usually pilose and small- to medium-sized. *Biscutella raphanifolia* s.l. is somewhat similar at first sight to *B. maritima*, and sometimes both have been misidentified in northern Africa. Note, for instance, that M. Choulette's "Fragmenta Florae Algeriensis Exsiccata" n° 9 (coll. 1853) included mixed material of both taxa (*B. maritima*: e.g., P-05438288, P-05438293, P-05438858; and *B. raphanifolia* var. *algeriensis*: K, LY-0003809), which was gathered in northeastern Algeria and distributed under the name "*B. apula*." Nonetheless, the true phylogenetic relationships of *B. raphanifolia* are poorly resolved in our analyses, and further research is still needed to clarify this issue.

Secondly, both Moroccan and Iberian specimens of *Biscutella boetica* (Clade E) showed a rather constant morphology, with oblanceolate and regularly dentate to pinnatifid leaves, and inflorescence usually loose and not unilateral with patent pedicels. They all possess $2n = 16$ [$n = 8$] chromosomes (Olowokudejo & Heywood, 1984; Ubera & Ruiz de Clavijo, 1984; Mejías & Luque, 1987; Santa Bárbara et al., 1994; Vogt & Oberprieler, 2009 p.p.). Only populations from northern Morocco (mostly the Tingitana Peninsula and neighboring Rif

areas) with similar morphology but a broad range of plasticity, were strongly supported as sister to the Spanish samples in the phylogenetic trees, whereas the remaining Moroccan specimens sometimes identified as "*B. boetica*" (Grau, 1999) or "*B. didyma* sensu lato" (Fennane, 1999) or "*B. maritima*" (Maire, 1967) nested together in a different clade sister to the former (see Clade F below). Therefore, according to our results, only the northern Rif populations belong to *B. boetica*, those results being contrary to the most recent treatment on northern Moroccan floras (Grau, 1999, 2002), which considered all the northern Moroccan annual entities as part of a widely circumscribed *B. boetica*, consequently very variable in morphology.

Taxa in Clade F are characterized by typically pinnatipartite to pinnatisect leaves (rarely only dentate) and/or long dense fruiting racemes (inflorescence types A–C+). Two morphologically well-defined entities can be recognized, which share the chromosome number $2n = 16$ [$n = 8$] (Schönfelder, 1968 as "*Biscutella lyrata*"; Ruiz de Clavijo, 1991 as "*B. lyrata*"; Vogt & Oberprieler, 2009 as "*B. baetica*" p.p.). On the one hand, most of the North African samples can be accommodated in an extended concept of *B. eriocarpa*, a species described from an undefined site between Mogador (Essaouira) and southern Spain (Candolle, 1811). Two morphotypes can be recognized sharing outstanding characters such as the very dense racemes (three to 10 fruits/cm: mean values: 6.5 and 5.3, respectively) often unilateral and leaves usually deeply lobed. However, this aggregate shows a wide morphological variation in the leaf division and distribution on stems or pedicel insertion pattern (Fig. 1). Firstly, *B. eriocarpa* var. *eriocarpa* usually includes small plants with one to numerous stems arising from a single, quite dense leaf rosette formed by pinnatipartite to pinnatisect (sometimes dentate) leaves, those on the stems absent or bract-like (or sometimes one to three well developed in the basal part of stems), and dense and long unilateral inflorescences. This variety is distributed mainly in the western and southern areas of Morocco and Algeria, mostly along the dry coastal areas of Morocco (from Casablanca to Agadir) extending to the Atlas and Anti-Atlas Mountain ranges and the neighboring desert territories up to southern Algeria. This treatment was previously outlined by Manton (1937), who implicitly restricted this species to the surroundings of Mogador, albeit later authors did not follow her suggestion. However, the morphological study of the holotype of that name (G-00202788), which was most probably gathered between Casablanca and Mogador (Vicente et al., 2019b), as well as the epitype (ABH-74998) and material from western and southwestern Morocco and southern Algeria, allows us to confirm that it has the priority at specific rank for the whole aggregate, in accordance with our phylogenetic results. Secondly, the other morphotype described here as *B. eriocarpa* var. *riphaea* (see below section 5) applies to plants usually larger, exhibiting mostly pinnatipartite to pinnatisect (rarely dentate to subentire) basal leaves, with some to many well-developed cauline ones, bearing long and dense unilateral inflorescences shorter than the stems. It occurs more frequently throughout the rainy mountain areas of central and northern Morocco (Middle Atlas and Rif), reaching the northwest border of Algeria. However, a broad morphological variation is observed in the group, with many intermediate individuals mainly distributed in areas where both morphotypes coexist, even in a single population where individuals from both varieties occur (e.g., Mogador: P-05438170; Taza, Djebel Tazzeka: ABH-68350, ABH-68351, ABH-69559; Meknès-Azrou: ABH-68336, ABH-68339; Taza to Tazerte, Djebel Ibone: ABH-68333; Beni-Snassen: ABH-68371, ABH-68372; or Tlemcen: P-05438222). This fact, together with the obtained molecular results (cf. Alonso et al., 2020), in which specimens from both morphotypes form several poorly supported clades, might be interpreted as a result of interbreeding (which is usual in recently diversified lineages) together with the lack of geographical or ecological isolation. Accordingly, at the moment we consider the varietal rank to be the most suitable option for both morphotypes, since isolation (mostly geographical or ecological) is usually assumed as necessary to recognition of higher taxonomic ranks (Avise & Ball, 1990; Hamilton & Reichard, 1992; Crespo et al., 1998, 2016; Ellison et al., 2014).

Some Moroccan populations have recently been described as *Biscutella pseudolyrata* (see Vicente et al., 2019a), which occur between Larache and Rabat in the Atlantic coastal areas of Gharb (or also Rharb) region, a Neogenic-Quaternary lowland basin in northwestern Morocco. Plants from that area (subclade F1) are always found on Quaternary deep sandy soils, and they exhibit a very distinct morphology clearly differing from the surrounding populations of both *B. boetica* and *B. eriocarpa* s.l., which at first sight relate them to *B. maritima*. The principal diagnostic characters of the Gharb plants are the lower density of racemes (mean value: 2.3 fruits/cm), lack of cauline leaves, and presence of elongated claviform median nectaries (0.4–0.6 mm), quite thickened in the upper part. According to Vicente et al. (2019a), they are an independent species, *B. pseudolyrata*, which very likely correspond to the Rif populations that Grau (1999) identified as "*B. boetica*" because of the lack of winged stamen filaments and that he related to the Iberian *B. lyrata* on account of their general habit and lyrate basal leaves. Acceptance of the specific rank for the Gharb plants might be controversial in the light of our phylogenetic tree (Fig. 4), since the *B. pseudolyrata* clade is embedded with other *B. eriocarpa* groups in a

larger poorly resolved clade (87% BS, 1.00 PP). This is probably due to a recent diversification of the group through either ecological and geographical drift or ongoing gene flow that may obscure patterns of differentiation at the DNA level and therefore make difficult a clear taxonomic arrangement based solely on the molecular phylogeny (see Alonso et al., 2020). Similar patterns of paraphyletic or non-monophyletic taxa are also found in other cruciferous genera such as *Arabidopsis* Heynh., *Aphragmus* Andrz. ex DC., *Eutrema* R. Br. (incl. *Taphrospermum* C. A. Mey. and *Thellungiella* O. E. Schulz) (Warwick et al., 2006), *Capsella* Medik. (Hurka et al., 2012), or *Cardamine* L. (Bleeker et al., 2002), in which recently evolved lineages present scarce molecular differentiation, albeit they usually are morphologically well defined (Alonso et al., 2020). The degree of morphological divergence observed in each concerned group should determine the most suitable taxonomic rank for application. In our case, however, the specific rank seems the best choice for the Gharb populations for several reasons. First, the outstanding and unique combination of morphological characters differentiating *B. pseudolyrata* and *B. eriocarpa* is not consistent with their inclusion in a single taxon (e.g., "*B. eriocarpa* s. l."), which would bring its morphological variation to an impracticable extreme. Secondly, populations of *B. pseudolyrata* are restricted to red sandy layers of the western Gharb, which were deposited recently (within the last 0.5–1 Ma). All those data suggest that *B. pseudolyrata* had arisen as a result of recent ecological specialization in a peculiar kind of Quaternary sand substrates, as suggested by Vicente et al. (2019a) and Alonso et al. (2020).

Parisod and Besnard (2007) suggested that genetic refuges during the Last Glacial Maximum (LGM; ca. last 20,000 years), together with polyploidy and reticulate evolution, triggered recent diversification of *Biscutella* ser. *Laevigatae* Malin. in Central Europe. In fact, processes including morphological divergence following introgression, polyploidization, and/or rapid adaptive radiation might be in the origin of diversification of lineages unresolved in traditional molecular phylogenies, as it often occurs in taxonomically complex Mediterranean genera such as *Limonium* Mill. (Lledó et al., 2005, 2011) or *Helianthemum* Mill. (Parejo-Farnés et al., 2013). The case of *Biscutella* ser. *Biscutella* also seems to point to this phenomenon. The current distribution of the series, mostly centered in the southern part of the Mediterranean basin and the Middle East, suggests a radiation process related to the major geological and climatic events occurring in the Mediterranean basin and Eurasia within the last 20 million years, as shown in the time-tree of Alonso et al. (2020). Most taxa traditionally recognized in the series (e.g., *B. boetica*, *B. didyma*, *B. lyrata*, *B. maritima*, and *B. raphanifolia*) together with other neglected or misunderstood ones (e.g., *B. eriocarpa* and *B. pseudolyrata*) form well-supported clades that are defined by recognizable syndromes of morphological characters. The varieties accepted here in *B. didyma*, *B. eriocarpa*, and *B. raphanifolia* represent extremes of variation (morphotypes) of lineages with a broad plasticity and incomplete divergence, which are based on characters (e.g., stem foliation, basal rosette presence and density, and leaf division) that likely evolved several times in their evolutionary history (Alonso et al., 2020). Their apparently weak genetic differences still are either not well correlated to ecological or distributional patterns or not entirely discriminated by the plastidial markers used in our phylogenetic analyses. Further molecular work including application of massive sequencing techniques will surely render better resolved phylogenetic relationships in non-model groups like *Biscutella* (cf. Sucher et al., 2012; Tonnabel et al., 2014), which perhaps will contribute to a more stable future proposal. In the meantime, the taxonomic arrangement presented here facilitates understanding of the morphological variation observed in the wild populations and helps to recognize the biological entities found in *Biscutella* ser. *Biscutella*.

Conclusions: A New Taxonomic Arrangement

Biscutella L., Sp. Pl. 2: 652. 1753, nom. cons. TYPE: *Biscutella didyma* L., typ. cons. (see Barrie, 2006: 796).

Biscutella L. ser. **Biscutella.**

Biscutella ser. *Lyratae* Malin., Bull. Acad. Sci. Cracovie, Ser. B, 1910: 124. 1911 [Art. 22.1 of the ICN; Turland et al., 2018].

Mostly annual to short-lived perennial plants, variable in size. Stem single to numerous, glabrous to hirsute in the basal part. Basal leaves usually in a rosette that can be loose or absent; blade entire, dentate to variously pinnatisect or lyrate to spatulate, hirsute to glabrescent. Cauline leaves bract-like to fully developed or sometimes absent, entire to variously divided, attenuate to amplexicaul. Inflorescence in simple or branched panicle, rarely a simple raceme. Sepals not markedly spurred or saccate at base. Petals gradually tapering at base, with short claw. Lateral nectaries intrastaminal. Staminal filaments filiform, sometimes the median ones with a wide membranous wing. Silicle glabrous to covered with clavate and/or tiny conical trichomes, with a wide range of distribution patterns; margins flat to clearly thickened (cf. Malinowski, 1911; Olowokudejo, 1986; Guinea & Heywood, 1993).

Basic chromosome number. $x = 8$ (Manton, 1937; Olowokudejo & Heywood, 1984; Olowokudejo, 1986; Alonso et al., 2020).

Habitat and distribution. Species in *Biscutella* ser. *Biscutella* occur in grasslands, disturbed ground, and open shrubby or forest vegetation, on limestone, schistose or sandy substrates, sometimes on stony slopes and rocks, at 0–2400 m. Their distribution ranges from northern Africa, Southwest Asia, and western Europe, mostly in the Mediterranean basin, extending southwards onto the pre-desert Saharan areas and eastwards to the Iranian coast of the Persian Gulf and Saudi Arabia.

KEY FOR IDENTIFICATION OF THE SPECIES IN *BISCUTELLA* SER. *BISCUTELLA*

1. Staminal filaments with wide membranous wing; silicles 2–3.2 × 4–6 mm . . . . . 4. *B. lyrata* L.
1′. Staminal filaments filiform, unwinged; silicles usually larger, (2.3–)3–8(–11) × (4.5–)6–15 mm 2
2. Rosette leaves mostly oblanceolate, dentate to irregularly pinnatisect 3
2′. Rosette leaves lyrate (occasionally the lowermost dentate, and then intrastaminal nectaries ≥ 0.4 mm long) 5
3. Intrastaminal median nectaries conspicuous, 0.2–0.4 mm long; infructescence usually as long as or longer than the stem and loose, 1 to 3(to 4) fruits/cm (mean value: 2.3), with silicles not unilateral . . . . . 1. *B. boetica* Boiss. & Reut.
3′. Intrastaminal median nectaries inconspicuous or to 0.25 mm long; infructescence usually shorter than the stem and dense, 3 to 10 fruits/cm (mean value: ≥ 5.3), with silicles unilateral or not 4
4. Leaves dentate, occasionally pinnatifid or pinnatisect; infructescence non-unilateral; mean length of 5 basal fruiting pedicels 2–6 mm long (rarely up to 8); fruit width 7–13.5 mm; style length/fruit width ratio 0.18–0.25; central Mediterranean to Middle East . . . . . 2. *B. didyma* L.
4′. Leaves often pinnatisect, sometimes dentate; infructescence often unilateral; mean length of 5 basal fruiting pedicels 4.5–10 mm long (rarely shorter to 3.5); fruit width 4.5–10 mm; style length/fruit width ratio 0.22–0.40; Morocco and Algeria . . . . . 3. *B. eriocarpa* DC.
5. Caulinar leaves well developed (occasionally the uppermost bract-like); infructescence a profusely branched panicle (type D), with 8 to 30 terminal racemes per branch; median nectaries inconspicuous to 0.4 mm long . . . . . 7. *B. raphanifolia* Poir.
5′. Caulinar leaves absent or bract-like (occasionally the lowermost well developed); infructescence a raceme to branched panicle (types A–C+), mostly with 2 to 8 terminal racemes per branch; median nectaries 0.4–0.8 mm long 6
6. Stem up to 120 cm tall; median nectaries 0.5–0.8 mm, usually cylindrical; racemes bearing (1 to)2 to 5(to 6) fruits/cm at base (mean value: 3.7); Algeria, Italy, and Tunisia . . . . . 5. *B. maritima* Ten.
6′. Stem up to 45(–60) cm tall; median nectaries 0.4–0.5 mm, usually clavate; racemes bearing 1 to 3(to 4) fruits/cm at base (mean value: 2.3); northwestern Morocco . . . . . 6. *B. pseudolyrata* A. Vicente, M. Á. Alonso & M. B. Crespo

1. Biscutella boetica Boiss. & Reut., Diagn. Pl. Orient. ser. 2, 1: 42. 1854. *Biscutella didyma* L. var. *boetica* (Boiss. & Reut.) Font Quer, Butl. Inst. Catalana Hist. Nat. 26: 102. 1926. TYPE: Spain. Málaga: in campis siccis montosis circâ Malagam et praecipué al Cerro, au nord de la Ville, 30 Apr. [probably collected in 1837 by *Boissier s.n.*] (lectotype, designated by Vicente et al. [2016b: 294], G-00418100 digital image!).

Biscutella apula L. var. *megacarpaea* Boiss., Voy. Bot. Espagne 2: 55. 1839, p.p. [syn. excl.]. TYPE: Spain. Málaga: in campis siccis montosis circâ Malagam et praecipué al Cerro, au nord de la Ville, 30 Apr. [probably collected in 1837 by *Boissier s.n.*] (lectotype, designated by Vicente et al. [2016b: 294], G-00418100 digital image!).

Biscutella bourgaei Jord., Diagn. Esp. Nouv.: 320. 1864. TYPE: Spain. Cádiz: Medina Sidonia, pelouse aride, 21 Mar. 1849, *E. Bourgeau 28* (lectotype, designated by Thiébaut & Tison [2016: 110], LY-0009641 digital image!).

Biscutella didyma L. var. *scabrida* Maire, Bull. Soc. Hist. Nat. Afrique N. 36: 92. 1945. *Biscutella microcarpa* DC. f. *scabrida* Pau & Font Quer, Iter Marocc. 1930, n° 235. 1932, nom. nud. TYPE: Morocco. Tanger-Tétouan-al Hoceima: Rincón de Medik, in arenosis inter Ceuta et Tetauen, 4 m, 13 Mar. 1930, *Font Quer 235* (lectotype, designated by Vicente et al. [2019b: 180], BC-137361!; isolectotypes, MA-44533!, MPU-006772 digital image!).

Biscutella didyma L. var. *micraspis* Maire, Bull. Soc. Bot. Afrique N. 36: 92. 1945. TYPE: Morocco. Tanger-Tétouan-al Hoceima: pr. El Ksar-el-Quebir, in quercetis suberis, 50 m, 27 Mar. 1930, *Font Quer 236* (lectotype, designated by Vicente et al. [2019b: 180], MPU-006771 digital image!; isolectotypes, BC-137362!, MA-44534!).

Biscutella didyma L. var. *muscariodora* Maire, Bull. Soc. Hist. Nat. Afrique N. 26: 187. 1935. TYPE: Morocco. Béni Mellal-Jenifra: inter Kenifra et Kasba Tadla, in pascuis lapidosis, 700 m, 15 Apr. 1934, *R. Maire s.n.* (lectotype, designated by Vicente et al. [2019b: 179], MPU-003387 digital image!).

Annual plants, 20–60(–70) cm tall. Stems 2 to 6(to 12), hirsute below. Basal leaves 2 to 13(to 20), usually disposed in a loose rosette or rosette absent, oblanceolate, regularly dentate to occasionally pinnatipartite, up to 11 × 3.5 cm, hirsute. Cauline leaves 1 to 5, well developed in most individuals, attenuate to semiamplexicaul. Inflorescence in simple racemes to branched panicles, types B–C(C+), with up to 8(to 15) terminal racemes per stem, broadly elongated, often covering up to 1/2 of the total stem length, and loose in fruit, bearing 1 to 3(to 4) fruits/cm at base (mean value: 2.3); pedicels patent to erect-patent, (5–)6–12 mm. Sepals 1.5–2.5 mm; petals 2.5–5 mm, gradually attenuate at base. Staminal filaments filiform. Median nectaries elongated, 0.2–0.4 mm. Style 1.8–3(–3.8) mm. Silicle (2.3–)3–5.6 × (4.5–)5–10 mm, generally showing

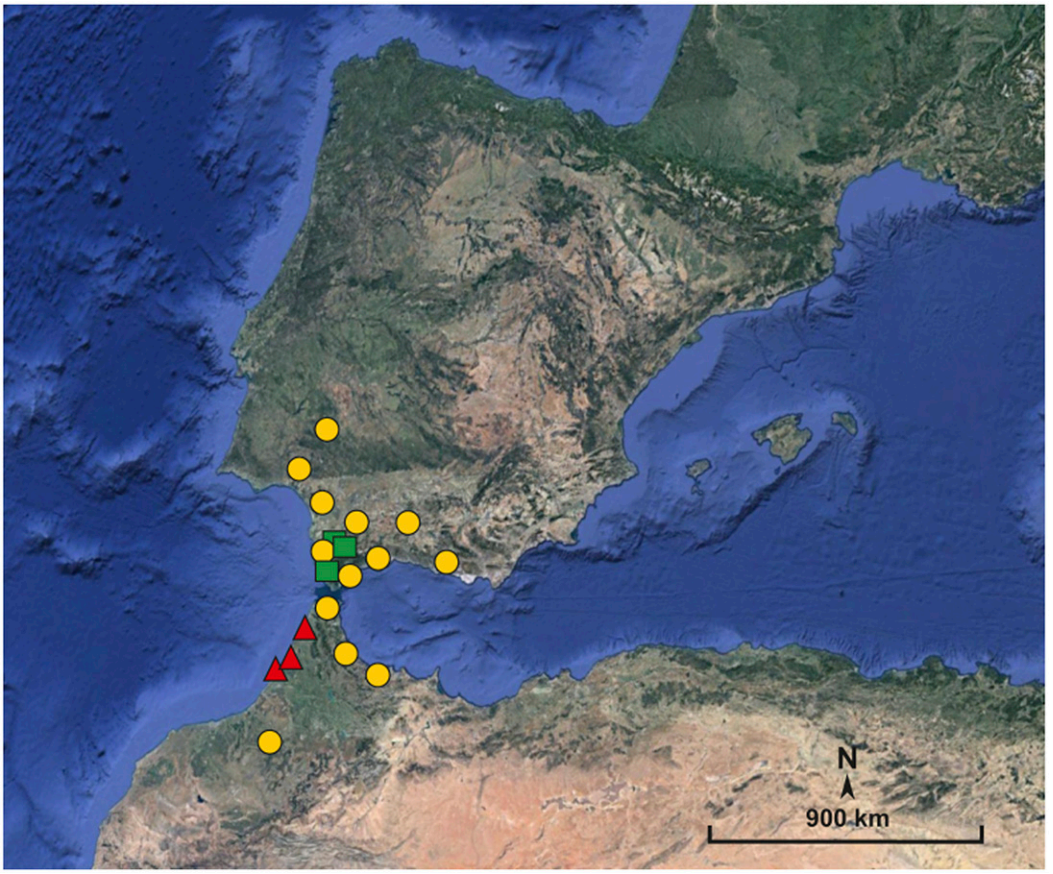

Figure 5. Distribution of the studied material of *Biscutella boetica* Boiss. & Reut. (yellow circles), *B. lyrata* L. (green squares), and *B. pseudolyrata* A. Vicente, M. Á. Alonso & M. B. Crespo (red triangles) in the western Mediterranean basin. Satellite image from Google Earth Pro.

a swollen margin and covered with tiny conical trichomes together with clavate ones, those being longer in the central part and shorter on margins; sometimes lacking the conical indumentum or totally glabrous (types S2–S3, S6).

Chromosome number. $n = 8$ (Schönfelder, 1968: Málaga, southern Colmenar; Ubera & Ruiz de Clavijo, 1984: Spain, Málaga, Cabo Calaburras, *Ubera s.n.*, COFC-10021; Mejías & Luque, 1987: Spain, Málaga, Casares, *Mejías s.n.*, SEV-118864; Santa Bárbara et al., 1994: Spain, Cádiz, Sierra del Aljibe, *J. Pastor & J. C. Diosdado s.n.*, SEV-118356); $2n = 16$ (Olowokudejo & Heywood, 1984: Spain, Cádiz, Castellar de la Frontera-Almoraina; Vogt & Oberprieler, 2009: Morocco, Tanger Peninsula, rd. 8303 from Souk-Tlata-Taghramet to Ceuta (Sebta), *R. Vogt 9858 & C. Oberprieler 4306*, B-10-1013205).

Icon. Grau and Klingenberg (1993: 295, lám. 107).

Habitat and distribution. *Biscutella boetica* occurs in grasslands, disturbed ground, and open shrubby or forest vegetation, at 10–1500 m. It is known from southern Spain and northern Morocco (mostly in the northern Rif Mountains). Figure 5.

Conservation status. Populations of this species are found in a wide area, and no severe threats appear to exist in its distribution. Therefore, it should be considered Least Concern (LC) (IUCN, 2012).

2. Biscutella didyma L., Sp. Pl. 2: 653. 1753. TYPE: "Habitat in Germania, Gallia, Italia" (lectotype, designated by Heywood [1964: 150], Herb. Clifford 329, *Biscutella* 2, BM-000646258 digital image!). EPITYPE: Italy. Puglia: Castellaneta, alongside the rd. SS-7, near the bridge across Gravina Grande, 33TXE642966, 105 m, 4 May 2014, *A. Vicente et al. s.n.* (epitype, designated by Vicente et al. [2015b: 291], ABH-70565!).

Biscutella apula L., Mant. Pl.: 254. 1771, nom. illeg. superfl. [Art. 52.1 of the ICN; Turland et al., 2018] (cf. Greuter et al., 1986: 62).

Annual plants, 6–50(–70) cm tall. Stems 1 to 7, hirsute below. Basal leaves 4 to 20, in a rosette that can be absent or loose, generally oblanceolate, dentate (occasionally pinnatifid or pinnatisect), up to 8 × 2.5 cm, hirsute. Cauline leaves usually well developed, 1 to 6(to 10), attenuate, or sometimes bract-like or absent. Inflorescence a simple raceme to branched panicle, types B–C+, with dense racemes usually short or slightly elongated in fruit at least at base, covering up to 1/4 of the total stem length and bearing 3 to 9 fruits/cm at base (mean value: ≥ 5.8); pedicels non-unilateral, erect to erect-patent, 2–6 mm, rarely to 8 mm in some individuals. Sepals 1.3–2.5 mm; petals 2–5 mm, gradually attenuate at base. Staminal filaments filiform. Medial nectaries inconspicuous or up to 0.20 mm. Style 1.5–2.5(–3) mm, short in relation to fruit width. Silicle (3–)3.5–7(–8) × (6–)7–13.5 mm, flat to thickened on margin, with broad range of indumentum types, from entirely glabrous to entirely covered with both, clavate and conical trichomes (types S1–S6).

Chromosome number. See varieties below.

Habitat and distribution. *Biscutella didyma* occurs in grasslands and open woodlands, at 50–1000 m. It is present in the central and eastern Mediterranean region and the Middle East, from Italy and eastern Algeria to the Iranian coast of the Persian Gulf and Saudi Arabia.

Conservation status. This species occupies the widest distribution range in the aggregate and the highest variety of habitats, where no special threats seem to exist. Therefore, it should be treated as Least Concern (LC) for both of its varieties (IUCN, 2012).

Notes. As said before, two morphotypes mostly differing in the number and development of cauline leaves have been usually recognized, which are accepted here at varietal rank. As opposed to Raffaelli (1991), it was not realistic to connect clear patterns of raceme density with both morphotypes, since numerous transitional forms were found throughout the distribution range of the species. Both varieties can be defined as follows:

Key to the Varieties of *Biscutella didyma*

1. Basal leaves crowded in a dense rosette, most cauline leaves bract-like (up to 2 cm long); racemes usually short and dense . . . . . 2a. *B. didyma* L. var. *didyma*
1′. Basal leaves usually not crowded in a dense rosette, several cauline leaves well developed, similar in shape and size to basal ones; racemes sometimes long and loose at least at basal part . . . . . 2b. *B. didyma* var. *ciliata* (DC.) Vis.

2a. Biscutella didyma L. var. didyma.

Biscutella columnae Ten., Fl. Napol. 1: 38. 1811. *Biscutella didyma* subsp. *columnae* (Ten.) Nyman, Consp. Fl. Eur.: 59. 1878. *Biscutella apula* L. var. *columnae* (Ten.) Arcang., Comp. Fl. Ital.: 62. 1882. *Biscutella didyma* var. *columnae* (Ten.) Halácsy, Consp. Fl. Graec. 1: 105. 1900. *Biscutella ciliata* DC. var. *columnae* (Ten.) Mach.-Laur., Bot. Arch. 13: 31. 1926. TYPE: [icon] "Iondraba Alyssoides Apula spicata" [alternatively referred to as "IonDraba apula alissoides spicata"] in Colonna, Ekphrasis 1: 285. 1616 [the figure on the left side] (lectotype, designated here). EPITYPE: Italy. Apulia, Gargano, in agris restilibus pr. Mt. S. Angelo, 24 Apr. 1875, *Porta & Rigo 534* (epitype, designated here, P-05362591!).

Biscutella morisiana Raffaelli, Webbia 45: 26. 1991, p.p. (holotypo excl.). ISOTYPE: Italy. Sardegna: dalla Caletta di Fuili alla Grotta del Bue Marino, 4 Apr. 1970, *P. V. Arrigoni & C. Ricceri s.n.* (isotype, FI-001355 digital image!).

Annual plants, (7–)15–50 cm tall. Basal leaves usually in a dense rosette. Cauline leaves absent or bract-like, sometimes only 1 well developed at the basal part of stem, but clearly smaller than those in the rosette. Inflorescence racemes usually dense and short, not much elongated in fruit, 5 to 9 fruits/cm (mean value: 7).

Chromosome number. $n = 8$ (Al-Shehbaz & Al-Omar, 1982: Iraq, above Sinjar, *IAS 7759* [not seen]); $2n = 16$ (Dolcher & Pignatti, 1960 as "*B. columnae*"; Olowokudejo & Heywood, 1984: Greece, Attica, Athens, & Egypt, Alexandria).

Icon. Colonna, Ekphrasis 1: 285. 1616 [the figure on the left side]; Raffaelli (in Webbia 45(1): 23, fig. 9. 1991; loc. cit.: 27, fig. 11. 1991, sub *B. morisiana*); Jaffri (Fl. Libya 23: 111, fig. 34. 1977).

Habitat and distribution. *Biscutella didyma* var. *didyma* occurs through most of the distribution area of the species, though it is more frequent in the western and central territories of the range. Figure 6A.

Notes. The type material of *Biscutella morisiana* at FI includes two collections. Those marked as isotypes fit with the concept of *B. didyma* var. *didyma*. However, the one marked as holotype shows a loose basal rosette and bears well-developed cauline leaves, and hence it is synonymized here to *B. didyma* var. *ciliata*. Regarding typification of *B. columnae*, the voucher BM-000750313 [digital image], from Nuttall's herbarium, includes a fragment marked as "type material" that matches the concept of that species. However, although that herbarium specimen is annotated "*B. columnae* Ten." and was said to be collected in Naples by Tenore (see Tenore, 1811), no solid evidence exists (e.g., date of collection) to consider it as original material, and therefore it is disregarded here as syntype.

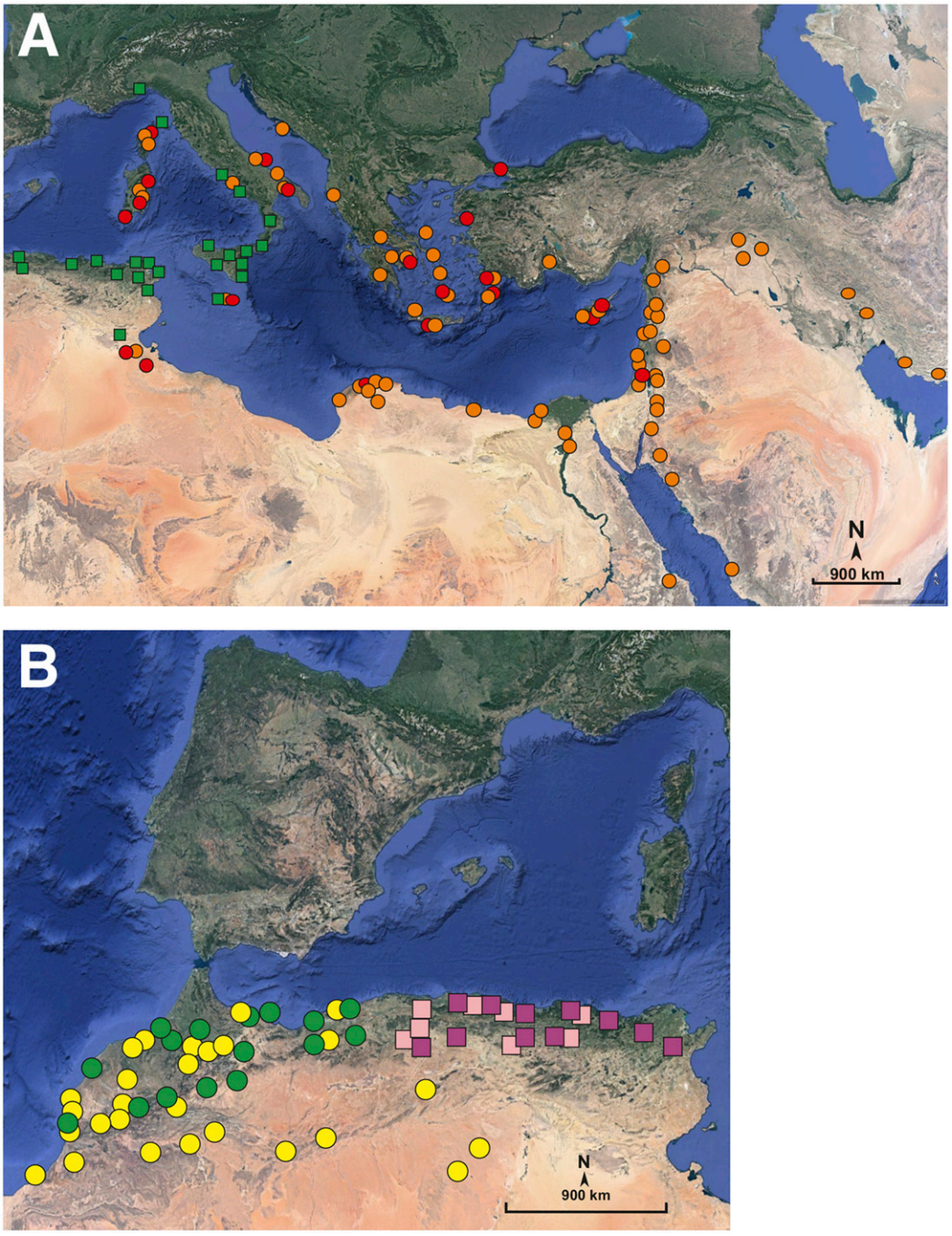

Figure 6. Distribution of the studied material. —A. *Biscutella didyma* L. var. *didyma* (red circles), *B. didyma* var. *ciliata* (DC.) Vis. (orange circles), and *B. maritima* Ten. (green squares) in the central and eastern Mediterranean basin. —B. *Biscutella eriocarpa* DC. var. *eriocarpa* (yellow circles), *B. eriocarpa* var. *riphaea* A. Vicente, M. Á. Alonso & M. B. Crespo (green circles), *B. raphanifolia* Poir. var. *raphanifolia* (violet squares), and *B. raphanifolia* var. *algeriensis* (Jord.) A. Vicente, M. Á. Alonso & M. B. Crespo (pinkish squares) in the central and western Mediterranean basin. A, B, satellite images from Google Earth Pro.

2b. Biscutella didyma var. **ciliata** (DC.) Vis., Fl. Dalmat. 3: 113. 1850. *Biscutella ciliata* DC., Ann. Mus. Hist. Nat. 18: 297. 1811. *Biscutella didyma* var. *ciliata* (DC.) Vis., Fl. Dalmat. 3: 113. 1850. *Biscutella apula* L. var. *ciliata* (DC.) Arcang., Comp. Fl. Ital.: 62. 1882. *Biscutella apula* subsp. *ciliata* (DC.) Rouy & Fouc., Fl. France 2: 116. 1895. *Biscutella didyma* subsp. *ciliata* (DC.) Maire, Fl. Afrique N. 13: 132. 1967. TYPE: [Herb. de Candolle] "*Biscutella didyma* W. m. Balbis 1810" [most probably an Italian plant] (lectotype, designated here, G-00202790 digital image!).

Biscutella apula L., Mant. Pl.: 254. 1771, p.p. e descr. [syn. excl.]. *Biscutella didyma* var. *apula* Coss., Bull. Soc. Bot. France 19: 223. 1872. *Biscutella didyma* subsp. *apula* Nyman, Consp. Fl. Eur.: 59. 1878. TYPE: Italy. "Habitat in Italia" (lectotype, designated by Raffaelli [1991: 24], LINN 831.4 digital image! [fragment marked "a," on the right]).

Biscutella depressa Willd., Enum. Pl.: 673. 1809. *Biscutella apula* L. var. *depressa* (Willd.) Asch. & Schweinf., Ill. Fl. Égypte: 39. 1887. *Biscutella columnae* Ten. f. *depressa* (Willd.) Malin., Bull. Acad. Sci. Cracovie, Ser. B, 1910: 126. 1911. TYPE: Egypt. "Habitat in Aegypto" (lectotype, designated by Vicente et al. [2019b: 176], B–W-11928–01 digital image!).

Biscutella leiocarpa DC., Ann. Mus. Hist. Nat. 18: 299. 1811. *Biscutella didyma* var. *leiocarpa* (DC.) Halácsy, Consp. Fl. Graec. 1: 105. 1900. TYPE: [Herb. de Candolle] [s. loc., *s. coll.*] n° 2769, 784 (lectotype, designated here, G-00202784 digital image!).

Biscutella ciliata DC. var. *applanata* Mach.-Laur., Bot. Arch. 13: 34. 1926. *Biscutella didyma* subsp. *applanata* (Mach.-Laur.) Hadač & Chrtek, Acta Univ. Carol., Biol. 1971(4): 238. 1973. TYPE: Iran. Gere, in rupestribus umbroses faucium pr. Gere, inter Buschir et Schiras, 14 Mar. 1842, *Th. Kotschy 42* (lectotype, designated here, JE-00002639 digital image!; isolectotypes, HAL-0145881 digital image!, JE-00002638 digital image!, P-06648081!, P-05362146 [specimen on the left]!).

Biscutella didyma var. *lenticularis* Pamp., Arch. Bot. (Forlì) 12: 30. 1936. TYPE: Libya. Cyrenaica: Apollonia-Bgua, 11 Apr. 1933, R. Pampanini 2917 (lectotype, designated by Cuccuini et al. [2015: 59], FI-003803 digital image!).

Biscutella didyma var. *macrocarpa* Pamp., Arch. Bot. (Forlì) 12: 36. 1936. TYPE: Libya. Cyrenaica: Uadi el-Kuf (fra Gasr Beni Gdam e Sidi Abd el-Uahed), 6 Apr. 1933, *R. Pampanini 2905* (lectotype, designated by Cuccuini et al. [2015: 59], FI-003479 digital image!).

Biscutella didyma f. *parviscutata* Maire & Weiller, Bull. Soc. Hist. Nat. Afrique N. 29: 406. 1939. TYPE: Libya. Cyrenaica, in planitie ad meridiem (27 km) oppidi Tokra, solo calcareo, 29 Apr. 1938, *R. Maire & M. Weiller 98* [*Iter libycum*] (holotype, identified by Vicente et al. [2019b: 180], MPU-004115 digital image!).

Biscutella didyma subsp. *dunensis* Chrtek & B. Slavík, Preslia 53: 50. 1981. TYPE: Cyprus. Paphros: loco arenoso in amphitheatri ruina prope pharum situ occ. ab opp. Paphos, 3 Apr. 1978, *J. Chrtek & B. Slavík 622* (holotype, PR not seen).

Biscutella alireza-dadjua Parsa, Fl. Iran 8: 275. 1960. TYPE: Iran. Shustar, Mar. 1949, *A. Parsa 20008* (holotype, unknown; isotype, K-000484153 digital image!).

Biscutella elbensis Chrtek, Čas. Nár. Mus., Odd. Přír. 145(4): 185. 1978 [1976 publ. 1978]. *Biscutella didyma* var. *elbensis* (Chrtek) El Naggar, Taeckholmia 11: 71. 1988. TYPE: Egypt. Gebel Elba distr.: Gebel Shandodai, 10 Feb. 1962, *V. Tackholm et al. s.n.* (holotype, CAI-000035 digital image!).

Biscutella morisiana Raffaelli, Webbia 45: 26. 1991. TYPE: Italy. Sardinia: Dalla Caletta di Fuili alla Grotta del Bue Marino, 4 Apr. 1970, *P. V. Arrigoni & C. Ricceri s.n.* (holotype, FI-001356 digital image!).

Annual plants, 25–50(–60) cm tall, usually robust. Basal leaves usually in a loose rosette or rosette absent. Cauline leaves well developed, usually numerous, those in the lower half of stem similar in size and shape to rosette leaves. Inflorescence racemes dense, sometimes elongated in fruit and rather loose at least in the lower part, 3 to 9 fruits/cm (mean value: 5.8).

Chromosome number. $2n = 16$ (Manton 1937, as "*B. ciliata*": Palestine, Jerusalem; Raffaelli & Fiorini, 1986 as "*B. didyma*": Italia, Statte, Taranto, Gravina della Mastuola (o Amastuola) in front of Masseria Amastuola, *M. Raffaelli & C. Ricceri s.n.*, FI [not seen]).

Icon. Maire (1967: 128, fig. 45); Raffaelli (1991: 25, fig. 10).

Habitat and distribution. Biscutella didyma var. *ciliata* occurs throughout the whole distribution area of the species, though it is more frequent in the eastern territories of the range. Figure 6A.

Notes. The names *Biscutella didyma* f. *genuina* Pamp. (Arch. Bot. [Forlì] 12: 27. 1936, nom. inval. [Art. 24.3 of the ICN]), *B. didyma* var. β "JonDraba alyssoides apula spicata" sensu L. (Sp. Pl.: 653. 1753, non Colonna, Ekphrasis 1: 285. 1616), and *B. ciliata* var. *genuina* Mach.-Laur. (Bot. Arch. 13: 30. 1926, nom. inval. [Art. 24.3 of the ICN]) indeed refer to *B. didyma* var. *ciliata*. Some populations described as *Biscutella depressa* by Willdenow (1809), and distributed in the littoral areas of Egypt and eastern Libya, show a remarkable swelling on the fruit margin. In addition, all specimens from Egypt and some plants from Libya exhibit very small plant size, with short ascendant stems up to 11 cm bearing some well-developed leaves, whereas other Libyan specimens with swollen fruits often reach 30–40 cm long, with numerous well-developed leaves on the stems. Although typical plants of *B. didyma* var. *ciliata* are also found in these countries, the "*depressa*" morphotype is rather constant and apparently exclusive from the southeastern Mediterranean basin. Similar plants with rather swollen fruits occur also in some areas of Greece, and therefore *B. depressa* is here treated in synonymy of *B. didyma* var. *ciliata*. Further phylogenetic studies including samples

from Libya and Egypt are needed to assign the proper taxonomical status to Willdenow's taxon.

3. Biscutella eriocarpa DC., Ann. Mus. Hist. Nat. 18: 298. 1811. *Biscutella didyma* L. var. *eriocarpa* (DC.) Maire & Weiller, Fl. Afr. Nord 13: 133. 1967. TYPE: Morocco. "Hab… in itinere trans Hispaniam ad Mogador reperit Broussonet" (holotype, identified by Vicente et al. [2019b: 176], G-00202788 digital image!). EPITYPE: Morocco. Casablanca-Settat: Grand Casablanca, ctra. P3011 entre Bouskoura y Dar el Haj Omar, pastos pisoteados en suelos poco profundos de zonas calizas, 169 m, 22 Mar. 2015, *I. Aizpuru et al. SA896* (epitype, designated by Vicente et al. [2019b: 176], ABH-74998!; isoepitype, SALA-155641!).

Annual plants, 10–50(65) cm tall. Stems 1 to 20, glabrescent to hirsute below. Basal leaves 3 to 25, usually in a rosette that can be absent or loose, oblanceolate, dentate to variously pinnatisect, up to 13 × 4.5 cm, hirsute. Cauline leaves usually well developed, 1 to 8, variously divided, attenuate to amplexicaul; sometimes mostly absent or bract-like. Inflorescence in simple or branched panicle, rarely a simple raceme, types (A)B–C(C+), usually yielding up to 8 (occasionally to 13) terminal racemes per stem, with fruiting inflorescences elongated and often dense, bearing 3 to 10 fruits/cm at base (mean value: ≥ 5.3); pedicels 3.5–10 mm, unilateral or non-unilateral, patent to erect. Sepals 1.5–2.6 mm; petals 2.3–5 mm, gradually attenuate at base. Staminal filaments filiform. Median nectaries usually slightly elongated, up to 0.25 mm. Style 1.5–3 mm. Silicle (2.8–)3–6(–8) × 5–10(–13) mm, glabrous to covered with clavate and/or tiny conical trichomes, with a wide range of distribution patterns (types S1–S3, S6); margins flat to clearly thickened.

Chromosome number. See varieties below.

Habitat and distribution. *Biscutella eriocarpa* is found in grasslands, disturbed ground, and open shrubby or forest vegetation, at 10–2400 m. It is known from Morocco and Algeria, reaching the southernmost foothills of the Atlas range.

Conservation status. The species is widespread in a broad territory in which populations are common and include many individuals. Furthermore, they occur in a variety of habitats not threatened, and hence it should be regarded as Least Concern (LC) for both of its varieties.

Notes. This species has often been misidentified as *Biscutella lyrata* or *B. didyma* var. *maritima*, two taxa not present in Morocco. As mentioned by Vicente et al. (2019a), the holotype specimen of Candolle (1811) is an incomplete fragment collected by Broussonet (G-00202788) that probably came from a larger plant and that cannot be critically identified for the precise application of that name. It sometimes has been related to *Biscutella didyma* (see Guinea & Heywood, 1993). The epitype (ABH-74998) recently designated by Vicente et al. (2019a) was collected near Casablanca and fits with plants occurring mostly in western and southwestern Morocco and southern Algeria. Although a remarkable variation is found in leaf morphology and distribution on stems, the concept accepted here for *B. eriocarpa* parallels the variation patterns occurring in other species in the series (e.g., *B. didyma*, *B. raphanifolia*, and *B. pseudolyrata*). Accordingly, two morphotypes can be recognized as follows:

Key to the Varieties of *Biscutella eriocarpa*

1. Basal leaves numerous, in a dense rosette; cauline leaves absent or bract-like, entire . . . 3a. *B. eriocarpa* DC. var. *eriocarpa*
1′. Basal leaves scarce, laxly disposed; cauline leaves numerous, well developed, usually deeply lobed . . . . . 3b. *B. eriocarpa* var. *riphaea* A. Vicente, M. Á. Alonso & M. B. Crespo

3a. Biscutella eriocarpa DC. var. **eriocarpa.**

Biscutella didyma L. var. *pseudoalgeriensis* Maire, Bull. Soc. Hist. Nat. Afrique N. 29: 406. 1938. TYPE: Morocco. Casablanca-Settat: Oulad Saïd, in pascuis ditionis, solo arenaceo, 6 Apr. 1937, *R. Maire s.n.* (lectotype, designated by Vicente et al. [2019b: 181], MPU-003915 digital image!; isolectotype, P-05438785!).

Biscutella didyma L. var. *haplotricha* Maire, Bull. Soc. Hist. Nat. Afrique N. 29: 406. 1938. TYPE: Morocco. Casablanca-Settat: in rupestribus arenaceis inter Sidi-Sbaa et Khatouat, 800 m, 3 Apr. 1937, *R. Maire s.n.* (lectotype, designated by Vicente et al. [2019b: 179], MPU-003914 digital image!).

Biscutella didyma L. var. *pseudociliata* Maire, Bull. Soc. Hist. Nat. Afrique N. 23: 166. 1932. TYPE: Morocco. Souss-Massa: Anti-Atlante, in rupestribus arenaceis montis Fidoust, 2000–2200 m, 20 Apr. 1931, *R. Maire s.n.* (lectotype, designated by Vicente et al. [2019b: 178], MPU-002855 digital image!). EPITYPE: Morocco. Souss-Massa: Ighirmillul at Djebel Tafraout et Kerkar, montagnes à l'Est du district de Tazeroualt, 1876, *Mardochée s.n.* (epitype, designated by Vicente et al. [2019b: 179], P-05438846! [specimen on the right side of the sheet]).

Biscutella didyma L. f. *glaberrima* H. Lindb., Acta Soc. Sci. Fenn., Ser. B, Opera Biol. 1(2): 59. 1932. TYPE: Morocco. Marrakech-Safi: Atlas Magnum in convalle fl. Aït Messane, in decliv. lapid. calc. pr. pag. Tinitine, ca. 1400 m, 3 June 1926, H. Lindberg 3493 (lectotype, designated by Väre [2012: 21], H-1509707 digital image!).

Biscutella didyma L. f. *chamaecarpa* Maire, Bull. Soc. Hist. Nat. Afrique N. 26: 187. 1935. TYPE: Algeria. Naama: Aïn-Sefra, 13 May 1934, *A. Faure s.n.* (lectotype, designated by Vicente et al. [2019b: 179], MPU-003389 digital image!).

Biscutella didyma L. var. *pseudomicrocarpa* Maire, Bull. Soc. Sci. Nat. Maroc 13: 264. 1933. TYPE: Morocco. Drâa-Tafilalet: Atlante Majore, Tizi-n-Tichka, in glareosis schistaceis, 2100 m, 8 May 1932, *R. Maire s.n.* (lectotype, designated by Vicente et al. [2019b: 178], MPU-003200 digital image!; isolectotype, P-05438226!).

Biscutella didyma L. f. *orivilla* Maire & Sam., Ark. Bot. 29: 9. 1939. TYPE: Morocco. Souss-Massa: Atlas major, ad sept. a transitus Tizi-n-Test, in glareosis ad Maison cantonnière; 200 m, 7 Apr. 1936, *R. Maire & G. Samuelsson s.n.* (holotype, identified by Vicente et al. [2019b: 181], MPU-006208 digital image!).

Biscutella didyma L. f. *parvivalvis* Maire, Bull. Soc. Hist. Nat. Afrique N. 26: 187. 1935. TYPE: Algeria. Naama: in pascuis arenosis ad Aïn-Sefra, 31 May 1934, *A. Faure s.n.* (lectotype, designated by Vicente et al. [2019b: 178], MPU-003390 digital image!).

Biscutella didyma L. var. *suaveolens* Maire, Bull. Soc. Hist. Nat. Afrique N. 27: 207. 1936. TYPE: Algeria. Médéa Prov.: Ben Chicao, pelouses sur les grès, 1100 m, 19 May 1935, *R. Maire s.n.* (lectotype, designated by Vicente et al. [2019b: 179], MPU-003590 digital image!).

Plants relatively small, 13–37 cm tall. Stems often numerous, (1 to)5 to 20, glabrescent to hirsute below. Basal leaves 3 to 25, oblanceolate, up to 7 × 2.5 cm, usually in a dense rosette, pinnatipartite to pinnatisect-sublyrate, occasionally dentate to crenate. Cauline leaves absent to bract-like, mostly entire (sometimes 1 to 3 well developed at the basal part, attenuate to semiamplexicaul). Fruiting inflorescence covering up to 1/3 of the total stem length (occasionally longer) and bearing (3 to)4 to 10 fruits/cm at base (mean value: 6.5); pedicels mostly unilateral (when non-unilateral, usually erect to erect-patent), (3.5–)4.7–9 mm. Median nectaries inconspicuous or shortly elongated, up to 0.25 mm.

Chromosome number. $n = 8$ (Schönfelder, 1968 as "*B. lyrata*": Morocco, Aoullouz, *A. Hohenester s.n.*).

Icon. Candolle (1811: tab. IX fig. 2a-b [plate 15]).

Habitat and distribution. *Biscutella eriocarpa* var. *eriocarpa* occurs throughout the distribution area of the species, albeit it is more abundant in the mountains and plains of western and southern Morocco (from Casablanca to Souss-Massa-Drâa region) to southern Algeria, mainly through the Atlas and Anti-Atlas, spreading onto the pre-desert Saharan areas. Figure 6B.

Notes. The name *Biscutella didyma* var. *gymnocarpa* Maire (Bull. Soc. Hist. Nat. Afrique N. 36: 92. 1945, nom. nud. inval. [Art. 39 of the ICN]) was applied to plants belonging to *B. eriocarpa* var. *eriocarpa*.

3b. Biscutella eriocarpa var. **riphaea** A. Vicente, M. Á. Alonso & M. B. Crespo, var. nov. TYPE: Morocco. Oriental province: Oujda, monts Beni-Snassen, prox. Taforalt, 30SWD544530, 700 m, 29 Apr. 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar* (holotype, ABH-68371!). Figure 7.

Diagnosis. *Biscutella eriocarpa* DC. var. *riphaea* A. Vicente, M. Á. Alonso & M. B. Crespo differs from *B. eriocarpa* var. *eriocarpa* by the basal leaves scarce and laxly disposed; cauline leaves numerous and well developed, usually deeply lobed; and infructescence often looser, bearing 3 to 8 fruits/cm at base (mean value: 5.3).

Plants usually large, (10–)20–50(–65) cm tall. Stems 1 to 9 (rarely more numerous), hirsute below. Basal leaves 5 to 20, pinnatipartite to pinnatisect, up to 13 × 4.5 cm. Cauline leaves well developed in most individuals, 1 to 8, pinnatipartite to pinnatisect, attenuate to amplexicaul. Fruiting inflorescence with relation raceme length/stem length up to 0.4, bearing 3 to 8 fruits/cm at base (mean value: 5.3); pedicels often unilateral (when non-unilateral, usually erect to erect-patent), 4.5–8.5(–10) mm. Median nectaries usually elongated, up to 0.25 mm.

Chromosome number. $n = 8$ (Ruiz de Clavijo, 1991 as "*B. lyrata*": Morocco, Tiouririne to Ain-Leuh, *B. Cabezudo et al. s.n.*, COFC-19871); $2n = 16$ (Vogt & Oberprieler, 2009 as "*B. baetica*": Morocco, Monts des Beni-Snassen, tracks from Beni Ammar to Taforalt via Talezzert, Oued Tlata-at-Talremt, *R. Vogt 11191 & C. Oberprieler 5639*, B-10-1013207).

Habitat and distribution. *Biscutella eriocarpa* var. *riphaea* mostly occurs through the northern part of the distribution area of the species, though it is more frequent in the mountains of central and eastern Morocco and western Algeria (Beni-Snassen mountain range). Figure 6B.

Notes. The name *Biscutella lyrata* var. *algeriensis* f. *minorisilicula* Sennen & Mauricio (Cat. Rif: 6. 1934, nom. nud. inval. [Art. 39 of the ICN]) was applied to plants belonging to *B. eriocarpa* var. *riphaea*.

4. Biscutella lyrata L., Mant. Pl. Alt.: 254. 1771. *Biscutella didyma* L. var. *lyrata* (L.) Coss., Bull. Soc. Bot. France 19: 223. 1872. *Biscutella apula* L. subsp. *lyrata* (L.) Ball, J. Linn. Soc., Bot. 16: 332. 1877. *Biscutella didyma* subsp. *lyrata* (L.) Nyman, Consp. Fl. Eur.: 59. 1878. *Biscutella apula* f. *lyrata* (L.) Batt., Fl. Algérie Dicot.: 37. 1888. *Biscutella apula* var. *lyrata* (L.) Parl., Fl. Ital. 9: 649. 1893. TYPE: Spain. "lyrata/A. 148" (lectotype, designated by Raffaelli [1985b: 696], LINN 831.3 digital image!).

Biscutella microcarpa DC., Ann. Mus. Hist. Nat. 18: 298. 1811. *Biscutella apula* L. var. *microcarpa* (DC.) Boiss., Voy. Bot. Espagne 2: 56. 1839. TYPE: Spain. Cádiz: ca. San Roch [San Roque], May, *Broussonet s.n.* (lectotype, designated here, FI-018213 digital image!).

Biscutella scutulata Boiss. & Reut., Diagn. Pl. Orient. ser. 2, 1: 41. 1854. *Biscutella lyrata* var. *scutulata* (Boiss. & Reut.) Ball, J. Linn. Soc., Bot. 16: 332. 1877. TYPE: Spain. Cádiz: Cádiz, *J. P. Monnard 250* (lectotype, designated by Burdet et al. [1984: 358], G-00389119!).

Figure 7. Holotype of *Biscutella eriocarpa* DC. var. *riphaea* A. Vicente, M. Á. Alonso & M. B. Crespo (ABH-68371).

Biscutella patulipes Jord., Diagn. Esp. Nouv.: 320. 1864. TYPE: Spain. Cádiz: Medina Sidonia, pelouse aride, 21 Mar. 1849, *E. Bourgeau 28* (lectotype, designated by Thiébaut & Tison [2016: 110], LY-0009625 digital image!).

Biscutella microcarpa DC. var. *taraxacifolia* Kunze, Flora 29: 694. 1846 [Chloris Austro-Hispanica: 48. 1846]. TYPE: Spain. [I]n cultis regione calidae Baeticae occidentalis: in agris desertis prope lapicidinas oppidi Puerto-Real in Prov. Gaditana, 14 Feb. 1845, *H. M. Willkomm 502* (lectotype, designated here, COI-00044218 digital image!).

Annual plants, 15–45 cm tall. Stem 1 to 6, glabrous or glabrescent at base. Basal leaves 5 to 14, rosulate, lyrate-pinnatipartite, up to 9 × 3 cm, with terminal lobe usually broadly ovate, glabrescent to occasionally laxly hirsute. Cauline leaves (0)1 to 5, dentate, attenuate, well developed, mostly in the lower part of stem. Inflorescence in racemes to simple panicles, types A–C(C+), non-unilateral, elongated in fruit up to 1/2 of the total stem length, rather loose, bearing 1 to 3(to 4) fruits/cm at base (mean value: 2.5); pedicels patent to erect-patent in fruit, 4.5–11 mm. Sepals 1.3–2 mm; petals 2–4 mm, gradually attenuate at base. Median staminal filaments with a wide membranous wing. Median nectaries clearly elongated, up to 0.4 mm. Style 1–2(–2.5) mm. Silicles 2–3.2 × 4–6 mm, with narrow swollen rings at margin; surface glabrous to covered with conical and/or clavate trichomes, usually shortly pedunculate (types S1, S4–S6).

Chromosome number. $n = 6$ (Schönfelder, 1968 as "*B. microcarpa*": Cádiz, Sierra de Luna, W Algeciras; Santa Bárbara et al., 1994 as "*B. microcarpa*": Spain, Cádiz, Sierra de Saladavieja, *C. Santa Bárbara et al. s.n.*, SEV 118375); $2n = 12$ (Manton, 1937 as "*B. microcarpa*": S Spain; Olowokudejo & Heywood, 1984 as "*B. microcarpa*": Spain, Cádiz, El Colorado, near Chiclana de la Frontera).

Icon. Grau and Klingenberg (1993: 297, lám. 108).

Habitat and distribution. *Biscutella lyrata* in found in open ephemeral grasslands in coastal pine (*Pinus pinea* L.) and cork–oak tree (*Quercus suber* L.) woodlands, usually on siliceous sandy soils, at 10–600 m. It is endemic to the southern Iberian Peninsula (Cádiz Province, Spain; references from Huelva and Málaga provinces have not been confirmed). Figure 5.

Conservation status. Although this species is confined to a narrow area in southern Spain, it occurs in habitats not severely threatened and hence should be regarded as Least Concern (LC) (IUCN, 2012).

Notes. Typification of *Biscutella lyrata* by Raffaelli (1985b) on a specimen from southern Spain restricted application of that Linnaean name to the Spanish plants usually identified as *B. microcarpa*, and also allowed recovering the name *B. maritima* for the Sicilian plants usually identified as *B. lyrata*.

North African plants with lyrate to sublyrate leaves have been usually misidentified with *Biscutella lyrata*, a species endemic to southern Spain. Two remarkable characters, the broadly winged filaments of stamen and the small silicles in loose racemes, are unique in the series, and they allow unequivocal identification of *B. lyrata*. North African citations of the latter are usually attributable to other relatives, mostly to *B. eriocarpa*, *B. pseudolyrata*, and *B. raphanifolia*.

The names *Biscutella microcarpa* var. *pseudoscutulata* Rouy (nom. nud. in sched.: LY-0004244), *B. tumidula* Lag. ex DC. (Syst. Nat. 2: 411. 1821, nom. inval. pro syn. [Art. 39 of the ICN]), and *B. microcarpa* f. *carpohirta* Muñoz Med. (Anales Inst. Bot. Cavanilles 10 [1]: 354. 1951, nom. nud. inval. [Art. 39 of the ICN]) were applied to plants belonging to *B. lyrata*.

5. Biscutella maritima Ten., Fl. Napol. Prodr. 1: 38. 1812; et Fl. Napol. 2: 77–78. 1820. *Biscutella lyrata* L. var. *maritima* (Ten.) Arcang., Comp. Fl. Ital.: 62. 1882. *Biscutella lyrata* subsp. *maritima* (Ten.) Raffaelli, Taxon 34: 697. 1985. *Biscutella didyma* L. var. *maritima* (Ten.) Batt., Fl. Algérie: 38. 1888. TYPE: Italy. *Biscutella maritima* Nob., [Naples,] Capri, Tenore (Herb. Tenore) (lectotype, designated by Raffaelli [1991: 16], NAP digital image!).

Biscutella marginata Ten., Fl. Napol. Prodr. 1: 38. 1812. SYNTYPE: Italy. [Naples,] "Capri, Tenore" (Herb. Tenore) (syntype, NAP not seen).

Biscutella laxiflora C. Presl, Delic. Prag.: 11. 1822; Fl. Sic. 1: 68–69. 1826. *Biscutella didyma* L. var. *laxiflora* (C. Presl) Batt., Fl. Algérie: 38. 1888. *Biscutella lyrata* L. subsp. *laxiflora* (C. Presl) Raffaelli, Webbia 39: 114. 1985. TYPE: unknown.

Biscutella erucifolia Rchb., Iconogr. Bot. Pl. Crit. 7: 5. 1829. TYPE: Icon 828, tabula DCVII (lectotype, designated here).

Annual (occasionally short-lived perennial) plants, 15–85(–120) cm tall. Stem 1 to 10, hirsute at base. Basal leaves 5 to 13(to 25), densely rosulate, lyrate to spatulate due to the lateral lobes diminution, up to 14(–20) × 4.5(–6) cm, with terminal lobe broadly ovate, occasionally oblanceolate, hirsute, with hairs mainly distributed on nerves. Cauline leaves absent or bract-like, occasionally 1 to 3 small leaves close to the stem base, attenuate-semiamplexicaul. Inflorescence in racemes to branched panicles, types B–C+, non-unilateral, with up to 8(to 15) terminal racemes per stem elongated in fruit, often rather dense, bearing (1 to)2 to 5(to 6) fruits/cm at base (mean value: 3.7); pedicels generally patent in fruit, erect-patent to a lesser extent, (5.5–)7–12 mm. Sepals (1.5–)2–3 mm; petals (3.5–)4–6.5 mm, gradually

attenuate at base. Staminal filaments filiform. Median nectaries always elongated, (0.4–)0.5–0.7(–0.8) mm, usually cylindric. Style 2–3.5 mm. Silicles (3–)3.5–6 × (6–)7–13 mm, margins flat to slightly thickened; surface covered with clavate and/or minute conical trichomes, with a broad range of distribution patterns, from glabrous to entirely covered with both types of trichomes (types S1–S6).

Chromosome number. $n = 8$ (Larsen & Laegaard, 1971 as "*B. radicata*": Italy, Sicily); $2n = 16$ (Manton, 1932 as "*B. lyrata*": Italy, Sicily; Olowokudejo & Heywood, 1984 as "*B. lyrata*": Italy, Sicily, Siracusa; Raffaelli & Fiorini, 1986 as "*B. lyrata* subsp. *maritima*": Italy, Isola di Ponza, close to the rd. and crops, Fondi, in the forest of *Quercus suber* L. a San Biagio; Fiorini & Raffaelli, 1990 as "*B. lyrata* subsp. *laxiflora*": Tunisia, coastal rd. to Biserta-Cap Blanc, *M. Raffaelli & C. Ricceri s.n.*).

Icon. Raffaelli (1985a: 117, fig. 3, sub *B. lyrata* subsp. *laxiflora*; 1991: 17, fig. 6).

Habitat and distribution. *Biscutella maritima* is found in coastal forests, grasslands, and open shrubby vegetation, usually in disturbed ground, at 50–1000 m. It is known from the western coast of the Italian Peninsula, Sicily, Tunisia, and eastern Algeria. Figure 6A.

Conservation status. This species should be regarded as Least Concern (LC) because of its broad distribution in the central Mediterranean and its populations being not specially threatened (IUCN, 2012).

Notes. In general terms, plants from Tunisia show smaller size (15–30 mm) and/or smaller fruits and petals (Vicente et al., 2017). Some Algerian individuals produce oblanceolate, subentire leaves, but a combination of characters, such as branching pattern and nectary or pedicel length, easily allows recognition of those individuals as belonging to *Biscutella maritima*. Part of the original material of *B. choulettei* Jord. (Diagn. Esp. Nouv.: 316. 1864, p.p.) really belongs to *B. maritima*.

6. Biscutella pseudolyrata A. Vicente, M. Á. Alonso & M. B. Crespo, Willdenowia 49: 158. 2019. TYPE: Morocco. Rabat-Sale-Zemmour-Zaer Prov., ctra. de Sale a Sidi Allal el Bahraoui, 29SQT239668 [34°01′04.7″N, 06°34′30.8″W], 178 m, bosque de *Quercus suber*, 6 May 2015, *A. Vicente & M. Á. Alonso s.n.* (holotype, ABH-72445!; isotypes, ABH74994!, ABH75001!, MA01−00931693!).

Annual plant, 25–45(–60) cm tall. Stems 1 to 10, glabrescent to hirsute below. Basal leaves 4 to 25, in a rosette, generally lyrate, keeping the terminal lobe relatively entire and ovate, occasionally spatulate or oblanceolate, due to the lateral lobes diminution, up to 12 × 3 cm, hirsute. Cauline leaves generally absent (occasionally 1 to 2 well developed in the basal part of stem, and attenuate at base). Inflorescence a simple raceme to simple panicle sometimes with some loose sub-panicles at base, types (A)B–C(C+), usually yielding up to 8 terminal racemes per stem with racemes elongated and loose in fruit, bearing 1 to 3(to 4) fruits/cm at base (mean value: 2.3); pedicels patent to erect, 6–12 mm. Sepals 1.8–3 mm; petals 2.8–5(–6) mm, gradually attenuate at base. Staminal filaments filiform. Median nectaries elongated, 0.4–0.6 mm, usually clavate. Style (1.6–)1.9–2.9 mm. Silicle 3–6 × 6.5–12 mm; margins from flat to clearly thickened; surface from glabrous to covered with clavate and/or tiny conical indumentum, with a wide range of distribution patterns (types S1–S6).

Chromosome number. $2n = 16$ (Vogt & Oberprieler, 2009 as "*B. baetica*": Morocco, Rharb, rd. S 216 betw. Arbaoua & Moulay Bousselham, *Vogt 10190 & Oberprieler 4638*, B-10-1013203).

Icon. Vicente et al. (2019: 159, fig. 1).

Habitat and distribution. *Biscutella pseudolyrata* occurs in grasslands, disturbed ground, and open *Quercus suber* L. woodlands, on siliceous sandy soils of Neogenic-Quaternary origin, at 1–300 m. It is only known from Atlantic coastal areas of the Gharb region (northwestern Morocco), from Larache to Rabat. Figure 5.

Conservation status. Populations of this narrow endemic species occur in fragile habitats of a rather extensive area where potential threats exist, including land-use change, habitat fragmentation, human interference, water and soil pollution, infrastructure development, and urbanization. All those factors could provoke rapid destruction of habitat, leading to regard *B. pseudolyrata* as Vulnerable (VU) (IUCN, 2012). Monitoring is therefore necessary to establish more accurately the number and size of populations and their temporal dynamics to detect further threats.

Notes. *Biscutella pseudolyrata* is morphologically close to both *B. lyrata* and *B. maritima*, with which it has sometimes been misidentified. However, an exclusive combination of morphological features, including basal lyrate leaves, loose inflorescences, and elongated median nectaries (Table 1), allow easy differentiation of *B. pseudolyrata* (see Vicente et al., 2019a). In some populations, plants with dentate basal leaves somewhat resembling *B. boetica* can be found, but the floral and vegetative characters of both species are different enough to warrant safe identification. Font Quer's (1932, unpubl.) exsiccata "Iter maroccanum, 1930" n° 233 and n° 234 were attributed to two forms of *B. didyma*, but they belong instead to *B. pseudolyrata*.

7. Biscutella raphanifolia Poir., Voy. Barbarie 2: 198. 1789. *Biscutella lyrata* L. var. *raphanifolia* (Poir.) Arcang., Comp. Fl. Ital.: 62. 1882. *Biscutella didyma* L. var. *raphanifolia* (Poir.) Coss., Comp. Fl. Atlant.: 287. 1887. TYPE: Algeria. Ex Numidia, *Poiret s.n.* (lectotype, designated by Raffaelli [1985: 114], P-00166955! [the plant on the right side of the sheet]).

Annual or perennial plants, 23–100 cm tall. Stems 1 to 4, hirsute to lanate at base. Basal leaves 4 to 10, in a rosette, mostly lyrate, occasionally pinnatipartite, up to 20 × 6 cm, with broad entire terminal lobe, hirsute to lanate. Well-developed cauline leaves generally present, 1 to 4, occasionally absent, amplexicaul to attenuate. Inflorescence in profusely branched panicles, type D, usually yielding much more than 8 terminal racemes per stem (up to 30), rather dense, with short racemes bearing (1 to)2 to 5 fruits/cm at base (mean value: ≥ 3.2); pedicels 5.3–13 mm, mostly non-unilateral, erect-patent. Sepals 1.4–3 mm; petals 3–6 mm, gradually attenuate at base. Staminal filaments filiform. Median nectaries inconspicuous or elongated up to 0.4 mm. Style 2–4.5(–5) mm. Silicles with a wide range of variation, 2.5–8 × 4.5–15 mm, from totally glabrous to mostly covered with tiny conical hairs together with clavate hairs in the central part and on margins (types S1–S6, but more usually S2 and S6).

Chromosome number. Unknown.

Habitat and distribution. Biscutella raphanifolia occurs in grasslands, disturbed ground, and open shrubby or forest vegetation, at 10–1800 m. It is known from northeastern Algeria and northwestern Tunisia, from Theriet el Had to Oued el Hadjar.

Conservation status. This species occupies a large distribution range and occurs in a variety of habitats not specially threatened. It therefore should be considered as Least Concern (LC) for both of its varieties (IUCN, 2012).

Notes. For further detailed data on the taxonomic aggregate of *Biscutella raphanifolia* see Vicente et al. (2016a). Two morphotypes occur that can be regarded at varietal rank as follows:

Key to the Varieties of *Biscutella raphanifolia*

1. Stem 30–100 cm; silicles (8.2–)9–15 mm wide, usually glabrous . . . . . 7a. *B. raphanifolia* Poir. var. *raphanifolia*
1′. Stem 23–40 cm; silicles 4.5–9(–11) mm wide, usually pilose . . . . . 7b. *B. raphanifolia* var. *algeriensis* (Jord.) A. Vicente, M. Á. Alonso & M. B. Crespo

7a. Biscutella raphanifolia Poir. var. **raphanifolia.**

Biscutella radicata Coss. & Durieu, Bull. Soc. Bot. France 19: 224. 1873 [1872 publ. 1873]. TYPE: Algeria. Annaba Prov.: Collines de Djebel-Edough, subdivision de Bône, May 1864, *V. Reboud s.n.* (lectotype, designated by Vicente et al. [2016a: 418], P-05438661! isolectotypes, B-10-0154798!, MPU-008649 digital image!, MPU-023098 digital image!, MPU-023099 digital image!, MPU-023100 digital image!, P-04632019!, P-05438730!).

Biscutella raphanifolia var. *ditrichocarpa* Maire, Bull. Soc. Hist. Nat. Afrique N. 28: 337. 1937. TYPE: Algeria. Médéa Prov.: In pascuis supra Ben Chicao, solo arenaceo, 24 May 1936, *R. Maire s.n.* (lectotype, designated by Vicente et al. [2016a: 419], MPU-003738 digital image!).

Biscutella raphanifolia var. *orivillosa* Maire, Bull. Soc. Hist. Nat. Afrique N. 28: 337. 1937. TYPE: Algeria. Constantine Prov.: Djebel-Ouach, près de Constantine, pentes arides, [end of] May 1880, *J. Reboud s.n.* (lectotype, designated by Vicente et al. [2016a: 419], MPU-003737 digital image!).

Perennial plants, usually with woody rhizome, 30–100 cm tall. Stems hirsute to lanate at base. Basal leaves up to 20 × 6 cm, hirsute to lanate. Cauline leaves occasionally absent, when developed, amplexicaul to auriculate at base, unusually sessile. Sepals 1.8–3 mm. Style 2.6–4.5(–5) mm. Inflorescence with (1 to)2 to 5 fruits/cm at base (mean value: 3.4). Silicles (4.5–)5–8 × (8.2–)9–15 mm, generally flat and glabrous, sometimes swollen at margin and hirsute, with clavate and/or tiny conical trichomes (often type S6, but also S1–S5).

Icon. Cosson (1884: tab. 50, as *B. radicata*); Maire (1967: 139, fig. 47); Raffaelli (1985: 115, fig. 1).

Habitat and distribution. Biscutella raphanifolia var. *raphanifolia* is found throughout the distribution range of the species, though it is more abundant in the rainy mountain areas. Figure 6B.

Notes. Plants identified as *Biscutella raphanifolia* var. *genuina* Maire (Bull. Soc. Hist. Nat. Afrique N. 28: 337. 1937, nom. inval. [Art. 24.3 of the ICN]) belong to this variety.

7b. Biscutella raphanifolia var. **algeriensis** (Jord.) A. Vicente, M. Á. Alonso & M. B. Crespo, Willdenowia 46: 419. 2016. *Biscutella algeriensis* Jord., Diagn. Esp. Nouv.: 318. 1864. *Biscutella didyma* L. var. *algeriensis* (Jord.) Batt., Fl. Algérie: 38. 1888. TYPE: Algeria. Alger Prov.: Env. d'Alger, Birmandreis, 16 Apr. 1862, *E. Revelière s.n.* (lectotype, designated by Vicente et al. [2015a: 237], MPU-024556 digital image!).

Biscutella confusa Pomel, Bull. Soc. Sci. Phys. Algérie 11: 231. 1874 [Nouv. Mat. Fl. Atl.]. *Biscutella didyma* L. var. *confusa* (Pomel) Batt., Fl. Algérie: 38. 1888. TYPE: Algeria. Tissemsilt Prov.: Teniet-el-Had, *Pomel s.n.*

(lectotype, designated by Vicente et al. [2016a: 419], MPU-005072 digital image!).

Biscutella didyma L. var. *coriophora* Batt., Fl. Algérie: 37. 1888. TYPE: Algeria. Aïn Defla Prov.: Duperré [Aïn Defla], Apr. 1882, *J. A. Battandier s.n.* (lectotype, designated by Vicente et al. [2016a: 419], P-00166951!).

Biscutella choulettei Jord., Diagn. Esp. Nouv.: 316. 1864. TYPE: Algeria. Constantine Prov.: Route de Stora à Philippeville, pentes scutagineuses du Mansourah à Constantine, 15 May 1853, *S. Choulette s.n.* (lectotype, designated by Vicente et al. [2015a: 238], LY-0003809 digital image!).

Annual plants, 23–40 cm tall. Stems hirsute in the lower part. Basal leaves up to 8.5 × 3.5 cm, hirsute. Cauline leaves well developed in most individuals, amplexicaul to sessile. Sepals 1.4–2.6 mm. Style 2–3 mm. Inflorescence with 2 to 5 fruits/cm at base (mean value: 3.2). Silicle 2.5–6 × 4.5–9(–11) mm, with wide range of indumentum types, mostly covered with tiny conical hairs together with clavate hairs in the central part and on margins; sometimes with glabrous surface, with clavate indumentum only present in the central part and on margin (mostly type S2, but also S1–S6).

Habitat and distribution. *Biscutella raphanifolia* var. *algeriensis* is found through most of the distribution range of the species, though it is more abundant in the coastal plains and low dry mountains. Figure 6B.

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Appendix 1. Selected herbarium material of the studied taxa.

Biscutella boetica Boiss. & Reut.

MOROCCO. **Béni Mellal-Jenifra:** inter Kenifra et Kasba Tadla, in pascuis lapidosis, 700 m, 15 Apr. 1934, *R. Maire s.n.* [*Iter maroccanum XXIV*] (lectotype of *B. didyma* subsp. *apula* var. *muscariodora*, MPU-003387). **Rabat-Salé-Kenitra:** ditione Gharb, prope Arbaoua, 14 Apr. 1927, *R. Maire s.n.* [*Iter maroccanum XIII*] (P-05438784); in ditione Gharb, prope Ouezzan, 13 Apr. 1927, *s. coll. s.n.* (P-05438783). **Tanger-Tétouan-al Hoceima:** Tangier & Tetuan, Apr. 1871, *Hooker* (K specimen on the right); Tanger, Bou Bana, in incultis, Mar. 1911, *C. J. Pitard s.n.* (P-05438772); Tangiers, Apr. 1931, *A. W. Trethewy 404* (K); environs de Tanger, *Broussonet s.n.* [reçu de M. Bouchet] (P-05438825 p.p. specimen on the right side); Tanger, cap Spartel, in aridis, 3 Mar. 1911, *C. J. Pitard s.n.* (P-05438761, P-05438765); Tanger-Tétuan, Zinat, in collibus, 11 Apr. 1913, *C. J. Pitard s.n.* (P-05438760); Tanger, Apr. 1921, *C. Pau s.n.* (MA-44396); Tanger, Apr. 1921, *C. Pau s.n.* (MA-44398); Tanger, Dj. Quebir, 6 Apr. 1939, *Font Quer s.n.* (BC-107759); Tétouan, cerca de Boureït, 1300 m, 29 May 1981, *S. Castroviejo, J. Fdez. Casas, F. Muñoz Garmendía & A. Susanna s.n.* (MA-232634); Tetuán, Arroyo Samoa, 15 Mar. 1947, *L. M. Simancas s.n.* (GDA-027991); Tétuan, Jerusa, in incultis, 5 Apr. 1911, *C. J. Pitard s.n.* (P-05438771); Tétouan, cerca de Boureït, Bab Berré, cauce pedregoso de un arroyo, 29 May 1981, *S. Castroviejo, J. Fdez. Casas, F. Muñoz Garmendía & A. Susanna s.n.* (MA-477642); Tanger-Tétouan, Bab Taza, P. N. Talasetmane, sustrato siliceo, 1300 m, 17 June 2008, *J. Calvo & A. Quintanar AQ2790* (MA-782670); Tanger-Tétouan, Chefchaouen, pr. Aguelman, 476 m, 17 June 2008, *E. Rico, S. Andrés Sánchez & M. Santos Vicente MS994* (MA-782810); Tanger Peninsula, rd. 8303 from Souk-Tlata-Taghramet to Ceuta (Sebta), limestone rocks above Souk-Tlata-Taghramet & around the quarry not far from the summit of the pass, 450–500 m, 35°48′N, 05°27′W, 17 Apr. 1993, *R. Vogt 9858 & C. Oberprieler 4306* (B-10-1013205); Tétouan, ca. 29 km from

Chefchaouèn, on rd. to Ouezzane, Douar-E-Kob, 115 m, 35°02′N, 5°26′W, 23 June 1992, *B. Valdés et al. 51-1710* (B-10-0298590); Rincón de Medik, in arenosis inter Ceuta et Tetauen, 4 m, 13 Mar. 1930, *Font Quer 235* [*Iter maroccanum 235*] (lectotype of *B. didyma* subsp. *apula* var. *scabrida*, BC-137361; isolectotypes, MPU-006772, MA-44533); Tayenza, Forêt Bouhachem, 30STE737042, 1518 m, 27 June 2013, *M. B. Crespo, M. Á. Alonso & A. Vicente s.n.* (ABH-69331); Fahs-Anjra, Ksar-es-Seghir, roquedos calcáreos, 3 July 2013, *M. B. Crespo, M. Á. Alonso & A. Vicente s.n.* (ABH-69317); Chauen, subida Djebel Kalaa, sustratos calcáreos, 995 m, 27 May 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68347); Tánger-Tétouan, Oued Laou, 174 m, 26 Mar. 2017, *T. Buira, J. Calvo & S. Hantson TB1152* (MA-807348); Tánger-Tétouan, entre Derdara y Ksar-el-Kebir, pr. Tankoub, 9 Apr. 2009, *J. Calvo & I. Espejo s.n.* (MA-791267); Jebala, djebel Sougna near rd. S603, betw. Chefchaouene & Ksar-el-Kebir, W of village Doumse ca. 14 km E Tanakoub, river banks, field margins & sources, 850 m, 35°05′N, 05°24′W, 23 Apr. 1993, *R. Vogt 10103 & C. Oberprieler 4551* (B-10-1013204); Ksar-el-Quebir, in quercetis suberis, 27 Mar. 1930, *Font Quer 236* [*Iter maroccanum 236*] (BC-137362, MA-44534, MPU-006771); Atlas Rifain, montagnes de Ketama [Issaguen], sol schisteux, 11 June 1935, *Sennen & Mauricio s.n.* (MA-162781). SPAIN. **Cádiz:** Cádiz, Jerez de la Frontera, prox. Pto. de Galis, 30STF64, 450 m, 13 May 2014, *A. Vicente s.n.* (ABH-70653, ABH-70654); Medina Sidonia, pelouse aride, 21 Mar. 1849, *E. Bourgeau 28* p.p. (P-05362287, P-05362291 plants on the left, LY-0009641 lectotype of *B. bourgaei*); Zahara de la Sierra, Cortijo del Álamo, 400 m, 29 Mar. 1983, *A. Aparicio & S. Silvestre s.n.* (GDA-34795); Cádiz, Grazalema, proximidades, 36°45′N, 05°21′W, 865 m, borde de camino en alcornocal, 14 May 2018, *C. Aedo et al. CA25808* (ABH-79392); Cádiz, Villaluenga del Rosario, Sierra del Caíllo, 30STF8763, 905 m, 16 May 2018, al pie de los cortados, *A. Buira et al. CN10131* (ABH-79496); Baetica, Cádiz, pr. Ubrique, terra class., in locis incultis, herbosis, 500 m, 18 June 1925, *P. Font Quer & M. Gros s.n.* (GDA-27990); Cádiz, Ubrique, alcornocales sobre suelos silíceos, etapas aclaradas y márgenes de caminos, 24 Mar. 1982, *M. Ladero, F. Navarro, M. Pérez Chiscano & C. Valle s.n.* (COFC46830); Cádiz, Cortes de la Frontera, ctra. de Cortes de la Frontera a Alcalá de los Gazules, 13 May 2014, *A. Vicente s.n.* (ABH-70651, ABH-70652); Cádiz, Jimena de la Frontera, P. N. de los Alcornocales, 30STF6828, 470 m, 10 May 2018, prado en alcornocal, *A. Buira et al. AB3378* (ABH-78981); Cádiz, Alcalá de los Gazules, Sierra del Algibe, 30STF6245, 380 m, 13 May 2014, *A. Vicente s.n.* (ABH-70655, ABH-70656); Cádiz, Castellar de la Frontera, 30STF7921, 14 May 2014, *A. Vicente s.n.* (ABH-70948); Cádiz, Castellar de la Frontera, cercanías del castillo, 30STF8119, 50 m, 13 May 2014, *A. Vicente s.n.* (ABH-70650, ABH-70657); Prov. Gaditana, Mt. Carbonera, pr. S. Roque, loc. graminosos cultis, sol. schistoso, 200–300 m, 11 Apr. 1895, *Porta & Rigo s.n.* (P-05362293, P-04661684); Cádiz, inmediaciones de Los Barrios, ca. 200 m, 22 May 1997, *E. González Giménez s.n.* (GDA-42375); in montibus supra Algeciras, June 1849, *Boissier & Reuter s.n.* (G-00418101); Algeciras, 15 Apr. 1876, *M. Winkler s.n.* (P-05426735 specimen on the right); Algeciras, 15 Apr. 1876, *M. Winkler s.n.* (P-05362159 specimen on the right). **Granada:** Granada, Silla del Moro, June 1964, *J. Varo s.n.* (GDA-3014). **Huelva:** Zufre, Sierra de Aracena, Cortijo La Carnicera, 11 Mar. 1997, *M. Morales s.n.* (COFC25905); La Palma del Condado, río Tinto, Camino Cortijo de Aradilla, 65 m, 5 Apr. 2005, *M. Á. Alonso, A. Juan, J. Monerris & J. J. Montoya s.n.* (ABH-51001); Huelva, Alájar, Sierra de Aracena, subida a la ermita Virgen de los Ángeles, 760 m, 9 Apr. 2004, *M. Martínez Azorín s.n.* (ABH-50293); Huelva, Niebla, pastizales sobre suelos silíceos, 26 Mar. 1980, *M. Ladero et al. s.n.* (GDA-12633); cercanías de Higuera de la Sierra, 1 May 1977, *J. Varo et al. s.n.* (GDA-4349, GDA-4583). **Málaga:** in agris reg. calid., May 1837, *E. Boissier s.n.* (G-00418099); Ronda, sur les sables calcaires, 1889, *É. Reverchon s.n.* (P-05362290); Ronda, Andalusien, auf kalk, 19 May 1890, *É. Reverchon s.n.* (P-05362261); Ronda, lieux incultes et sablonneux, sur le calcaire, 500 m, June 1890, *É. Reverchon s.n.* (GZU-00318718, GZU-00318719, GZU-00318720); Málaga, Frigiliana, hacia Torrox, pr. Cetrerías, laderas esquistosas, 450 m, *V. J. Arán 6251* (ABH-52054); Málaga, Sierra de Tolox, May 1978, *O. Socorro, F. Valle, G. Blanca & F. Pérez Raya s.n.* (GDA-5639, GDA-7716); ibid., alrededores de los Baños, 30SUF26, 800 m, lugares pedregosos calizos, 29 Apr. 1981, *F. Pérez Raya & J. Molero Mesa s.n.* (GDA-20815); pr. Málaga, loc. aridis in vineis collium supra torre S. Telmo, 28 Apr. 1879, *Huter, Porta & Rigo 163* (P-05362272); Málaga, entre Alozaina y Casarabonela, 29 Apr. 1982, *E. Domínguez, E. Ruíz de Clavijo & J. L. Ubera s.n.* (COFC51585); Málaga, de Colmenar a Olías, Montes de Málaga, Km. 535, W de la Axarquía, Finca Rubira el Viejo, 30SUF7975, 750 m, 23 Apr. 2004, *L. Baena & P. García s.n.* (ABH-49200, GDA-49938); ibid., Km. 535, W de la Axarquía, Finca Rubira el Viejo, 30SUF7976, 900 m, 20 Apr. 2004, *C. Morales et al. s.n.* (GDA-53011); Málaga, Casares, 30STF9737, 480 m, 24 Apr. 2012, *A. Vicente & A. Pardo s.n.* (ABH-59974); Casares, entre arroyo Hondo y cerro Muñiz, 30STF9835, 320 m, taludes y matorral silicícola, 20 Mar. 2015, *J. Fuentes s.n.* (GDA-62168); Málaga, sierra Tejeda, ctra. hacia Salares, 30SVF0680, 699 m, 21 Apr. 2012, *A. Vicente & A. Pardo s.n.* (ABH-59821); Málaga, Sedella, sierra Tejeda, ruta del Pozancón, 30SVF0781, 840 m, 21 Apr. 2012, *A. Vicente & A. Pardo s.n.* (ABH-59820); Málaga, Montes de Málaga, Lagar de Torrijos, 30SUF7876, 755 m, 22 Apr. 2012, *A. Vicente & A. Pardo* (ABH-59822); in campis siccis montosis circâ Malagam et praecipué al Cerro, au nord de la Ville, 30 Apr. 1837 (lectotype of *B. boetica*, G-00418100); Málaga, entre Mijas y Fuengirola, 11 Apr. 1991, *A. Pujadas & F. Navarro s.n.* (COA-20078); Manilva, cerca del Poblado Goleto, 30STF9825, 50 m, herbazales terofítico sobre suelo silíceo, 20 May 2015, *J. Fuentes s.n.* (GDA-62124).

Biscutella didyma L. var. *didyma*

CYPRUS. In montibus pr. Kythraea, May 1880, *Sintenis & Rigo 271* (P-05404915); ibid., Apr. 1880, *Sintenis & Rigo 271* (K); Kythraea above Sirganiá, 29 Mar. 1941, *Davis 2922* (K); Akrotiri forest, Mar. 1939, *G. A. Mavromoustakis 119* [*Flora of Cyprus 119*] (K); Gerasa, 1000 ft., 20 Mar. 1948, *G. A. Mavromoustakis s.n.* (K); Agios Philon, m. Rizokarpaso, fixed sand dunes at sea level, 19 Feb. 1941, *Davis 2279* (K); Halefka Forest Station, 1500 ft., 4 Apr. 1950, *E. Chapman 121* [*Flora of Cyprus 121*] (K); Komi tou Yialou, Karpas, 150 ft., frequent in maquis in pineforest, 7 Apr. 1950, *E. Chapman 220* [*Flora of Cyprus 220*] (K); Episkopi, 100 ft., 14 Mar. 1964, *J. B. Suart 183* (K); Kokkinotrimithia-Kafkalla, 7 Apr. 1933, *A. Syngrasside 322* (K); République de Chypre, district de Limassol, 140 m, pelouses à annuelles sur terre reuge calcaire entre fourrés de *J. phoenicea*, *Pistacia lentiscus*…, 10 Apr. 1992, *J. Lambinon 92/Cy/169 & Van den Sande* (MA-526338). FRANCE. **Corsica:** Corse, June, *Soleirol s.n.* (P-05362153); Corse, collines arides près Bastia, 23 Mar. 1856, *A. André s.n.* (K); Bastia, 1845, *Barnard s.n.* (P-05384426); Bastia, lieux arides, 23 Mar. 1856, *A. André s.n.* (P-04631955); Bastia, coteaux pierreux, 5–20 Apr. 1865, *P. Mabille s.n.* (K, P-05362154 specimens on the right); Bastia, collines micaschisteuses, 8 Mar. 1867, *O. Debeaux s.n.* (P-05384419); Bastia, rochers á St. Lucie, 6 Aug. 1865, *G. C. Joad s.n.* (K). GREECE.

Attica: Athenas, in collibus aridis pr. Athenas, 13 Mar. 1848, *Heldreich s.n.* (P-05362154 specimen on the left); Attica, in M. Pentelico, reg. infer., 3 Apr. 1892, *Heldreich s.n.* (P-04661686); Attikí, Ática, cabo Sounion, templo de Poseidón, 22 Apr. 2011, *J. L. Villar & E. Martínez s.n.* (ABH-58628); ibid., 39 Mar. 1964, *J. Brunner s.n.* (GZU-318716); Attica, *Spruner s.n.* (K). **South Aegean:** Rhodes, *Aucher Eloy 291* (P-05362265 specimen on the lower left side). IRAN. **Fars Prov.:** Kuh-Barfi, prope Schiras, May 1842, *Th. Kotschy s.n.* (P-06648076). ITALY. **Puglia:** Puglia, castel del Monte, 6 Apr. 1976, *Nydegger s.n.* (P-04717853); Puglia, Martina Franca, bosque delle Pianelle, ctra. a Massafra, 4 May 2014, *A. Vicente, M. B. Crespo & M. Á. Alonso s.n.* (ABH-70566); Puglia, Castellaneta, cruce de la SS7 cerca de Gravina Grande, 33TXE642966, 105 m, 4 May 2014, *A. Vicente, M. B. Crespo & M. Á. Alonso s.n.* (ABH-70565, epitype of *B. didyma* var. *didyma*); Apulia, Gargano, in agris restilibus pr. Mt. S. Angelo, 24 Apr. 1875, *Porta & Rigo s.n.* (P-05362281, P-05362591). **Sardegna:** Sardinia, ad Kalarim, 1860, *Gennari s.n.* (P-05404917 specimen on the left); Sardinia, *E. Thomas s.n.* (P-05362265 specimen on the upper left side); Sardinia, Siniscola, ctra. Siniscola a Lula, Mt. Albo, 9 May 2014, *M. B. Crespo, A. Vicente & M. Á. Alonso s.n.* (ABH-70560); Sardinia, comune di Urzulei, cantoniera Bidicolai, 9 May 2014, *M. B. Crespo, A. Vicente & M. Á. Alonso s.n.* (ABH-70561). LIBYA. **Cyrenaica:** Apollonia-Bgua, 11 Apr. 1933, *R. Pampanini 2917* (lectotype of *B. didyma* var. *lenticularis*, FI-003803); altipiano betw. Barce & Tecnis, 3 Apr. 1939, *N. Y. Sandwith 2317* (K). MALTA. Malte, 25 Feb. 1847, *s. coll. s.n.* (P-05362131); Malta, *s. coll. s.n.* (K). TUNISIA. **Gabés Govern.:** Tamezret, Djebel Matmata, 21 Apr. 1884, *A. Letourneux s.n.* (P-05438272, P-05438859 specimen on the left). **Tataouine Govern.:** Djebel Bou Hadíd prope Douiret, 7 Apr. 1887, *A. Letourneux s.n.* (P-05438818 specimen below on the right). PALESTINE. Palestine, bords du Cedron, vallée de Josafhat, Apr. 1933, *s. coll. s.n.* (P-04718136). TURKEY. **A2. Istanbul:** in ditione Constantinopolitana [İstanbul], 30 Apr. 1844, *W. Noei s.n.* (P-05362140). **B1. Balikesir:** Ayvalık Şeytan Sofrası, 70 m, 28 Mar. 1986, *Ö. Seçmen s.n.* (EGE-19956).

Vouchers with Both Varieties of *Biscutella didyma* L. (variety *didyma* and variety *ciliata*)

FRANCE. **Corsica:** Bastia, lieux arides, 23 Mar. 1856, *A. André s.n.* (P-05404870); Bastia, rochers á Sta. Lucia, 16 Mar. 1867, *O. Debeaux s.n.* (P-05362152). CYPRUS. Agios Philon, in Rizokarpaso, fixed sand dunes in sea level, 19 Feb. 1941, *Davis 2279* (K). GREECE. **Attica:** in Atticae collibus, Mar. 1848, *Heldreich s.n.* (K). **Soutgh Aegean:** Rhodes, Mar. 1845, *Heldreich s.n.* (P-05362266); Insel Thera [= Santorini], zwischen Phira und Pyrgos, 14 Apr. 1911, *Hayek s.n.* (GZU-00318723). **Crete:** Kreta, trockene Hügel bei Suoia [Sougia?], 4 May 1904, *Vončina s.n.* (GZU-0054594). ITALY. **Puglia:** Apulia, Gargano, in agris restilibus pr. Mt. S. Angelo, 24 Apr. 1875, *Porta & Rigo s.n.* (K). **Sardegna:** Sardinien, Prov. Núoro, Tal des Rio Pardu bei Gáiro SW Lanusei, ca. 600–650 m, Steineichenwald, Silikatfelsen, 4 May 1986, *J. Poelt s.n.* (GZU-00318711); Sardinia, Jerzu, ctra. a Perdasdefogu, 8 May 2014, *M. B. Crespo, A. Vicente & M. Á. Alonso s.n.* (ABH-70569). LIBYA. **Cyrenaica:** Barce-Sidi Ahmed el-Cheila, 6 Apr. 1933, *R. Pampanini 2919* (FI-003805). TURKEY. **C1. Muğla:** Datça, Hizirsah village, 45 m, 1 Mar. 2016, *H. Yıldırım s.n.* (ABH-76352).

Biscutella didyma var. *ciliata* (DC.) Vis.

ALBANIA. Borsh, rocky limestone slopes above rd. to Valona, 4 June 1933, *A. H. G. Alston & N. Y. Sandwith 1402* (K). CROATIA. Dalmatia, in insula Lesina, *Streinz s.n.* (P-05404908); Lesina, in scopulis, Apr., *R. C. Alexander s.n.* (K); Dalmatia, Scoglio Spalmadore, Apr. 1843, *A. Prior s.n.* (K). CYPRUS. Distr. de Paphos (div. géobot n° 1), Paphos, entassement de cailloux calcaires en bordure des ruines du château byzantin, 10 m, 11 Apr. 1992, *J. Lambinon & van den Sande s.n.* (MA-526436); Paphos, piste de long de l'Ezoussas en aval de Ayia, sur 4 à 5 km à partir du carrefour des pistes de Panayia et de Kannaviou, complexe volcanique, 400–450 m, 23 Apr. 1991, *G. Alziar, P. Ewar et al. 1228* [*OPTIMA Iter Mediterraneum IV no. 1228*] (MA-496208); Larnaka, entre Xylophagou et Ayia Thékla (Larnaca), 0–5 m, champ (blé) abandonné et pseudosteppe á *Sarcopoterium*, 0–5 m, 12 Apr. 1991, *G. Alziar, P. Ewar et al. 44* [*OPTIMA Iter Mediterraneum IV 44*] (MA-495529); Yaïlá, Kyrenia range, 2000 ft., banks by roadside, 28 Mar. 1941, *Davis 2892* (K); Mi. 5, Nicosia, F'gusta rd., 500 ft., frequent in wastelands in Asphodel association, *E. Chapman 42* [*Flora of Cyprus 42*] (K). EGYPT. **Alexandria Govern.:** Bourg el Arab, 10 Oct. 1944, *H. Davis 7249* (K). **Matruh Govern.:** betw. Matruh & Barrani, 2 Apr. 1932, *J. R. Shabetai F4766* (K). **Red Sea Govern.:** Gebel Elba, 1 Feb. 1933, *J. R. Shabetai F1661* (K). FRANCE. **Corsica:** Calenzana, 20 June 1920, *Fuchs s.n.* (P-04632231); Bastia, rochers á Sta. Lucia, 18 Mar. 1867, *O. Debeaux s.n.* (P-05362149); Bastia, environs, lieux vagues, June 1998, *M. Brun, E. Malinvaud & Fre Jh. Héribaud s.n.* (P-05404888); Bastia, *Goulard s.n.* (P-05384423); Bastia, *Roth s.n.* (GZU-00318724); Toga, prés Bastia, sur les pelouses, 9 Apr. 1876, *A. Autheman s.n.* (P-04710159, K); Aléria, lieux meubles, Apr. 1874, *Mauri s.n.* (P-05384424); Aléria, lieux sablonneux, Apr. 1875, *Hanry s.n.* (P-04719100, P-00214104, P-05384425, P-05404910, P-05362151 specimen on the right). GREECE. **Attica:** Athens, Mar. 1930, *J. A. Rogers 0706* (K); [Athens] below Zographu monastery, stony ground in macchia, 16 Apr. 1934, *A. W. Hill, N. Y. Sandwith & W. B. Turrill 2426* (K); in collibus Atticae, Apr. 1855, *Heldreich s.n.* (P-05362135, P-05362263). **Crete:** Créte, La Canée, les moissons, 5 Apr. & 24 May 1883, *É. Reverchon s.n.* (P-05362138, P-05362141, P-05362148, P-05362254, P-05362284, P-05362596, P-05451710, K); ibid., 12 Mar. & 16 May 1883, *É. Reverchon s.n.* (GZU-00318727); La Caneé, Akrotiri, 19 Mar. 1914, *M. Gandoger 3285* (K); Ile de Crête, 1817, *Sieber s.n.* (P-05362188, K); Ile de Crète, prairies autour de Khania, 1845, *V. Raulin s.n.* (P-05362278); Créte, Kissamos, lieux incultes, 21 Mar. & 19 May 1884, *Reverchon s.n.* (K, P-05362137, P-05362285); Creta, in campis, Mar. 1846, *Heldreich s.n.* (K); Kreta, Auf steinigen Anhöhen NW von Dybaki, 13 Apr. 1914, *Eberstaller s.n.* (GZU-00318717). **Peloponnese:** Arche-Korinthos, champs, 30 Apr. 1976, *G. Dominicique s.n.* (P-00036895); Peloponese, Mistra, 14 Apr. 1964, *C. C. Townsend 640415/3* (K); Skyros, 1927, *Rechinger 751* (K). **South Aegean:** Rhodes, Mar. 1845, *Heldreich s.n.* (P-05362276, K); Rhodes, collines, rocailles prés Trianda, 20 June 1870, *Bourgeau s.n.* (P-04718696); Rhodes, collines rocailles prés Rhodes, 20 June 1870, *Bourgeau s.n.* (P-05362268 specimen on the top); Rhodes, NE side of Mt. Attavirios by rd. to Ag. Issidoros near Embona, 5 Apr. 1971, *J. P. M. Brenan 11033* (K); Cycladum insula Andros, in aridis prope Korthion, 5 Mar. 1901, *Heldreich 1609* (P-04719176); Cyclades, Amorgos, at Janghada, 15 Apr. 1940, *Davis 1508* (K); Delphos, Apr. 1930, *s. coll. s.n.* (P-05404913). IRAN. **Bushehr Prov.:** Kazarum Plain, near Bushire, 22 Mar. 1928, *S. Horner 161* (K); Dalaki in graminosis (Pers. austr.), Apr. 1868, *C. Haussknecht s.n.* (P-05362269 specimen on the lower part). **Fars Prov.:** Kuh-Barfi, prope Schiras, May 1842, *Th. Kotschy s.n.* (P-06648076 specimen in the center); Gere, in rupestribus umbroses faucium pr. Gere, inter Buschir et Schiras, 14 Mar. 1842, *Th. Kotschy s.n.* (lectotype of *B. ciliata* var. *applanata*, JE-00002639; isolectotypes, HAL-0145881, JE-00002638, P-06648081, P-05362146 specimen on the

left); Shah Allamdar, Yarz-e-Khast, on rocky limestone slopes, 1250 m, 8 Mar. 1959, *Coferton 3647* (K); 5 km from Masiri to Basht, 700 m, 20 Mar. 1974, *Davis & Bokhari D.55640* (K). **Khuzestan Prov.:** Shustar, Mar. 1949, *Parsa 20008* (isotype of *B. alireza-dadjua*, K000484153). **Lorestan Prov.:** Luristan, 60 km W of Khorramabad, 1160 m, 10 Apr. 1966, *J. C. Archibald 1644* (K); Lorestan, 3 km W of Mirabad, N of Kashgan R. gorges, 16 Apr. 1960, *H. E. Wright Jr. & A. M. Bent s.n.* (K); 1 mi. N Khorramabad, 5000 ft., 10 Apr. 1929, *Cowan & Darlington 1033* (K). IRAQ. Dabanjuk, 1500–3000 ft., Apr. 1932, *Acra 3100* (K). **Al Anbar Govern.:** S bank of Euphrates opposite Rawa, 150 m, 28 Mar. 1947, *Gillett & Rawi 7054* (K). **Dohuk Govern.:** Zawita Gorge, 23 Apr. 1932, *E. Jubert 2187* (K); Zawita Gorge, ca. 950 m, 29 Apr. 1956, *Emberger, Guest, Long, H. E. S. Schuvan & S. Y. Serhahia s.n.* (K); near Zakho, 825 m, 11 Apr. 1967, *F. Karim, Al Dabbagh & K. Hamad s.n.* (K); Jasina, 11 Apr. 1975, *S. Omar 42785* (K). **Erbil Govern.:** Haibat Sultan Dagh, N of Koy Sanjaq, 850 m, 7 May 1969, *Rnawi, Nuri & Al-Kan 28149* (K); Koy Sanjaq, 7 May 1959, *Rawi, Nuri & Al-Kan 28102* (K); Kurdistania, in montis Kuh-Sefin reg. infer. ad pagum Schaklava, 1000 m, 9 May 1893, *Bornmüller 903* (K). Kani Kirmaj, 19 Mar. 1958, 1600 ft., *M. E. D. Poore 464* (K). **Kirkuk Govern.:** Kirkuk liwa, gorge in Tuni Baba Amera Hills, 10 km S of Durbendikan, 9 Apr. 1964, *F. A. Barkley & S. Y. Haddad 7446* (K). **Niniveh Govern.:** Mésopotamie, Mossoul, 1845, *M. P. E. Botta* (P-06648077); Mosul, Apr. 1920, *R. J. D. Graham 669* (K); Nimrud dagh supra Orfa, Mar. 1867, *C. Haussknecht s.n.* (P-05362269 specimen on the upper part). ITALY. unspecified locality, *Herb. Poiret s.n.* (P-05362151 specimens on the left). **Campania:** Ital. Austr., ca. Neapolim, *N. A. Pedicino s.n.* (P-05362193). **Puglia:** Bari, parking del aeropuerto, 4 May 2014, *M. B. Crespo, A. Vicente & M. Á. Alonso s.n.* (ABH-70564); Puglia, Martina Franca, bosque delle Pianelle, ctra. a Massafra, 4 May 2014, *A. Vicente, M. B. Crespo & M. Á. Alonso s.n.* (ABH-70559); Puglia, Crispiano, ctra. a Statte, cerca de Gravine de Amastuola, 4 May 2014, *A. Vicente, M. B. Crespo & M. Á. Alonso s.n.* (ABH-70570, ABH-73578). **Sardegna:** Sardinia, 1835, *Moris s.n.* (K); Sardinia, Jerzu, ctra. a Perdasdefogu, 8 May 2014, *M. B. Crespo, A. Vicente & M. Á. Alonso s.n.* (ABH-70563); Sardinia, comune di Urzulei, ctra. a Dorgali, Genna Croce, 9 May 2014, *M. B. Crespo, A. Vicente & M. Á. Alonso s.n.* (ABH-70562); Sardaigne, 1850, *Gennari s.n.* (P-05404917 specimen on the right). JORDAN. **Ammann Govern.:** Ammann, Rücken wenig E des Berdes Nebo (Dschebel Siyagha) bei Madaba, beweidete Flur mit Kalkblöcken, 650 m, 4 Mar. 1992, *J. Poelt s.n.* (GZU-00318728); Amman, old peach orchard near university, 28 Mar. 1995, *F. N. Hepper 10016* (K); Amman, pasture, 2500 ft., 7 Mar. 1922, *V. E. Buseton s.n.* (K); Amman, 5 Apr. 1953, *H. F. Mooney s.n.* (K). **Aqaba Govern.:** Wadi Rum, rocky slope, 13 Apr. 1945, *Bundaois 9025* (K). LEBANON. Saïda, près de village de Scanderouna [Saraouniye], 29 Feb. 1853, *s. coll. s.n.* (P-05362265 specimen on the right); Saïda [Sidon], rochers calcaires de Kanderom, 28 Feb. 1853, *G. Gaillardt s.n.* (P-04745934); Kherbet Qanafar, slopes above Schneller School, 22 Apr. 2004, *F. N. Hepper 13289* (K); Beka'a, Hoch Moch (Rayak), mountainous area (rocky), 22 Apr. 2004, *J. Breidy & S. Khairallah LEB244* (K); Harissa, 2300 ft., 17 Apr. 1959, *O. Polunin 5288* (K). **Ma'an Govern.:** Petra, 970 m, 10 Apr. 1935, *J. E. Dinsmore 11349* (K). **Tafilah Govern.:** Dana Reserve, plateau near top of Rumana Mtn., SW aspect, 1338 m, 7 Apr. 2013, *M. Al Awaji, R. Al Khawaldah, H. Amafadi, R. Borosova, S. Ghazanfar, J. Hearsum, J. Osborne, H. Taifour & E. Williams s.n.* (K). **Zarqa Govern.:** Zarqa, from Kamsheh toward Alouk, 663 m, 24 Mar. 2004, *K. Abulaila, M. A. Hamoun, S. Saifan & Z. Tehabsem s.n.* (K). LIBYA. **Cyrenaica:** Uadi el-Kuf (fra Gasr beni Gdam e Sidi Abd el-Uahed), 6 Apr. 1933, *R. Pampanini 2918* (FI-003804); Cirenaica, el-Beida–Uadi el Kuf Bu Breica, 27 Apr. 1934, *R. Pampanini & R. Picchi-Sermoli 2920* (FI-003806); Cirenaica, Uadi el-Kuf, fra Gasr Beni Gdam e Sidi Abd el-Uahed, 6 Apr. 1933, *R. Pampanini 2905* (lectotype of *B. didyma* var. *ciliata* var. *macrocarpa*, FI-003479); Cirenaica, El Gubba, Siret Bettamer, 7 Apr. 1933, *R. Pampanini 2906* (FI-003480); Cirene, Melchifaf, 7 Apr. 1933, *R. Pampanini 2907* (FI-003481); Cirenaica, Apollonia, Rgua, 11 Apr. 1933, *R. Pampanini 2909* (FI-003483); Cirenaica, Lamluda, 28 Apr. 1934, *R. Pampanini & R. Pichi-Sermolli 2911* (FI-003485); Cirenaica, Apollonia, Uadi Scechaba, 1 May 1934, *R. Pampanini & R. Pichi-Sermolli 2912* (FI-003486); Wadi el Kuf, on limestone rock, 13 Apr. 1939, *N. Y. Sandwith 2614* (K); ibid., 13 Apr. 1939, *N. Y. Sandwith 2615* (K); Benghasi, 1883, *G. Ruhmer s.n.* (P-05438759); Slonta to Marawa, S rd. from Derna to El Merj, 750 m, 1 Apr. 1970, *Davis 50567* (K); Benghazi, Rommel's Pool, 15 Feb. 1961, *Kranz s.n.* (K); Cirenaica, Lamluda, 9 Apr. 1933, *R. Pampanini s.n.* (K); wadi descending from Cyrene to Apollonia, 350 m, 5 Apr. 1939, *N. Y. Sandwith 2398* (K); Cirenaica, el-Mechili, wadi Ramla, 27 Mar. 1933, *R. Pampanini s.n.* (K); Attag, Fueihat, 21 Jan. 1959, *Keith s.n.* (K); Attag, Fueihat, 3 Mar. 1959, *Keith s.n.* (K); Attag, Fueihat, 24 Feb. 1959, *Keith s.n.* (K); Cyrenaica, in planitie ad meridiem (27 km.) oppidi Tokra, solo calcareo, 29 Apr. 1938, *R. Maire & M. Weiller 98* [*Iter libycum*] (holotype of *B. didyma* f. *parviscutata*, MPU-004115). MALTA. Malta, Feb., *C. de Fountenay s.n.* (P-05362146 specimen on the right); Île de Malte, 1845, *V. Raulin s.n.* (P-05362192); Malte, pelouses, 25 Feb. 1847, *s. coll. s.n.* (P-04632429); Île de Malta, environs de Citta-vecchia, 13 Mar. 1865, *Lagrange s.n.* (P-05362295); Malte, Feb., *C. de Fontenay s.n.* (P-05362146 specimen on the right); Malta, Feb. 1894, *C. de Fontenay s.n.* (P-04661687); Malta, *M. G. Churet s.n.* (P-05362132). PALESTINE. Palestina, Apr. 1846, *E. Boissier s.n.* (K, P-05362190 specimen on the right); Ramath-Gan, near Tel-Aviv, sandy fields & field borders, 21 Feb. 1928, *M. Zohary, N. Feinbrun & M. Spindel s.n.* (P-06648079); Jerusalem, Apr. 1863, *B. T. Lowne s.n.* (K); Jerusalem, Apr. 1933, *s. coll. s.n.* (P-04718135); Jerusalem, by Jerusalem to Jericho rd., just below sea level, in gravel, Mar.–Apr. 1967, *A. C. Western s.n.* (K); Jerusalem, am Syrischen Waisenhause, 24 Mar. 1899, *H. Eggers s.n.* (GZU-00318736); [Jerusalem] St. Saba, Hyerosolymae, Apr., *Roth s.n.* (K); Haifa, ad montem Carmel, 9 Apr. 1906, *H. Petry s.n.* (P-04719045); Israel, Judean Mtns., 749 m, 1 May 2007, *A. Singer Bidi0202010507* (K); Bethlehem, 21 Apr. 1999, *F. N. Hepper & P. S. Davies 13052* (K); Wadi Kelt, 4 Mar. 1942, *P. H. Davis 4020* (K); above Jabbok River, 500 m, 2 May 1911, *F. S. Meyers & J. E. Dinsmore 81349* (K); Palestine, wady-El-Jib, 1 July 1919, *G. C. Johnson s.n.* (K); Mashita, 750 m, 25 Apr. 1911, *F. S. Meyers & J. E. Dinsmore s.n.* (K); Palestine, E of Jordan, 1873, *J. A. Paine s.n.* (K); Jericho, Apr. 1863, *B. T. Lowne s.n.* (K). SAUDI ARABIA. N Hijaz, jebel Dibbagh, 5500 ft., 22 Mar. 1978, *I. S. Collenette 460* (K); Wadi Sawawin, 550 mi. N of Jeddah, 2200 ft., 25 Feb. 1979, *I. S. Collenette 837* (K); viewpoint behind Police Post, top of the Taif escarpment, 6300 ft., 5 Feb. 1980, *I. S. Collenette 1745* (K); Hema Figra, 50 km W of Madinah, 5000 ft., 3 Mar. 1989, *I. S. Collenette 6986* (K). SYRIA. Yatta, 24 Jan. 1851, *Michon s.n.* (P-06648076 specimen on the right); env. de Saida, 29 Feb. 1853, *Blanche s.n.* (P-04719044); Ariha, Apr. 1945, *Fre. Louis s.n.* (P-05123709); Alep (Syrie du Nord), 10 Apr. 1927, *s. coll. s.n.* (P-05434872); Khan Abon Charnat (Désert de Syrie), 10 Apr. 1933, *Daumail s.n.* (P-05434862); Qalaat el Hosn, 29 Apr. 1934 (P-05434871); W-Syrien, Krak des Chevaliers, in Spalten des Mauerwers der Kreuzfahrerburg, 14 Apr. 1988, *H. Pittoni s.n.* (GZU-00318732). TUNISIA. Ad rupes in cacumine

collis prope Gueçar, El Kubbar non procul a Techin, 1 Apr. 1887, *A. Letourneux s.n.* (P-05438818 specimen above on the right). TURKEY. **C1. Muğla:** Datça, 45 m, 6 Mar. 2016, *H. Yıldırım s.n.* (ABH-64354, ABH-76351); Muğla, Datça, 5 m, 9 Mar. 2015, *H. Yıldırım s.n.* (ABH-76353). **C3. Antalya:** Düdengaz (9 km N of Antalya), 14 Apr. 1959, *Leiden Expedition s.n.* (P-06648083); Adalia, dans les collines à Chaire, 26 Apr. 1860, *E. Bourgeau s.n.* (P-06648082).

Biscutella didyma L. var. *ciliata* (DC.) Vis. ("Depressa" Morphotype)

EGYPT. **Alexandria Govern.:** Aegypto, *s. coll. s.n.* (lectotype of *B. depressa*, B–W11928010); in Aegypto, ca. Alexandriam, 14 Mar. 1836, *Th. Kotschy s.n.* (K); near Alexandria, Apr. 1871, *H. A. Hurst s.n.* (K); ex Aegypto inferiori prope Alexandriam, Feb.–Mar. 1877, *A. Letourneux s.n.* (K); Ramlé, Apr. 1874, *A. Letourneux s.n.* (P-05362143); Ramlé, in arenosis, inter segetes, in vervactis, 9 Mar. 1877, *A. Letourneux s.n.* (P-05362271, P-05438301, K); Ramleh, dry sandy or stony rocks, 8 Mar. 1911, *G. F. Scott Elliot 3687* (P-05438284). **Cairo Govern.:** Cairo, 1903, *R. Muschler s.n.* (K); Heluan, ad Nili ripas, Mar. 1906, *R. Muschler s.n.* (K). LIBYA. **Cyrenaica:** Martuba, a est di Barce, Uadi El Bgar, 08 Apr. 1933, *R. Pampanini 2908* (FI-003482); Cirenaica, Derna, 21 Apr. 1934, *R. Pampanini & R. Pichi-Sermolli 2910* (FI-003484).

Biscutella eriocarpa DC. var. *eriocarpa*

ALGERIA. **Béchar Prov.:** Beni Ounif, rocailles gréseuses à la base Nord du Mt. Sidi Youssef, 10 Apr. 1939, *Léouffre s.n.* (P-05438777). **Ghardaïa Prov.:** Bounoura prope Ghardaïa, in incultis palmeti et in herbidis, 2 Apr. 1899, *L. Chevallier s.n.* (P-05438296); ibid., 3 Apr. 1899, *L. Chevalllier s.n.* (P-05438748, P-05438806); Oued Zegrir près Guerrara, dans le Mzab, 20 May 1858, *E. Cosson s.n.* (P-05438837 specimen on the left); El Farch, dans le Mzab, 19 May 1858, *s. coll. s.n.* (P-05438815); Mzab, El Ateuf, 7 Apr. 1899, *s. coll. s.n.* (P-05438749). **Médéa Prov.:** Ben Chicao, pelouses sur les grès, 1100 m, 19 May 1935, *R. Maire s.n.* (lectotype of *B. didyma* var. *suaveolens*, MPU-003590). **Naama Prov.:** Naama, Aïn Hadhjadj, al sud d'Aïn Sefra, 1300 m, 3 June 1989, *C. Benedí, G. Montserrat Martí & J. M. Montserrat Martí JMM-2357* (BC-813786); entre Ain Sefra et ain el Hadjadj, 13 Apr. 1888, *E. Bonnet & P. Maury s.n.* (P-05438178, P-05404871); Aïn el Hadjadj, 13 Apr. 1888, *E. Bonnet & P. Maury s.n.* (P-05438149); Aïn el Hadjar, *J. A. Battandier s.n.* (P-05438776); Aïn-Sefra, 13 May 1934, *A. Faure s.n.* (lectotype of *B. didyma* f. *chamaecarpa*, MPU-003389); in pascuis arenosis ad Aïn-Sefra, 31 May 1934, *A. Faure s.n.* [*Itinera Algerica*] (lectotype of *B. didyma* f. *parvivalvis*, MPU-003390); Mograr Tathani, 17 Apr. 1888, *E. Bonnet & P. Maury s.n.* (P-05404879, P-05404898, P-05438148); ibid., 15 Apr. 1888, *E. Bonnet & P. Maury s.n.* (P-05438801); Col de Founassa, 18 Apr. 1888, *E. Bonnet & P. Maury s.n.* (P-05438150, P-05438180 specimen on the right); Djenian Bou Rezk [Djéniane Bourzeg], 17 Apr. 1888, *E. Bonnet & P. Maury s.n.* (P-05438180). **Oran Prov.:** Prov. Oran, coteaux à Lalla-Maghnia, 28 Apr. 1869, *A. Wariou s.n.* (P-05438305); Sidi Bel Abbés, 1858, *s. coll. s.n.* (P-05438259); ibid., May, *s. coll. s.n.* (K). **Ouargla Prov.:** steppes désertiques à 100 km E de Ksar el Hirane, sur la piste de Dzioua, 29 Apr. 1965, *L. Faurel s.n.* (P-04745857, P-04745858, P-04745862). **Saïda Prov.:** Saïda, gorges de l'oued, rocailles, 28 Apr. 1928, *Le Cesve s.n.* (P-04632008, P-05326060, P-05438829). **Tlemcen Prov.:** Tlemcen, 26 May 1843, *M. Durieu s.n.* (P-05438256 specimen on the left); Tlemcem, Apr. 1912, *Ch. d'Alleizette s.n.* (P-05438184). MOROCCO. "Mauritania" [probably referred to somewhere in N Morocco, Mauritania-Tingitana], Feb. 1872, *Schousboe s.n.* (K). S Morocco, June 1872, *Rein & von Fritsch s.n.* (K). **Béni Mellal-Khénifra:** Tirsel, Demnat, 1 July 1881, *Ibrahim s.n.* (P-05438168). **Casablanca-Settat:** Casablanca, Apr. 1897, *M. Mellerio s.n.* (P-05438736); environs de Casablanca, 20 Mar. 1887, *M. Mellerio s.n.* (P-05438257, P-05438825 p.p. specimen on the left side); Casablanca, 13 Feb. 1918, *R. Benoist s.n.* (P-05438769); Casablanca, friches caillouteuses, sur le chemin de Beauséjour à Aïn-Diab, Feb. 1934, *J. Jallu s.n.* (MA-425421, P-05404894); Grand Casablanca, ctra. P3011 entre Bouskoura y Dar el Haj Omar, pastos pisoteados en suelos poco profundos de zonas calizas, 169 m, 22 Mar. 2015, *I. Aizpuru, S. Andrés-Sánchez, D. Gutiérrez-Larruscaín, C. Molina, J. Pedrol, A. Prunell, E. Rico, A. Rodríguez & C. Urones SA896* (epitype of *B. eriocarpa* var. *eriocarpa*, ABH-74998; isoepitype, SALA-155641); [Skihrate], Sehd Eddhed, Oued Ykem, 16 Apr. 1984, *A. Aparicio, J. G. Rowe & S. Silvestre s.n.* (SEV-203374); entre Berrechid y Sidi Mohammed el Kebir, depresión encharcable, 18 Apr. 1989, *M. A. Carrasco, S. Castroviejo, S. Cirujano & M. Velayos s.n.* (MA-592328); Fedhala [Mohammedia], Mar. 1933, *A. W. Trethewy 34* (K); Mohammedia, pastos primaverales, 50 m, 23 Mar. 1989, *Guzmán, Luceño, Martínez Escribano & Vargas s.n.* (MA-642943); Mohammedia, Oued Nefifik, 29SPT537322, 1 m, 4 May 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68462); Oulad Saïd, in pascuis ditionis, solo arenaceo, 6 Apr. 1937, *R. Maire s.n.* [*Iter maroccanum XXVIII*] (lectotype of *B. didyma* var. *pseudoalgeriensis*, MPU-003915; isolectotype, P-05438785); in rupestribus arenaceis inter Sidi-Sbaa et Khatouat, 800 m, 3 Apr. 1937, *R. Maire s.n.* [*Iter maroccanum XXVIII*] (lectotype of *B. didyma* var. *haplotricha*, MPU-003914). **Drâa-Tafilalet:** Tazzouguert, Djebel Mechmech, Apr. 1925, *H. Humbert s.n.* (P-05438741); Ouarzazate, inter Tizi n'Tichka et Irherm n'Ougdal, 2000 m, 30 May 1985, *C. Blanché, J. Fernández Casas, J. Molero, J. M. Montserrat & A. M. Romo s.n.* (BC-807601, BC-813071, MA-340586); Atlante Majore, Tizi-n-Tichka, in glareosis schistaceis, 2100 m, 8 May 1932, *R. Maire s.n.* [*Iter maroccanum XXII*] (lectotype of *B. didyma* subsp. *lyrata* var. *pseudomicrocarpa*, MPU-003200; isolectotypes, P-05438226, P-05438231); Marrakech-Tensift-Al Hauz, Alto Atlas, collado de Tizi'n-Tichka, 2140 m, 19 Sep. 2013, *M. Martínez Azorín et al. s.n.* (ABH-69882); Marrakech-Tensift-Al Haouz, desvío en la carretera de Marrakech a Ouazazat, cerca de Col de Tichka hacia Imouzer des Glaoua, 2382 m, 12 June 2009, *R. Gonzalo et al. 1196* (MA-799996); Jbel Anaour, Tizi-n-Tinififft, ca. 650 m, felsige halbwüstenartige Hänge, 27 Mar. 1989, *J. Poelt s.n.* (GZU-00318730); Errachidia, steppe rocailleuse, 27 Apr. 1986, *J. Lewalle s.n.* (MA-509404); Er Rachida, rd. N from Erfoud, Ait Amira, 31°47.22′N, 4°14.05′W, 1040 m, 4 June 2004, *S. L. Jury, M. Rejdali & T. M. Upson s.n.* (ABH-46591); Callée du Dadés, Tinerhir, wüstenhafter Hang oberhalb der Altstadt, 29 Mar. 1989, *J. Poelt s.n.* (GZU-00318729). **Fès-Meknès:** Meknès, ctra. Azrou-Meknès, pr. Ito, 30STC844144, suelos esquistosos, 1420 m, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68339 p.p.); Meknès, ctra. Azrou-Meknès, pr. Ito, 30STC829152, 1420 m, 2 May 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68336); Fez, May 1930, *A. W. Trethewy 280* (K); ibid., May 1931, *A. W. Trethewy 279* (K); Aïn Cheggag [Fez], in petrosis, Feb. 1913, *Mouret s.n.* (P-05438764); Cheraga, entre Aïn Aicha y Ourtzarh; 250 m, 5 May 1990, *G. Blanca et al. MA90-25* (GDA-57465); Taza-Al Hoceima, Djebel Tazzeka, 30SVC9671, 22 Apr. 2009, *M. B. Crespo, A. Juan, M. Á. Alonso et al. s.n.* (ABH-69559). **Marrakech-Safi:** "Teneriffa [strikethrough]" [Probably near Mogador], 1807, *Broussonet s.n.* (holotype of *B. eriocarpa*, G-00202788); S Morocco, near Mogadore, Ain-el-Hadjar, Apr.–May 1871, *Dr. Hooker s.n.* (P-05438824 specimen above on the left); Mogador, *s. coll. s.n.* (P-05438824 specimen at the lower

part); M. Tafetecht, entre Chichaouna et Mogador, 5 May 1921, *s. coll. s.n.* (P-05438734); Essaouira, a 1 km de Moulay-Bouzerktour, sabinares de *Juniperus phoenicea* y *Argania spinosa*, 19 Apr. 2003, *S. Talavera, T. Stuessy, R. Berjano & G. Cruz s.n.* (SEV-270562); Ourika Tal, unter Setti Fatma; degradierter mediterraner Buschwald, ca. 1150–1200 m, 9 Apr. 1979, *W. Möschl & H. Pittoni s.n.* (GZU-00318734); Chemaia, cultivos sobre pizarras, 500 m, 18 Apr. 1984, *A. Aparicio, J. G. Rowe & S. Silvestre s.n.* (SEV-203362); Marrakech, Feb.–Mar. 1936, *A. W. Trethewy 148* (K); Middle-High Atlas, Souk el Khemis, ca. 2500 ft., 29 Mar. 1958, *M. M. Whiting & K. Richmond 115* (K); Marrakech, Asni rd., 10 mi. from Marrakech, Mar. 1930, *A. W. Trethewy 223* (K); in planitié Haouz prope Marrakech, 8 Apr. 1929 (P-05438228); Grand Atlas, Riraya, au desous du Tizi-Tamatert, 17 June 1921, *Jahandiez 818bis* (P-05438225); Sud-Ouest de la ville de Maroc [Marrakech], Djebel Afougneur, 11 July 1876, *Ibrahim s.n.* (K, P-05438267); Sud-Ouest de Maroc, Djebel Afougneur, 8 June 1875, *Ibrahim* (K); ibid., 1876, *Ibrahim s.n.* (P-05438266); Maroc, Djebel Aziwel, 1883, *Ibrahim* (P-05438261); Djebel Aziwel, Aït Adouyous, 1883, *Ibrahim s.n.* (P-05438796); W Amzmiz & Tizi-Hemiri, Oct. 1888, *J. Thomson s.n.* (K); 64 km from Marrakech on rd. to Ouarzazate, just beyond Touama, 3 June 2002, *S. L. Jury, M. Ait Lafkih, M. A. Carine, F. J. Rumsey & R. W. Rutherford s.n.* (MA-698283); 71 km S from Marrakech along minor roads, 2 km below Oukaïmeden, 2520 m, 5 July 1987, *S. L. Jury, M. Rejdali & M. F. Watson 8999* (MA-392207); Distr. de Beni-Mellal, en valle de la Felicidad, inmediaciones de Aït Ziri, 1663 m, 4 June 2006, *L. Medina et al. s.n.* (MA-746284). **Oriental:** Region 19 (Beni-Snassen), S Beni-Snassen Mtns., ca. 20 km NW of Oujda, 34°47′N, 2°08′W, 480 m, 5 Mar. 1994, *T. M. Upson et al. 13893* (K); Provinz of Oujda, Monts des Beni-Snassen, rd. S 403 betw. rd. P 27 (Nador-Berkane) & Taforalt, rocks in a quarry N of the rd. ca. 4 km, S of the junction with rd. P 27, 320–340 m, 34°51.614′N, 02°25.380′W, 4 May 1995, *R. Vogt 14230 & C. Oberprieler 8539* (B-10-0114140); Provinz of Oujda, Monts des Beni-Snassen, track betw. Trassoute & Beni Amer, field margins around Beni Amer, 710 m, 34°48.535′N, 02°20.403′W, 5 May 1995, *R. Vogt 14318 & C. Oberprieler 8627* (B-10-0114141); Monts des Beni-Snassen, Taforalt, N-facing slopes Djebel Achaoun ca. 1 km E Taforalt, stony slope and limestone rocks, 850–900 m, 34°49′N, 02°24′W, 4 May 1993, *R. Vogt 10786 & C. Oberprieler 5234* (B-10-1013206); Oujda, Montes de Beni-Snassen, roquedos calcáreos y prados anejos, 30SWD544530, 700 m, 29 Apr. 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68372); pentes du Djebel Melias, Apr. 1913, *C. J. Pitard s.n.* (P-05438823). **Rabat-Salé-Kénitra:** Rabat, in aridis maritimis, Jan. 1912, *Mouret s.n.* (P-05438870). **Souss-Massa:** Agadir, Feb. 1935, *A. W. Trethewy 153* (K); Dj. Hadid, 1886, *Ibrahim s.n.* (P-05438306); Agadir, col du Kerdouss, solo calcareo, 1270 m, 24 May 1985, *C. Blanché, J. Fernández Casas, J. Molero, J. M. Montserrat & A. Romo s.n.* (BC-813069, MA-340939); Agadir, vallée d'Imouzzer des Ida-ou Tatane, près de Souk el Khemis d'Imouzzer, 1100 m, 10 June 1988, *J. Molero, A. M. Romo & A. Susanna s.n.* (SEV-201908); Souss-Massa-Drâa, Garganta del Todra, 30RTA5500, 1600 m, 16 May 2007, *M. Martínez Azorín et al. s.n.* (ABH-69727) entre Agadir y Tafraoute, a 18 km al S de Aid-Baha, 20 Apr. 2003, *S. Talavera, T. Stuessy, R. Berjano, G. Cruz, L. Félix, J. L. García Castaño, M. A. Ortiz, A. Terrab, K. Tremesberger & C. Vega s.n.* (SEV-270619, SEV-270620); Souss-Massa-Drâa, Amerzgane, Sirouna, 1584 m, laderas descarnadas sobre rocas ígneas, 27 Mar. 2015, *I. Aizpuru, S. Andrés-Sánchez, D. Gutiérrez-Larruscaín, C. Molina, J. Pedrol, A. Prunell, E. Rico, A. Rodríguez & C. Urones DG614* (ABH-75000); Souss-Massa-Drâa, entre Ait Mansour y Afella Ighir, 1195 m, laderas pedregosas secas del cañón, 25 Mar. 2015, *I. Aizpuru, S. Andrés-Sánchez, D. Gutiérrez-Larruscaín, C. Molina, J. Pedrol, A. Prunell, E. Rico, A. Rodríguez & C. Urones SA965* (ABH-74999); Atlas major, ad sept. a transitus Tizi-n-Test, in glareosis ad Maison cantonnière; 200 m, 7 Apr. 1936, *R. Maire & G. Samuelsson* (holotype of *B. didyma* f. *orivilla*, MPU-006208); Chaine du Grand-Atlas, sur la route du Tizi-n'Test, près de l'hotel Alpina, 1500–1700 m, 31 Mar. 1952, *B. de Retz 31642* (P-04657211); Gran Atlas, ctra. Taroudant-Marrakech, 25 km al S de Tizi-n-Test, suelo calcáreo, 950 m, 21 Apr. 2003, *S. Talavera, T. Stuessy, R. Berjano, G. Cruz, L. Félix, J. L. García Castaño, M. A. Ortiz, A. Terrab, K. Tremesberger & C. Vega s.n.* (SEV-270651); Atlas Magnum in convalle fl. Aït Messane, in decliv. lapid. calc. pr. pag. Tinitine, ca. 1400 m, 3 June 1926, H. Lindberg 3493 (lectotype of *B. didyma* f. *glaberrima*, H-1509707); in rupestribus arenaceis prope Tirmi, in ditione Tazeroualt, Anti Atlas, 500 m, 12 Apr. 1934, *R. Maire & E. Wilczek s.n.* (MPU-008627, P-05438781); in faucibus sidi-el-Ghiat, ditionis Tazeroualt, Anti Atlantis, 2 Apr. 1934, *R. Maire & E. Wilczek s.n.* (P-05438782); districts de Tazeroualt et Issighiwar jusque à Si Ahmed ou Moussa, Maroc méridional occidental indépendant, 1876, *Mardochée s.n.* (P-05438869); Montagnes de Siggrat et Ghiliz, jusque verst Ighirmillul, à l'est du district de Tazeroualt, 1876, *Mardochée s.n.* (P-05438849); Ighirmillul at Djebel Tafraout et Kerkar, montagnes à l'Est du district de Tazeroualt, 1876, *Mardochée s.n.* (P-05438846); Anti-Atlante, in rupestribus arenaceis montis Fidoust, 2000–2200 m, 20 Apr. 1931, *R. Maire s.n.* [*Iter maroccanum XXI*] (lectotype of *B. didyma* subsp. *lyrata* var. *pseudociliata*, MPU-002855); Foumalili et partie septentrionale du district d'Ida Ouchendal, SW du Maroc, 1876, *Mardochée s.n.* (P-05438864); Ida Ouchendal et Adrar Mqorn, 1876, *E. Cosson s.n.* (P-05438820); Amaluz et Tidli Ighichan, montagnes das le district d'Ida Ouchendal, 1876, *s. coll. s.n.* (P-05438835, K).

Biscutella eriocarpa var. *riphaea* A. Vicente, M. Á. Alonso & M. B. Crespo

ALGERIA. **Oran Prov.:** Prov. d'Oran, champs a Gharrouban, 21 May 1856, *E. Bourgeau s.n.* (P-05438245, P-05438851); Gharrouban, May 1855, *s. coll. s.n.* (K). **Tlemcen Prov.:** Tlemcem, subida al Plateau Lalla Setti, 30SXD5149, 1000 m, 20 May 2012, *A. Juan, M. Á. Alonso, B. Gesslahui & C. Mollá s.n.* (ABH-59292); Tlemcem, 30SXD5860, 800 m, 11 Apr. 2012, *M. Á. Alonso & C. Muñoz s.n.* (ABH-69560, ABH-69561). MOROCCO. **Béni Mellal-Khénifra:** Azilal, subida al Jbel Azourki, 29SQR335950, 1150 m, 27 May 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68360); Azilal, bajada a Beni Mellal, 29SQR410651, 830 m, 2 May 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68354); Beni-Mellal, Jab Tassemit au-dessus de Beni-Mellal (Moyen Atlas), 32°18′N, 6°15′W, 1900 m, 6 June 1980, *A. Charpin, F. Jacquemoud & D. Jeanmonod MAR616* (MA-236739); Grand Atlas, entre Afourer y Bin-el-Ouidane, 1200 m, taludes pedregosos, 9 July 1996, *S. Cirujano, J. B. Peris, A. Romo, R. Roselló & G. Stübing s.n.* (MA-625029); Krinfla [Kenifra?], June 1887, *A. Grant s.n.* (K). **Fès-Meknès:** Taza-Al Hoceima, Djebel Tazzeka, 30SVC062787, 1150 m, 30 Apr. 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68352, ABH-68353); Taza-Al Hoceima, bajada del Djebel Tazzeka, 30SUC791796, 385 m, 22 Apr. 2009, *M. B. Crespo, L. Sáez, M. Á. Alonso et al. s.n.* (ABH-54350); Taza-Al Hoceima, Taza, Bab-Azhar, montes Tazzeka, 578 m, 30 Apr. 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68350, ABH-68351); Taza-Al Hoceima, ctra. bajando a Tafferte, djebel Bou Iblane, 30SUC844286, 1562 m, 27 May 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68381); Sidi Abdallah, entre Taza et Fès, 24 Feb. 1921,

R. Maire s.n. (P-05438233); entre Boulemane y Fès, Tizi Abekhmanes, 1700 m, 22 Apr. 1984, *A. Aparicio, J. G. Rowe & S. Silvestre s.n.* (SEV203303); Meknès, entre Mulay-Idriss y el puerto de Zeggota, 450 m, 6 Apr. 1994, *J. M. Montserrat & B. Valdés BV2428/94* (SEV203370); Moulay-Idriss, pr. Oulad Youssef, 650 m, 6 May 1990, *G. Blanca et al. MA90-28* (GDA-57483); Region 9 (Zorhoun), ruins of Roman city of Volubilis, 4 June 1994, *S. L. Jury, M. Ait Lafkih & B. Tahiri s.n.* (BC-906062); Meknès, ctra. Azrou-Meknès, pr. Ito, 30STC829152, 1420 m, 2 May 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68337); Azrou, hacia Khenifra, encinares, 14 Apr. 1990, *J. L. Solanas & M. B. Crespo s.n.* (ABU33146); Timhadit, 29 June 1918, *R. Benoist s.n.* (P-05438794); Fez, Mar. 1930, *A. W. Trethewy 282* (K); ibid., Mar. 1930, *A. W. Trethewy 280* (K); ibid., May 1931, *A. W. Trethewy s.n.* (K); entre Fes y Taounate, pr. Aïn Kansena, Cheraga, 400 m, 5 May 1990, *G. Blanca et al. MA90-23* (GDA-57464); Fes, Bab Zitouna, collado del Jbel Zalagh, 630 m, 10 May 1994, *A. Achhal, Y. Ben Yacoub, F. Bombardó, J. M. Montserrat & M. Soler JMM-5152/3* (BC-906076). **Marrakech-Safi:** Cap Cantin [Cap Beddouza], in rupestribus calcareis maritimis ad promontorium Soloim, 1937, *R. Maire s.n.* (P-05438780); Moulay Brahim, Atlantis Majoris, 7 Apr. 1929, *R. Maire s.n.* (P-05438227). **Oriental:** Nador, Mont Gourougou, terrain calcaire, 13 Apr. 1988, *A. Acchal, A. Benibid, Z. Díaz, J. C. Diosdados, C. Santa-Bárbara & B. Valdés s.n.* (SEV-202628); Gurugú, marges, éboulis, vers Taquigriat, 21 June 1931, *Sennen & Mauricio s.n.* (MA-44514); Taza-Al Hoceima, cabo Tres Forques, 18 Apr. 2009, *M. B. Crespo, A. Juan, M. Á. Alonso, L. Sáez et al. s.n.* (ABH-58630, ABH-69558); Nador, vertiente meridional del Jbel Arwadi, entre Arbaa Tawrirt y Bou Saida, 16 June 1993, *T. Abdelkader, J. Molero, J. M. Montserrat, J. Pallàs, J. Vicens & M. Veny JMM-3435/5* (BC-906047); Nador, Arbaa Tawrirt, vertiente meridional del Jbel Arwadi, 11 June 1993, *T. Abdelkader, J. Molero, J. M. Montserrat, J. Pallàs, J. Vicens & M. Veny JMM-33645/2* (BC-906048); Nador, Oulad Berzayer, estribaciones Jbel Guens, 6 Apr. 1994, *A. M. Romo 6447, M. Bouhmadi, J. B. Peris & G. Stübing s.n.* (SEV201683); pr. Midar, 460 m, 9 Apr. 1989, *G. Blanca et al. MA89-19* (GDA-34024); entre Midar y Nador, 450 m, 9 Apr. 1989, *G. Blanca et al. MA89-20* (GDA-34028); Segengane, pr. Nador, 300 m, 29 Apr. 1990, *G. Blanca et al. MA90-1* (GDA-57462); Berkane, Oued Zeg Zel, entre Tazarhine y Takerboust, 8 June 1993, *J. Molero, J. M. Montserrat, J. Pallàs, J. Vicens & M. Veny JMM-3126/5* (BC-906054); Monts des Beni-Snassen, rd. P 27 betw. Berkane & Ahfir, ca. 3.2 km W Ahfir, rd. embankments and field margins, 270 m, 34°56.240′N, 02°08.354′W, 6 May 1995, *R. Vogt 14438 & C. Oberprieler 8747* (B-10-0114142); Monts des Beni-Snassen, track 5308 betw. Gorge du Zegzel & Ain-Almou, ca. 4.7 km E of the gorge du Zegzel, limestone cliffs, 730 m, 34°50.866′N, 02°20.611′W, 15 May 1995, *R. Vogt 15028 & C. Oberprieler 9337* (B-10-0114143); Monts des Beni-Snassen, tracks from Beni Ammar to Taforalt via Talezzert, Oued Tlata-at-Talremt ca. 2.5 km S of the marabout "Sidi Boubker," roadsides, limestone cliffs, 220 m, 34°48′N, 02°39′W, 7 May 1993, *R. Vogt 11191 & C. Oberprieler 5639* (B-10-1013207); Oujda, Montes de Beni-Snassen, roquedos calcáreos y prados anejos, 30SWD544530, 700 m, 29 Apr. 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68371, ABH-68373, ABH-68374); environs de Taforalt, broussailles, 900 m, 20 May 1931, *A. Faure s.n.* (K); Oujda, betw. Beni Drar & Ahfir, Col de Guerbourss, 530 m, 29 May 1993, *M. Etlaftski, M. A. Mateos & B. Valdés BV289/93* (SEV-203364); [Ahfir], Martimprey-du-Kiss, au Guerbouz, bords des champs, 26 Apr. 1933, *A. Faure s.n.* (MA-44487). **Rabat-Salé-Kénitra:** Chaouia-Ouardigha, ctra. de Rabat a Slimane, 29SPT782331, 179 m, 7 May 2015, *A. Vicente & M. Á. Alonso s.n.* (ABH-74996); Chaouia-Ouardigha, Sidi Feali, ad Dar Chaffai, in segetibus, 2 June 1912, *C. J. Pitard s.n.* (P-05438813); Chaouia-Ouardigha, Sidi Feali, in collibus aridis, 2 June 1912, *C. J. Pitard s.n.* (P-05438873); Temara, friche herbeuse, 2 Mar. 1986, *J. Lewalle & J. Lambinon s.n.* (BC-807888, MA-464306, P-04657207). **Tanger-Tétouan-al Hoceima:** Axdir (Littore rhiphaeo), 50 m, in herbosis, 30 Apr. 1927, *Font Quer 218* (MA-44502, GDA-028007); Targuist, hacia Cala Iris, pr. Beni Boufrah, 400 m, 8 Apr. 1989, *G. Blanca et al. MA89-11* (GDA-34025). SPAIN. Melilla, 14 June 1915, *A. Caballero s.n.* (K).

Vouchers with Both Varieties of *Biscutella eriocarpa* DC. (variety *eriocarpa* and variety *riphaea*)

ALGERIA. **Tlemcen Prov.:** de Tlemcem à Lalla Maghnia, *J. A. Battandier s.n.* (P-05438222). MOROCCO. **Fès-Meknès:** Fès-Boulemane, Fès, Birtam-Tam, 30SUC589516, 860 m, 30 Apr. 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68408); Meknès, Mequines, Azrou, mirador de Ibo, 30STC844144, suelos esquistosos, 1420 m, 1 May 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68339); Djebel Sadig, 28 May 1888, *Grant s.n.* (P-05438837 specimen on the right); Taza, Djebel Ibone, ctra. bajando a Tazerte, 30SUC844286, 1562 m, 30 Apr. 2013, *M. B. Crespo, M. Á. Alonso, A. Vicente & J. L. Villar s.n.* (ABH-68333). **Marrakech-Safi:** environs de Mogador, Apr. 1867, *B. Balansa s.n.* (P-05438170). **Tanger-Tétouan-Al Hoceima:** pr. Al Hoceima, 150 m, 9 Apr. 1989, *G. Blanca et al. MA89-14* (GDA-34026).

Biscutella lyrata L.

SPAIN. **Cádiz:** In cultis regione calidae Baeticae occidentalis, in agris desertis prope lapicidinas oppidi Puerto-Real in Prov. Gaditana, 14 Feb. 1845, *H. M. Willkomm 502* (lectotype of *B. microcarpa* var. *taraxacifolia*, COI-00044218); Puerto Real, 4 Apr. 1850, *E. Bourgeau s.n.* (P-05362235, P-05426737); Cádiz, Jerez de la Frontera, pr. puerto de Gáliz, 11 Apr. 2009, *J. Calvo & I. Espejo s.n.* (MA-790862); Cádiz, ibid., 30STF6749, 430 m, 13 May 2018, prado en alcornocal, *A. Buira et al. AB3419* (ABH-79015); Medina Sidonia, pelouse aride, 21 Mar. 1849, *E. Bourgeau 28* p.p. (P-05426734 specimen on the upper left side, LY-0009625 lectotype of *B. patulipes*); Cádiz, Chiclana, 7 Apr. 1873, *M. Winkler s.n.* (P-05426736 specimen on the left); ibid., *Monard 250* (P-05426734 specimen on the upper right); Cádiz, Chiclana, pinar sobre suelos arenosos, 9 Apr. 1976, *Ladero & Rivas Goday s.n.* (MA-233571); Cádiz, Chiclana, laguna campano, 22 Apr. 1990, *A. Pujadas, P. Poyato, R. García-Salmones & G. Manzano s.n.* (COA-20087); Cádiz, inter Chiclana et Vejer de la Frontera, Cabo Roche, in arenosis maritimis, 13 Apr. 1978, *T. Luque & B. Valdés s.n.* (P-04717874, MA-377631); Cádiz, Conil de la Frontera, del Pinar de Roche a la Cala del Arenal, 36°19′N, 06°06′W, 15 m, pinar sobre arenas, 9 May 2018, *C. Aedo et al. CA25650* (ABH-79272); Cádiz, Alcalá de los Gazules, sierra del Algibe, 22 Apr. 1993, *J. C. Cristóbal, M. B. Crespo et al. s.n. (*ABH-5663); Cádiz, Alcalá de los Gazules, sierra del Algibe, inicio ruta al Picacho, 8 July 2014, *A. Vicente s.n.* (ABH-70648, ABH-70649); Cádiz, subida al pico del Algibe desde el refugio del Picacho, 6 May 1995, *A. Lora & A. Pujadas s.n.* (COA-020854); Cádiz, Jimena de la Frontera, P.N. de los Alcornocales, 30STF6828, 400 m, 10 May 2018, prado en alcornocal, *A. Buira et al. AB3305* (ABH-79031); Cádiz, [Castellar de la Frontera,] La Almoraima, 3 May 1950, *s. coll. s.n.* (GDA-027992); ca. San Roch [San Roque], May, *Broussonet s.n.* (lectotype of *B. microcarpa*, FI-018213); Cádiz, San Roque, finca La Alcaidesa, 25 Apr. 1979, *G. López s.n.*

(MA-402081); Cádiz, Tarifa, Campo de Gibraltar, Sierra de Ojén, en el Llano del Juncal, pr. antenas del Tajo de las Escobas, 30STE7198, 810 m, 12 May 2018, melojar con durillos y rododendros, substrato silíceo, *A. Quintanar et al. AQ6711* (ABH-79206); in sylvaticis supra Algeciras, June 1849, *Reuter s.n.* (P-05426734 specimen below) Cádiz, [Sierra de] Ojén, 7 June 1987, *E. Hernández, M. Clemente, J. M. Montoro & A. Pujadas s.n.* (COA-013098); barranco de Ojén, 23 Apr. 1976, *D. S. Mata s.n.* (GDA-14051); Algeciras, 15 Apr. 1876, *M. Winkler s.n.* (P-05426736 specimen on the right); Cádiz, Algeciras, barranco del Canuto del capitán, 14 Apr. 1989, *M. L. Gil Zúñiga, L. F. Sánchez & J. A. Alejandre s.n.* (MA-485962). UNITED KINGDOM. **Gibraltar:** Gibraltar, *Broussonet s.n.* (P-05426735).

Biscutella maritima Ten.

ALGERIA. see Vicente et al. (2017). ITALY. **Calabria:** Calabria, loc. arenos. vinearum ca. Rhegium Julium (Reggio), 13–17 Apr. 1877, *Huter, Porta & Rigo s.n.* (K); Calabria, Stalletti, 33SXC360913, 110 m, 5 May 2014, *M. B. Crespo, M. Á. Alonso & A. Vicente s.n.* (ABH-70567, ABH-70571, ABH-70572, ABH-70573). **Campania:** Capri, Marina piccola, 11 Apr. 1885, *G. Evers s.n.* (GZU-00318737); in aridis montis in Capri, 1832, *s. coll. s.n.* (P-05362156 specimen on the left); Capri, 1832, *M. Tenore s.n.* (P-05362164); ibid., Feb. 1827, *M. Tenore s.n.* (K); in Insula Caprearum (P-05362156 specimen on the right); ex Insula Capraearum prope Neapolim, Apr. 1874, *J. Ball s.n.* (K); Capri, Jan. 1905, *J. S. Slater s.n.* (K); Isola di Capri, 10 May 1907, *M. Guadagno s.n.* (MA-44512). **Lacio:** Terracina, Apr. 1845, *M. M. Tulasne s.n.* (P-05362163). **Liguria:** [Genova] Sampierdarena, Vilae Balbi prope Genuan, May, *F. Baglietto s.n.* (P-05325945). **Sicilia:** Prov. Messina, Letoianni, 31 Mar. 1969, *S. Kai Larsen, I. N. Laegaard & B. Øligaard s.n.* (MA-491195); Sicily, Palermo, in campis, May 1890, *H. Rofr. s.n.* (MA-44507); Palermo, in campis sterilibus, Mar., *Todaro 717* (K); Palermo, collibus reg. infer. et montanae, Apr. 1898, *R. Coll s.n.* (K); Palermo, Mt. Pellegrino, 33SUC555257, 422 m, 6 May 2014, *M. B. Crespo, M. Á. Alonso & A. Vicente s.n.* (ABH-70519); Sicily, Mt. San Giuliano, near Erice, 31 May 1990, *F. M Raimondo, S. L. Jury, R. M. Gebauer, A. Charpin, S. Brullo, H. Hofmann, M. Mastracci, D. Lakusic, E. Pérez Caro, P. Minissale, G. Certa, A. Gambino, F. Gendusa & L. Gianguzzi s.n.* (SEV-270084); Sicily, Missilmeri, 31 Mar. 1847, *s. coll., s.n.* (K); Sicilia, Sicilia, Cerami, 33SVB559849, 923 m, 6 May 2014, *M. B. Crespo, M. Á. Alonso & A. Vicente s.n.* (ABH-70574, ABH-70575, ABH-70576); Girgenti [Agrigento], Temple de la Concorde, May 1895, *D. Lattem s.n.* (P-04632425); Sicilia, Nicosia, 33SVB486845, 957 m, 6 May 2014, *M. B. Crespo, M. Á. Alonso & A. Vicente s.n.* (ABH-70558); Sizilien, Catania, Auffahrt zum Atna, 1200 m, 6 Apr. 1958, *J. Brunner s.n.* (GZU-00318712); Sizilien, Syracus [Siracusa], Merkurtempel, 4 Apr. 1958, *J. Brunner s.n.* (GZU-00318713); Sizilien, Auf Anhöhen bei Taormina, 6 Apr. 1958, *J. Brunner s.n.* (GZU-00318715); Sizilien, Castello, 1 Apr. 1958, *J. Brunner s.n.* (GZU-00318714). **Toscana:** Livorno, île de Gorgona, près de la Punta di Cala Maestra, alt. 100–110 m, 19 Apr. 1988, *G. Moggi, M. Rizzotto, E. Luccioli, P. Cuccuini & C. Gori s.n.* (MA-497102, P-04717872). TUNISIA. see Vicente et al. (2017).

Biscutella pseudolyrata A. Vicente, M. Á. Alonso & M. B. Crespo

MOROCCO. **Rabat-Salé-Kénitra:** Mamora forest, May 1888 (K); Forêt de Mamora, 4 Apr. 1888, *Grant s.n.* (P-05438793); Larache, 1914, *Pérez Camarero s.n.* (BC-05077); in planitie Gharb, in silva Mamora, 22 Apr. 1925, *R. Maire s.n.* (P-05438224); Kenitra, Rabat, Mamora forest, Feb. 1930, *A. W. Trethewy s.n.* (K); Kenitra, Ma'mora, 12 km from Rabat on rd. to Meknès, Forêt de la Mamora Quercus suber forest, 80 m, 34°02′N 6°42′W, 9 June 1992, *B. Valdés et al. 01–0032* (B-10-0298334); Kenitra, Mar. 1931, *A. W. Trethewy s.n.* (K); Kenitra, plantation d'agrumes au N de la ville, sol sableux, 14 Feb. 1974, *J. Lewalle 7438* (MA-268268, P-04657216, P-04743559); Sidi Sliman, 60 km from Meknès, 1936, *A. W. Trethewy 288* (K); Région de Rabat, bois du Souissi, aux environs immédiats de Rabat, sur sol sableux, 15 Dec. 1966, *J. Veilex s.n.* (MA-802415, P-04657219, P-04718125, P-04745864, P-05432970); Rharb [Gharb], rd. S 216 betw. Arbaoua & Moulay Bousselham, ca. 3.4 km W of junction with rd. to Lalla-Rhano and Ksar-el-Kebir, ungrazed field margin, 10 m, 34°51′N, 6°10′W, 24 Apr. 1993, *R. Vogt 10190 & C. Oberprieler 4638* (B-10-1013203); Rabat-Salé-Zemmour, ctra. de Sidi Allal el Bahraoui a Kenitra, *Quercus suber* forest, 29SQT235881, 78 m, *A. Vicente & M. Á. Alonso s.n.* (ABH-75002); Rabat-Salé-Zemmour, ctra. de Salé a Sidi Allal el Bahraoui, *Quercus suber* forest, 29SQT239668, 178 m, *A. Vicente & M. Á. Alonso s.n.* (holotype of *B. pseudolyrata*, ABH-72445; isotypes, ABH-74994, ABH-75001, MA-01–00931693); Gharb-Charda-Béni Hse, Ain Felfe, ctra. 4214, sobre sustrato arenoso, 29SQU534586, 6 May 2015, *A. Vicente & M. Á. Alonso s.n.* (ABH-74997). **Tanger-Tétouan-Al Hoceima:** Larache, Feb. 1886, *M. Mellerio s.n.* (P-05438255); El Araix, in arenosis, 20 m, 16 Mar. 1930, *Font Quer 233* (MA-4448, GDA-027996); ibid., *Font Quer 234* (MA-44486, GDA-027995); Tanger-Tétouan, Larache, ctra. de Larache a Ksar-el-Kebir, 29SQU615893, 19 m, 6 May 2015, *A. Vicente & M. Á. Alonso s.n.* (ABH-74993, ABH-74995).

Biscutella raphanifolia Poir.

See Appendix in Vicente et al. (2016a).

Appendix 2. Samples included in the phylogenetic analyses of *Biscutella* L. ser. *Biscutella* (from Alonso et al., 2020) summarized in Figure 4.

Code	Taxon	Locality	Voucher	GenBank ref. *rpl32-trnL*	GenBank ref. *trnV*	GenBank ref. ITS
L. draba ES	*Lepidium draba*	SPAIN. Alicante: San Vicente del Raspeig	ABH71952	KU746330	KU746332	KU746329
M. speluncarum RU	*Megadenia speluncarum*	RUSSIA. Primorskii Krai, Lozovy	VLA10454	KX943557	KX943556	KX943555
B. pseudolyrata MO8	*Biscutella pseudolyrata*	MOROCCO. Rabat-Salé-Zemmour, rd. from Salé to Sidi Allal el Bahraoui	ABH74994	MF521261	MF521296	MF521226
B. pseudolyrata MO9	*Biscutella pseudolyrata*	MOROCCO. Rabat-Salé-Zemmour, rd. from Sidi Allal el Bahraoui a Kenitra	ABH75002	MF521262	MF521297	MF521227
B. pseudolyrata MO10	*Biscutella pseudolyrata*	MOROCCO. Larache rd. from Larache to Ksar-el-Kebir	ABH74993	MF521263	MF521298	MF521228
B. erioc. var. *riphaea* DZ1	*Biscutella eriocarpa* var. *riphaea*	ALGERIA. Tlemcem	ABH69561	KU570220	KU574029	KU570210
B. erioc. var. *riphaea* DZ2	*Biscutella eriocarpa* var. *riphaea*	ALGERIA. Tlemcem, Plateau Lalla Setti	ABH59292	MF521239	MF521274	MF521204
B. erioc. var. *riphaea* MO3	*Biscutella eriocarpa* var. *riphaea*	MOROCCO. Taza, Bab-Azhar, Djbel Tazzeka	ABH68350	MF521238	MF521273	MF521203
B. erioc. var. *riphaea* MO4	*Biscutella eriocarpa* var. *riphaea*	MOROCCO. Oujda, Beni-Snassen, prox. Taforalt	ABH68371	KU570219	KU574028	KU570209
B. erioc. var. *riphaea* MO5	*Biscutella eriocarpa* var. *riphaea*	MOROCCO. High Atlas, Afourer to Bin-el-Ouidane	MA625029	MF521240	MF521275	MF521205
B. erioc. var. *riphaea* MO6	*Biscutella eriocarpa* var. *riphaea*	MOROCCO. Azilal, Djbel Azourki	ABH68360	MF521241	MF521276	MF521206
B. erioc. var. *riphaea* MO7	*Biscutella eriocarpa* var. *riphaea*	MOROCCO. High Atlas, Tizi'n-Tichka	ABH69882	MF521266	MF521301	MF521231
B. erioc. var. *riphaea* MO11	*Biscutella eriocarpa* var. *riphaea*	MOROCCO. From Marrakech to Ouarzazat	MA799996	MF521268	MF521303	MF521233
B. erioc. var. *riphaea* MO12	*Biscutella eriocarpa* var. *riphaea*	MOROCCO. Chaouia-Ouardigha, rd. Rabat to Slimane	ABH74996	MF521265	MF521300	MF521230
B. erioc. var. *eriocarpa* MO1	*Biscutella eriocarpa* var. *eriocarpa*	MOROCCO. Fès, Birtam-Tam	ABH68408	MF521237	MF521272	MF521202
B. erioc. var. *eriocarpa* MO2	*Biscutella eriocarpa* var. *eriocarpa*	MOROCCO. Meknés, rd. Azrou-Meknés, pr. Ito	ABH68336	MF521264	MF521299	MF521229
B. erioc. var. *eriocarpa* MO13	*Biscutella eriocarpa* var. *eriocarpa*	MOROCCO. Betw. Agadir & Tafraoute	SEV270620	MF521267	MF521302	MF521232
B. erioc. var. *eriocarpa* MO14	*Biscutella eriocarpa* var. *eriocarpa*	MOROCCO. Grand Casablanca	ABH74998	MF521269	MF521304	MF521234
B. erioc. var. *eriocarpa* MO15	*Biscutella eriocarpa* var. *eriocarpa*	MOROCCO. Souss-Massa-Drâa, betw. Ait Mansour & Afella Ighir	ABH74999	MF521270	MF521305	MF521235
B. erioc. var. *eriocarpa* MO16	*Biscutella eriocarpa* var. *eriocarpa*	MOROCCO. Chemaia	SEV203362	MF521271	MF521306	MF521236
B. boetica MO17	*Biscutella boetica*	MOROCCO. Chefchauen, pr. Aguelman	MA782810	MF521242	MF521277	MF521207
B. boetica MO18	*Biscutella boetica*	MOROCCO. Tánger-Tétouan, Oued Laou	MA807348	MF521244	MF521279	MF521209
B. boetica MO19	*Biscutella boetica*	MOROCCO. Fahs-Anjra, Ksar-es-Seghir	ABH69317	MF521245	MF521280	MF521210
B. boetica MO20	*Biscutella boetica*	MOROCCO. Chauen, Djebel Kalaa	ABH68347	MF521246	MF521281	MF521211

Appendix 2. Continued.

Code	Taxon	Locality	Voucher	GenBank ref. *rpl32-trnL*	GenBank ref. *trnV*	GenBank ref. ITS
B. boetica MO21	*Biscutella boetica*	MOROCCO. Tayenza, Forêt Bouhachem	ABH69331	MF521243	MF521278	MF521208
B. boetica ES4	*Biscutella boetica*	SPAIN. Cádiz: Alcalá de los Gazules	ABH70652	MF521247	MF521282	MF521212
B. boetica ES5	*Biscutella boetica*	SPAIN. Málaga: Sedella, ruta del Pozancón	ABH 59820	MF521248	MF521283	MF521213
B. raph. var. *algeriensis* DZ29	*Biscutella raphanifolia* var. *algeriensis*	ALGERIA. Médéa, Berrouaghia	ABH72640	KU570216	KU574025	KU570206
B. raph. var. *algeriensis* DZ35	*Biscutella raphanifolia* var. *algeriensis*	ALGERIA. Blida, Chrea Natl. Park	ABH72641	KU570217	KU574026	KU570207
B. raph. var. *raphanifolia* DZ10	*Biscutella raphanifolia* var. *raphanifolia*	ALGERIA. Wilaya de Tizi-Ouzou, l'Akfadou, près de la maison forestière de Tala Kitane	VAL33967	KU570218	KU574027	KU570208
B. maritima IT1	*Biscutella maritima*	ITALY. Sicilia: Cerami	ABH70575	MF521249	MF521284	MF521214
B. maritima IT2	*Biscutella maritima*	ITALY. Calabria: Punta Stalleti	ABH70571	MF521250	MF521285	MF521215
B. *maritima* TN1	*Biscutella maritima*	TUNISIA. Nabeul, cap Bon	MA797732	KU570214	KU574023	KU570204
B. maritima TN2	*Biscutella maritima*	TUNISIA. Rouhia, 30 km from Rouhia to Maktar	MA724301	KU570215	KU574024	KU570205
B. maritima TN3	*Biscutella maritima*	TUNISIA. Tabarka	Herb. Fac. Sci. Bizerta	MF521251	MF521286	MF521216
B. didyma var. *didyma* GR	*Biscutella didyma* var. *didyma*	GREECE. Attikí, Cape Sounion	ABH58628	KU570212	KU574021	KU570202
B. didyma var. *didyma* IT4	*Biscutella didyma* var. *didyma*	ITALY. Sardinia: Siniscola Mt. Albo	ABH70560	MF521252	MF521287	MF521217
B. didyma var. *ciliata* IT5	*Biscutella didyma* var. *ciliata*	ITALY. Sardinia: Jerzu	ABH70563	MF521253	MF521288	MF521218
B. didyma var. *ciliata* IT6	*Biscutella didyma* var. *ciliata*	ITALY. Puglia, Bari	ABH70564	MF521254	MF521289	MF521219
B. didyma var. *ciliata* IT7	*Biscutella didyma* var. *ciliata*	ITALY. Puglia, Martina Franca	ABH70559	KU570213	KU574022	KU570203
B. didyma var. *ciliata* TR1	*Biscutella didyma* var. *ciliata*	TURKEY. Muğla Prov., Datça	ABH76351	MF521256	MF521291	MF521221
B. didyma var. *didyma* TR2	*Biscutella didyma* var. *didyma*	TURKEY. Balkesir, Ayvalık Şeytan Sofrası	EGE19956	MF521257	MF521292	MF521222
B. didyma var. *didyma* CY	*Biscutella didyma* var. *didyma*	CYPRUS. Paphos, ruines du château byzantin	MA526436	MF521255	MF521290	MF521220
B. didyma var. *ciliata* JO	*Biscutella didyma* var. *ciliata*	JORDAN. Prov. Ammann, Dschebel Siyagha, bei Madaba	GZU00318728	MF521258	MF521293	MF521223
B. lyrata ES1	*Biscutella lyrata*	SPAIN. Cádiz: Alcalá de los Gazules, ruta al Picacho	ABH70649	KU570211	KU574020	KU570201
B. lyrata ES2	*Biscutella lyrata*	SPAIN. Cádiz: Alcalá de los Gazules, ruta al Picacho	ABH70648	MF521259	MF521294	MF521224
B. lyrata ES3	*Biscutella lyrata*	SPAIN. Cádiz: Jerez de la Frontera	MA790862	MF521260	MF521295	MF521225

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