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New annotated checklist of the Portuguese oaks (*Quercus*, Fagaceae)

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Abstract. We present a comprehensive taxonomic and nomenclatural review of the Portuguese oaks (*Quercus*), issuing from thorough biogeographical, historical, bibliographic, field and herbarium data. We propose a new annotated checklist for all taxa and nothotaxa belonging to *Quercus* L. genus in the Portuguese national territory, extending the analysis to the broader biogeographical context of the Western Mediterranean subregion. Fifteen herbaria collections were exhaustively studied and complemented by information retrieved from digital collections, resulting in the recognition of eleven native oaks. Further treatment at infraspecific level includes one subspecies and additional 23 nothotaxa. We designate lectotypes for 27 names and add a preliminary list of 148 cultivated taxa, resulting in a total of 183 oaks found in Portugal.

Moreover, we clarify the taxonomical status and reinstate *Q. pseudococcifera* and *Q. airensis* as native to the western Mediterranean subregion. We recover the concept of *Q. faginea*, as the widespread gall oak in Portugal and update its synonym list. We propose *Q. orocantabrica* and *Q. estremadurensis* as autonomous species within the broad European *Q. robur s.l.* group, alongside two newly circumscribed subsections within Section *Quercus.* We describe five new nothotaxa, including four unreported to nature and one missing a suitable name (*Q.* ×*almeidae*, *Q.* ×*alvesii*, *Q.* ×*capeloana*, *Q.* ×*eborense* and *Q.* ×*sampaioana*) and we approach the nomenclatural resolution of the remaining natural hybrids. Lastly, we provide an identification ke , intelligible for non-specialists, including both native taxa and most frequent nothotaxa.

We emphasise the importance of historical and literature review, combined with accurate biogeographical information, as paramount to coherent taxonomical resolution. Both specimens and their associated records were found of crucial significance to a taxonomical model that is, in the end, useful for biodiversity conservation.

Keywords: biodiversity, biogeography, forest conservation, floristics, historical collections, Iberian Peninsula, Mediterranean forests, nomenclature, taxonomy.

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Introduction

As one of the most important genera of woody plants in the northern hemisphere, *Quercus* Linnaeus (1753: 994) possesses circa 435 species, spanning across Temperate, Mediterranean, and Tropical biomes. Oaks are key components of mature woodlands and tall scrubland vegetation in the Iberian Peninsula (Axelrod, 1983; Carrero *et al*., 2020; Costa *et al*., 2012; Manos *et al*., 1999; Rivas-Martínez *et al*., 2011).

In Portugal, eight oak species have been considered native (Franco, 1971; Pereira et al., 2016). These were: Mirbeck's oak (*Quercus canariensis* Willdenow (1809: 975)), kermes oak (*Q. coccifera* Linnaeus (1753: 995), Portuguese oak (*Q. faginea* Lamarck (1785: 725), Lusitanian dwarf oak (*Q. lusitanica* Lamarck (1785: 725)), Pyrenean oak (*Q. pyrenaica* Willdenow (1805: 451), pedunculate oak (*Q. robur* Linnaeus (1753: 996), round-leaf oak (*Q. rotundifolia* Lamarck (1785: 723) and cork oak (*Q. suber* Linnaeus (1753: 995)).

Several botanists have produced standard reviews of oak taxonomic diversity in the Iberian Peninsula (Coutinho, 1888; Schwarz, 1936; Vicioso, 1950; Vasconcellos & Franco, 1954; Franco & González, 1987; Franco, 1990). Nevertheless, recent updates to the

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Portuguese and western Mediterranean scenario asks for a new synthesis (Vázquez et al., 2003; Vázquez et al., 2004; Capelo & Costa, 2005; Vila-Viçosa, 2012; Vila-Viçosa et al., 2014; Vinagre, 2014; Vázquez et al., 2015; Vila-Viçosa et al., 2015; Vázquez & Coombes, 2016; Vázquez et al., 2018; Vazquez et al., 2020; Vila-Viçosa et al., 2022a).

Moreover, we should be aware that the current image of oak taxonomy is that of a 'never-ending story', with an entangled nomenclature, that is inflated by intrinsic natural variation. Downstream, due to natural history artifacts, this drains in a wealth of names that are given to different subsets of taxonomic entities, creating manifold artificial species, instead of valid taxa with 'real' biological meaning. First, many simplistic descriptions lacked further typification and created dubious or phantom names. Second, a wealth of atypical heterogeneous herbarium material, that are not necessarily representative of natural variation, led authors to produce an inflation of species, by endorsing many several artificial 'herbarium taxa' (Vila-Viçosa *et al*., 2022a). In addition, the known low interspecific barriers to gene flow and proliferation of several nothotaxa, enhanced by anthropogenic action, shuffles the potential combinations of shared characters (Vila-Viçosa et al., 2014; Vila-Viçosa et al., 2015; Vázquez et al., 2018). This led to more taxonomic misperceptions and the ongoing profusion of names (Vila-Viçosa *et al*., 2022a). However, modern access to online collections and biodiversity libraries leverages the detailed resolution of such cryptic information. An example is that is easier to find elusive type material in original collections

Thus, our primary objective is to provide a resolved overview of the Portuguese oaks names with a direct taxonomic update and species delimitation, based on the current available information. We also note the biogeographic and synecological characteristics of the recognized taxa and provide straightforward diagnoses and an identification ke , accessible to non-specialists.

Material & Methods

This work relies on the combined observations of authors, along with extensive fieldwork in Portugal and Spain since 2006. We performed a full *in-situ* review of Iberian *Quercus* L. collections in fifteen Herbaria, ten Portuguese (AVE, BRESA, COI, HVR, LISE, LISFA, LISI, LISU, PO and UEVH); three Spanish (BCN; HSS and MA); one in the Netherlands (L); and one French (P). Furthermore, we consulted eight online collections (B, FI, G-BOIS, K, LINN, MAIA, S and MPU) (Thiers, 2021), covering a few thousand specimens. A SYNTHESIS grant (FR-TAF-280), targeting Iberian oaks, at P-Lam, P-Desf, P-Juss and the general collection in the Herbarium of the Paris Muséum National d'Histoire Naturelle (P) was crucial for the presented results.

We complement new name propositions or taxa circumscription with drawings, type images, ecological and chorological features. We provide morphological descriptions in Latin and English. For all taxa, we supply the most relevant synonyms, including many names often misplaced in taxonomic literature. For unambiguous, but already well-documented names, we add updated descriptions, focusing mainly on combinations of diagnostic-characters, presented in the final ke .

Taxa and nothotaxa circumscription follows the proposals of Brotero (1805); Coutinho (1888, 1913, 1930, 1935); Schwarz (1935, 1936a, 1936b); Camus (1935, 1936, 1938, 1939); Villar (1935; 1938; 1943; 1949; 1958); Vicioso (1942, 1950); Vasconcellos & Franco (1954); Saénz (1967, 1969, 1975); Saénz & Rivas-Martínez (1971); Penas et al. (1994); Rivas-Martínez & Saénz (1991); Llamas (1995); Vázquez (1995); Llamas et al. (2003); Vázquez *et al*. (2003); Vázquez *et al*. (2004); Vázquez *et al*. (2015) Capelo & Costa (2005); Andrés *et al*. (2009); Vázquez & Coombes (2016); Vila-Viçosa et al. (2014); Vázquez et. al. (2018); Vázquez et al. (2020) and Vila-Viçosa et al. (2022a).

Taxonomy was adapted from the infrageneric review of Denk *et al*. (2017) and the world oaks' phylogenetic backbone retrieved from Hipp *et al*. (2020) (Supplementary information S1). Furthermore, we account for recent and ongoing molecular studies dealing with infrageneric classification (Manos & Hipp, 2021; Vila-Viçosa *et al*., 2021). For cultivated specimens we used Cullen & Maxwell (1989), Nixon (1997) and Huang *et al*. (1999), altogether supported by the original protologues, subsequent authors comments and combined with the previously mentioned works. Trichome analysis was made using a binocular magnifier (SZX16), coupled with a digital camera (OlympusSC-30) and a scanning microscope (Carl Zeiss EQ-01784). Authorship orthography follows the International Plant Names Index: http://www.ipni.org [accessed in December 2020].

Bioclimatic and biogeographic typology follows, respectively, Rivas-Martínez *et al*. (2011); Rivas-Martínez *et al*. (2017) and the update of Vila-Viçosa *et al.* (2017). Syntaxonomic references followed Costa *et al*. (2012). We collected information about exotic cultivated species, either cultivated in gardens or used as ornamentals, herbarium records, the nursery of the Botanical Garden of the University of Porto (Vila-Viçosa *et al*. 2022b) and personal communication by experts.

Results

We present a full list of 183 oaks recognized in Portugal, 35 native and 148 cultivated. The list of native taxa includes eleven species, one subspecies and 23 nothotaxa with 287 heterotypic (=) and 57 homotypic synonyms (≡), that were revisited and updated, with substantial exchanges across taxa. We provide the annotated checklist of native oaks, ordered by sub-genus, section, subsection and species (Supplementary Information S1). We also provide the list of cultivated taxa (Supplementary Information S2). Finally, we

provide a synthetic key for native taxa and nothotaxa, based in differential characters inside groups.

We update from eight to eleven the list of native oaks, previously published by Franco (1990). The list of nothotaxa includes four yet unreported hybrids and one missing nomenclatural reassignment. We designate the lectotypes of 27 names, mentioning three important isolectotypes and seventeen holotypes, eighteen syntypes, four paratypes and twelve explicit references to previously designated lectotypes, in a total of eighty-one significant herbarium type-specimens.

We propose that the Iberian white oaks, together with the western Palearctic Section *Quercus,* to be distributed in two subsections, in agreement with previous proposals (Camus, 1934; Maleev, 1935) that are being supported by ongoing molecular analysis, based in next-generation sequencing (RADSeq) (Vila-Viçosa et al., 2021).

Taxonomy

Quercus L. (1753: 994)

I. *Quercus* subgen. *Cerris* Oerst. (1866: 74)

Section *Cerris* Dumortier (1829: 15)

1. *Quercus suber* L. (1753: 995) =*Quercus suberosa* Salisbury (1796: 392) =*Quercus occidentalis* Gay (1857: 243) ≡*Quercus suber* L. subsp. *occidentalis* (Gay) A. Camus (1938: 510) =*Quercus cintrana* Welw. ex Nyman (1881: 662)
Lectotype (designated by Iamonico & Peruzzi, 2013: 1044)**:** LINN - 1128.11 [digital image]!: http://linnean-online.org/11701/

Ecology: Found mostly on silicate-derived and acidic soils, seldom on leached limestones or marble-derived soils. Dominant in zonal woodlands in oceanic climates, from upper dry to hyper-humid ombrotypes. Occurs also as azonal (edaphoxerophile) or secondary forest, in the context of zonal deciduous forests; or as edaphohygrophile in lower dry ombrotype. It is commonly excluded by low winter temperatures (absolute minimum below -10º C), in continental areas, supramediterranean and supratemperate belts.
Biogeography: Entire Portuguese mainland, excluding areas above 1000 m.
Syntaxonomy: *Quercetalia ilicis*

Section *Ilex* Loudon (1838: 1899)

Subsection *Ilex* Oerst (1866: 69).

Round-leaf oak

2. *Quercus rotundifolia* Lam. (1785: 723) ≡*Quercus ilex* L. var. *rotundifolia* (Lam.) Trabut (Battandier & Trabut 1905: 309) ≡*Quercus ilex* L. subsp. *rotundifolia* (Lam.) O. Schwarz ex Taborda de Morais (1940: 122) =*Quercus ballota* Desfontaines (1791: 395) ≡*Quercus ilex* L. var. *ballota* (Desf.) Candolle (1864: 39) ≡*Quercus ballota* (Desf.) Nyman (1881: 662) ≡*Quercus ilex* subsp. *ballota* (Desf.) Sampaio (1909: 102) =*Quercus calycina* Poiret (Lamarck & Poiret, 1811: 216) =*Quercus ilex* L. subf. *coutinhoi* Villar Lectotype (designated here): MPU010434! [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu010434 =*Quercus ilex* var. *dolichocalyx* C. Vicioso (1950: 170) =*Quercus rotundifolia* L. var. *macrocarpa* (Cout.) F.M. Vázquez, S. Ramos & S. García (2004: 31).
Lectotype (designated by Vazquez et al. (2020)): (P-Lam - P00382458! [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p00382458)

Ecology: Edaphic indifferent, either in ultramafic, limestone or poor acidic soils, without waterlogging. Found under a large range of continental climate in lower-dry Mediterranean areas, but reaching supratemperate and hyper-humid bioclimatic belts in Northwest Portugal as edaphoxerophile woods (Pinto-Gomes *et. al*. 2010).
Notes: Widely distributed taxon, frequently considered as a distinct species from *Quercus ilex* by ecological and biogeographic segregation and morphological distinctive characters (Franco, 1971, 1990; Schwarz, 1964; Rivas-Martinez & Saénz, 1991; Vila-Viçosa *et. al*. 2022a). Phylogeographic assessments sustain the latter hypothesis (Lumaret et al., 2002).
Biogeography: All Portuguese mainland.
Syntaxonomy: *Quercetalia ilicis*

Holm oak

2.1 *Quercus ilex* L. (1753: 995) =*Quercus smilax* Linnaeus (1753: 994) =*Quercus sempervirens* Miller (1768: 508) ≡*Quercus ilicifolia* Salisbury (1796: 392) =*Quercus ilex* var. *angustifolia* Lamarck =*Quercus ilex* L. var. *oblongifolia* Lamarck (1805: 313) =*Quercus prasina* Persoon (1807: 568) =*Quercus expansa* Poiret (Lamarck & Poiret, 1811: 217) =*Quercus integrifolia* Steudel (1821: 673) =*Quercus variifolia* Sweet (1830: 465) =*Quercus ilex* L. subvar. *dehnhardtii* Tenore =*Quercus ilex* L. var. *macrophylla* Ten. =*Quercus ilex* L. var. *undulata* Ten. (1831: 472) =*Quercus ilex* L. var. *intermedia* Ten. =*Quercus ilex* L. var. *oleifolia* Ten. =*Quercus ilex* L. var. *operculata* Ten. =*Quercus ilex* L. var. *polycarpa* Ten. (1831: 473) =*Quercus ilex* L. var. *strangulata* Ten. (1831: 474) =*Quercus cookii* Loudon (1838: 1926) ==*Quercus ilex* L. var. *fordii* Loudon (1843: 35) =*Quercus alpina* Endlicher (1847: 25) =*Quercus fordii* (Loudon) Carr (1861: 114) =*Quercus ilex* L. var. *lanceolata* Kotschy (*Exsicc.* 1855: 204) =*Quercus gracilis* Lange (1862: 36) =*Quercus ilex* L. var. *revoluta* Martrin-Donos & Timb.-Lagr. =*Quercus sinuata* Martrin-Donos & Timb.-Lagr. (1864:11) =*Quercus ilex* L. subvar. *micracylos* Martrin-Donos & Timb.-Lagr. (1864:12) =*Quercus ilex* L. var. *aperta* Martrin-Donos & Timb.-Lagr. (1864:13) =*Quercus ilex* L. var. *rostrata* Martrin-Donos & Timb.-Lagr.=*Quercus*

ilex L. var. *argentata* Martrin-Donos & Timb.-Lagr. (1864:14) =*Quercus ilex* L. subvar. *capreifolia* Martrin-Donos & Timb.-Lagr. (1864:15) =*Quercus ilex* L. var. *glaucocaesia* Martrin-Donos & Timb.-Lagr. =*Quercus glauca* Martrin-Donos & Timb.-Lagr. (1864: 16) =*Quercus pseudoilex* Chatin (1869: 22) =*Quercus crispa* K. Koch (1873: 56) =*Quercus fagifolia* K. Koch =*Quercus oblonga* K.Koch, (1873: 56) =*Quercus ilex* L. var. *angustifolia* Gillot (1877: 48) =*Quercus ilex* L. var. *salicifolia* Borzí =*Quercus ilex* L. var. *parvifolia* Borzí (1880: 169); =*Quercus cyclophylla* Welw. ex Nyman (1881: 662) =*Quercus ilex* var. *laurifolia* Laguna (1883: 254) =*Quercus ilex* L. var. *gracilis* (Lange) Laguna (1883: 255) =*Quercus ilex* L. subvar. *oleoides* Trabut (Battandier & Trabut 1890: 824) Lectotype (designated here): MPU007892 [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu007892 =*Quercus ilex* L. var. *diversifolia* G.Nicholson (1896: 189) =*Quercus ilex* L. var. *phillyreoides* (A.Gray) Franch. (1899: 152) =*Quercus ilex* L. var. *rufescens* Franch. (1899:151) =*Quercus ilex* L. var. spinosa (David) Franch =*Quercus ilex* L. var. *bullata* (Seemen) Franch. (1899: 152) =*Quercus ilex* L. var. *acrodonta* (Seemen) Skan (1902: 516) =*Quercus mixta* Reyn. (1903: 129) =*Quercus smilax* L. var. *fordii* (Loudon) Halácsy (1904: 132) =*Quercus ilex* L. var. *eucalyptoides* Lojac. (1907: 384) =*Quercus ilex* L. var. *oosperma* Albert (1908: 439) (Albert & Jahandiez, 1908) =*Quercus ilex* L. subvar. *brevicalyx* Albert =*Quercus ilex* L. var. *depressa* Albert =*Quercus ilex* L. var. *elegans* Albert =*Quercus ilex* L. var. *ovatiacutifolia* Albert =*Quercus ilex* L. var. *myrtifolia* Albert =*Quercus* ilex L. var. *ovifolia* Albert =*Quercus ilex* L. subvar. *parvifolia* (Borzí) Albert =*Quercus ilex* L. var. *sinuosifolia* Albert =*Quercus ilex* L. var. *undulata* Albert (1908: 440) (Albert & Jahandiez, 1908) =*Quercus ilex* L. var. *cerasifolia* Albert =*Quercus ilex* L. var. *mirabilis* Albert =*Quercus ilex* L. var. *revoluta* Albert =*Quercus ilex* L. var. *cordifolia* Albert (1908: 441) (Albert & Jahandiez, 1908) =*Quercus ilex* L. var. *reducta* Albert =*Quercus ilex* L. var. *spinulosa* Albert (1908: 442) (Albert & Jahandiez, 1908) =*Quercus ilex* L. var. *ellipticifolia* Albert =*Quercus ilex* L. var. *pisiformis* Albert =*Quercus ilex* L. var. *serratifolia* Albert (1908: 443) (Albert & Jahandiez, 1908) =*Quercus ilex* L. subvar. *laurifolia* (Laguna) Albert =*Quercus ilex* L. var. *ambigua* =*Quercus ilex* L. var. *crispata* Albert (1908: 444) (Albert & Jahandiez, 1908) =*Quercus ilex* L. var. *fagifolia* Sprenger (1908: 154) =*Quercus marcetii* Pau (1909: 95) =*Quercus ilex* L. subvar. *marginata* Rouy =*Quercus ilex* L. subvar. *plicata* Rouy (1910: 321) =*Quercus ilex* L. var. *smilax* (L.) Asch. & Graebn. (1911: 472) =*Quercus ilex* L. var. *genabii* Bean (1914: 312) =*Quercus laurei* Coutange (1928: 157) =*Quercus ilex* var. *genuina* Cout. f. *laurifolia* Laguna (Coutinho 1930: 5) Lectotype (designated here): LISU P-10617! =*Quercus ilex* L. var. *plicata* (Rouy) A.Camus (1935: 8) =*Quercus murbeckii* Sennen (1936: 29) Lectotype (designated here): MA-01-00467547! [digital image]!: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00467547) =*Quercus ilex* L. subvar. *brevicalyx* Trab. ex A.Camus (1939: 88) =*Quercus ilex* L. subvar. *cordifolia* (Albert) A.Camus (1939: 54) =*Quercus ilex* L. subvar. *caduca* A.Camus (1939: 54) =*Quercus ilex* L. subvar. *reducta* (Albert) A.Camus (1939: 54) =*Quercus ilex* L. var. *gracilis* (Lange) A.Camus (1939: 64); =*Quercus ilex* L. var. *subrevoluta* A.Camus (1939: 57) =*Quercus ilex* L. subsp. *montserratensis* Svent. & Marcet (Marcet 1945: 37) ≡*Quercus montserratensis* (Svent. & Marcet) Sventenius & Marcet (1952: 335) Marcet (1952) =*Quercus ilex* L. var. *subsphaerocarpa* Albert (1946: 104) =*Quercus ilex* L. subsp. *genuina* (Cout.) C.Vicioso =*Quercus ilex* L. var. *vulgaris* (Cout.) C.Vicioso (1950: 161) =*Quercus ilex* L. f. *ambigua* (Albert) C. Vicioso (1950: 163) =*Quercus ilex* L. subsp. *genuina* (Cout.) C. Vicioso var. *gracilis* (Lange) C.Vicioso (1950: 164); =*Quercus ilex* L. var. *marcetii* (Pau) C.Vicioso (1950: 166) =*Quercus ilex* L. subsp. *refugiorum* Radic (1983: 18) =*Quercus ilex* L. f. *conoidea* Radic =*Quercus ilex* L. f. *lingulata* Radic =*Quercus ilex* L. f. *patula* Radic =*Quercus ilex* L. f. *rubella* =*Quercus ilex L. var. gymnobalanus Radic* (1983: 22) =*Quercus ilex* L. f. *pallida* Radic =*Quercus ilex* L. f. *tristigmata* Radic (1983: 23) =*Quercus ilex* L. f. *almissana* Radic =*Quercus ilex* L. f. *bistonensis* Radic =*Quercus ilex* L. f. *subtillima* Radic (1983: 24) =*Quercus ilex* L. f. *introversa* Radic (1983: 25) =*Quercus ilex* L. f. *glauca* Radic =*Quercus ilex* L. f. *mucurensis* Radic =*Quercus ilex* L. var. *glauca* Radic (1983: 26) =*Quercus ilex* L. subsp. *gracilis* Rivas Mart. & Sáenz de Rivas (2002: 705).

Lectotype (designated by Vázquez & Coombes (2017: 1473–1475)): (LINN 1128.4 [digital image]!: http://linnean-online.org/11694/).

Ecology: Thermo to meso-temperate bioclimatic belts, normally in mesotrophic soils. Biogeography: Potential native distribution in Northeast Portugal (Luso-Duriense Sector). Syntaxonomy: *Quercetalia ilicis* | *Quercenion ilicis* Notes: Despite not being usually considered a Portuguese native species, Coutinho (1930) names a specimen from Vimioso in northeast Portugal (LISU P-10617!) as *Quercus ilex* var. *genuina* f. *laurifolia* (=*Quercus ilex* var. *laurifolia* Laguna (1883: 254)). Given the biogeographic affinities with the northwest Iberian Peninsula (Saénz de Rivas, 1967), along with the recognition of *Q. ilex* hybrids with *Q. coccifera* (*Q.* ×*auzandri*) (LISI 10278/1999!) in the same biogeographic area (Luso-Duriense Sector), we cannot exclude the hypothetic survival of *Q. ilex* as rare relict in the Portuguese Douro Basin, despite *Q. ilex* not being found there so far.

Subsection *Cocciferae* (Spach) Gürke (1897: 70)

Kermes oak

3. *Quercus coccifera* L. (1753: 995) =*Quercus coccifera* var. *vera* Candolle (1864: 52) non Cout. (1888: 101) =*Quercus coccifera* f. *exserta* Coutinho (1888: 101)
Lectotype (designated by Iamonico & Peruzzi 2013: 1042): UPS V-175683 (Herb. Burser): XXII: 113.

Description: Dense shrubs, up to 3 m high; branching from the base. Leaves: curled, concolorous, green, glabrous with 5-8 (9) pairs of secondary veins, shinny; petiolate, with spiny, serrate to dentate margins. Petiole and lower quarter of the midrib and secondary veins, sometimes with sparse fused-stellate trichomes; Cup: short (length/breadth ratio up to 0.5*) broad cupuliform (acetabuliform) to cylindrical. Cup-scales: elongated, partially connate, terete to irregular, trigonous, cuspidate, sometimes free, stinging, and erect.

Ecology: Essentially in xerophytic habitats (outcrops), being indifferent to lithology. Found in both subhumid oceanic and dry and continental bioclimate. In Portugal, it is mostly found in successional stages of *Quercus rotundifolia* dry woodlands.
Biogeography: Coastal Lusitanian and West Andalusia Province | West Iberian Mediterranean Province | Duriense Lusitanian Sector
Syntaxonomy: *Asparago albi-Rhamnion oleoidis*
Notes: *Quercus coccifera sensu stricto* was originally described by Linnaeus (1753) and recently lectotypified by Iamonico & Peruzzi (2013). The taxonomic reasoning about the western Mediterranean arboreal kermes oaks and related taxa, is discussed as follows.

Arboreal kermes oaks

Mediterranean arboreal kermes oaks are immersed in nomenclatural controversy. The widely used name *Quercus calliprinos* Webb (1838: 15) has been addressed to the eastern Mediterranean arboreal kermes oaks, while the original taxon was described from Northwest Africa (Tétouan) by Webb (1838), referring to a tree with tomentose leaves (Vázquez *et al.,* 2018, Vila-Viçosa *et. al*., 2022a). This original concept of an '*arboreal Kermes oak*' with fully downy leaves was enlarged by the author, to include Near East (Lebanon) plants, earlier named as *Q. pseudococcifera* Labillardière (1812: 9) (Vila-Viçosa *et. al*. 2022a). The putative type-specimen for this Palestinian oak (FI 171706!) was labelled by Webb as "*Quercus calliprinos N. / pseudococcifera Labill. non Desf.*" (Burdert, 1979). This specimen has sub-glabrous leaves and petioles, with erect to patent-flat and large cup scales and annual fructification. Subsequently, De Candolle (1864) applied the name *Q. calliprinos* var. *eucalliprinos* Candolle (1864: 55) to the same Lebanese materials, that were later addressed by Zohary *in schedula*: "*To this specimen Webb is referring in his Iter Hispanicum! It is this specimen which is the Type of Q. calliprinos Webb"* (1970-05-24). As a result, this name (*Q. calliprinos*) was applied to the Palestinian oak until the present time. However, the latter tree has glabrous and oblong to lanceolate leaves, with few stellate and fused-stellate trichomes in the proximal half of the leaf-blade and midrib, with characteristically large and free cup scales. This set of characters enhances the proximity of this eastern Mediterranean representant of the arboreal kermes oaks, as vicarious taxon of the western distributed *Q. pseudococcifera* Desf. (1799: 349) (Vázquez *et. al*. 2018, Vila-Viçosa *et. al*. 2022a). The latter has also a cup with free scales, that are smaller, becoming sometimes retroflexed in maturity and commonly a sub-occult (hidden) fruit (more than 1/3 of the length) (Vila-Viçosa *et. al*. 2022a). The Portuguese arboreal kermes oak forests, first referenced by Webb (1838) and Boissier & Reuter (1842), were later studied by Capelo & Costa (2001; 2005) from Arrábida and Olissiponense District (Rivas-Martínez et al., 2017) where *Quercus rivasmartinezii* (Capelo & J.C.Costa) Capelo & J.C. Costa (2005: 268), is a well-documented taxon, related to *Q. pseudococcifera* Desf (Vila-Viçosa *et. al*. 2022a). *Q. rivasmartinezii* shares a set of taxonomic and ecological traits with the latter, namely broad linear, but conic scales (3.0-7.0 mm), appressed in the proximal half of the cup, then strongly curled upwards near the distal half. Both above-described trees co-occur in the western Mediterranean Basin, thus, the taxonomic treatment of the Portuguese arboreal kermes oaks is proposed as follows:

False-kermes Oak

4. *Quercus pseudococcifera* Desf. =*Quercus mesto* Boissier (1842: 579) (Lectotype: G00358092!; Syntype: G00358094!) =*Quercus coccifera* L. var. *imbricata* DC. (1864: 53) =*Quercus coccifera* L. var. *vera* DC. f. *laxispinosa* Coutinho (1888: 101) (LISU!) =*Quercus coccifera* f. *subintegrifolia* Coutinho. (1888: 101) (LISU!) =*Quercus coccifera* var. *vera* DC. f. *subinclusa* Coutinho (1888: 101) =*Quercus coccifera* var. *vera* DC. f. *densispinosa* Coutinho (1888: 101) =*Quercus coccifera* f. *lanceolata* Coutinho (1888: 101) (LISU!) =*Quercus coccifera* f. *latifolia* Trab. (Battandier & Trabut 1890: 825) Lectotype (designated here): (MPU007902 [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu007902) =*Quercus* ×*battandieri* A. Camus (1939: 792) Lectotype (designated here): (MPU010410, [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu010410).

Lectotype (designated by Vázquez et. al. (2018: 35): (P00667225! [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p00667225)

Description: Trees up to 18 m, with a clear single bole, including young individuals, reaching a diameter at breath height 0.6-0.7m; smooth grey bark with vertical cracks in maturity. Leaves: flat, oblong to elliptic-lanceolate or narrowly obovate (obovate-spathulate), normally sub-sessile to sessile; margins often sub-

entire sometimes with spiny teeth, with 7-9(11) pairs of divaricate secondary veins, glabrous to sub-glabrous, sometimes with sparse, deciduous, fused-stellate trichomes in the leaf basis, near the midrib. Cup: dark brown, hemispheric to cylindrical (length/breadth ratio greater than 0.5). Cup with free scales, dense, elongated and slightly thicker, irregular and trigonous, 3,3-5,5 mm long, heavily retroflexed, acuminate or cuspidate in maturation; hidden acorn (1/2; >1/2), ovate to narrow obovate.

Ecology: Mesophytic species, living in oceanic areas, with higher ombrothermic features, normally as natural fringes of marcescent forests.
Biogeography: Coastal Lusitanian and West Andalusian Province

4.1. *Quercus pseudococcifera* Desf. subsp. ***rivasmartinezii*** (Capelo & J.C. Costa) Capelo, Vila-Viçosa & F.M. Vázquez ***comb. nov***.

Basyonym: *Quercus coccifera* L. subsp. *rivasmartinezii* Capelo & J.C. Costa (2001: 270) (Holotype: LISI!) ≡*Quercus rivasmartinezii* (Capelo & J.C. Costa) Capelo & J.C. Costa (2005: 268)

Diagnose: Leaves sometimes slightly spathulate**;** cups with obvious thick conic to terete, sometimes nearly cylindrical, and acuminate free scales, that become retroflexed in maturity. This subspecies is, for the most, circumscribed to the thermophilic forests above dolomitic limestone substrata from the Coastal Lusitanian Province, but especially in the Arrábida District (Rivas-Martinez, 2017; Vila-Viçosa et. al. 2017) and punctual elsewhere, across the range of *Q. pseudococcifera*.

Downy-kermes Oak

5. *Quercus airensis* Franco & Vasconcelos (1954: 119) prop. hybr. =*Quercus coccifera* L. var. *tomentosa* Candolle (1864: 53) =*Quercus coccifera auct. pl.* non Linnaeus (1753:995) =*Quercus coccifera* L. f. *tomentosa* (A. DC.) Coutinho (1888: 101) =*Quercus webbei* Amo (1861:351) *nom. nud*.

Holotype (Vasconcellos & Franco, 1954: 119): (COI – 18715!; [digital image]!: http://coicatalogue.uc.pt/specimen/18715)

Description: Trees to dendroid shrubs. Leaves: sclerophyllous, flat and spiny, 1,5-4 cm x 1-3 cm, ovate-oblong to semi-lanceolate, from sub-glabrous to fully tomentose in both adaxial and abaxial surfaces. Trichomes: multiradial and ramified, long rays with different lengths (300-400 (500) µm) and stipitate (stip up to 100 µm). Cups: hemispheric with free, erect slim, terete to irregular trigonous scales, arcuate in maturity, with half-hidden to hidden fruits.

Notes: The main distinctive character that led Webb (1838) to propose a new species (*Quercus calliprinos*), inside the Kermes oak complex, was its "downy" leaves from both faces. This fully tomentose and dendroid kermes oak, with typical *loci* from Tétouan (Morocco), occurs in the Atlantic coast of Portugal (Lisbon-Alenquer) where it was collected and recognized by Coutinho (1888; COI - 18906!) as *Q. coccifera* f. *tomentosa* (A.DC.) Cout. (1888: 101). This nomenclatural endorsement was based on the variety proposed by De Candolle (1864) (*Q. coccifera* L. var. *tomentosa* Candolle (1864: 53)), corresponding to the upper specimen in the same herbarium sheet that contains the firs ascribed plant by Webb (1831) deposited in FI 011747! (Vázquez *et. al*. 2018). Furthermore, Candolle (1864) addresses a potential proximity of this taxon to its eastern Mediterranean vicariant taxon *Quercus aucheri* Jaub. & Spach (Jaubert, 1843: 113), which was also hypothesized as a putative hybrid between *Q. ilex* and *Q. calliprinos* by Kasapligil (1981), but possessing quite distinctive cups, if compared to those of the putative parents' species. Likewise, the Portuguese plant communities of *Q. coccifera (Quercetum coccifero-airensis*) from Montejunto and Aire e Candeeiros mountains were assumed to be co-dominated by a putative natural hybrid between *Q. coccifera* and *Q. rotundifolia*, named as *Quercus ×airensis* Franco & Vasc. (1954: 119) (Espirito-Santo et. al. 1995). By analogy to *Q. aucheri, Q. airensis* also has fully tomentose leaves (Fig. 1) and reveals comparable ecological features: karst limestones in hyperoceanic and coastal areas, protected from winter cold (Serteser *et. al*, 2009). Therefore, we share the assumption made by Candolle (1864), relating the proximity between *Q. airensis* and *Q. aucheri* as vicariant taxa across the Mediterranean Basin. Both taxa deserve further molecular scrutiny, to be included in a global phylogeographic assessment of all kermes oaks from the Mediterranean Basin.

As stated above, the name *Q. calliprinos* was originally enlarged to the Near East arboreal kermes-oak (Webb, 1838; Vila-Viçosa *et. al*. 2022a), being in use for more than 50 years (Zohary, 1960). Thus, according to the Art. 14.9 of the ICN (Turland *et. al*. 2018) and to preserve the nomenclatural stability, we hereby recover the onward available name for the western Mediterranean tomentose kermes oak as *Q. airensis*, in accordance with Vasconcellos & Franco (1954). The name *Q. calliprinos* Webb (1838: 15) should be properly preserved, with the respective elected type (FI-171706!) for the eastern Mediterranean arboreal Kermes oak (Palestinian oak) in future nomenclatural works (pro nom. cons. prop. nob.).

Ecology: Fringe-mantles of edaphoxerophile round-leaf oak (*Q. rotundifolia*) and Portuguese oak (*Q. faginea*) forests, normally in Cenozoic's karst limestone, marls or clay substrata.
Biogeography: Coastal Lusitanian and West Andalusia Province
Syntaxonomy: *Quercion fagineae*

Figure 1. Fully tomentose abaxial leaf surface of *Q. airensis* Franco & Vasconcellos.

In Portugal, if the most common nothotaxa are also considered, four arboreal Kermes oaks can be found: i) the taxa *Q. pseudococcifera* and *Q. airensis* and ii) the nothotaxa *Quercus ×eborense nob.* and *Q. ×almeidae nob.,* further discussed in the hybrids section.

To address the taxonomy of tomentose kermes oaks and segregate autonomous taxa from the aforementioned hybrids, we rely on trichome analysis (see Fig. 2). The nothospecies respectively inherit *Q. ilex* and *Q. rotundifolia* trichomes, which are exclusively fused stellate, subsessile and totally appressed (see Fig. 2b and 2d), with short rays (<150 µm in *Q. rotundifolia*; and slightly larger (<180 µm) in *Q. ilex*; (Saénz de Rivas, 1967; Vila-Viçosa *et. al*. 2022a)) (see Fig. 2a and 2b). In contrast, *Quercus airensis* (Fig. 2e and 2f) possesses ramified multiradial trichomes, with large rays (>300-400 (500) µm) and a well-developed stipe (*ca.* 100 µm) (Figure 2e and 2f). A synopsis of taxonomic criteria and nomenclature of the aforementioned Portuguese Kermes oaks is presented in Table 1.

II. *Quercus* subgen. *Quercus* Hickel & Camus (1921: 379)

Section *Quercus* Menitsky (1972 : 107); Nixon & Muller (1997); Denk *et. al*. (2017: 13) ≡Section *Robur* Reichb. (1831 : 177 ≡Section *Robur* Loudon (1838: 1731))

Subsection *Hartwissianae* (Maleev) Vila-Viçosa, Capelo, P. Alves, R. Almeida & F.M. Vázquez *comb. & stat. nov.*

Basionym: *Quercus* L. subgen. *Lepidobalanus* DC *emend*. Oerst. Sect. *Eulepidobalanus* Oerst. subsect. *Robur* (Rchb.) Maleev ser. *Hartwissianae* Maleev, *Bot. Zhur. URSS*, 20(2): 164. 1935.

Type species: *Quercus hartwissiana* Steven (1857: 387)

Includes: *Q. brutia* Ten., *Q. dalechampii* Ten., *Q. estremadurensis* O. Schwar, *Q. haas* Kotschy, *Q. huguetiana* (Franco & G.López) Rivas Mart., *Q. iberica* Steven ex M.Bieb., *Q. imeretina* Steven ex Woronow, *Q. orocantabrica* Rivas Mart. & al., *Q. pedunculiflora* K.Koch, *Q. petraea* (Matt.) Liebl, *Q. pinnatiloba* K. Koch, *Q. robur* L.

Description: Deciduous to brevi-deciduous trees, subsessile to long petiolate leaves with lobate to lobulate margins, and mostly irregular lobes. Less often regularly lobate to dentate, with or without vestigial intercalary nerves, seldom with tertiary ones that are subparallel to each other, coarsely and regularly reticulate. Glabrous to glabrescent or pubescent leaves and twigs, with simple, bifurcate, stellate or more rarely fasciculate trichomes.

Estremadura Oak

6. *Quercus estremadurensis* O. Schwarz (1935: 463) ≡*Quercus robur* subsp. *estremadurensis* (O. Schwarz) A. Camus (1935a: 50) =*Quercus racemosa* Brotero (1804: 31) *non* Lamarck (1785: 715) =*Quercus pedunculata* f. *longipedunculata* Coutinho (1888: 58) =*Quercus robur* subsp. *broteroana auct. pl. non* Schwarz (1935: 463)
Lectotype (designated by Vázquez et al. (2018)): Portugal. Extremadura: Sintra, May, 1840, *Wellwitsch s.n.* (P06857436!); Syntype 1: Portugal. Beira Litoral: Coimbra, Arregaça, October 1904, *M. Ferreira s.n.* (P06857428!; Isosyntypes: LISU – 10353!, Fl. Lus. Exs. 1743; COI – 19267!; PO-V2073 G.S.!); Syntype 2: Portugal. Beira Litoral: Coimbra, Pinhaes da Fonte da Telha, April 1890, *A. Moller s.n.* (COI – 19268!, Fl. Lus. Exs. 876)

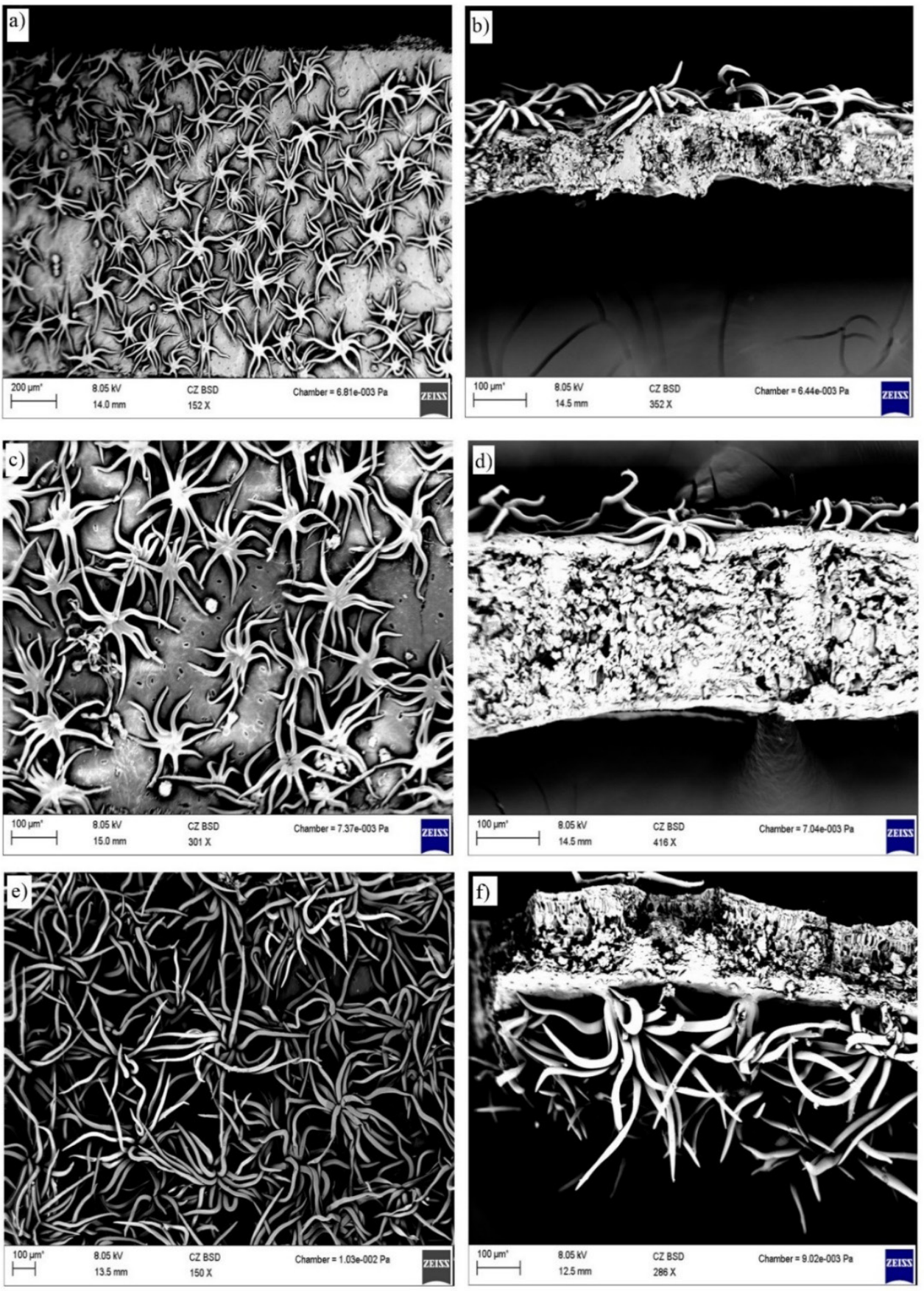

Figure 2. Trichome analysis comparison (SEM) of Iberian hybrids between kermes oak and holm oak and *Quercus airensis* - (a), b) - *Quercus* ×*eborense nob.*; c), d) – *Q.* ×*auzandri;* e), f) – *Q. airensis*); (a), c) – Detail of abaxial leaf surface with fused-stellate and stellate trichomes (152x magnifying in *Q.* ×*eborense nob.* and 301x in *Q.* ×*auzandri*); (b), d) – transversal overview and detail of appressed fused-stellate and stellate indumentum (abaxial leaf surface) (352x in *Q.* ×*eborense nob.* and 416x in *Q.* ×*auzandri*); (e), f) - Detail of multiradial and stipitate trichomes (e)-150x; f) - 286x) in *Q. airensis* with large rays (>300 µm).

Table 1. Synthetic table of the differential characters for the western Mediterranean kermes oaks and related nothotaxa.

Species/ Characters	*Q. airensis*	*Q. coccifera*	*Q. ×eborense*	*Q. pseudococcifera*	*Q. pseudococcifera* subsp. *rivasmartinezii*	*Q. ×almeidae*
Leaf traits						
Margin						
	Irregular, Dentate, Flat	Irregular, Dentate, curly	Irregular, Dentate, curly	Sub-entire to serrate, Flat	Sub-entire to serrate, Flat	Irregular, Dentate, to sub-entire, fla
Shape						
	Ovate-oblong to semi-lanceolate	Ovate to obovate, sometimes semilanceolate, Petiolate	Ovate to obovate, sometimes semilanceolate, Petiolate	Lanceolate to ovate-oblong, Sub-sessile	Lanceolate to ovate-oblong, Sub-sessile	Ovate to obovate-oblong, Petiolate
Cup traits						
Cup / Acorn						
	Hemispheric cup Half hidden to hidden fruits	Short cupoliform (acetabuliform) to short cylindrical (length/breadth <0.5), large fruit not hidden	Hemispheric, large fruit not hidden,	Hemispheric to long cylindrical (length/breadth > 0.5) cup, dark brown, large to strait fruits, partially hidden	Hemispheric to long cylindrical (length/breadth > 0.5) cup, dark brown, large to strait fruits, partially hidden	Hemispheric cup, dark brown, large to straitfruits, partially hidden
Scales						
	Large, retroflexed, thick and acute scales	Short, Thick, erect-patent to retroflexed in maturity	Short, half-free to imbricate, thick, erect-patent to slightly retroflexed in maturity	Free, large, flat and appressed in maturity, lax	Free, large, cylindrical and retroflexed in maturity, pungent	Plicate, appressed to slightly free
Trichome types						
Presence/density						
	Both adaxial and abaxial faces pubescent to heavily tomentose	Glabrous to glabrescent in petiole, lower part of midrib and branches	Pubescent to tomentose in abaxial face and pubescent to glabrescent in adaxial face	Glabrous to subglabrous, sometimes pubescent in abaxial leaf face (proximal edge) in the midrib, insertion of secondary nerves and petiole	Glabrous to subglabrous, sometimes pubescent in abaxial leaf face (proximal edge) in the midrib, insertion of secondary nerves and petiole	Pubescent in both abaxial and adaxial leaf faces
Bulbous	-	-	+	-	-	-
Stellate	++	-	+	+	+	+
Fused-Stellate	++	++	+++	++	++	+++
Stipitate	+++	-	-	-	-	-
Simple/uniseriate	++	++	+	+	+	++
Multiradial	+++	-	-	-	-	+

Ecology: Thermophilic species, found in oceanic humid and submediterranean areas, with short summer drought period. Preferring silicate-derived soils, but may be found in leached limestones normally under slight temporary influence of the water table.

Notes: *Quercus estremadurensis* specimens have been commonly misidentified as putative hybrids between *Q. robur* and *Q. faginea* (*Q. ×coutinhoi* Samp.). This misconception comes from both trees being marcescent to evergreen and to the similar rhomboidal leathery leaf, with acute lobes. If compared to *Q. robur* or *Q. robur* subsp. *broteroana* (Schwarz, 1937), *Q. estremadurensis* tend to have lobes in a higher number (≥ (7)8) that are subequal, less deeply cut, with acute tips and sometimes mucronate. The petiole is normally larger (> 5 mm up to 15 mm) and the peduncle is often longer (> 8 cm). Leaf indumentum is composed of single/bifurcated trichomes throughout the midrib and ramified trichomes throughout the abaxial leaf surface, which varies from glabrescent to pubescent (Vázquez et al., 2018) (Indumentum differences comparing *Q. estremadurensis* to *Q ×coutinhoi* will be further discussed further on). The Portuguese herbaria review, performed by Schwarz (COI! and LISU!), that served as base for the original protologue of *Q. estremadurensis* (Schwarz, 1935), suggests an already frequent introgression with *Q. robur* (*Q. robur* subsp. *broteroana*). Such clinal variation led Vasconcellos & Franco (1954) to regard this taxon as mere phenotypic plasticity of *Q. robur s.l.*. The

original protologue of Schwarz (1935) emphasizes differential characters, like early leaf-development in spring shoots, leaves with a very regular structure, higher number of lobes and almost absence of sinual nerves. The higher number of cup-scales, larger towards the base and quickly becoming short towards the apex, is a character considered to belong to Ser. *Primitivae*, inside Section *Quercus* (Schwarz, 1936a). These are shared with other southern European roburoid oaks, like *Q. hartwissiana* Steven (1857: 387) (=*Quercus armeniaca* Kotschy (1860: 25)) (K000832028!; P06813011!; 06813013! 06861134!; L-1571371!; L-157376!). Accordingly, Camus (1939), Vicioso (1950) and Montserrat (1957) concur with recent essays (Vila-Viçosa et al., 2014; Vázquez et al. 2018; Vila-Viçosa et al., 2020b) by reasoning that *Q. estremadurensis* can be a relict oak from the tertiary period (Schwarz, 1935). Such hypothesis is supported by the presence of this taxon in north Africa (P05622871!; P06860974!; P06857427!), and southwest Iberian Peninsula, which enhances a biogeographic alliance to paleoclimatic, thermophilic and subtropical relictual taxa with Tertiary affinity, like *Q. canariensis, Rhododendron ponticum* and *Prunus lusitanica* (Vila-Viçosa et al., 2020b).
Biogeography: Coastal Lusitanian and West Andalusia Province | West Iberian Province | Duriense Lusitanian Sector
Syntaxonomy: *Quercion fagineae* | *Quercenion pyrenaicae*

Galician oak

7. *Quercus orocantabrica* Rivas Mart. & al. (2002: 706) =*Quercus robur* subsp. *broteroana* O. Schwarz (1937: 108) ≡*Quercus broteroana* **(**O. Schwarz) Vila-Viçosa, Capelo, P. Alves, R. Almeida & F.M. Vázquez, *alibi, nom. illegit.* Art. ICN 11.2 (Turland, 2018) Lectotype (designated here): Portugal. Minho. Serra do Soajo, Várzea, 600m, 9-VIII-1926, *A. Mendonça s.n.* (COI-19256!) [digital image]!: http://coicatalogue.uc.pt/specimen/19256; Syntype 1: Portugal. Extremadura: Sintra: Palácio da Pena, 12-V-1905- Kuegler s.n. (JE28997!); Syntype 2: COI-19263!; Syntype 3: COI-19264!; Syntype 4: COI-91634!; Syntype 5: COI-19244!; Syntype 6: COI-19243!; Syntype 7: COI-19238!; Syntype 8: COI-19249!; Syntype 9: COI-19258!
Ecology: Silicate-derived soils, in humid to ultra-hiperhumid areas, or in temporihygrophile stations in areas with a short summer drought.
Notes: The Iberian pedunculate oaks have been examined by Schwarz (1935; 1937). The protologue of *Q. robur* subsp. *broteroana* O. Schwarz (1937: 108), addresses this taxon as the hybridization-front and transitional gradient between *Q. estremadurensis* and the European *Q. robur* L. Later, the author himself withdrew both his Iberian pedunculate oaks (Schwarz, 1964) since the observed differential characters can be found in non-Iberian populations. Despite the morphological plasticity across Europe, we found that Schwarz's perception of a higher frequency of distinctive character combination supporting *Q. robur* subsp. *broteroana* still holds and it's supported by molecular data (Vila-Viçosa et al., 2021). This analysis reveals *Q. orocantabrica* to be conspecific with *Q. robur* subsp. *broteroana* and that this western Iberian pedunculate oak, to be a well-circumscribed sister-species of the European *Q. robur.* Further, the same molecular analysis (Vila-Viçosa *et. al*. 2021) also segregates *Q. estremadurensis* together with *Q. robur* subsp. *broteroana* from the European pedunculate oaks (*Q. robur* L. *s. str.*). Nevertheless, in the light of the ICN (Turland et al., 2018), at the species rank, the headlong available name for the western Iberian pedunculate oak is *Q. orocantabrica* as prioritary according to the Article Art.11.2. When comparing with typical *Q. robur,* the diagnostic characters are related with leaf length, shape, and texture. Typically, *Q. orocantabrica* has a thicker and leathery blade, with oblong to oblong-transovate shape. Moreover, the leaves are wider and glossy with unequal lobes, more than 6(8) secondary nerves and larger cups, with brownish and acute not-fused scales. *Q. orocantabrica* often presents both longer petiole (up to 15 mm) and peduncle (up to 15 cm) in comparison with *Q. robur*. These characters are collectively distributed across all syntypes, that are cited by the authors (Schwarz, 1937; Rivas-Martínez *et al.* 2002) in the protologues of both *Q. robur* subsp. *broteroana* and *Q. orocantabrica*. Some of these characters often overlap the description of *Q. estremadurensis* (Schwarz, 1935), which led to the indifferent use of both names (*Q. robur* subsp. *broteroana* and *Q. estremadurensis*) in several pedunculate oak herbaria specimens from center-west and northwest Portugal (LISI!; LISU!; HVR!).
Biogeography: Portuguese Divisorian Subprovince | Atlantic Oro-Lusitanian Subprovince | Toledanian-Taganian Sector
Syntaxonomy: *Querco-Fagetea sylvaticae*

Subsection *Macrantherae* (Stef.) Maleev (1935: 163)

Type species: *Quercus macranthera* Fisch. & C.A. Mey. ex Hohen (1838: 259)

Includes: *Q. boissieri* Reut., *Q. brachyphylla* Kotschy, *Q. canariensis* Willd., *Q. congesta* Presl. *Q. faginea* Lam., *Q. frainetto* Ten., *Q. ichnusae* Mossa, Bacch. & Brullo, *Q. infectoria* G.Olivier, *Q. kotschyana* O. Schwarz, *Q. lusitanica* Lam., *Q. pubescens* Willd., *Q. pyrenaica* Willd., *Q. virgiliana* Ten., *Q. vulcanica* Boiss. et Heldr.

Diagnose: Trees with brevi-deciduous or marcescent leaves. Crenate or ± deeply lobed to pinnatifid margins, coarsely toothed when crenate. Divaricate and irregular secondary nerves. Pubescent to tomentose abaxial leaf surfaces with simple, stellate, multistellate or fasciculate trichomes. Cups with small, flat to fat or gibbose scales, always appressed

and never free or loosely imbricated and long. Commonly distributed across submediterranean areas from southern Europe, North Africa, and Near East to Transcaucasia and Iran.

Algerian oak

8. *Quercus canariensis* Willd. (1809: 975) =*Quercus lusitanica* Lam. var. *salzmanniana* Webb (1838: 12) =*Quercus mirbeckii* Durieu (Duchatre 1847: 426) Lectotype (designated here): P06860975! [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p06860975 ≡*Quercus lusitanica* Webb var. *mirbeckii* (Durieu) Candolle (1864: 19) ≡*Quercus infectoria* Boiss. subsp. *mirbeckii* (Durieu) Nyman (1881: 661) ≡*Quercus lusitanica* Webb subsp. *mirbeckii* (Durieu) Ball (1878: 666) ≡*Quercus lusitanica* Webb var. *mirbeckii* (Durieu) Coutinho (1888: 69) ≡*Quercus canariensis* Willd. var. *mirbeckii* (Durieu) C. Vicioso (1950: 94) =*Quercus esculenta* K. Koch (1873: 80) =*Quercus lusitanica* Lam. subsp. *mirbeckii* (Durieu) Ball, (1878: 666) =*Quercus corymbifolia* Ehrenb. ex Boiss. (1879: 1167) =*Quercus mirbeckii* Durieu var. *angustifolia* Trab. =*Quercus mirbeckii* Durieu var. *subpedunculata* (1890: 820) =*Quercus mirbeckii* Durieu var. *microphylla* =*Quercus mirbeckii* Durieu var. *brevipetiolata* Trab. =*Quercus mirbeckii* Durieu var. *fagifolia* Trab. (1890: 821) Battandier & Trabut (1890) =*Quercus faginea* Lam. var. *salzmanniana* (Webb) Sampaio (1910: 164) ≡*Quercus lusitanica* Webb subsp. *salzmanniana* (Webb) Coutinho (1913: 165) ≡*Quercus salzmanniana* (Webb) Coutinho (1935: 36) Lectotype (designated here): (LISU – 10407!) ≡*Quercus canariensis* Willd. var. *salzmanniana* (Webb) C.Vicioso (1950: 94) =*Quercus lusitanica* var. *maroccana* Braun-Blanq. & Maire (1924: 155) ≡*Quercus faginea* Lam. var. *maroccana* (Braun-Blanq. & Maire) Jahand. & Maire (1932: 165) ≡*Quercus faginea* var. *maroccana* (Braun-Blanquet & Maire) A. Camus (1935a: 26) ≡*Quercus faginea* subsp. *maroccana* (Braun-Blanq. & Maire) F.M. Vázquez & Coombes (2016: 27) =*Quercus faginea* Lam. var. *spinosa* Maire & Trabut (Maire 1931b: 314) Lectotype (designated here): (MPU002693, [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu002693) =*Quercus faginea* var. *fagifolia* Jahandiez. & Maire (1932: 165) =*Quercus faginea* var. *mirbeckii* (Durieu) Maire (1932: 178) =*Quercus carpinifolia* Sennen (1932: 807) ≡*Quercus canariensis* var. *carpinifolia* (Sennen) C. Vicioso (1950: 96) =*Quercus nordafricana* Villar (1938: 450) =*Quercus alpestris* f. *glabrescens* Villar (1938: 454) =*Quercus mirbeckii* var. *typica* A. Camus (1939: 156) =*Quercus faginea* var. *microphylla* (Trab.) Maire & Saccardy (1939: 364)

Lectotype (designated by Schwarz (1936a))**:** Spain, Teneriffa, *Brussounet s.n.* (B –W - 17608 -01 [digital image]!: http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=BW17608010).

Isolectotype: P06860905 [digital image] !: http://coldb.mnhn.fr/catalognumber/mnhn/p/p06860905

Ecology: Growing extensively on limestones in North Africa, the Iberian Peninsula subpopulations are exclusive from siliceous lithology. In Portugal occurs in the sienitic batholith of Monchique, in humid to hyper-humid ombrotypes, expanding through riverine forests in neighbouring areas, above schists. (Odemira and Aljezur). The main ecological feature associated to this species distribution is summer horizontal precipitation, originated either by advection fogs, either by thermic inversion in deep valleys or interior mountain areas (Vila-Viçosa et al., 2015; Vila-Viçosa et al., 2020a; Vila-Viçosa et al., 2020b; Vila-Viçosa & Arsénio, 2021).
Note: A notable distinctive feature of *Quercus canariensis* is the indumentum type. The leaves are glabrescent only with a floccose indumentum of fasciculate, uniseriate single ramified trichomes concentrated near the midrib and secondary nerves. The absence of a stellate indumentum is a marked differential character of the species (*e.g*. compared with *Q. faginea*) as emphasized by Schwarz (1936b); whereas the presence of stellate trichomes indicates introgression with other *Galliferae* oaks (Gurke, 1897). Hence, this issue is discussed further on *Q.* ×*tlemcenensis*, that relates such introgression between *Q. canariensis* and *Q. faginea* in the western Mediterranean Basin.
Biogeography: Monchique County (Vila-Viçosa & Arsénio, 2021)
Syntaxonomy: *Euphorbio monchiquensis-Quercetum canariensis*

Portuguese oak

9. *Quercus faginea* Lam. (1785: 725) =*Quercus pseudosuber* Desfontaines (1799: 348) =*Quercus hybrida* Brotero (1805: 31) =*Quercus aegilopifolia* Persoon =*Quercus ovalifolia* Bosc *ex* Pers., (1807: 570) =*Quercus castellana* Bosc *ex* Pers. (1807: 571) =*Quercus castellana* Bosc (1808:24) **=***Quercus castellana* Bosc *ex* Poir., (Lamarck, 1811: 226) =*Quercus australis* Link *ex* Spreng (1826: 861) =*Quercus australis* Link, 1831: 466) =*Quercus cookii* Loudon (1838: 1926) =*Quercus lusitanica* var. *baetica* Webb (1838:12) Lectotype (designated here): P06857819! [digital image] http://coldb.mnhn.fr/catalognumber/mnhn/p/p06857819) ≡*Quercus lusitanica* subsp. *baetica* (Webb) A.DC. (1864: 19) ≡*Quercus faginea* var. *baetica* (Webb) Samp. (1910: 123) ≡*Quercus faginea* Lam. subsp. *baetica* (Webb) Maire, (1931: 65) ≡*Quercus baetica* (Webb) Villar (1938: 455) =*Quercus alpestris* Boiss. (1838: 83) ≡*Quercus faginea* subsp. *alpestris* (Boiss.) Maire (1961: 100) ≡*Quercus lusitanica* subsp. *alpestris* (Boiss.) Nyman (1881: 661) ≡*Quercus lusitanica* var. *alpestris* (Boiss.) Cout. (1888: 68) ≡*Quercus lusitanica* subsp. *alpestris* (Boiss.) Mouill. (1897: 1161) =*Quercus quexigo* Cook *ex* Willk. & Lange (1862: 240) =*Quercus lusitanica* subsp. *faginea* (Lam.) A.DC. in A.P.de Candolle =*Quercus lusitanica* subsp. *faginea* (Lam.) A.DC. α *clusii* A.DC. (1864: 17) *nom.*

nud., *p.m.p.* ≡*Quercus lusitanica* α *faginea* (Lam.) Boiss. ex Cout. =*Quercus lusitanica* subsp. *faginea* (Lam.) A.DC. (β) var. *brevipetiolata* A.DC. (1864: 17) =*Quercus lusitanica* subsp. *baetica* (Webb) A.DC. (β) var. *pedunculata* A.DC. (1864: 19) =*Quercus baetica* (Webb) H. Buek (De Candolle, 1874: 322) =*Quercus lusitanica* var. *broteroi* Coutinho (1888: 68) Lectotype (designated here): COI - 18933 [digital image]!: http://coicatalogue.uc.pt/specimen/18933 ≡*Quercus lusitanica* subsp. *broteroi* (Cout.) Mouillefert (1898: 1162) ≡*Quercus faginea* subsp. *broteroi* (Cout.) A. Camus (1939: 179) ≡*Quercus broteroi* (Cout.) Rivas-Martínez & C. Sáenz 1991: 104) =*Quercus lusitanica* Webb f. *salicifolia* Coutinho (1888: 68) ≡*Quercus alpestris* var. *salicifolia* (Cout.) A. Camus (1939: 166) =*Quercus lusitanica* Webb f. *ellipticifolia* Coutinho (1888: 68) ≡*Quercus alpestris* var. *ellipticifolia* (Cout.) A. Camus (1939: 166) =*Quercus lusitanica* var. *broter[o] i* Cout. f. *pedunculata* Cout. (1888: 69) =*Quercus lusitanica* Webb subsp. *faginea* (Lam.) Coutinho (1913: 165) ≡*Quercus lusitanica* α *faginea* (Lam.) Boiss. ex Cout. f. *vulgaris* Cout. *nom. inval*. (Melbourne Code, Art. 23) ≡*Quercus faginea* subvar. *vulgaris* (Cout.) A. Camus, (1935: 113) *nom. inval.* (Melbourne Code, Art. 23); ≡*Quercus faginea* var. *vulgaris* A.Camus (1939: 177) *nom. inva*l. (Melbourne Code, Art. 23) ≡*Quercus faginea* subsp. *eufaginea* A.Camus (1939: 172) *nom. inval*. (Melbourne Code, Art. 23) =*Quercus lusitanica* α *faginea* (Lam.) Boiss. ex Cout. f. *submembranacea* Cout. (1888: 67) =*Quercus lusitanica* α *faginea* (Lam.) Boiss. ex Cout. f. *subsuberosa* Cout. (1888: 68) =*Quercus faginea* var. *submembranacea* (Cout.) A.Camus (1939: 177) ≡*Quercus lusitanica* var. *submembranacea* (Cout.) C. Vicioso (1950: 112) =*Quercus lusitanica* f. *obtusidens* C. Vicioso. (1950: 108); =*Quercus lusitanica* var. *submembranacea* (Cout.) C. Vicioso (1950: 112); =*Quercus lusitanica auct. pl*. non Lamarck (1875: 719) =*Quercus lusitanica* Lam. subsp. *faginea* (Lam.) Candolle (1864: 17) =*Quercus* ×*villariana* A. Camus (1939: 791) =*Quercus lusitanica* subsp. *broteroi* (Cout.) Muill. var. *lanceolata* C. Vicioso (1950: 112) Lectotype (designated here): [digital image]!: MA - 54728! http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00054728 =*Quercus* ×*clementei* C.Vicioso (1950: 140) Lectotype (designated here): MA-01-00057382! [digital image]!: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00057382 ≡*Quercus* ×*villariana* nothosubsp. *clementei* (C.Vicioso) F.M.Vázquez, S.Ramos & S.García (2004: 31) =*Quercus alpestris* f. *grandifolia* C. Vicioso, (1950: 102) Lectotype (designated here): MA-02-00054718! http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00054718 =*Quercus lusitanica* f. *obtusidens* C.Vicioso (1950: 108) =*Quercus gaditana* Vázquez *et. al*. (2014: 142) =*Quercus* ×*rosa-pintii* Vila-Viçosa, F.M. Vázquez, Meireles & C. Pinto-Gomes (2014: 146)

Lectotype (designated by Vázquez et al. (2018)): P-Lam P00382459!) [digital image] http://coldb.mnhn.fr/catalognumber/mnhn/p/p00382459

Isolectotype: P-Juss P00320341!; Spain. Andalusia. XVIII century *Antoine Laurent de Jussieu s.n.* [digital image] http://coldb.mnhn.fr/catalognumber/mnhn/p/p00320341)

Ecology: Preferentially basophile taxon, but indifferent to lithology. From sub-humid to humid ombrotypes, or in temporihygrophile positions in drier stations. Notes: This taxon has been enrolled in a wealth of unclear nomenclatural and taxonomic assignations since the study performed by Vasconcellos and Franco (1954), upon the original materials of Lamarck kept in P-Lam (P00382459!) and P-Juss (P00320341!). Only the recent review elaborated by Vázquez et al. (2020) upon the historical herbarium of Antoine Laurent de Jussieu (JUSS), clarified the misinformation around this taxon name. Prior to that, Saénz de Rivas (1969) addressed as candidate type for this species, the material of *Q. faginea,* in Lamarck's herbarium (P-Lam - 000382459 – 2 (upper left exemplar)) (Saénz de Rivas, 1969). Nevertheless, the herbarium-sheet has four different small fragments referable to different taxa. Schwarz (1954) proposed that the upper right specimen corresponds to an epitype of *Q. faginea* Lam., but all remaining fragments, drawn from Jussieu's herbarium, correspond to other taxa (P-Lam – 000382460!), namely *Q. pubescens* subsp. *palensis* (Palassou) O.Schwarz (1936: 97). The fragment number "2" effectively has a short petiole and glabrescent leaves, that led to the subsequent nomenclatural change to what became later the broad *Q. faginea* concept, brought by Saénz de Rivas (1969) and adopted in Flora Iberica (Franco, 1990) as *Q. faginea* subsp. *faginea*. However, this fragment corresponds to a second specimen and herbarium sheet of *Q. faginea* beneath P-Juss (P00320341!), that presents such characters (glabrescent leaves, possessing stellate trichomes with shorter rays), but not the one elected and annotated by Lamarck (P0032034! http://coldb.mnhn.fr/catalognumber/mnhn/p/p00320341), which corresponds to a tomentose plant with stellate trichomes with large rays. Consequently, Franco (1990) considered two subspecies of *Q. faginea,* based on the length of the rays of the stellate trichomes, thus segregating *Q. faginea* subsp. *faginea* by its glabrescent leaves and stellate trichomes with short rays (<150 μm), in accordance with Saénz de Rivas (1969), from *Q. faginea* subsp. *broteroi,* with tomentose leaves and a stellate indumentum with larger rays (> 180 μm). The originally claimed as typical subspecies (*Q. faginea* subsp. *faginea*) has shorter and curly leaves, small petioles and serrate to dentate leaf margins and is distributed mostly through the Northern and Eastern Iberian Peninsula. In turn, *Q. faginea* subsp. *broteroi* would have larger leaves and bigger petioles, plus a crenate margin. The latter is distributed through the southern and western halves of the Iberian Peninsula. As stated above, the name *Q. faginea* was mistakenly given to the first morphotype (fragment number "2" of P00382459!), while the lectotype of *Q. faginea* shows a fully tomentose abaxial leaf surface, with large petioles. This was previously diagnosed by Vasconcellos and Franco (1954) and recently reinstated by Vázquez et. al. (2020), as the correct name to be addressed to this taxon. It distributes across the western Iberian Peninsula and north Africa, with a multistellate indumentum and denser

trichomes and medium-sized rays ((7)8-14(16); (150)180-250(280) µm), also in accordance with *Q. faginea* subsp. *eufaginea* Maire (1931: 65).

Some botanists recognized individuality to a few Portuguese oaks from southwest Iberian Peninsula, with lanceolate and serrate leaves that are erroneously attributed to *Q.* ×*hispanica* Lam. (Brotero, 1805; Webb, 1838; Colmeiro & Boutelou, 1854; Candolle, 1864; Laguna, 1883), which are assignable to the morphological plasticity of *Q. faginea* (Vila-Viçosa et. al. 2022a). The original protologue of *Q. faginea* and *Q. hispanica* (Lamarck, 1785) states the morphological affinity of both taxa, due the lanceolate and dentate leaf blade. This also led to the later proposal of an independent species inside broad *Q. faginea*, as *Q. gaditana* Vázquez *et. al*. (Vila-Viçosa *et. al*. 2014: 142).

Biogeography: Coastal Lusitanian and West Andalusian Province | West Iberian Province | Carpetan Leonese Province

Syntaxonomy: *Quercion fagineae*

Lusitanian dwarf-oak

10. *Quercus lusitanica* Lam. (1785: 719) =*Quercus humilis* Lam. (1785: 719) *nom. illegit.* =*Quercus fruticosa* Brot. (1805: 31) =*Quercus humilis* f. *prasina* (Bosc) Coutinho (1888: 79) ≡*Quercus humilis* var. *prasina* Sampaio (1910: 123) ≡*Quercus faginea* raç. *lusitanica* var. *prasina* (Bosc.) Sampaio (1947: 147) =*Quercus fruticosa* var. *pedunculata* (Cout.) A. Camus

Lectotype (designated by Vázquez et al. (2020)): P00382467! [digital image] http://coldb.mnhn.fr/catalognumber/mnhn/p/p00382467).

Epitype (P00938261!, [digital image] http://coldb.mnhn.fr/catalognumber/mnhn/p/p00938261).

Ecology: Exclusive to siliceous lithology, in sub-humid to humid or hyperoceanic areas, mainly in the understory of semi-deciduous or evergreen woods. It has a high intolerance to low winter temperatures, so it is mostly found in the thermomediterranean to thermotemperate bioclimatic belts.

Notes: The name *Quercus lusitanica* Lam. (1785: 719) was proposed simultaneously to *Q. humilis* Lamarck (1785: 719). Both names belong to two taxa that are clearly conspecific and therefore one of the two is a superfluou name. This problem was solved, without a specific choice of any of the available two, when Sampaio (1910) correctly addressed the name *Q. lusitanica* to the Lusitanian dwarf-oak, clarifying the interpretations provided by other botanists (Boissier, 1838; Webb, 1838; Candolle, 1864; Coutinho, 1888; Vicioso, 1950) that commonly linked the name *Q. lusitanica* to trees of *Q. faginea s.l*., were incorrect. The sheet corresponding to *Q. lusitanica* presents two varieties (α and β): the first (α - P00320340!; P-LAM – 00382467 (left exemplar)) was collected in the Portuguese Estremadura. This specimen refers *in schedulla*: "*cerqueiro-bravo*", which is the common name for the shrub that grows around Lisbon and below Tagus regions and was validated by Vasconcellos & Franco (1954). It presents a sessile, thick-sclerophyll and glabrescent blade, with an entire margin in the proximal third of the leaf. These characters, when in comparison to the protologue (Lamarck, 1785) and all studied specimens of *Q. lusitanica* (P-Lam and P-Juss) and respective synonyms (*Q. fruticosa*), allows us to agree with the proposal of Vasconcellos & Franco (1954) that addressed, without any doubt, the name *Q. lusitanica* to this taxon. These latter authors analysed three locations, mentioned in the original notes of Antoine de Jussieu, with comments on the origin of both *Q. lusitanica* Lam. and *Q. humilis* Lam. All references mentions the Tagus and Sado Cenozoic Basin, where *Q. lusitanica* forms known scrublands (*Erico-Quercetum lusitanicae*) according to Costa *et. al*. 2012), as follows: 1-between Vendas Novas and Montijo (Aldeia Galega), 2 - between Moita and Palmela and 3 - Alvalade do Sado. The second variety (β - P00320339!) shows a different set of characters that stands in the origin of the following nomenclatural conundrum, around the name *Q. lusitanica*. Vasconcellos & Franco (1954) suggests this plant contains aestival leaves of the same taxon, but the studied specimen has no information beside that it was collected in Portugal. Additionally, the leaf shape links it to a roburoid oak, included in the broad plasticity of *Q. faginea,* or even to hybrids assignable to *Q.* ×*coutinhoi* Samp. or *Q.* ×*alentejana* Pinto-Gomes & Vázquez. This hybrid hypothesis is corroborated by Schwarz in his Lamarck herbarium review (1954), who regarded it as *Q. cerrioides* Willk. & Lange, which was his interpretation of the hybrid between *Q. faginea* and *Q. pubescens* subsp. *palensis* (Palassou) O. Schwarz (1936: 97) as *Quercus lusitanica* subsp. *cerrioides* (Willk. & Costa) O. Schwarz (1936: 72).

Biogeography: Coastal Lusitanian and West Andalusia Province | West Iberian Province | Galician-Portuguese Sector

Pyrenean oak

11. *Quercus pyrenaica* Willd. (1805: 451) =*Quercus toza* Gillet ex Bosc (1792: 155)
=*Quercus pubescens* Brotero (1805: 31) =*Quercus cerris* var. *tomentosa* DC. =*Quercus humilis* DC. (Lamarck & Candolle, 1805: 311) =*Quercus tauzin* Persoon (1807: 571) =*Quercus brossa* Bosc (1807: 319) =*Quercus toza* Bastard (1809: 346) =*Quercus stolonifera* Lapeyrouse (1813: 582) =*Quercus toza* Bosc var. *cœnomanensis* N.H.F.Desp. (Lamarck & Candolle, 1815: 352) =*Quercus castellana* Bosc ex Persoon (1807: 571) =*Quercus tauza* Desfontaines (1815: 245) =*Quercus cenomanensis* N.H.F.Desp. ex Endl. (1848: 24) =*Quercus camata* Petz. & G.Kirchn. (1864: 628) =*Quercus toza* Gillet ex Bosc var. *humilis* (A. DC.) Nyman =*Quercus toza* Gillet ex Bosc var. *pyrenaica* (Willd.) Wenz. (1886: 198) =*Quercus toza* Gillet ex Bosc var. *aurea* (Wierzb. ex Rochel) Nyman (1890: 279) =*Quercus toza* Gillet ex Bosc subsp. *conferta* (Kit.) Nyman (1890: 279) =*Quercus toza* Gillet ex Bosc var. *spectabilis* (Kit. ex Simonk.) (1891: 2) =*Quercus tauzinii* Bubani (1897: 67) =*Quercus toza* Gillet ex Bosc var. *spicata* Tourlet (1903: 423) =*Quercus toza* Gillet ex Bosc

subsp. *conferta* Kit. (1908: 199) =*Quercus toza* Gillet ex Bosc var. *stenocarpa* Rouy (1910: 316) =*Quercus toza* Gillet ex Bosc var. *sphaerocarpa* Rouy (1910: 317) =*Quercus toza* Gillet ex Bosc var. *vulgaris* (Bastard) Cout. (1913: 164) =*Quercus toza* Gillet ex Bosc var. *normalis* Rouy (1913: 164) =*Quercus pyrenaica* Willd. f. *brachyloba* O. Schwarz =*Quercus pyrenaica* Willd. f. *laciniata* O. Schwarz =*Quercus pyrenaica* Willd. lus. pendula (Dippel) O. Schwarz =*Quercus pyrenaica* Willd. f. *pinnatifida* O. Schwarz (1937: 143); =*Quercus pyrenaica* Willd. f. *pinnatipartita* C. Vicioso (1950: 52) =*Quercus pyrenaica* Willd. var. *expansa* C. Vicioso (1950: 52) =*Quercus pyrenaica* Willd. f. *sphaerocarpa* (Rouy) F.M. Vázquez =*Quercus pyrenaica* Willd. f. *stenocarpa* (Rouy) F.M. Vázquez (1998: 82) =*Quercus pyrenaica* Willd. f. *normalis* (Rouy) F.M. Vázquez =*Quercus pyrenaica* Willd. f. *expansa* (C. Vicioso) F.M. Vázquez (1998: 82).

Lectotype (designated by Saénz de Rivas, 1975: 780): (B-W - 17651 – 03 [digital image] http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=BW17651030).

Ecology: Supports mesophytic conditions as edaphic indifferent, although preferring siliceous bedrock. From sub-humid to hyper-humid ombrotypes, coping with summer-drought, normally with marcescent behaviour in thermophilic areas. Biogeography: All Portuguese mainland, except for *Baixo Alentejo-Andevalense* and *Promontório-Algarvio* Subsectors (Vila-Viçosa *et al*. 2017). Syntaxonomy: *Quercion pyrenaicae*

Hybrids

1. *Quercus* ×*alentejana* C. Pinto-Gomes & F.M. Vázquez (Vázquez *et al.* 2015: 49)
Q. faginea × *Q. pyrenaica*

Holotype: Vázquez *et al.* (2015: 49): HSS – 49040!

Description: Tree up to 15 m, growing with the parents. Leathery leaves with pinnately lobed to crenate margins, lamina (7)10-15(20) × (4)5-8(10) cm. Adaxial lamina surface pubescent to tomentose. Abaxial leaf surface heavily tomentose, with the presence of a double indumentum with stellate trichomes with long rays (>180 µm) and large fasciculate trichomes.

Notes: Very polymorphic plant, normally having obovate leaves, with deep lobes and divaricate secondary nerves. Besides the stellate indumentum, it also has fasciculate trichomes with long rays belonging to *Q. pyrenaica*, especially across the midrib and secondary nerves. This nothotaxon originally inherited the name *Q.* ×*neomairei* A. Camus (1937: 28; 1939: 408), from a specimen labelled by Coutinho (1988) as « *Quercus toza* × *Q. lusitanica* » (LISU 10402!). The latter specimen was collected by Welwitsch on the margin of the Mondego River (LISU!) and corresponds to a hybrid with the participation of different parental species (see '*Q.* ×*welwitschii*'). Therefore, the natural hybrid between *Q. faginea* and *Q. pyrenaica* lacked an appropriate name.

2. *Quercus* ×*almeidae* Vila-Viçosa, Capelo, P. Alves & F.M. Vázquez **nothosp.nov.** (Figure 3)
Q. pseudococcifera × *Q. rotundifolia*

Holotype: HSS - 081083! (Figure 3) – Portugal, Alto-Alentejo: Évora, Herdade dos Padres, 342 m, 38.5885253; -8.1469238, 2014, *Carlos Vila-Viçosa s.n.* (Isotype: PO-V70053; LISE-96338)

Descriptio: *Arbor parva ad usque 6 m alta, inter parentibus incolente; foliis concoloribus atroviridibus 3-5(7) × 1-3(4) cm sursum glabrescentibus deorsum pubescentibus indumento ex trichomatibus stellatis radiis parvis (160µm) ut illis Q. rotundifolia; obovatis oblongis vel lanceolatis dentatis spinosis. Maturatione fructus annua cupulae squamis imbricatis adpressis maturatione praecipue supernis liberis facientibus.*

Description: Tree up to 6 m, among parents, Dark green concolorous leaves 3-5(7) × 1-3(4) cm, obovate to oblong and sometimes lanceolate leaves, with dentate and spiny margins. Glabrescent adaxial leaf surface and pubescent abaxial leaf surface, with an indumentum of stellate trichomes with short rays (160 µm), like *Q. rotundifolia.* Annual fructification with cups possessing intricate and appressed scales that become free in maturity, especially the upper ones.

Dedicated: To the distinguished botanist and friend Rubim Almeida da Silva (1960).
Notes: Occurs among parentals, especially across the Coastal Lusitanian and West Andalusia Province in humid areas, where *Q. pseudococcifera* grows at the edge of marcescent thermophilic forests, contacting with *Q. rotundifolia* secondary forests in xerophytic outcrops or lithosols.

3. *Quercus* ×*alvesii* Vila-Viçosa, Capelo, R. Almeida & F.M. Vázquez **nothosp.nov.** (Figure 4)
Q. lusitanica × *Q. rotundifolia*

Holotype: PO - 62235! (Figure 5) - Portugal. Baixo-Alentejo: Almodôvar, São Barnabé, Carvais de Baixo, 447 m, 37≡20'7.92" N; -8≡ 6'8.82" W, 09 November 2015, *Carlos Vila-Viçosa & Arlindo Rim s.n.* Isotype: HSS – 65657.

Descriptio: Frutex usque ad 100 cm altus, inter utrosque parentes intermedius, sed saepe Q. lusitanicae similior; folia ex ovato-obovatis ad lanceolata laminis (9)12-20(24) x (4)6-14(17)mm tertia parte infera marginibus integris autem secunda primaque sursum partibus ex serratis ad denticulatas, parvis mucronibus, supra glabrescentibus vel trichomatibus sparsis stellatis multistellatis simplicibus immo subtus tomentosis trichomatibus stellatis multistellatis fasciculatis radiatis simplicibusque, petiolo 2-7 mm pubescenti, nervis secundariis a base quam angulo maiore 45≡ abeuntibus prope marginibus saepe bifurcatis tamen eisdem supernis a Querco rotundifoliae similis sint.

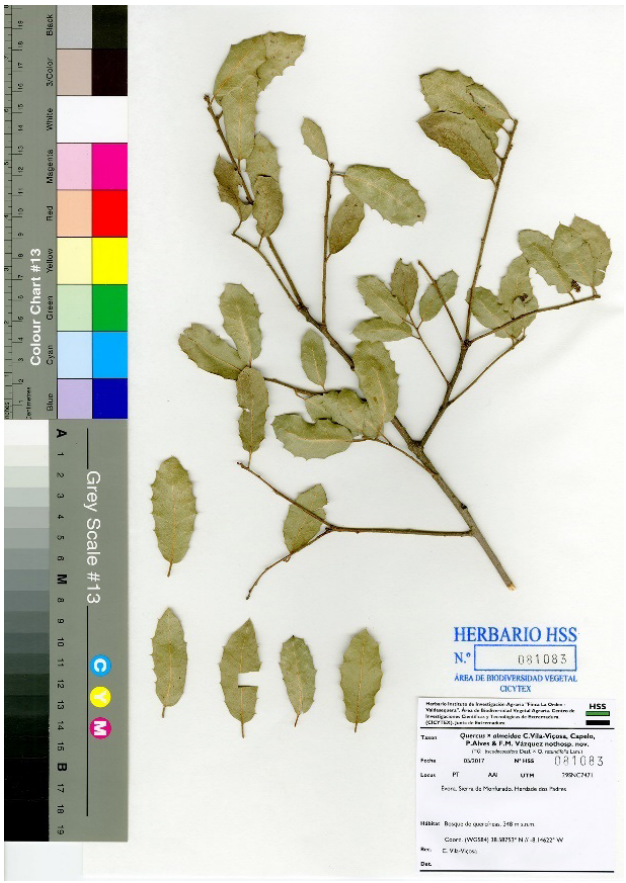

Figure 3. Holotype of *Q.* ×*almeidae* Vila-Viçosa, Capelo, P.Alves & F.M. Vázquez nothosp.nov. HSS - 081083!

Description: Shrub up to 100 cm among parents. Leaves ovate-obovate to lanceolate, blade with (9)12-20(24) x (4)6-14(17) mm, entire margin in the first third (proximal), the second and distal thirds serrate to denticulate, with mutic mucrons and a 2-7 mm wide pubescent petiole (Figure 6). Adaxial leaf surface glabrescent, with stellate, multi-stellate, and simple trichomes. Abaxial leaf surface tomentose, with stellate, multi-stellate, radiate, single and fasciculate trichomes. Secondary veins bifurcated in the apex and forming almost rectilinear angles with the midrib in the proximal half of the leaf, like in *Quercus rotundifolia* Lam.

Dedicated: To the distinguished botanist and friend Paulo Jorge Mendes Alves (1975).
Notes: Grows with the parents, on sub-humid and thermophilic areas, namely on edaphoxerophile round-leaf-oak (*Q. rotundifolia*) forests. Also found in Serrano-Monchiquense district through fieldwork and herbarium review (COI) in Portuguese Divisorian Sector.

4. *Quercus* ×*aruciensis* C. Vicioso (1950: 139).
Q. faginea ×*Quercus lusitanica*

Lectotype (designated here): Spain. Andalucia: Huelva, Los Marines, Sierra de Aracena, 21 June 1942, *C. Vicioso s.n.* (MA 57386!). [Digital image] http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00057386

Notes: Detected in *Ulici welwitschianii-Quercetum faginea*, where sandy soil horizons overlap limestones, enabling the co-occurrence of *Q. lusitanica* and *Q. faginea*. It was not possible to locate the type materials of *Q.* ×*tingitana* A. Camus (1939) to study this putative prior name and we retain the name given by Vicioso (1950), corresponding to this hybrid, as we have directly studied its type.

Figure 4. Illustration of *Q.* ×*alvesii* Vila-Viçosa, Capelo, R. Almeida & F.M. Vázquez nothosp.nov. Branch and leaf type morphologies (F.M. Vázquez).

Figure 5. Holotype of *Q.* ×*alvesii* Vila-Viçosa, Capelo, R. Almeida & F.M. Vázquez nothosp.nov. PO-V62235! (Porto University, Natural History and Science Museum).

Figure 6. Leaf detail of *Q.* ×*alvesii* Vila-Viçosa, Capelo, R. Almeida & F.M. Vázquez nothosp.nov. PO-V62235! (Porto University, Natural History and Science Museum).

5. *Quercus* ×*auzandri* Gren. & Godr. (1855: 119) =*Quercus ilicococcifera* Saporta (1893: 206) =*Quercus* ×*reynieri* Albert (1902:129) =*Quercus* ×*comari* Albert (1902: 130) =*Quercus* ×*denudata* Albert (1902: 131) =*Quercus* ×*integrata* Albert (1902: 131) =*Quercus* ×*catalaunica* Sennen (1912: 243) Lecotype (designated here): (BCN-BC-Cadevall 823018!) =*Quercus* ×*rouxii* A. Camus (1935a: 54)
Q. coccifera × *Q. ilex*

Notes: The studied materials (LISI 10278/1999!) from Douro valley, contains hybrids of *Q. coccifera,* with the participation of *Quercus ilex* as a parent, apparent from the lauroid leaf shape and higher number of secondary nerves (>8). The label of the studied specimens also includes João do Amaral Franco's hand-notes, discussing the probable participation of *Q. ilex* instead of *Q. rotundifolia*.

6. *Quercus* ×*avellaniformis* Colmeiro & E. Boutelou (1854: 9) =*Quercus* ×*mixta* Villalobos ex Colmeiro (1888: 677) non Candolle (1864: 83) *nom. inval.* =*Quercus ilex* var. *avellaniformis* (Colmeiro & E. Boutelou) Cout. (1888: 95) =*Quercus ilex* f. *crassicupulata* Cout. (1888: 95)
Lectotype (designated here): COI-19409! [digital image]!: http://coicatalogue.uc.pt/specimen/19409
Q. rotundifolia × *Q. suber*
Lectotype (designated by Vázquez et al. (2018): Spain. Extremadura: Badajoz, Cabeza la Vaca, Dehesa de Murillo, *E. Boutelou s.n.* MA-01-00026153! [digital image]!: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00026153

Notes: Common among parents, in bioclimatic areas where flowering and pollination periods of both often overlap. Normally in neighbouring areas of cork oak and round-leaf oak vegetation series.

7. *Quercus* ×*capeloana* Vila-Viçosa, P. Alves, P. Lemos, R. Almeida & F.M. Vázquez **nothosp.nov.** (Figure 7)
Q. pseudococcifera × *Q. suber*

Holotype: PO V-70068! (Figure 7) - Portugal. Estremadura, Caldas da Rainha: Paúl da Tornada; Rua dos Bernardinos, 32 m, 39.444674 -9.145928, 28 October 2021, *Paulo Lemos s.n.* Isotypes: HSS-079482; LISE- 96336.

Descriptio: Arbor ad 4 m alta apud parentibus inventa cortice tenuiter suberoso ad albescentem a aurantiaco. Foliae inter parentibus intermediis lanceolatas (3)4-7(8) ×(1)2-3(4) cm glabrescentibus vel pubescentibus margine denticulata petiolo pubescenti sursum atroviridibus glabrescentibus trichomatis stellatis sparsis deorsum pubescentibus trichomatis stellatis multistellatisque, nervis secundariis bifurcatis anastomosantibus praesertim a basi nervo medio recto inserto sed hoc paulatim accedentibus ab apice. Glans biennis cupulae squamis erectis longis teretibus crassis liberisque.

Description: Tree up to 4 m, growing with the parents, with whitish to orangish corky bark. Glabrescent to pubescent and lanceolate leaves, (3)4-7(8) × (1)2-3(4) cm, denticulate margin, and pubescent petiole. Dark-green and glabrescent adaxial surface, with scarce stellate trichomes. Pubescent abaxial surface,

with stellate and multi-stellate, trichomes. Bifurcate (anastomosed) secondary veins, that are perpendicular with the midrib, especially at the base of the leave, normally forming progressively acute angles towards the apex. Leaf architecture between the parents. Biennial fruit maturation. Cups with large-free erect and thick cylindrical scales, retroflexed in maturit .
Dedicated: To the distinguished botanist and friend Jorge Henrique Capelo Gonçalves (1965).
Notes: Among the parents, in coastal hyperoceanic areas, of the Portuguese Divisorian Sector, above mixed Jurassic lime and sandstone derived soils. It is distinguished from *Q. coscojosuberiformis* by the totally free cup scales, compared to the slightly free to appressed-fused scales in the latter.

Figure 7. Holotype of *Quercus* ×*capeloana* Vila-Viçosa; P. Alves, P. Lemos, R. Almeida & F.M. Vázquez nothosp. nov. (PO-V70068!) (Porto University, Natural History and Science Museum).

8. *Quercus* ×*celtica* F.M. Vázquez, Coombes, Rodr.-Coombes, Ramos & Doncel (2003: 52)
Q. lusitanica × *Q. suber*

Holotype: Vázquez et al. (2003): Portugal. Alto-Alentejo: Ponte-de-Sôr, Ervideira, 21 November 1999, *F.M. Vázquez s.n.* (HSS – 3718!)

Notes: Common taxon among the parents, in the understory of cork oak (*Q.* suber) forests, in Ribatagan-Sadense Sector.

9. *Quercus* ×*coscojosuberiformis* Baonza (2007: 365)
Q. coccifera × *Q. suber*

Holotype: Baonza (2007: 365): Spain. Madrid: Monte el Pardo, 3 March 2006, *J. Baonza Díaz s.n.* MA-01-00737668!; [digital image]!: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00737668

Notes: Not observed through fieldwork or in herbaria, but with high probability of existence in nature due to the extensive area of parents overlap.

10. *Quercus* ×*coutinhoi* Samp. (1910: 123) ≡*Quercus faginea* var. *coutinhi* Samp. (1947: 147) =*Quercus lusitanica* var. *faginea* (Lam.) Boiss. ex Cout. f. *subpinnatifida* Cout. (1888: 67) ≡*Quercus faginea* var. *subpinnatifida* (Cout.) A. Camus (1939: 177) =*Quercus lusitanica* var. *faginea* (Lam.) Boiss. ex Cout. f. *bullata* Cout. =*Quercus lusitanica* var. *faginea* (Lam.) Boiss. ex Cout. f. *pedunculata* Cout. (1888: 68) Lectotype (designated here): COI: 18934! [digital image]!: Available at: http://coicatalogue.uc.pt/specimen/18934 ; Syntype 1: Portugal, Beira Litoral, Coimbra, Carapinheira do Campo, IX-1981 (COI: 18930!) ≡*Quercus faginea* var. *pedunculata* (Cout.) A. Camus (1939: 178) ≡*Quercus lusitanica* Lam. var. *pedunculata* (Cout.) C. Vicioso (1950: 110) =*Quercus lusitanica* var. *broter[o]i* Cout. f. *bullata* Cout. ≡*Quercus faginea* var. *bullata* (Cout.) A. Camus (1939: 178) =*Quercus lusitanica* var. *broter[o]i* Cout. f. *sublobata* (1888: 69) ≡*Quercus faginea* subvar. *sublobata* (Cout.) A. Camus (1939: 180) =*Quercus lusitanica* var. *broteroi* Cout. f. *subpinnatifida* Coutinho (1888: 67) ≡*Quercus faginea* var. *subpinnatifida* (Cout.) A. Camus (1938: 177) =*Quercus pedunculata* f. *brevipedunculata* Coutinho (1888: 58) =*Quercus* ×*molleri* A. Camus (1934: 44) Lectotype (designated here): LISU – 10358**!** (right specimen) =*Quercus* ×*ferreirae* A. Camus (1934: 45) Camus (1938: 406): Lectotype (designated here): (COI: 19024!) [digital image]!: http://coicatalogue.uc.pt/specimen/19024 ≡*Quercus* ×*coutinhoi* A.Camus nothosubsp. *ferreirae* (A. Camus) F.M. Vázquez, S. Ramos & S. García. (2004: 31) =*Quercus* ×*subalpestris* A. Camus (1935a: 59) Lectotype (designated here): (LISU - P-10361!) ≡*Quercus* ×*coutinhoi* nothosubsp. *subalpestris* (A. Camus) F.M. Vázquez *et al.* (2004: 31) =*Quercus* ×*carrissoana* A. Camus (1935a: 59) =*Quercus* ×*coutinhoi* nothosubsp. *beturica* F.M. Vázquez *et.al.* (2003: 53) ≡*Quercus* ×*beturica* (F.M. Vázquez, *et al.*) F.M. Vázquez, *et al.* (Vila-Viçosa *et al.* 2014: 148): Holotype (Vázquez *et al.* 2014): (HSS: 22279!))
Q. estremadurensis × *Q. faginea*

Lectotype (designated here): Portugal. Beira Litoral: Coimbra. Fornos. Agri Conimbricense, August 1848, *Welwitsch s.n.* (LISU – 10364!)

Notes: All specimens determined by Coutinho (1888) (LISU!; COI!) as "*Quercus pedunculata* × *Q. lusitanica*", and posteriorly referenced by Sampaio (1910) and Camus (1934), from Coimbra and Sintra, match the

typical location from where *Q. estremadurensis* was described (Schwarz, 1935).

11. *Quercus* ×*diegoi* F.M. Vázquez, C. Pinto-Gomes, C. Vinagre & Vila-Viçosa (Vinagre *et al.* 2014: 95)
Q. lusitanica × *Q. pyrenaica*

Holotype Vinagre *et al.* (2014): HSS – 62975!

Notes: Rare taxon, found among the parents, namely in thermophilic areas of *Arisaro simorrhini-Quercetum pyrenaicae* (Vila-Viçosa, 2012).

12. *Quercus* ×*duriensis* (Franco & Vasconcellos) Vila-Viçosa, Capelo, Alves, Almeida & Vázquez ***stat. nov.*** ≡*Quercus* ×*coutinhoi* f. *duriensis* Franco & Vasconcellos [basion.] (Vasconcellos & Franco 1954: 33) ≡*Quercus* ×*coutinhoi* nothosubsp. *duriensis* (Franco & Vasc.) Monteiro-Henriques *et al.* (Costa *et al.* 2012: 122)
Q. faginea × *Q. orocantabrica*

Holotype Vasconcellos & Franco (1954): LISI – 6046! -9702/1999-1! Portugal, Viseu, Lamego, entre Lamego e Várzea de Abrunhais, próximo de Alvéolos, 1943-06-12

Description: Tree, growing among parents, with intermediate leaf characters,: leaves oblong to obovate (80(8.7) x 45(52) mm), sub-sessile to short petiolate (<5(10) mm), auriculate; irregular margin lobate-sinuate to crenate, with 7 (8) blunt rounded and uneven lobes (resembling *Q. orocantabrica*); short or very few secondary nerves 7(8), often sinual; glabrescent to pubescent leaves on the abaxial leaf surface with scarce uniformly distributed stellate and multi-stellate trichomes; often pedunculate fruits (<6 cm).

Notes: These northern Portuguese (Douro Basin) hybrid swarms, generally correspond to the type-location of *Quercus* ×*coutinhoi* f. *duriensis* Franco & Vasconcellos. Field work, complemented by molecular analysis corroborates that the roburoid oak, sympatric with *Q. faginea* in those populations is *Q. orocantabrica* (Vila-Viçosa et al. (2021). Accordingly, we propose to elevate the previous name, given by Vasconcellos and Franco (1954), to nothospecies rank.

13. *Quercus* ×*eborense* Vila-Viçosa, Capelo, P. Alves, J. Junqueira, R. Almeida & F.M. Vázquez **nothosp.nov** (Figure 8).
Q. coccifera × *Q. rotundifolia*

Holotype: PO-V70054! (Figure 8) – Portugal, Alto-Alentejo: Évora, Alto de São Bento 367 m, 38.580084 -7.937871, 12, June, 2022, *João Junqueira s.n.* Isotypes: HSS-081136; LISE- 96337.

Descriptio: Frutex arborescens ad usque 3 m altum, inter parentibus incolente; foliis paene concoloribus sursum atroviridibus glabris sive glabrescentibus dum deorsum subviridibus sed cinerascentibus decentibus propter ipsis petiolisque pubescentibus vel sparso tomentosis in modo Querco rotundifolia hoc maxime iuvenibus sed tandem glabescentibus veteribus, orbicularibus a ovatis seu obovatis 2-4(5) × 1-3 (3,5) cm integris sive dentatis spinosis clare mucronatis a Q. coccifera similiter. Indumentum foliorum ex trichomatibus stellatis sive multistellatis foliis adpressis componuntur (Figure 2). Architectura formam foliorum ex Q. rotundifolia simili saepe venis secundariis bifurcatis anastomosantibus praesertim a basi nervo medio rectis insertis. Maturatione fructus annua sicut Quercus rotundifolia; glans ut Quercus rotundifolia cupulae squamis crassis adpressis nonnunquam ut Q. coccifera liberis facientibus.

Figure 8. Holotype of *Quercus* ×*eborense* Vila-Viçosa, Capelo, P. Alves, J. Junqueira, R. Almeida & F.M. Vázquez nothosp. nov. PO-V70054! (Porto University, Natural History and Science Museum).

Description: Dendroid shrub up to 3 m high, growing among the parents. Green concolorous leaves, with a glabrous to glabrescent dark green adaxial leaf blade, while the abaxial leaf blade is light green, becoming greyish due to a pubescent indumentum and petiole, like *Q. rotundifolia,* that is notorious in younger leaves and branches, becoming glabrescent in older ones. Orbicular to ovate or obovate leaves, 2-4(5) × 1-3 (3,5) cm, with entire to dentate and spiny margins, with well-developed and non-mutic mucrons like *Q. coccifera*. Foliar indumentum composed by stellate and multistellate trichomes that are appressed to the leaf blade (Figure 2). *Q. rotundifolia* architectural leaf

shape, with often bifurcate (anastomosed) secondary veins, that are perpendicular with the midrib, at the base of the leave. Annual fruit maturation like *Q. rotundifolia*. Cups with appressed and thick scales like *Q. rotundifolia*, but sometimes becoming free like in *Q. coccifera*, especially the upper ones.

Dedicated: To the city of Évora, the Capital of the Alentejo Region, where this hybrid is rather frequent across the typical Montado/Dehesa landscape.
Notes: Common hybrid in the Marianense and Portuguese Divisorian Sectors, as edaphic indifferent. It is distinguished from *Q. airensis* by the presence of stellate and multistellate appressed trichomes with rays <160 µm, that are inherited from *Q. rotundifolia* and the total absence of multiradial and stipitate trichomes with large rays (300-400 (500) µm) (Figure 2) that are typical from *Q. airensis*.

14. *Quercus* ×*fontqueri* O. Schwarz (1936b: 85).
Q. canariensis × *Q. pyrenaica*

Lectotype (designated here): Spain. Catalonia: Barcelona, Canyamas, Montalt, Font del Mal Pas, 1 September 1946, *P. Monserrat s.n.* (MA - 81789!).

Notes: Rare tree, present in *Euphorbio monchiquensis-Quercetum canariensis* forests in Southwest Portugal (Vila-Viçosa *et. al*. 2012; Vila-Viçosa *et. al*. 2015).

15. *Quercus* ×*gallaecica* F. Llamas, Lence & C. Acedo (2003: 87)
Q. lusitanica × *Q. orocantabrica*

Holotype (Llamas et al., 2003): LEB – 53647!

Notes: Rare shrub, in Duriense Littoral District.

16. *Quercus* ×*lousae* Vila-Viçosa, F.M. Vázquez, Meireles & C. Pinto-Gomes (Vila-Viçosa *et al.* 2014: 145)
Q. canariensis × *Q. estremadurensis*

Holotype: Vila-Viçosa *et al.* (2014): HSS – 54488!

Notes: After an accurate analysis of all Welwitsch collected specimens, determined as *Q. mirbeckii* Durieu (LISU!; COI!), we concluded that they correspond to broad-leafed *Q. faginea*. Thus, the hybrid between this former taxon and *Q. estremadurensis,* reiterated by Camus (1939) as *Q. ×carrissoana,* corresponds to *Q. ×coutinhoi* Samp. In turn, the lectotype of *Q. ×lousae* was collected in a population where *Q. canariensis* was recently confirmed and the specimen exhibits intermediate features between the here established nothotaxon.

17. *Quercus* ×*pacensis* F.M. Vázquez (1996: 249)
Q. faginea × *Q. suber*

Holotype: Vázquez (1995): HSS: 9092!. Isotype: MA-01-00526300! [digital image]!: http://161.111.171.57/herbarioV/visorVCat.php?img=MA-01-00526300

Notes: The hybridization of *Q. faginea* and *Q. suber* has been assumed as being common and is often related with the concepts of *Q. ×hispanica* Lam. and *Q. pseudosuber* Desf. (Webb, 1838; Vicioso, 1950; Vázquez *et. al*, 2018; Vila-Viçosa et. al. 2022a). Nevertheless, many such individuals are pure *Q. faginea*, which occasionally develops a 'corky' bark, because of secondary growth. This was already stated by Coutinho (1888) when describing *Quercus lusitanica* α *faginea* f. *subsuberosa* Cout. Although this nothotaxon exists, it is rare in Southern Portugal (Ribatagan-Sadense sector and Alentejano District) in *Ulici-Quercetum faginea* and *Pistacio-Quercetum faginea* woodlands, demanding further molecular in-depth analysis to demonstrate genetic admixture.

18. *Quercus* ×*prasina* Bosc ex Endlicher (Bosc 1807: 330) Endlicher (1847: 25) =*Quercus ×angustifolia* Villar ex Gonz.Albo (1936: 1)
Q. coccifera × *Q. faginea*

Lectotype (designated by Vázquez et al. (2018)): P06847432! [digital image]!: http://coldb.mnhn.fr/catalognumber/mnhn/p/p06857698

Notes: Recognized through fieldwork and herbaria review (LISE – 45056!), in Portuguese Divisorian Sector.

19. *Quercus* ×*sampaioana* Vila-Viçosa, Capelo, P. Alves, R. Almeida & F.M. Vázquez **nothosp. nov.** (Figure 9) =*Quercus humilis* α *genuina* f. *subcrenatolobata* Coutinho (1888: 79) Lectotype (designated here): COI-19014! [digital image]!: http://coicatalogue.uc.pt/specimen/19014 .
Q. estremadurensis × *Q. lusitanica*

Holotype: Monserrate-Sintra, 26 August 1863, *Welwitsch s.n.* (LISU – 10359!). *Paratype 1: Serra de Sintra, entre o Alto do Monge e o Convento dos Capuchos, 26 August 1952, J. do Amaral Franco s.n* LISI - N≡ 13 - 14395/1999!; Paratype 2: Portugal. Beira Litoral. Figueiró dos Vinhos, próximo ao Matadouro, 450 m.s.m., 9 October 1954, *A.R. Pinto da Silva s.n.* (LISI - 16741/1999!); Paratype 3: Portugal. Beira Litoral: Mealhada, Luso, Mata do Buçaco. October 1962, *Álvaro de Brito Pires s.n.* LISI - N≡ 8 - 22038/1999!; Paratype 4: Portugal. Beira Litoral, C. de Montemor. 1888, *Bernardino A. de Barros Gomes s.n.* COI-19014.

Descriptio: Frutex ad usque 150cm seu arbor, inter parentibus; folia paene sessilis petiolis brevis (<5mm) glabrisque; laminae foliorum obovatis seu rhomboidalis (5)813(15) x (2)4-5(8) cm, tertia parte infera marginibus integris autem secunda primaque sursum partibus ex crenatis ad dentatas lobulatasque, supra glabris immo subtus glabrescentibus trichomatibus stellatis multiradialisque 8-13 radiis brevibus (<15µm) praeterhac simplicibus petiolis nervis centralisque necnon sparsibus per laminam; pedunculi longi aliquando 9cm.

Description: Shrub up to 150 cm or tree, growing with the parents. Leaves with obovate to rhomboidal lamina, (5)8-13(15) x (2)4-5(8) cm, with entire margin in the first third (proximal), the second and distal thirds crenate to dentate and lobulate, almost sessile with short (<5 mm) glabrous petiole. Lamina adaxial surface glabrous, abaxial surface glabrescent, with dispersed stellate and multiradial trichomes (8-13 rays), with short rays (<15µm) and simple trichomes in the midrib and scattered through the blade in the abaxial face. Large peduncle, up to 9 cm.
Dedicated: To distinguished botanist Gonçalo António da Silva Ferreira Sampaio (1865-1937).

Figure 9. Holotype of *Quercus* ×*sampaioana* Vila-Viçosa, Capelo, P. Alves, R. Almeida & F.M. Vázquez nothosp. nov. (LISU – 10359!)

Notes: Dispersed across the Coastal Lusitanian and West Andalusia Province, namely in the understory of *Asparago aphylli-Quercetum suberis*, *Arisaro simhorrini-Quercetum faginea* and *Avenello strictae-Quercetum faginea* (Vila-Viçosa *et. al*, 2012; Vila-Viçosa et al., 2015, Vila-Viçosa *et. al*. 2017).

20. *Quercus* ×*tavaresii* Samp. (1910: 123) ≡*Quercus* ×*subandegavensis* A. Camus (1935a: 60) ≡*Quercus* ×*andegavensis* nothosubsp. *subandegavensis* (A. Camus) Vila-Viçosa, F.M. Vázquez, Meireles & Pinto-Gomes (Vila-Viçosa 2012: 28)
Q. orocantabrica × *Q. pyrenaica*

Lectotype (designated here): Portugal. Beira Baixa: Soalheira, September 1902, *Joaquim da Silva Tavares s.n*. (LISU - P-10355!); Isolectotype: COI – 19233! [Digital image]!: http://coicatalogue.uc.pt/specimen/19233

Notes: Common among the parents, in Cantabrian Atlantic Subprovince. The lectotype, deposited in LISU (P-10355!) under *Quercus pyrenaica* and duplicated in *Q. robur* collection in COI (COI - 19233!), corresponds to the hybrid between *Q. orocantabrica* and *Q. pyrenaica*. It has large glabrescent leaves, with scarce fasciculate trichomes in the midrib and abaxial leaf surface, short petiole and auriculate leaf-base, plus a pinnately lobed to pinnatifid margin. It was later determined as *Q. pyrenaica* by Vasconcellos and Franco (1954) who argued the putative absence of *Q. orocantabrica* at the typical location, that is biogeographically ascribed to the potential forests of *Viburno tinii-Quercetum broteroanae* (Costa *et. al*. 2012).

21. *Quercus* ×*tentudaica* (F.M. Vázquez) F.M. Vázquez (Vázquez *et al.* 2015: 45) =*Quercus lusitanica* f. *microphylla* Coutinho (1888: 69) =*Quercus lusitanica* var. *broter[o]i* f. *microphylla* Cout. (1888: 69) ≡*Quercus faginea* subvar. *microphylla* (Cout.) A. Camus (1939: 180)
Q. faginea × *Q. rotundifolia*

Basionym: *Quercus* ×*senneniana* A. Camus nothosubsp. *tentudaicus* F.M. Vázquez. (1995: 250)
Holotype: (Vázquez, 1995): HSS – 1314!
Notes: Rare taxon, among the parents.

22. *Quercus* ×*tlemcenensis* Trab. (1905: 308) ≡*Quercus mirbeckii* f. *tlemcenensis* (A.DC.) Trab. (1890: 821); ≡*Quercus faginea* var. *tlemcenensis* (A.DC.) Jahand. & Maire (1932: 165); ≡*Quercus broteroi* (Cout.) Rivas-Martínez & C. Saénz subsp. *tlemcenesis* (DC.) F.M. Vázquez & A. Coombes (2016: 29); =*Quercus lusitanica* Lam. var. *rhiphaea* Pau & Font Quer (1928: 132) =*Quercus faginea* subsp. *eufaginea* var. *tlemcenensis* Jahand & Maire (1932: 165) =*Quercus* ×*tlemcenensis* (A.DC.) Villar (1938: 452), *nom. inval. non* Trab. (Battandier & Trabut 1905: 308) ≡*Quercus faginea* subsp. *broteroi* (Cout.) var. *tlemcenensis* (A.DC.) A. Camus (1939: 180) =*Quercus* ×*maroccana* (Braun-Blanq. & Maire) Villar (1943: 3) ≡*Quercus tlemcenensis* (A.DC.) Villar f. *maro[ca]ccana* (Braun-Blanq. & Maire) Villar (1938: 453) =Quercus ×*fagineomirbeckii* Villar (1938 450) =*Quercus* ×*jahandiezii* A. Camus (1939: 791) =*Quercus* ×*pseudofaginea* A.Camus (1939: 792) =*Quercus* ×*marianica* C. Vicioso (1950: 129) =*Quercus faginea* subsp. *tlemcenensis* (A.DC.) Maire & Weiller var. *tlemcenensis* f. *villiramea* Maire & Weiller (Maire 1961: 101), *comb. inval.* =*Quercus faginea* subsp. *tlemcenensis* (A.DC.) Maire & Weiller ex Greuter & Burdet. (Greuter & Raus 1982: 44)
Q. canariensis × *Q. faginea*

Lectotype (designated by Vázquez & Coombes, 2016): MPU007868! (right specimen) [digital image]!: https://science.mnhn.fr/institution/um/collection/mpu/item/mpu007868)

Notes: This hybrid type material was extensively collected between Tlemcen and Bouira (Algeria), in mixed forests with *Q. canariensis,* and received the name *Quercus* ×*tlemcenensis* by Trabut (Battandier & Trabut, 1905). Here the author overlooked the presence of *Q. faginea* in the oak flora of Algeria, thus assuming the participation of *Q. ilex* in his nothospecies, due to the set of characters that combines both sclerophyll and spiny leaves with the presence of the floccose indumentum of *Q. canariensis* (=*Q. mirbeckii*) (Battandier &Trabut, 1905). Such set of characters is also verifiable in the proposed lectotype (MPU007868!) (Vázquez et al., 2018), as in the several syntypes collected in the typical *locus* "Bouira, Tlemcen" (P06861500!; P06861501!; P06861504!; P06861505!; Figure 10). This agrees with the original description, and the participation of *Q. canariensis* is indisputable, while *Q. faginea* characters are also evident by the leaf shape and co-dominance of a stellate indumentum (see Figure 10) in all type-specimens. Moreover, Schwarz states *in schedula* that the lectotype specimen correspond to *Q. faginea,* endorsing the participation of the Portuguese oak in the admixture. This morphotype, that matches *Q. faginea* leaf shape, and the floccose indumentum of *Q. canariensis,* also occurs in Southern Portugal. Conversely, the reverse morphotype, presents wide lanceolate leaves, like those of *Q. canariensis*, with more than eleven secondary nerves, becoming glabrescent with the presence of scattered stellate trichomes. This morphotype traditionally received the name given by Vicioso (1950) as *Q.* ×*marianica*, becoming the widespread name for this nothospecies when following several recent authors (Vasconcellos & Franco, 1954; Saénz de Rivas & Rivas-Martínez, 1971; Rivas-Martínez & Saénz, 1991; Vila-Viçosa, 2012; Vila-Viçosa et al., 2014; Vila-Viçosa et al., 2015). Nonetheless, the recent molecular analysis performed by Vila-Viçosa et al. (2021) reveals that both morphotypes broadly correspond to the introgression between *Q. canariensis* and *Q. faginea*, being *Q.* ×*tlemcenensis* the prior name for this nothotaxon in the western Mediterranean Basin. Several synonyms should be considered, as the most common ones are *Q.* ×*fagineomirbeckii* Villar (1938: 450), *Q.* ×*jahandiezii* A. Camus (1939: 791), *Q.* ×*maroccana* (Braun-Blanq. & Maire) Villar (1943: 3), *Q.* ×*pseudofaginea* A. Camus (1939: 792), and *Q.* ×*marianica* C. Vicioso (1950: 129).

Biogeography: Monchique County (Vila-Viçosa & Arsénio, 2021)

Syntaxonomy: *Quercenion rivasmartinezii-suberis*

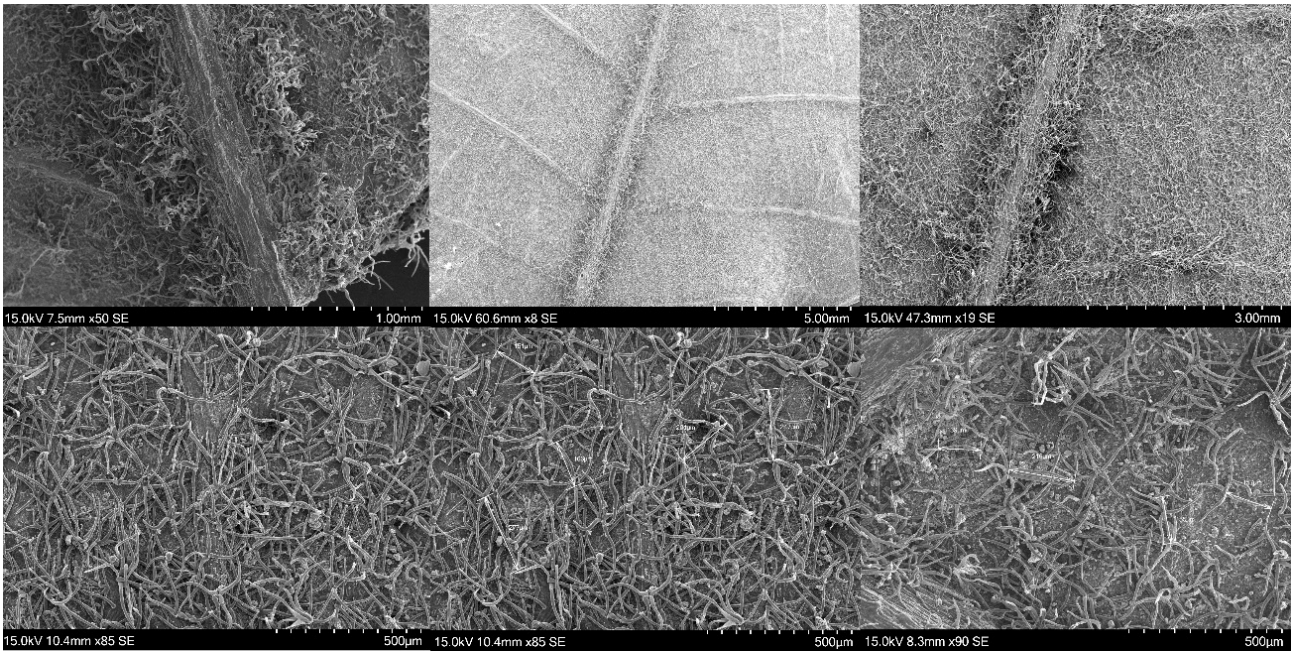

Figure 10. SEM imagery of the abaxial leaf surface, retrieved from the syntype of *Q.* ×*tlemcenensis* Trab. from Bouira (Algeria) (P06861505! http://coldb.mnhn.fr/catalognumber/mnhn/p/p06861505). Upper row showing both fuzzy fasciculate indumentum in the midrib, characteristic of *Q. canariensis* (*Q. mirbeckii*) and the stellate indumentum of *Q. faginea* on the leaf blade. Bottom row shows detailed images of *Q. faginea* stellate trichomes with rays up to *ca.* 280 µm long.

23. *Quercus* ×*welwitschii* Samp. (1910: 123) *non* Gandoger *nom. illegit.* ≡*Quercus* ×*neomairei* A. Camus (1937: 28) Camus (1938: 408) =*Quercus* ×*henriquesii* Franco & Vasconcellos (Vasconcellos & Franco 1954: 25) ≡*Quercus* ×*andegavensis* Hy nothosubsp. *henriquesii* (Franco & Vasc.) Rivas-Martínez & Sáenz (1991: 104).

Q. estremadurensis × *Q. pyrenaica*

Lectotype (designated here): Portugal. Beira-Litoral: Coimbra, Mondego, 5 August 1848, *Welwitsch s.n.* (LISU – 10402!)

Notes: Type material (LISU: 10402!), collected by Welwitsch under *Quercus pubescens* Brot. was labelled as "*Q. toza* × *Q. lusitanica*" by Coutinho (1888), regarding the putative hybridization between *Q. pyrenaica* and *Quercus faginea*. Sampaio (1910) named it for the first time as *Q.* ×*welwitschii,* dedicated to the collector. Later, the binomial *Q.* ×*neomairei* Camus (1937; 1938) was applied to the same specimen and was used by Vasconcellos & Franco (1954) and Franco (1990). The name *Q.* ×*welwitschii* Samp. was

neglected by Govaerts & Frodin (1998), under the argument of an absent Latin description, but the same authors paradoxically accept the name *Q.* ×*coutinhoi* Samp. (1910:123) described likewise, in the same work and page. Despite the alleged participation of *Q. faginea* and *Q. pyrenaica* in the type specimen (LISU: 10402!), Welwitsch refers *in schedulla* "*…frutex in sylvaticis…socialis c. Q. pedunculata et Q. lusitanica*" reporting the presence of a pedunculate oak in the population. Accordingly, the studied type material presents a pubescent to glabrescent abaxial leaf surface, with a single indumentum of fasciculate trichomes and total absence of stellate ones. In addition, the plant possesses a quite short petiole and a rhomboidal leaf shape, with acute lobes, which led us to infer that it has the participation of *Q. estremadurensis* and not *Q. faginea*, besides *Q. pyrenaica*. Furthermore, the studied types of *Q.* ×*henriquesii* Franco & Vasconcellos (LISI!) from Sintra, with the alleged introgression of *Q. orocantabrica* and *Q. pyrenaica* (Saénz de Rivas & Rivas-Martínez, 1991) also correspond to *Q. estremadurensis* as parent species, as it is observed in all type locations for *Q.* ×*welwitschii* and its synonyms.

Key for native and sub-spontaneous taxa

1. Evergreen trees or shrubs; sclerophyllous leaves, with entire, dentate, or serrate margins. 2
1'. Marcescent, brevi-deciduous to deciduous trees or shrubs, with softened leaves, dentate, serrate, crenate to lobate or pinnately lobed, to pinnatifid margins. 8
2. Shrubs; sometimes trees, with concolor adult green leaves, varying from completely glabrous in both abaxial and adaxial leaf surface to pubescent and sometimes heavily tomentose. 3
2'. Trees, with discolours leaves, having a thick greyish indumentum of stellate and fused stellate indumentum on abaxial leaf surface. 6
3. Shrubs, sometimes trees with glabrous to sub-glabrous mature leaves, especial in abaxial leaf surface with free to weakly appressed (imbricate) cup scales, the median mostly patent or recurved in maturity, the upper ones soft, the lower sometimes acuminate and pungent. 4
3'. Shrubs, sometimes trees with mature pubescent to heavily tomentose leaves. 5
4. Shrubs with glabrous, curled, and green leaves, with spiny serrate to dentate margin; short broad cupoliform (acetabuliform) to short cylindrical cups (ratio length/breadth up to 0.5) with elongated partially connate scales, sometimes spiny and erect; petiolate leaves. ..... *Q. coccifera*
4'. Trees to dendroid shrubs reaching 17 m high, with a distinct bole; adult leaves glabrous to sub-glabrous, sometimes with fused-stellate indumentum in the limb base, near the midrib; normally sub-sessile to sessile and flat, or with short petiole (<3 mm); dark brown and thick hemispheric to long cylindrical cups (ratio length/breadth greater than 0.5), with elongated fla scales, free, sometimes acuminate, partially hidden acorn (>1/2)..... *Q. pseudococcifera*
a) As above (4') with thick nearly cylindrical trigonous and acuminate scales, often retroflex in maturity. .....*Q. pseudococcifera* subsp. *rivasmartinezii*
b) As above (4') with corky orangish bark and lanceolate leaves, dark green on adaxial leaf surface and pubescent on abaxial leaf surface, large and totally free cup-scales, retroflex in maturit . ..... *Q.* ×*capeloana*
c) As above (4'), with appressed-fused scales. ... *Q.* ×*coscojosuberiformis*
5. Trees to dendroid shrubs; adult leaves pubescent to heavily tomentose (indumentum sometimes with light-brown rusty colour) on both abaxial and adaxial leaf faces; with multiradial, ramified and stipitate (stipe up to 100 µm) trichomes with large rays (> (250) 300 µm-400 (500) µm) on both abaxial and adaxial leaf faces; Hemispheric cups with free arcuate and thin scales and half-hidden to hidden acorns. ...*Q. airensis* (Figures 1 and 2e,f)
5'. Shrubs with pubescent leaves, having a greyish indumentum of simple and fused-stellate trichomes with short rays (<150 µm) in both abaxial and adaxial faces; total absence of stipitate trichomes; either with appressed cup scales or free rigid and thick ones; proximal secondary veins perpendicular with the midrib, bifurcating heavily; leaf shape architecture like *Q. rotundifolia*. .....*Q.* ×*eborense* (Figures 1a, b)
6. Presence of well-developed cork or corky bark (phellem) with discolour adult leaves, convex towards the adaxial face; pubescent with greyish indumentum of simple, stellate and fused-stellate trichomes; sinuous midrib; the secondary veins inserted with acute angles, (< 40-50≡); never bifurcating in tertiary venation; free cup scales, frequently biennial fructification. ..... *Q. suber*
a) Suberoid to fusiform bark, or with incipient cork; secondary veins inserted in > 45≡ angles, often bifurcating and turbinate cup.... *Q.* ×*avellaniformis*
6'. Absence of a corky bark (phellem); adult leaves with straight midrib; the secondary veins uncertain, forming in the proximal half angles higher than 50-80≡, normally bifurcating in tertiary venation. 7
7. Oblong-obovate to ovoid, or suborbicular leaves; with less than 7 pairs of secondary veins, petiole < 8 mm..... *Q. rotundifolia*
a) As above, with greenish abaxial leaf surface, fully pubescent, greyish to dark brown cup, with plicate to slightly free and patent scales. ..... *Q.* ×*almeidae*
7'. Lanceolate to oblong-lanceolate leaves with entire to sub-entire margins, normally with more than (7) 8 pairs of secondary veins and petiole > 1cm. .**Q. ilex*
8. Trees or shrubs with glabrous to glabrescent mature leaves, sometimes with scarce indumentum in abaxial leaf surface, mainly in the midrib and secondary veins. 9

8'. Trees or shrubs with mature pubescent to tomentose leaves. 13
9. Glabrous to glabrescent and cuneate leaves, with lobed to pinnately lobed margins, sometimes slightly pubescent with short simple (and bifurcated) trichomes in the abaxial leaf face and pedunculate fruits (> 5 cm). .....10.
9'. As above with glabrescent to pubescent abaxial leaf surface, with scarce stellate or fasciculate trichomes with lobed to crenate or pinnately lobed and dentate leaf margins. 12
10. Regular rhomboidal and sclerophyllous leaves, with acute and equal lobes and (6)8-12(14) secondary nerves, rectilinear and parallel; without or rarely with sinual nerves in the base; glabrescent to pubescent, provided with single/bifurcate trichomes throughout the midrib and ramifie trichomes throughout the abaxial leaf surface; with a developed petiole (5)8-15(18) mm; large peduncle (> 8 cm), sometimes with dark simple trichomes; with numerous scales that are large in the base of the cup, becoming smaller fast towards the apex. ..... *Q. estremadurensis*
10'. Irregular leaf shape, with sinuate-lobulate or pinnatilobate margins, with uneven and deep obtuse and round lobes, 4-8(9) secondary nerves; with glabrous to glabrescent branches; glabrescent peduncle and short petiole (<5 mm). 11
11. Thick and progressively obovate leaves (larger in the apical half); obtuse and uneven lobes (>6 (8)), with frequent sinual and intercalary veins; variable petiole ((2) 5-12(15) mm) sometimes marcescent; young branches and abaxial leaf surface, with scarce simple trichomes; big cups 18-25 mm, with brown scales, larger and free in the base becoming smaller and merged in the apex. ..... *Q. orocantabrica*
11'. Young shoots glabrescent to pubescent, thick blade, matt in adaxial leaf surface; pubescent leaves with crenate to pinnatifid ma gins. 12
12. As 10, with pinnatifid to pinnately lobed thick leaves, with acute lobes, glabrescent to pubescent, with scarce fasciculate and simple trichomes, mainly in the midrib or denser in the abaxial leaf surface, often with pedunculate fruits..... *Q. ×welwitschii*
a) As 10 with lobulate to crenate margins, glabrescent to pubescent with scarce stellate trichomes in the abaxial leaf surface, sympatric with *Q. estremadurensis* ..... *Q. ×coutinhoi*
12'. As 11 with pinnatifid to pinnately lobed leaf margins and glabrescent to pubescent abaxial leaf surface, short petiole, and regularly pedunculate fruits, with scarce indumentum of fasciculate trichomes with long rays (>0.5 mm), mainly in the midrib and secondary veins. ..... *Q. ×tavaresii*
a) As 11, mostly shrubs, with serrate to sinuate-lobulated margins, sub-sessile leaves; sometimes with entire leaf margin in the proximal third, with scarce stellate and multistellate trichomes in abaxial leaf surface, sympatric with *Quercus orocantabrica*. ..... *Q. ×gallaecica*
b) As 11, with dentate to crenate leaves, with cuneate basis and scarce or homogeneously distributed stellate trichomes in the abaxial leaf surface, sympatric with *Q. orocantabrica*. ..... *Q. ×duriensis*
13. Leaves with more than 10 pairs of secondary veins that are rectilinear (almost parallel), with obovate or progressively obovate towards the apex, crenate to serrate margins, usually glabrescent or slightly pubescent, with cotton-like deciduous indumentum of fasciculate-stipitate trichomes (sometimes reddish in drier stations and total absence of stellate trichomes) in the midrib and axils of the secondary veins, that becomes deciduous. .....*Q. canariensis*
a) As above, with single indumentum of stellate trichomes and absence of fuzzy fasciculate indumentum in the midrib and secondary nerves. ..... . *Q. ×tlemcenensis*
13'. Leaves with less than 10 pairs of secondary veins, with sinuate-lobulated to crenate-serrate or pinnately lobed to pinnatifid margins, from pubescent to tomentose abaxial leaf surface with fasciculate and/or stellate trichomes. 14
14. Trees with leathery leaves, velvety in both leaf surfaces, mostly with pinnatifid margins, but sometimes crenate to pinnately lobed, from pubescent to tomentose abaxial leaf surface, with dominance of fasciculate trichomes, with large rays (> (0.3)0.5 mm). ..... *Q. pyrenaica*
14'. Trees or shrubs with serrate, crenate, denticulate to lobulated margin, from glabrescent to tomentose abaxial leaf surface with dominance of stellate, multistellate and multiradial trichomes. 15
15. Shrubs up to 3 m high, with flat and almost sessile (petiole up to 3 mm) cuneate leaves, commonly with partial entire margin in the proximal third, serrate to dentate (occasionally lobulated) in 2/3 thirds of the leaf; glabrous to tomentose, with stellate and multistellate indumentum, sometimes pedunculated fruits. ..... *Q. lusitanica*
a) As above (15), with crenate to serrate margin, with entire first third of the leaf margin and double thick indumentum of stellate and multistellate trichomes with long rays (>180 μm), sympatric with *Q. faginea*. ..... *Q. ×aruciensis*
b) As above (15), with greyish indumentum, with ovate-obovate to lanceolate leaves; entire in the first third (proximal), the second and distal thirds serrate to denticulate, with mutic mucrons and pubescent petiole. Adaxial surface lamina glabrescent, abaxial surface lamina tomentose, with stellate, multistellate, radiate, and simple trichomes. Secondary veins bifurcate in the apex, perpendicular with the midrib in the proximal half of the leaf. ..... *Q. ×alvesii*
c) As above (15), up to 2 m, with serrate and mucronated leaves and greyish indumentum, secondary veins forming acute angles with the midrib, with stellate, multistellate and simple trichomes in the midrib, leaf architecture similar to *Q. suber*. ..... *Q. ×celtica*
d) As above (15), up to 3 m with serrate to pinnatifid margins, fully tomentose with both stellate and

multistellate trichomes, plus fasciculate trichomes with long rays (>0.5 mm), sympatric with *Quercus pyrenaica*. .....*Q.* ×*diegoi*

15'. Trees or shrubs with serrate-dentate to crenate margins, glabrescent to tomentose, with stellate, multistellate, multiradial, fasciculate or single trichomes. 16

16. Trees or shrubs with almost sessile leaves (petiole up to 0.5 cm), lobulate (acute lobes), to serrate-dentate margins, glabrescent, with stellate and multistellate trichomes below, and pedunculate fruits (Subsection *Hartwissianae* × Subsection *Macrantherae*). 17

16'. Trees with flat or curly leaves, pubescent to tomentose abaxial leaf surface, crenate to serrate-dentate margin with single indumentum of stellate and multistellate trichomes. 20

17. Shrubs, sometimes trees, with entire margin in the first third, lobed or lobulate (acute lobes), to serrate margins, glabrescent abaxial leaves, with stellate and multistellate trichomes, through the lamina and simple trichomes in the midrib, fruits with a well-developed peduncle. 18

17'. Trees with crenate-lobulate to dentate-serrate margins, normally with cordate leaf basis, glabrescent with single and scarce stellate indumentum, and pedunculate fruits. 19

18. Rhomboidal cuneate leaves, with entire margin in the first third, lobed or lobulate (acute lobes), to serrate margins, glabrescent abaxial leaves, with stellate and multistellate trichomes, through the lamina and simple trichomes in the midrib, fruits with a well-developed peduncle, sympatric with *Q. estremadurensis*. ..... *Q.* ×*sampaioana*

18'. Mostly shrubs, with cuneate and sub-sessile leaves, with serrate to sinuate-lobulate margins, with obtuse and uneven lobes, sometimes with entire leaf margin in the proximal third, having sinual and intercalary veins; with scarce stellate and multistellate trichomes on abaxial leaf surface, short petiole (< 3 mm), sympatric with *Q. orocantabrica*. ..... *Q.* ×*gallaecica*

19. Glabrescent leaves with dentate to serrate margins, or crenate to lobulate sometimes mucronate, with cordate base, short petiole (< 0.5 cm); scarce stellate indumentum with short rays (<150 μm) on abaxial leaf surface; simple trichomes mainly through the midrib, with pedunculate fruits, sympatric with *Q. estremadurensis*..... *Q.* ×*coutinhoi*

19'. As above, with uneven lobes and sinual nerves, sympatric with *Q. orocantabrica*. ....*Q.* ×*duriensis*

20. Trees with long flat oblong to obovate and ovate leaves, pubescent to tomentose abaxial surface; crenate-lobulate to serrate or dentate margins; with stellate and multistellate indumentum. ..... *Q. fagineaa*) As above with spiny leaves, greyish indumentum, of both stellate with large rays, with proximal secondary veins perpendicular with the midrib, bifurcating heavily. ..... *Q.* ×*tentudaica*

b) As above with crenate to pinnatilobed margin, fully tomentose with double indumentum of stellate and fasciculate trichomes with large rays (>0.5 mm), sympatric with *Q. pyrenaica*. ..... *Q.* ×*alentejana*

20'. Trees with oblong to obovate and ovate leaves, with crenate to serrate margin, with a double indumentum formed of the same stellate and multiradiate trichomes, plus the fasciculate, fuzzy and cotton like indumentum on the midrib and leaf base, sympatric with *Q. canariensis*. .....*Q.* ×*tlemcenensis*

Discussion

The taxonomical model here proposed is found to be largely coherent with recent synchorological, syntaxonomical and with molecular analysis, concerning the white oak (Vila-Viçosa *et al*., 2021). At the infrasectional level, our results are congruent with the segregation of two subsections (*Macrantherae* (Maleev, 1935) and *Hartwissianae* (Maleev, 1935) inside section *Quercus*. These are supported by morphological trait combinations, that are transitional across both subgroups and is consistent with the southern European and circummediterranean biogeography and ongoing molecular surveys (Vila-Viçosa *et al*., 2021). Submediterranean taxa (Subsection*Macrantherae*), usually found around the borders between Temperate and Mediterranean biomes - i.e. the transition of Euro-Siberian and Mediterranean subregions in southern Europe - share the same type of trichomes and similar edaphoclimatic envelopes. On the other hand, subsection *Hartwissianae* encompasses those taxa, in need of the increment of annual and summer precipitation, dominantly distributed across the Temperate bioclimatic belt, but preserved in Atlantic refugia, inside the submediterranean ecotone across southern European Peninsulas (Vila-Viçosa *et al*., 2020b). Therein, azonal conditions of soil moisture and horizontal precipitation compensate for summer aridity months, thus functioning as a proxy of temperate conditions by diminishing precipitation seasonality (Vila-Viçosa *et al*., 2015; Vila-Viçosa *et al*., 2020b). Subsection *Hartwissianae* incorporates broad *Q. petraea* and *Q. robur* species-syngameon, while subsection *Macrantherae* aggregate former Sections *Galliferae* and *Dascia* (Schwarz, 1936a), as the elected type-species combines transversal morphological characters to the species inside their respective section.

Regarding the populations of the Iberian pedunculate oaks (*Q. gr. robur*), *Quercus estremadurensis* seems to be a consistent species, as the confusion with *Q. orocantabrica* (=*Quercus robur* subsp. *broteroana*) is clarified. Nomenclatural difficulties in sorting out subordinate taxa, lead historical authors to the parsimonious solution of considering such taxa in the broad variation of *Q. robur*. Nevertheless, both *Q. orocantabrica* and *Q. estremadurensis,* possess high morphological plasticity and preserve high molecular

differentiation against the European *Q. robur* (Vila-Viçosa *et al*., 2021). The latter analysis confirmed that the western Iberian pedunculate oak populations, belong to *Q. orocantabrica*, and not the European *Q. robur,* as stated by past references (Schwarz, 1937; Rivas-Martinez & Saénz de Rivas, 1911. The presence of substantial morphological and molecular divergence of the Iberian pedunculate oaks, enhances its important role in the evolutionary history of these lineage of temperate oaks, namely as tertiary relicts inside subsection *Hartwissianae,* as suggested by Schwarz (1935; 1936a) and Montserrat (1957).

We recover the name *Q. faginea* Lam. to stand for the whole of the southern and western Iberian populations of the Portuguese oak, as proposed by Vasconcellos and Franco (1954). The morphological and type material analysis complemented with the ongoing molecular studies cannot find coherent infraspecific differentiation inside *Q. faginea*, especially regarding to the western Iberian subpopulations (Vázquez *et. al*. 2020; Vila-Viçosa *et. al*., 2021). The latter molecular works fully corroborates the assumptions of Villar (1958), that amplifies the area of this taxon up to the Douro thermophilic Basin, incorporating the *Spiraeo obovatae-Quercetum faginea* (Bolós & Montserrat, 1984; Loidi & Herrera, 1990) forests, contrarily to the widely assumed northern-limit between its putative subspecies around the Salamanca Sector (Franco, 1990; Rivas-Martinez & Saénz, 1991; Rivas-Martinez, 2017).

We should remark that forest fragmentation and land use changes after the Last Glacial Maximum contraction scenario, followed by periods of climatic amelioration, especially the Bølling–Allerød period, and the Early and Mid-Holocene, favoured interleaving expansions and contractions of oak forests (Lowe and Walker, 1984; Carrión *et al*., 2010; Vila-Viçosa *et al*., 2020b). This promoted genetic exchange between previously isolated populations and the establishment of hybrid swarms (Vila-Viçosa *et al*., 2020b). However, the recurrence of certain morphological characters as, for example, the conservative character of trichome-type, still observable in selective environments, provides insights on the hypothesis of putative phylogenetic relationship between existing species. This phenomenon most likely relies on the auto-ecological segregation of constant taxonomic character correlations, in response to environmental filtering. Likewise, the same phenomenon probably happened among both *Q. estremadurensis* and *Q. orocantabrica* with *Q. faginea* in Western Portugal and the Douro valley. During the Holocene, reduced seasonality and less severe summers and winters promoted bidirectional migrations of the roburoid oaks along a Northern-Southern and Western-Eastern gradients, leading to the formation of the known hybrid-swarms (*Q.* ×*coutinhoi* and *Q.* ×*duriensis*).

The western Mediterranean Kermes oak complex (*Quercus coccifera s.l.*) encompasses three taxa that are, in a way, coherently vicariant to the proposal of Kasapligil (1981) for eastern Mediterranean oaks. We here highlight the recover of *Q. airensis* Franco & Vasconcellos*.,* related with the original concept of *Q. calliprinos* Webb, as a western species and so far, misunderstood with broad hybrids between *Q. coccifera* and *Q. rotundifolia*. This proposal is congruent with the vicariancy presented by *Q. aucheri* (Serteser *et al*., 2009). *Q. airensis* is prominently distributed through northern Morocco and Portugal, with a Tingitan-Onubo-Algarvian distribution (Latorre *et al.*, 1996), and grows in Cenozoic karst and marly limestones in hyperoceanic areas, being however recognized by Laguna (1883: 266) in Montes de Toledo (Albarda, Spain). The recognition of a western Mediterranean arboreal kermes oak (*Q. pseudococcifera* Desf.) is in accordance with the original concepts of Desfontaines, 1799, Webb (1838) and Amo (1861), in which *Q. rivasmartinezii* is incorporated (Vila-Viçosa *et al*., 2022a). Nevertheless, an in-depth molecular work, preferably with next-generation sequencing tools, inside the western Mediterranean Section *Ilex* is a demanding task to solve at the population and species level, all these inferences brought by the nomenclatural and morphological analysis.

Conclusions

We provided a full update of the Portuguese oak species and nomenclature, which was enrolled in a conundrum and lacked an in-depth approach to the type materials and literature, since the most recent reference-works. By combining herbaria and literature review, with fieldwork, and supported by ongoing molecular surveys, we disclosed ongoing taxonomic and nomenclatural uncertainties to a high number of taxa and nothotaxa.

The higher diversity of morphological traits observed among the white oaks in the western and southern Iberian Peninsula, allows us to consider the western Iberian Peninsula as a likely candidate for a diversification centre for this group of oaks, when compared to European and circummediterranean counterparts. The notorious wealth of paleoclimatic relictual elements assumes an exceptional territorial cohesion, in western Portuguese mainland, including southern mountains and seashore. Notably, we can highlight the occurrence-areas of *Quercus canariensis* and *Q. estremadurensis* as tertiary paleoclimatic relicts for this biogeographic enclosure, that is enhanced by *Q. orocantabrica* in the north-central quadrant of the Iberian Peninsula.

Accordingly, we supported the rearrangement of former infrasectional classifications (Subsections *Macrantherae* and *Hartwissianae*)*,* based in consistent morphological and biogeographic transitional traits. Broadly, marcescent species are related to both tertiary paleoclimatic relictual areas and submediterranean ecotones and exhibit a disjunct amphimediterranean distribution. The forests they form have been biogeographical bridges between Eurosiberian and Mediterranean subregions, often hybridizing with other oaks inside Sections *Quercus*. Oaks in these sections are mesophytic but simultaneously adapted to Mediterranean conditions. Examples of such drought-adapted traits are leaf scleromorphy and an often-persistent indumentum-type in the abaxial surface.

We expect our proposals to be compared with extensive phylogeographic and molecular analysis to validate morphological analysis and to evaluate any involuntary taxonomic inflation, especially among the evergreen oaks (Section *Ilex*).

Finally, we highlight the urgent necessity to rehabilitate the classic practice of taxonomy, linked with the exercise of biogeography and geobotany, as valuable sources for stablishing stronger taxonomic and evolutionary hypotheses. We think our work stresses the contributions of extensive fieldwork, museology, and historical botany as key cornerstones for taxonomic awareness, that can be perfected by molecular tools.

We contributed to the knowledge of the Iberian and western Mediterranean oak forest biogeography and plant diversity, updating the nomenclature and taxonomic delimitation of an important group of woody plants. This work better serves any conservation efforts and decision making in a paradigmatic Biome like the Mediterranean forests and scrubs.

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Author contribution statement

All authors cotribute similarly to the manuscript.

Conflict of interest

None

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