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Notes on the original materials of the three western Mediterranean oaks (*Quercus*, Fagaceae) described by Desfontaines

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Abstract. We examined specimens from René Louiche Desfontaines, deposited in the "Herbier de la Flore Atlantique" (P-Desf) from MNHN-P and homologue specimens from P-Lam, LINN-HS, MPU, FI-Webb, and B-W, to assess three names of western Mediterranean oaks (*Quercus* L.) that are distributed across the Iberian Peninsula and North Africa. Specifically, we bring insights to the names *Quercus ballota, Q. pseudococcifera*, and *Q. pseudosuber*, after a thorough examination of the original specimens, combined with the analysis of the respective protologues. The results highlight the need for wider and detailed natural history and classic herbaria surveys to promote the discussion and better understanding of species delimitation and biogeographic awareness, especially in crucial groups, that are still involved in taxonomic and evolutionary discussion, as the trees that form the potential climacic forests of the Northern Hemisphere.

Keywords: Kermes oak, Gall oak, Holm oak, *Quercus ballota*, *Quercus pseudococcifera*, *Quercus pseudosuber*.

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Introduction

The genus *Quercus* Linnaeus (1783: 994) is one of the most important groups of woody plants in the Northern Hemisphere, with around 435 species (Manos *et al.*, 1999; Carrero *et al.*, 2020). This genus taxonomy is target of substantial debate and is not yet consensual, mainly due to the intrinsic difficulty of defining species boundaries among groups of species, defined as a syngameon (Burguer, 1975; Van Valen, 1976; Grant, 1981; Carrero *et al.*, 2020; Cannon & Petit, 2020; Hipp *et al.*, 2019). Consequently, there are diverse groups still under deep evolutionary and taxonomic study, especially around circummediterranean oaks in need of molecular scrutiny (Di Pietro *et al.*, 2020; Douaihy *et al.*, 2020; Hipp, 2015; Jiang *et al.*, 2019; Pham *et al.*, 2017; Vázquez *et al.*, 2020; Vázquez *et al.*, 2018; Vila-Viçosa *et al.*, 2014; Vila-Viçosa *et al.*, 2021). This situation has been originated from the often-brief descriptions of many oak taxa and on the fact that some of their names have never been typified, hampering an established and commonly accepted nomenclature. In addition, original *Quercus* spp. specimens were not adequately studied, and a wealth of heterogeneous materials led to various assumptions, nomenclatural endorsements and hasty typifications by different authors. Consequently, this caused a profusion of names and synonyms, which remain an increasing problem in the accurate identification of well-delimited evolutionary entities, their accurate nomenclature and taxonomic rank. Downstream, this hempers biodiversity conservation, especially in the Mediterranean forests, woodlands and scrub Biome that is is the richest of extra-tropical areas, aggregating 20% of all planetary plant species (Cody, 1986; Regato, 2001; Mittermeier *et al.*, 2011; Bellard *et al.*, 2014).

Desfontaines (1791, 1799) described three oaks from North Africa, two belonging to the western Mediterranean clade of section *Ilex* (Denk *et al.*, 2017; Hipp *et al.*, 2019) - *Quercus ballota* Desfontaines (1791: 375), corresponding to the holm oaks group and *Quercus pseudococcifera* Desfontaines (1799: 349) corresponding to the kermes oaks group. The third oak, *Quercus pseudosuber* Desfontaines (1799: 348), is a member of the western Mediterranean gall oaks, that are placed in section *Quercus* (Denk *et al.*, 2017; Hipp *et al.*, 2019) in the traditionally circumscribed subsection *Galliferae* (Spach, 1842; Gürke, 1897; Tschan & Denk, 2012).

The Mediterranean arboreal kermes oaks are traditionally assigned to *Quercus calliprinos* Webb

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(1838: 15), a tree originally described from northwest Africa (Tétouan, Morocco). The author (Webb, 1838) extended this original concept and species to the Middle East (Lebanon), in a comment to a plant, earlier named as *Q. pseudococcifera* Labillardière (1812: 9) (*non Q. pseudococcifera* Desfontaines 1799: 349). The western Mediterranean arboreal kermes oaks assigned to *Q. pseudococcifera* Desf. and *Quercus mesto* Boissier (1842: 579) (Vázquez *et al.*, 2018) are extensively documented by Webb (1838), Boissier & Reuter (1842), Amo (1861), Martinoli (1953) and, more recently, by Capelo & Costa (2005). The latter authors proposed an endemic arboreal kermes oak (*Quercus rivasmartinezii* (Capelo & J.C.Costa) Capelo & J.C.Costa) from the Atlantic coast of Portugal. This taxon deserves further molecular in-depth studies once the highlighted characters related with leaf shape and cup scales are also observed and overlap most of the distribution of *Q. pseudococcifera* Desf. specimens across the western Mediterranean Basin.

The western Mediterranean holm-oaks traditionally includes two distinct taxa: the holm oak itself (*Quercus ilex* Linnaeus 1753: 995) and the round-leaf oak (*Quercus rotundifolia* Lamarck 1785: 723) (Rivas-Martínez & Saénz, 1991; Schwarz, 1993). Both taxa are discriminated by Saénz de Rivas (1967), Rivas-Martinez (1990) and Franco (1990), followed by the molecular analysis of Lumaret *et al*. (2002) and respectively typified by Vázquez & Coombes (2017) and Vázquez *et al.* (2020). These species are taxonomically distinguishable by the wider lanceolate leaves of *Q. ilex* with a higher number of nerves (>(7)8) with a rectilinear midrib, in face of the smaller round-orbicular leaves with 5 7 secondary nerves and sinuous midrib, especially in the apex, of *Q. rotundifolia* (Rivas-Martínez, 1990). Furthermore, *Q. ilex* is reported to have tomentose leaves as a result of an indumentum formed with stellate trichomes with a higher number of rays (12 14) and larger in length (185 200 µm), in contrast to *Q. rotundifolia* with fewer (9 10) and smaller rays (135 150 µm) (Saénz de Rivas, 1967).

Traditional approaches and interpretations of the original protologue of *Quercus ballota* (Desfontaines, 1971), mentioning sweet edible acorns, led to the prompt synonymy to *Q. rotundifolia* (Sampaio, 1909, 1910, 1947; Taborda-de-Morais, 1940; Vasconcellos & Franco, 1954). Therefore, this taxon was included in Flora iberica (Franco, 1990) as *Quercus ilex* subsp. *ballota* (Desf.) Sampaio (1909: 102). Later, *Q. ballota* was lectotypified with material preserved at MPU (MPU014008!) by Ferrer-Gallego & Sáez (2019), although the author original materials deposited in Desfontaines personal herbarium (P-Desf), were disregarded by the latter authors.

The name of the approached gall oak (*Q. pseudosuber* Desf.) has been overlooked, once it was considered conspecific and a homonym of *Q. pseudosuber* Santi (1795: 156). Both names have been traditionally incorporated as synonyms of *Q.*×*crenata* Lamarck (1785: 724), the broad-known hybrid between *Q. cerris* and *Q. suber* (Vázquez *et al*., 2018).

Since consultations of authors' herbaria is a needed natural step, that is strongly recommended before further typifications, the main objective of this work was to revisit the previous typification of the three names (*Quercus ballota, Quercus pseudococcifera* and *Quercus pseudosuber*), complemented by the study of historical literature and the observation of the original materials, thus contributing to a better awareness of the western Mediterranean oaks' biogeography.

Materials & Methods

The present study was directed to address previous typifications of the original plants collected in North Africa by Desfontaines and kept in his herbarium "Herbier de la Flore Atlantique" (P-Desf) at the Paris Muséum National d'Histoire Naturelle, and duplicated in P-Lam, the Smith Herbarium of Linnean Society (LINN-HS!), the herbarium of the Botanic Garden and Botanical Museum Berlin-Dahlem (B-W), at MPU! (Herbier de l'Université de Montpellier) and FI-Webb! (Webb herbarium from Herbarium Universitatis Florentinae).

Original Desfontaines materials were studied at the Paris Muséum National d'Histoire Naturelle herbarium: *Quercus* spp. specimens (P-Desf!: P00667223!; P00667224!; P00667227! and P00667225!), P-Lam (P00382520!), P! (P06861579!), together with Desfontaines (1791, 1799) original descriptions and protologues. This was done to assess their validity and role pertinence as type materials.

This task was complemented with further online analysis of (a) LINN-HS herbarium specimens (1478.5! and 1478.9!), collected and sent by Desfontaines to Linnaeus *filius*, alongside (b) B-W herbarium relevant specimens (B-W 17597!) and (c) specimens conserved in MPU collected, that were sent by Desfontaines (UM-MPU-MPU014006-9!).

Additionally, *Q. pseudosuber* Desf. was submitted to SEM analysis, to ascertain past inferences and typifications around this taxon. This was done *in loco,* following a SYNTHESIS grant (FR-TAF-280) and performed in the MNHN (Muséum national d'Histoire naturelle) Plateau Technique de Microscopie Electronique for SEM and BAOBAB facilities, UMS2700 2AD, for stereo-microscope imagery.

Results and Discussion

Nomenclatural and taxonomic notes

***Quercus ballota* Desfontaines (1791: 375)**
=*Quercus rotundifolia* Lamarck (1785: 723)

The specimen of *Q. ballota* Desf. deposited in the Smith Herbarium of the Linnaean Society of London (LINN-HS 1478.5!) collected by Desfontaines in 1786 (see LINN-HS 1478.5!; http://linnean-online.

org/47990/) from the original and first location specified by Desfontaines (1791) as *locus classicus*: "Mount Atlas", with his handwriting is identifiable as *Q. ilex* (Desfontaines 1791). Accordingly, the original materials examined in the Herbier de la Flore Atlantique (P-Desf: P00667223! http://coldb.mnhn.fr/catalognumber/mnhn/p/p00667223); and P00667224! http://coldb.mnhn.fr/catalognumber/mnhn/p/p00667224; see Figure 1), also correspond to *Q. ilex* and concur with the original collection site as written in several detailed manuscript notes by Desfontaines *in schedula* "(Alger, Maroc, Belide, Mascar, Tlemsen)". Remarkably, we noticed that the specimen P00667224! (left exemplar) corresponds to the symmetrical image of the drawing presented by Desfontaines (1791) in his original protologue (see Figure 2), being the putative original plant used for such drawing. Additionally, the original description of *Q. ballota* (Desfontaines, 1971: 376-377) addresses two distinctive forms, referring *in schedula* "*J'en ai observé deux varietés bien saillantes, l'une à feulles orbiculaires, dont le diamètre n'etoit que de cinq à six lignes, celles de la seconde ètoient très-allongèes & terminées en pointe"*, referring clearly that the collected materials span the two addressed species inside the western Mediterranean holm oaks (Saénz de Rivas, 1967; Rivas-Martinez & Saénz, 1991), one with rounded and orbicular leaves with less than six secondary nerves, that corresponds to *Q. rotundifolia* and the second with large, acuminate and lanceolate leaves, that corresponds to *Q. ilex*. The specimens from Berlim (BW!) (Schwarz *in sched.*), together with P-Lam and LINN-HS were originated from P-Desf. and all correspond to the original protologue description (Desfontaines, 1797), besides the original diagnosis and image provided by Desfontaines (1791) (see Figure 2), where is common to count more than 8 secondary nerves in several acuminate leaves. Therefore, it is clear that these plants correspond to *Q. ilex*. However, the specimens from Montpellier herbarium (MPU014006!, MPU014007! and MPU014008!), referring to materials collected by Desfontaines in North Africa, were deposited only in 1791, and can be broadly assignable to the round-leaf oak (*Q. rotundifolia* Lam.), especially MPU014006! and MPU014007!. These MPU specimens are characterized by rounded leaves with entire to denticulate and spiny margins and less than 6-7 pairs of secondary nerves. However, the elected lectotype specimen from Ferrer-Gallego & Sáez (2019) (MPU014008!) presents heterogeneous specimens, including leaves with 8 nerves, that could be broadly, but uncertainly, ascribed to *Q. rotundifolia*. The fact that Desfontaines collected heterogeneous materials, that might not correspond to the lectotype elected by Ferrer-Gallego & Sáez (2019) does not invalidate that there are more collected materials that are also original and were not mentioned in the previous lectotipification work. As Desfontaines (1791) proposed several places as *locus typicus* in *"Mount Atlas"* alongside "*Belide, Mascar & Tlemsen*", it enables multiple origins for the original materials, beyond the elected lectotype. Therefore, the original specimens collected by Desfontaines and kept at P-Desf (see Figure 1) are hereinafter discussed.

Figure 1. Original materials of *Quercus ballota* Desf. studied *in-situ* at P-Desf; a, P00667224! and b, P00667223!, corresponding to *Q. ilex* L.

We consider that the specimens originally collected by Desfontaines in 1786, unmistakably match the original description of the taxon, and should have been selected from the author's personal herbarium (P-Desf) as the most appropriate types. However, the code (Turland *et al.*, 2018) prevents the superseding of the proposed MPU lectotype since the previous designation by Ferrer-Gallego & Sáez (l.c.) is not conflictual with the original protologue. Althought, it is necessary to attain that the original gathered materials, collected in North Africa by Desfontaines, including the lectotype, are heterogeneous. Especially, the original materials at P-Desf (P00667224! and P00667223!) that presents leaves with up to 10 secondary nerves and notorious lauroid-lanceolate leaves (see Figure 3), are assignable to *Quercus ilex* L. This should address further questioning and scientific discussion around the holm oak nomenclature and biogeography in North Africa and western Mediterranean Basin For this matter, we highlight a particular specimen (P00382520!) kept in Lamarck herbarium (P-Lam) (see Figure 4), that incorporates duplicate materials from P-Desf, including the three specimens distributed through P00667224! and P00667223!. The label from P00382520 mentions that all the three branches were offered by *"Monsieur Desfontaines"* and includes the note "*appariement au meme arbre",* certifying that all specimens included in Desfontaines collection (P00667224! and P00667223!) belong to same tree (see Figure 4). This is also the case of the materials from B-W (B-W 17597!), that emulates the same segments of the branches, retrieved from the three specimens kept at P00667224 and P00667223, as stated *in schedula* by Schwarz, confirming that they are the original plants associated to *Q. ballota* Desf.

Figure 2. Original image used to illustrate *Q. ballota* Desf. (Desfontaines 1791) – Symmetrical drawing of Figure 1 a) - P00667224! (left exemplar).

Figure 3. a, Lectotype specimen of *Quercus ballota* Desfontaines (MPU014008!) with leaves presenting 8 pairs of secondary nerves; b, P-Desf specimen (P00667224!) with lauroid-lanceolate leaves presenting 10 pairs of secondary nerves; c, P-Desf specimen (P00667223!; left specimen) with lauroid-lanceolate leaves presenting 10 pairs of secondary nerves.

The major output of this revision cohesively addresses that the name *Q. ballota* should be a synonym of *Q. ilex* rather than *Q. rotundifolia*, according to the original protologue, drawings, studied specimens and the abovementioned references and arguments. Herein, Desfontaines (1971), clearly described a different species without rounded and more tomentose leaves in opposition to the taxon previously described as "*chêne a feuilles rondes*", by Lamarck (1785). The own locations stated *in schedula "'en ai vu de valles forêts fur les montagnes de Belide, de Mascar, de Tlemsen…"* corresponds to the northern Algerian Atlas. In these

locations, *Q. ilex* is a common tree, as known from herbaria review, namely the Holotype of *Quercus ilex* L. subvar. *oleoides* Trabut ((MPU007892!; Figure 5), and fieldwork (Figure 6). This contradicts the major works of oak taxonomy and syntaxonomy of north Africa, that mostly recognises *Q. rotundifolia* as the dominant taxon in most forest associations (Barbero *et. al.* 1981; Benabid, 1982; Quézel *et. al.* 1987; Benabdellah *et. al.*; 2010; Chkhichekh *et. al.* 2015; Taleb & Fennane, 2018).

Figure 4. Specimen deposited in P-Lam (P00382520!), that is duplicated from P-Desf (P00667224! and P00667223!), with the statement that the three fragments belong to the same tree (Desfontaines pers. comm.).

Yet, Meddour *et al.* (2017) recognize morphological uniqueness to the holm oak populations of Tlemcen, thus addressing the name *Q. ballota* to the local taxon. The local surrounding potential vegetation corresponds to marcescent forests of *Q. canariensis* Willd. (1809: 975) and *Q. faginea* Lam. (1785: 725) which distribution pattern supports an increase in higher mean rainfall, that is also related to ecologically favour *Q. ilex*. (Saénz de Rivas, 1967; Alcaraz, 1989; Djellouli, 2012; Meddour *et al.*, 2017; Meddour & Mucina, 2021) Furthermore, these northern Algerian Atlas populations, that includes the limestone mountains (up to 1600 m), where *Q. ilex* var. *oleioides* (Battandier, 1890) is referenced, enhances its biogeographic and ecological vicariancy with the eastern Iberian and Italian known populations of *Q. ilex* (Saénz de Rivas, 1967; Barbero *et. al.* 1992; Biondi *et. al.* 2003). These are also known for entailing heavy morphological plasticity and corroborates the molecular results obtained by Lumaret *et al*. (2002).

In spite that most of the original materials collected by Desfontaines, that are directly related to the original protologue, are assignable to *Q. ilex*, we preserved the traditional synonymy to *Q. rotundifolia*, once the only materials that were initially available online at the time of the lectotypification, were the ones from MPU that were allusive to *Q. rotundifolia*.

Figure 5. Holotype of *Quercus ilex* L. subvar. *oleoides* Trabut (Battandier, 1890: 824; MPU007892!); https://science.mnhn.fr/institution/um/collection/mpu/item/mpu007892

Quercus pseudococcifera Desfontaines (1799: 349)

This name was lectotypified by Vázquez *et al.* (2018), foreseeing the original materials from the Herbier de la Flore Atlantique (P00667225!; Figure 7; http://coldb.mnhn.fr/catalognumber/mnhn/p/p00667225). Additional specimens were then studied, namely the ones preserved in Firenze (FI-011768!/ Webb-172233!), a LINN herbarium specimen (LINN-HS 1478.9!; http://linnean-online.org/47997/), sent to Linnaeus *Filius* by Desfontaines. and a Cosson herbarium specimen (P-Cosson P06861579!; http://coldb.mnhn.fr/catalognumber/mnhn/p/p06861579).

This last specimen (P06861579!) is simultaneously the Lectotype (here designated) of *Quercus obtecta* Poiret (Vereecke, 2021). All these specimens were collected in populations distributed across the western Mediterranean basin (left of Tunisia).

Quercus pseudococcifera lectotype corresponds to the broad descriptions of the arboreal Kermes oaks present in the western half of the Mediterranean basin (Desfontaines, 1799; Webb, 1838; Boissier, 1842; Martinoli, 1953; Capelo & Costa, 2005; Vázquez *et*

al., 2018). Regularly, the abovementioned lectotype presents sub-sessile, flat and oblong to elliptic-lanceolate or narrowly obovate leaves, sometimes with stellate trichomes near the midrib and proximate half of the leaf and petiole. Two key characters that distinguish this taxon from *Quercus coccifera* Linneaus (1753: 995) are (1) the presence of free large and flat scales on the cup (see Figure 8), that become retroflexed and acuminate or cuspidate in maturity, and (2) the acorn not exceeding the cup in more than 1/2 of the length of the cup (Capelo & Costa, 2005; Vázquez *et al*., 2018).

Figure 6. Specimens of *Quercus ilex* L. (PO-V 64578 and PO-V 64575) from Tlemcen (Algeria) at PO Herbarium collection (Porto University, Natural History and Science Museum).

Figure 7. Lectotype of *Quercus pseudococcifera* Desf. (P00667225!) designated by Vázquez *et. al.* (2018).

Biogeographically this taxon is related to the Atlantic areas of the western Mediterranean basin, normally located on the fringe of marcescent forests of *Quercus faginea* and *Q. canariensis*, included in the Iberian Peninsula and North Africa. Recentely, Capelo & Costa (2005) described an independent species of kermes oak dedicated to Prof. Salvador Rivas-Martinez, in the already known populations of *Q. pseudococcifera* from Sintra and Arrábida (Portugal), with triangular-cuspidate and retroflexed cup-scales and natural arboreal development. This western Mediterranean distributed taxon has been related with the eastern arboreal kermes oak, which preserves similar characters (Vázquez *et al*., 2018), linked with the eastern vicariant taxon that corresponds to the traditional concept of *Q. calliprinos* Webb (1838).

Quercus pseudosuber Desfontaines (1799: 348)
=*Quercus faginea* Lamarck (1785: 725)

The name previously typified by Vázquez *et al*. (2018), overlooked the deposited specimen in P-Desf herbarium. Therefore, this taxon was assigned to the hybrid between *Quercus faginea* and *Q. suber* L. according to the original protologue that mentions a corky bark and following the proposal of Vicioso (1950). These trees (*Q. pseudosuber* Desf.) with lanceolate and serrate leaves, that can develop a

corky bark, are common in the southern and western Iberian Peninsula and received several names by separate authors. For example, Webb (1838) relates it to *Q. hispanica*, while Vicioso (1950: 112) brings the concept of *Q. lusitanica* subsp. *broteroi* var. *lanceolata* C. Vicioso (1950: 112), and in Vila-Viçosa et. al. (2014) it was described as a new species (*Q. gaditana* F.M. Vázquez, C. Pinto-Gomes & C. Vila-Viçosa). However, this taxon is enclosed in the morphological plasticity of *Q. faginea*.

Figure 8. Detail of cup scales in *Quercus pseudococcifera* Desf. (P-Desf: P00667225!).

In the present study, the observation of the sheets preserved in P-Desf led to the conclusion that the lectotype of *Q. pseudosuber* corresponds to *Q. faginea*. (Figure 9, P-Desf P00667227! (left specimen); http://coldb.mnhn.fr/catalognumber/mnhn/p/p00667227). This conclusion was achieved by following the recent study of the historical types of the Iberian oaks described by Lamarck (Vázquez *et al*., 2020). This latter study helped to comprehend the extensive morphological plasticity and biogeographic outreach of *Q. faginea*, being conspecific of the P-Desf mentioned specimen (P00667227!). The name *Q. pseudosuber* has been traditionally synonymized with *Q.* ×*hispanica* and *Q.* ×*pseudosuber* Santi, both of which belong to subg. *Cerris* (Hipp *et al*., 2019) and to the concept of *Q.* ×*crenata* L., as priority name (Cristofoloni *et al*., 2017). The trichome analysis performed in this study (see Figure 10), confirms the presence of a single stellate indumentum with a high variation on the trichome ray length (100-230 µm). Thus we chose the left specimen (Figure 9, P-Desf P00320363-798!; http://coldb.mnhn.fr/catalognumber/mnhn/p/p00320363), while the right exemplar presents a double indumentum of the same type of stellate trichomes, plus the floccose-fasciculate, yellowish to orangish and fuzzy indumentum typical from *Q. canariensis*, especially on the midrib and secondary nerves. Thus, this exemplar was excluded, as it corresponds to a putative hybrid between *Q. faginea* and *Q. canariensis*.

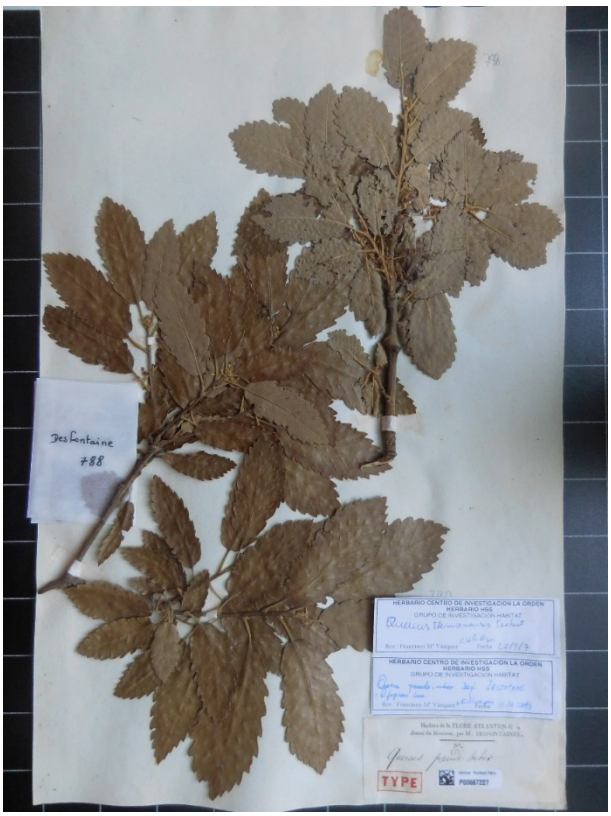

Figure 9. Lectotype of *Quercus pseudosuber* Desf. (P-Desf P00667227!; left specimen (790).

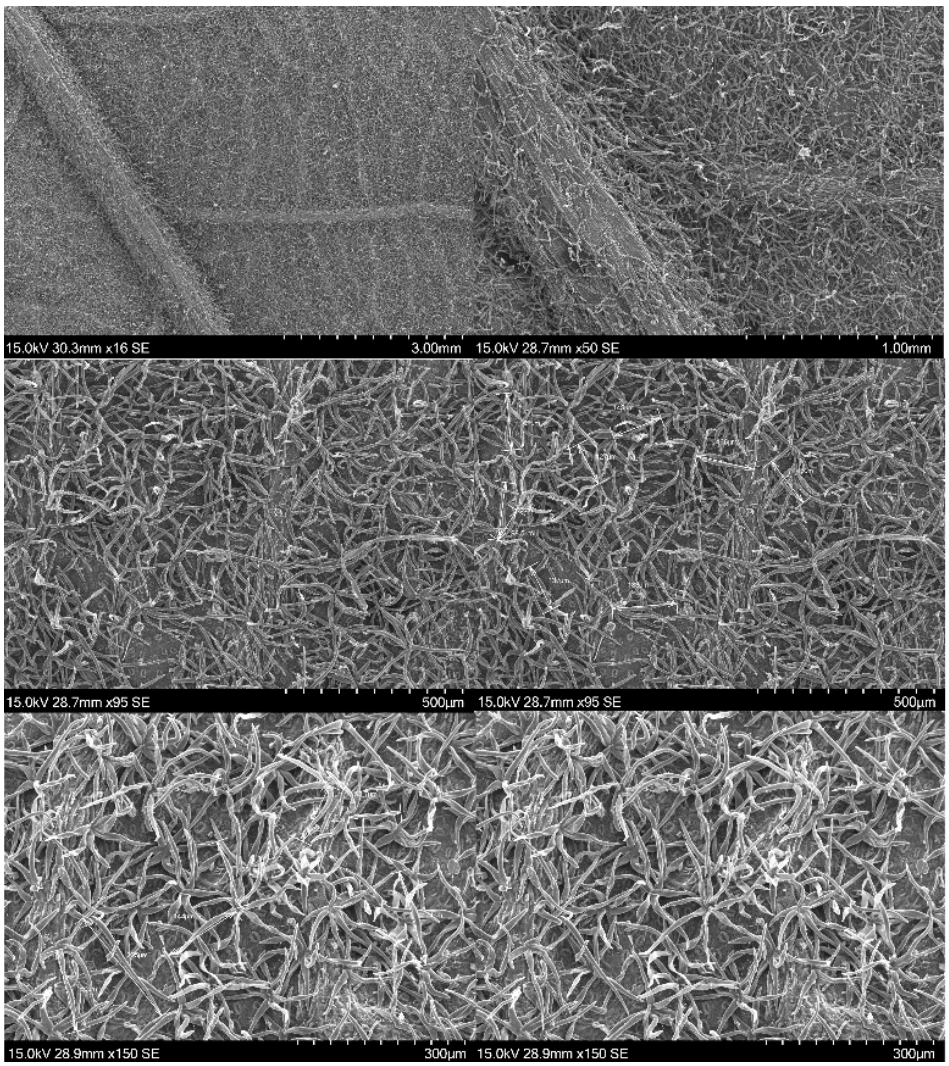

Figure 10. SEM imagery of the abaxial leaf surface indumentum from *Q. pseudosuber* Desf. (P-Desf P00667227-790!; left specimen), revealing a single indumentum of stellate trichomes with large rays (100-230 µm).

Conclusion remarks

This work reveals that the thorough review and examination of classic and personal herbaria is essential for accurate species delimitation, and nomenclatural endorsements with special implications to the oak forest biogeography of the Mediterranean basin. This exercise is especially fundamental for continuing to explore the realms of evolution and plasticity of oaks, and can bring new biogeographic insights and updates, that are otherwise elusive, following prompt typifications and synonyms. This constructive exploration and incorporation of new insights are especially important in groups of species with blurred species boundaries still being established by modern phylogenetic tools. Also, we recognize the importance of establishing and addressing the correct species names with a newly circumscribed biogeography, which influences the accurate conservation status of significant groups of oaks (ex: Sect. *Ilex* and *Quercus*). This is particularly fundamental for Mediterranean forests, which is a keystone biome that is severely threatened by Anthropocenic land use and climate change.

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