Phytotaxa 641 (3): 183–190
https://www.mapress.com/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.641.3.1

Finding the last missing white oak hybrid from the Iberian Peninsula (Fagaceae, *Quercus*, sect. *Quercus*)

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Abstract

The genus *Quercus* is widely known for its ability to hybridize among sympatric species, especially inside the same Section. The Iberian Peninsula is a major phylogeographic hotspot for oak diversity, with almost all possible combinations of hybrids already described inside sect. *Quercus*. In this work we present the remaining hybrid not yet described among the Iberian white oaks; we found it in one of the few areas (in the Southern Iberian Peninsula) where both parents (the Algerian oak, *Q. canariensis*, and the Lusitanian dwarf oak, *Q. lusitanica*) grow sympatrically. We provide a description of this nothotaxon (which we named *Quercus* ×*gaonae*) based on morphological characters related to leaf shape and trichome analysis. This work emphasizes the practice of natural history and encourages botanists to keep up their work on describing plant diversity in a major hotspot like the Mediterranean Basin.

Key words: Mediterranean forests, nothotaxa, taxonomy, biogeography

Introduction

The genus *Quercus* Linnaeus (1753: 994) is one of the most important of woody plants, mostly comprising the top climax stages of various Northern Hemisphere forest ecosystems (Manos & Stanford 2001, Aldrich & Cavender-Bares 2011, Carrero *et al.* 2020). Oaks are consistently regarded as one of the models to question the biological species concept, since they possess minimal barriers to gene flow in natural populations (Petit *et al.* 2004, Lepais *et al.* 2013, Hauser *et al.* 2017). This genus is regarded as a species syngameon, wherein species can maintain their primary and well-defined morphological and molecular barriers, while also undergoing considerable genetic information exchange through hybridization (Lotsy 1925, Grant 1981, Cannon & Petit 2020). With nearly half of the Mediterranean oak species, the Iberian Peninsula is appropriately regarded as a hotspot and refugium, particularly for the white oaks (sect. *Quercus*) (Schwarz 1964, Rivas-Martínez & Saénz 1991, Olalde *et al.* 2002, Carrero *et al*. 2020).

Classical natural history has reported on the idea of known widespread hybridization among Iberian oaks, with Brotero (1805) and Coutinho (1888) the first authors to mention hybridization among Portuguese oak species. In the twentieth century, several works provided comprehensive and extensive reviews of oak hybrid classification and nomenclatural endorsements for a high number of nothotaxa occurring in the Iberian Peninsula (Sampaio 1910, Camus 1934, 1935, Schwarz 1936, Camus 1939, Vicioso 1942, 1950, Rivas-Martínez & Saénz 1991, Vázquez 1995). In the 21st century several works almost finished the review of nothotaxa for the Iberian oaks with the most recent checklist for the Portuguese oaks enumerating twenty-three nothotaxa for the country (Vázquez *et al.* 2000, 2003, 2004, 2015, 2018, Vila-Viçosa *et al.* 2014, 2023).

Among the Eurasian white oaks, the Roburoid clade (sect. *Quercus*) presents high rates of diversification during the Late Miocene (Hipp *et al.* 2020), with the more recent and comprehensive subsectional division being proposed

Accepted by Angelo Troia: 7 Mar. 2024; published: 20 Mar. 2024

by Vila-Viçosa (2023). This segregation into two clades reflects two subsections inside sect. *Quercus,* supported by morphological and phylogenetic data (*Hartwissianae* (Maleev) Vila-Viçosa, Capelo, P. Alves, R. Almeida & F.M.Vázquez (2023: 7) and *Macrantherae* (Stef.) Maleev (1935: 163)).

With all past nomenclatural, taxonomic and phylogenomic reviews, just one hybrid combination of two sympatric Iberian white oaks remained unnamed, both belonging to subsection *Macrantherae* (Vila-Viçosa *et al*. 2023). This corresponds to the hybrid between *Q. canariensis* Willdenow (1809: 975) and *Q. lusitanica* Lamarck (1785: 719). Both species can co-occur in the southern Iberian Peninsula, where *Q. lusitanica* shrublands appear in the understory of both forest associations dominated by *Q. canariensis* in southern Portugal and Spain. These are *Rusco hypophylli-Quercetum canariensis* Rivas-Martínez (1975) from Cádiz and *Euphorbio monchiquensis-Quercetum canariensis* Rivas-Martínez (1990) from Southern Portugal (Monchique) and Aracena (Spain), the only three places of overlap of both species in the western Mediterranean basin (Rivas-Martínez *et al.* 2011a).

Thus, the main objective of this work, is to describe the remaining white oak hybrid from the Iberian Peninsula, after fieldwork and botanical expeditions directed to the areas of relictual *Q. canariensis* forests, where both parent species are known to occur in sympatry.

Material and methods

Study area: The study area is located in southern Iberian Peninsula, in Andalusia (Cádiz Province). The area is in the *Los Alcornocales* Natural Park, particularly in Sierra del Bujeo (Figure 1). The lithology is inserted in the carbonate formations of the Aljibe Unit, from the Flysch Complex, which are clayey and sandy with detritic and/or carbonate composition (Luján Martínez *et al.* 2016). The bioclimatology includes the thermo- to mesomediterranean thermotypes and subhumid to hyperhumid ombrotypes (Rivas-Martínez *et al.* 2011b). The vegetation comprises the paleoclimatic relict forest of *Q. canariensis* (*Rusco-Querco canariensis* Rivas-Martinez, 1975), enriched with evergreen large-leafed lauroid elements with *Senecioni lopezii-Quercetum lusitanicae* Rivas Martínez in Rivas-Martínez *et al.* (2002) in the understory of the fog-forest.

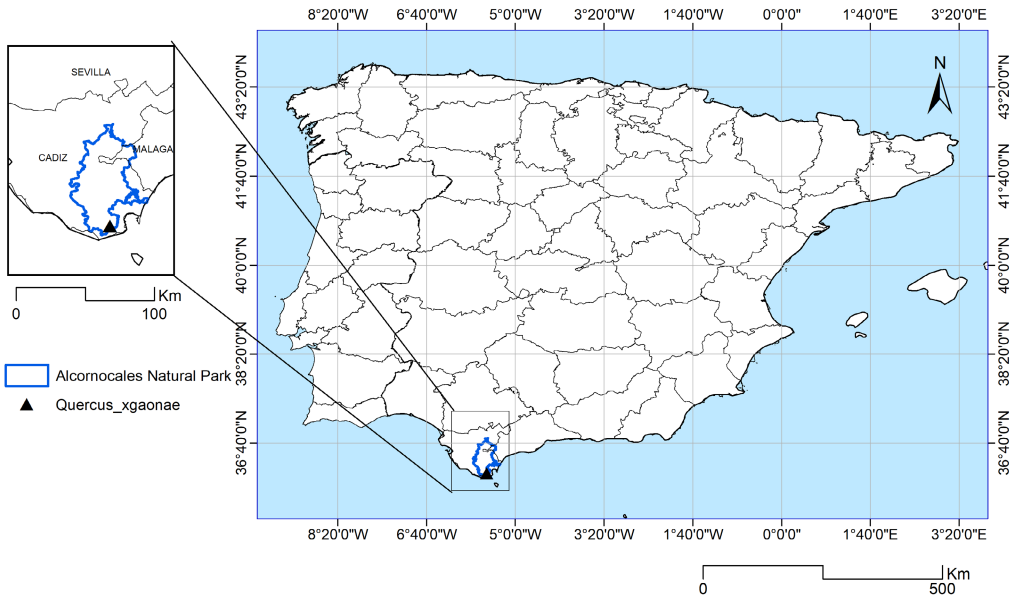

FIGURE 1. Location of the study area (Los Alcornocales Natural Park, in blue), in the Province of Cádiz and the location of the hybrid *Quercus ×gaonae*.

Taxonomic and morphological analysis and treatment of the new nothotaxon: The taxonomic approach relies on the taxonomic expertise and knowledge of the authors, combined with extensive field and taxonomic work of almost two decades on oak taxonomy in the Iberian Peninsula. The distinctive taxonomic characters rely on the observation of the clearly intermediate shape and structure of the observed specimen, found among both parental species, with clear intermediate leaf shape characters, and by possessing both types of indumentum that are exclusive to the parental species. Trichome analysis was made using the binocular magnifier of the Modular Stereo Microscope ZEISS SteREO Discovery.V20, coupled with a digital camera (ZEISS Axiocam 305 color).

Specimen for deposit as herbarium vouchers: Specimens of the new nothotaxon to be described were collected in the field and deposited at the Herbarium PO (Universidade do Porto, Portugal). Isotypes were deposited in Herbarium HSS (Research Centre of "La Orden-Valdesequera", Spain) and Herbarium LISE (Instituto Nacional de Investigação Agrária e Veterinária, Portugal). A branch of the specimen was collected in the field and grafted onto a *Q. orocantabrica* Rivas Martínez, Penas, T.E.Díaz & Llamas (2002: 706) rootstock, to be grown in the Botanical Garden of the University of Porto (Portugal).

Results

Taxonomy

Quercus* ×*gaonae Vila-Viçosa, Frias & F.M. Vázquez *nothosp. nov.* (Figs. 2,3,4 and 5)

Quercus canariensis Willd. × *Quercus lusitanica* Lam.

Type:—SPAIN. Andalusia: Cádiz, Parque Natural de los Alcornocales, Sierra del Bujeo, Ascent to Llanos del Juncal, 36.095457, -5.534832, 650 m, 09 August 2023, *Carlos Vila-Viçosa*, *Iúri Frias & José Gaona Ríos s.n.* (Holotype: PO V 72216 (Fig. 3), Isotypes: HSS 87103; LISE 96338).

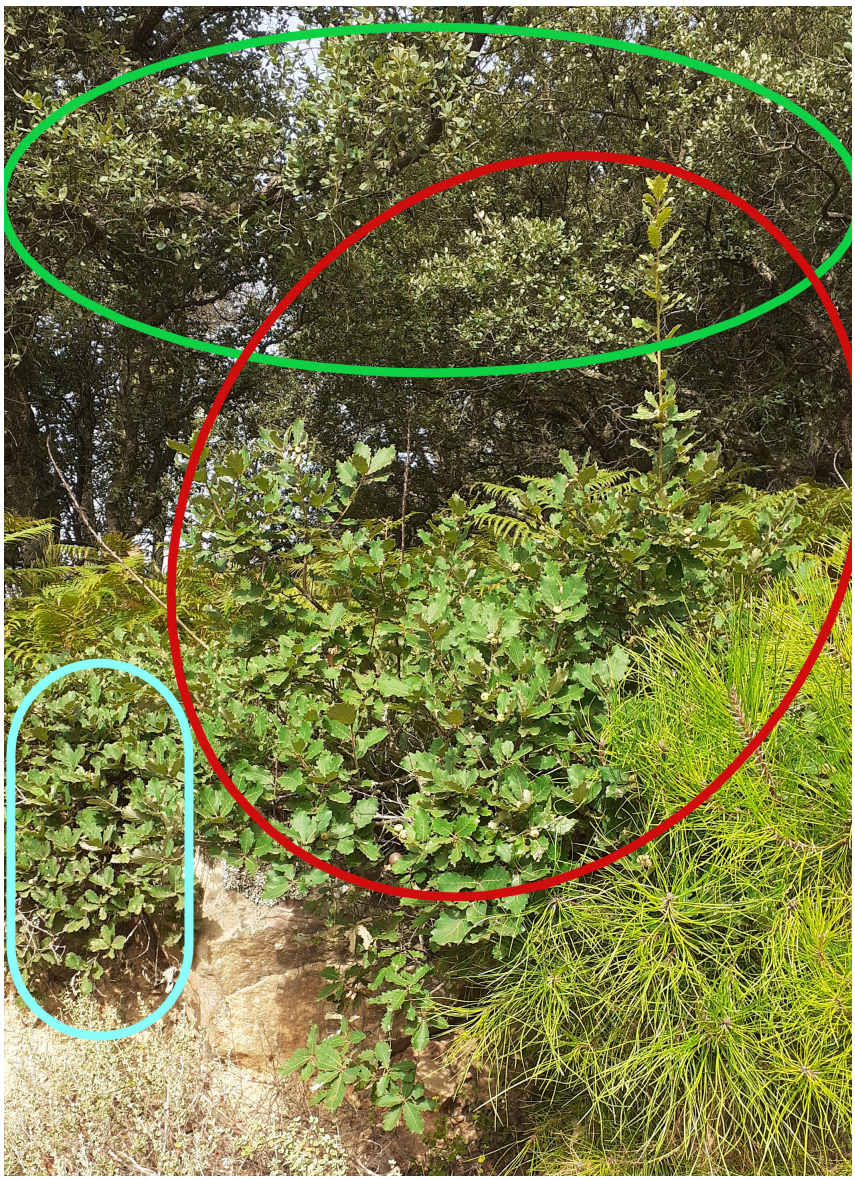

FIGURE 2. Type location of *Quercus* ×*gaonae* (middle—red oval), developing conspicuously erect shoots, among the parents, the prostrate *Q. lusitanica* (left—turquoise oval) and growing below the *Q. canariensis* arboreal layer (above—green oval).

FIGURE 3. Holotype of *Quercus* ×*gaonae* Vila-Viçosa, Frias & F.M. Vázquez PO V72216! (Porto University, Natural History and Science Museum).

Diagnosis: *Q.* ×*gaonae* is distinguished from both parents by possessing intermediate characters, such as leaves having the proximal third with entire margins, as in *Q. lusitanica*, with larger, lanceolate to rhomboidal leaves with serrate margins and some deep lobes and divaricate secondary nerves, as in *Q. canariensis* (Figs. 3 and 4). In addition to the stellate and multistellate trichomes that are characteristic of *Q. lusitanica*, it also has the deciduous, fuzzy and cotton-like yellowish tomentum, composed of fasciculate trichomes, typical of *Q. canariensis,* on the midrib and axillary veins (Fig. 5).

Description: Prostrate to erect shrub up to 150 cm tall, intermediate between the parents (Figure 2). Leaves with ovate-obovate to lanceolate and sometimes rhomboidal, blade (3)4–7(8) × (1.5) 2–4(5) cm. Most leaves with entire margin in the proximal third, the second and distal thirds serrate to dentate, sometimes deeply lobed, and a 3–9 mm short and pubescent petiole. Glabrescent adaxial leaf surface, with sparse stellate, multi-stellate, and simple trichomes on the midrib and the proximal half of the leaf. Abaxial leaf surface pubescent, covered with single, stellate, and multi-stellate trichomes, plus the presence of a deciduous fuzzy fasciculate and yellowish tomentum on the midrib, more prominent at the leaf base and the intersection of the secondary nerves with the midrib. Secondary veins often

divaricate towards the lobes with irregular shape and, as in *Quercus canariensis*, producing several leaves with deep lobes and very irregular margins.

Etymology: Dedicated to the eminent Gaditan naturalist and friend José Manuel Gaona Ríos (1971).

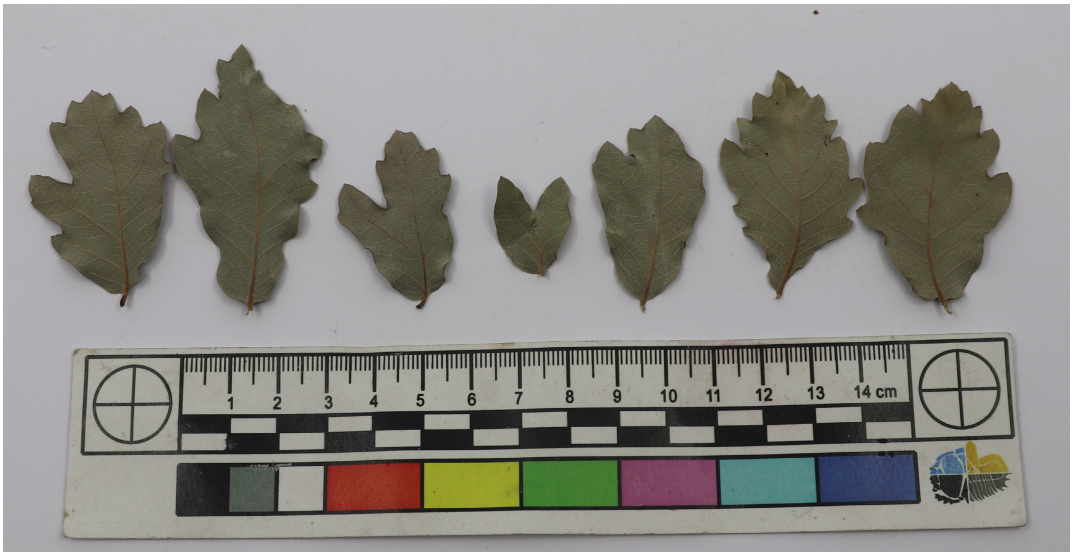

FIGURE 4. Abnormal leaf shapes of *Q.* ×*gaonae*, some with the proximal half of the leaf entire, as in *Q. lusitanica* and simultaneously with serrate margins, possessing deep lobes and divaricate secondary nerves, showing the influence of *Q. canariensis*, and indicating hybridization between these taxa.

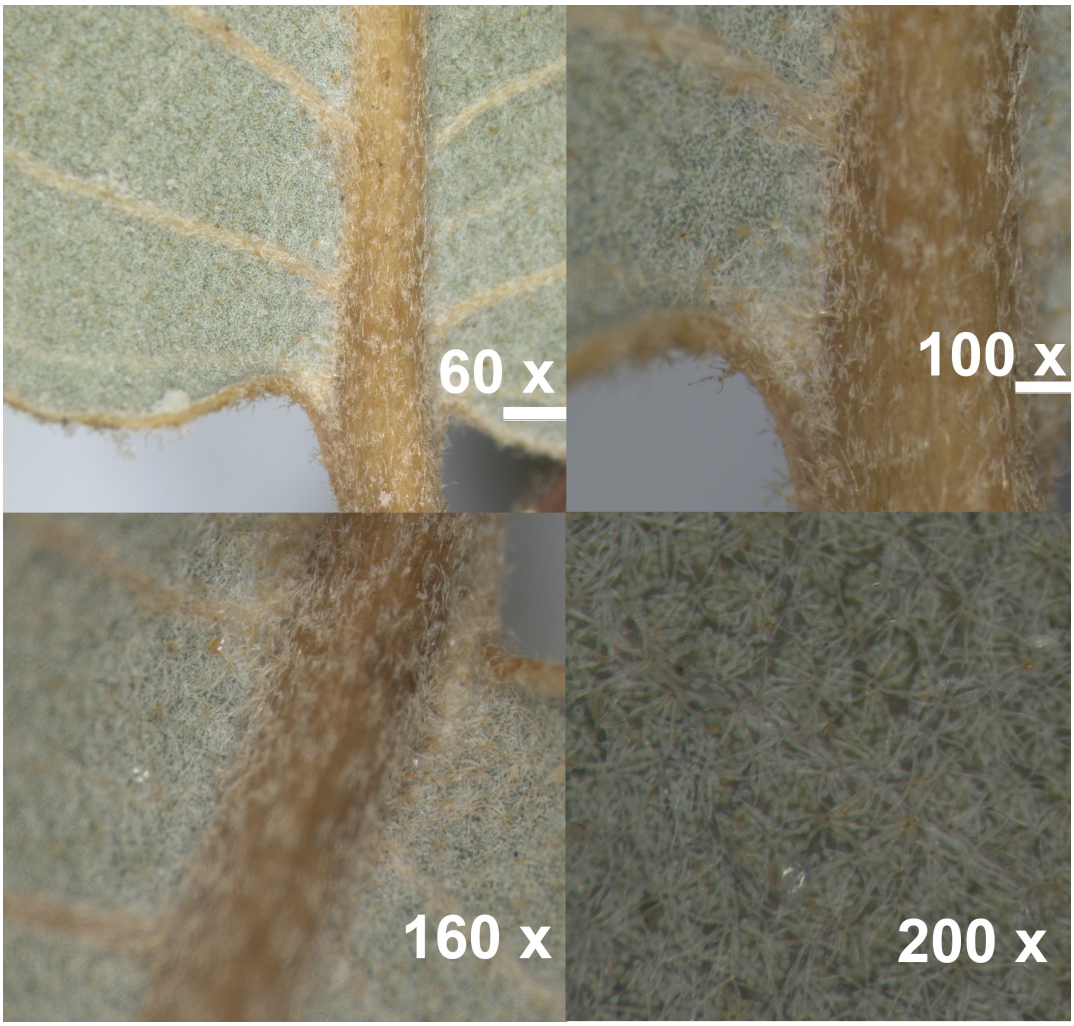

FIGURE 5. Indumentum details of *Q.* ×*gaonae*: 60×, 100× and 160×, yellowish fuzzy indumentum deriving from the parent *Q. canariensis* on the midrib and axillary veins; 200×, dominance of stellate and multistellate trichomes, deriving from the parent *Q. lusitanica*, on the abaxial leaf surface.

Discussion and concluding remarks

The Iberian Peninsula emerges as a major biogeographic landmark for understanding the evolutionary history of a paramount genus like *Quercus* in the western Palearctic Region, which is characterized by a complex and reticulate evolutionary history (Hipp *et al*. 2020, Kremer & Hipp 2020, Vila-Viçosa 2023). The global biogeographic and geobotanical knowledge about the Iberian oak forests was of paramount importance for predicting the occurrence and description of the remaining nothotaxon to be unveiled among the Iberian white oaks, where both parents potentially overlap and occur in sympatry (Vila-Viçosa *et al.* 2015). This is particularly important for the *Q. canariensis* relictual forest type that is related with the preservation of peculiar paleoclimatic conditions, in extreme Atlantic areas of the Iberian southwest, which results in an hotspot for oak species conservation (Vila-Viçosa *et al.* 2020a, Vila-Viçosa *et al.* 2020b, Vila-Viçosa & Arsénio 2021).

In spite of the existence of thorough reviews about white oak hybridization and nothotaxa description, especially provided by Camus (1939) and Vicioso (1950), these authors only endorsed the hybridization between *Q. lusitanica* and *Q. faginea* Lamarck (1975: 725) as *Q.* ×*tingitana* A. Camus (1939: 792) and *Q.* ×*aruciensis* C.Vicioso (1950: 139). The former is reported to have the participation of *Q.* ×*tlemcenensis* Trabut (1905: 308), which could uncover the putative participation of *Q. canariensis* in the admixture. However for Camus (1939), this taxonomic endorsement was related with infraspecific variation inside *Q. faginea* subsp. *broteroi* (Cout.) A. Camus (1939: 179), which is a synonym of *Q. faginea,* when following the most recent review provided by Vila-Viçosa *et al*. (2023).

The diversity of white oak species in the Iberian Peninsula turns it as a major living laboratory to understand oak species diversity and the role of hybridization in white oak evolution (Olalde *et al*., 2002; Vila-Viçosa *et al*., 2021; Vila-Viçosa, 2023). We described the remaining white oak hybrid to be found in nature, in an area that biogeographically was expected to harbor the natural cross between the Algerian and Lusitanian dwarf oak. The description was based on unequivocal intermediate morphological features between both species, with *Q.* ×*gaonae* being found exactly among both parents. This well-stablished tool of describing oak species diversity and hybridization is useful and of paramount importance to nurture future evolutionary questioning about oak evolution, together with conservation efforts and decision-making about Mediterranean forests.

We advocate that additional research should be maintained about studying and describing plant diversity and hybridization, especially by focusing on the reticulate historical biogeography of oaks in the western Palearctic Region and enlarging these efforts to vicariant populations of oak species from northern Africa, the Near East, and the southern European Peninsulas.

Acknowledgements

CVV was funded by the Scholarship UIDB/50027/2020, from the Project UP4REHAB, COMPETE 2020, contract n. 13/REACT-EU/2021.

Fieldwork obtained total or partial finance from Agenda Transform, project number C644865735-00000007, following the Mobilization Agendas for Business Innovation (Notice No. 02/C05-i01/2021), supported by the Recovery and Resilience Plan (PRR) and European Funds NextGeneration EU. More concretely Project PRR TRANSFORM – "Genetic conservation and recovery of populations of endangered indigenous species (*Quercus canariensis*)" Research Consultancy for RAIZ (Instituto de Investigação da Floresta e Papel), Navigator Forest Portugal.

We acknowledge the fruitful fieldtrips guided by José Gaona Ríos to Los Alcornocales Natural Park to study *Q. canariensis* forests.

References

Aldrich, P.R. & Cavender-Bares, J. (2011) Quercus. *In: Wild crop relatives: Genomic and breeding resources*. Springer, pp. 89–129. https://doi.org/10.1007/978-3-642-21250-5_6

Andrews, S. (1984) A reappraisal of Ilex aquifolium and I. perado (Aquifoliaceae). *Kew bulletin* 39: 141–155. https://doi.org/10.2307/4107862

Bolòs, O. de (1954) De Vegetatio notulae, I. *In: Collectanea Botanica, 1954, vol. IV.* Consejo Superior de Investigaciones Científicas (CSIC).

Brotero, F.A. (1805) *Flora Lusitanica, seu plantarum, quae in Lusitania vel sponte crescunt, velfrequentius coluntur, ex florum praesertim sexubus systematice distributarum, synopsis.* Lisboa: Typographia regia. https://doi.org/10.5962/bhl.title.45110

Camus, A. (1934) Quelques diagnoses de Fagacées. *Bulletin de la Société Botanique de France* 81: 814–818. https://doi.org/10.1080/00378941.1934.10834028

Camus, A. (1935) *Les chênes: Monographie du genre Quercus. Atlas.* (Vol. 2). Paris: Lechevalier.

Camus, A. (1939) *Les Chênes. Monographie du genre Quercus. Genre Quercus, sous-genre Euquercus (sections Lepidobalanus et Macrobalanus).* Paris: Lechevalier.

Cannon, C.H. & Petit, R.J. (2020) The oak syngameon: more than the sum of its parts. *New Phytologist* 226: 978–983. https://doi.org/10.1111/nph.16091

Carrero, C., Jerome, D., Beckman, E., Byrne, A., Coombes, A.J., Deng, M., González Rodríguez, A., Van Sam, H., Khoo, E., Nguyen Van, N., Robiansyah, I., Rodríguez Correa, H., Sang, J., Song, Y-G., Strijk, J.S., Sugau, J., Sun, W., Valencia-Ávalos, S. & Westwood, M. (2020) The red list of oaks 2020. The Morton Arboretum: Lisle, IL, USA, pp. 11–12.

Coutinho, A.X.P. (1888) Os Quercus de Portugal. *Boletim da Sociedade Broteriana* 6: 47–116.

Devesa, J.A. (1983) Notas taxonómicas y corológicas sobre la flora de Andalucia occidental. 153. El género Althenia Petit. *Lagascalia* 11: 81–117.

Grant, V. (1981) The Syngameon. *In: Plant speciation*. Columbia University Press, pp. 234–241. https://doi.org/10.7312/gran92318-037

Hauser, D.A., Keuter, A., McVay, J.D., Hipp, A.L. & Manos, P.S. (2017) The evolution and diversification of the red oaks of the California Floristic Province (Quercus section Lobatae, series Agrifoliae). *American Journal of Botany* 104: 1581–1595. https://doi.org/10.3732/ajb.1700291

Hipp, A.L., Manos, P.S., Hahn, M., Avishai, M., Bodénès, C., Cavender-Bares, J., Crowl, A.A., Deng, M., Denk, T., Fitz-Gibbon, S., Gailing, O., González-Elizondo, M.S., González-Rodríguez, A., Grimm, G.W., Jiang, X.-L., Kremer, A., Lesur, I., McVay, J.D., Plomion, C., Rodríguez-Correa, H., Schulze, E.-D., Simeone, M.C., Sork, V.L. & Valencia-Avalos, S. (2020) Genomic landscape of the global oak phylogeny. *New Phytologist* 226: 1198–1212. https://doi.org/10.1111/nph.16162

Kremer, A. & Hipp, A.L. (2020) Oaks: an evolutionary success story. *New Phytologist* 226: 987–1011. https://doi.org/10.1111/nph.16274

Lamarck, J.B. (1785) *Encyclopédie méthodique. Botanique*. Paris: Panckoucke. https://doi.org/10.5962/bhl.title.824

Lepais, O., Roussel, G., Hubert, F., Kremer, A. & Gerber, S. (2013) Strength and variability of postmating reproductive isolating barriers between four European white oak species. *Tree Genetics & Genomes* 9: 841–853. https://doi.org/10.1007/s11295-013-0602-3

Linnaeus, C. (1762) *Species Plantarum* (2 ed. Vol. 1). Stockholm: Impensis Laurentii Salvii.

Lotsy, J. (1925) Species or linneon. *Genetica* 7: 487–506. https://doi.org/10.1007/BF01676287

Luján Martínez, M., Gracia Prieto, J., Jordán López, A., Domínguez Bella, S. & Sánchez Bellón, Á. (2016) *Geología del PN de los Alcornocales en torno a Alcalá de los Gazules.* Geología.

Maleev, V.P. (1935) A Review of Oak Trees in Caucasus through theirs Taxonomical and geographical relations and concerning to evolution of group Robur. *Botanicheskiy Zhurnal* 20: 156–172.

Manos, P.S. & Stanford, A.M. (2001) The historical biogeography of Fagaceae: tracking the tertiary history of temperate and subtropical forests of the Northern Hemisphere. *International Journal of Plant Sciences* 162: S77–S93. https://doi.org/10.1086/323280

Olalde, M., Herrán, A., Espinel, S. & Goicoechea, P.G. (2002) White oaks phylogeography in the Iberian Peninsula. *Forest ecology and management* 156: 89–102. https://doi.org/10.1016/S0378-1127(01)00636-3

Petit, R.J., Bodénès, C., Ducousso, A., Roussel, G. & Kremer, A. (2004) Hybridization as a mechanism of invasion in oaks. *New Phytologist* 161: 151–164. https://doi.org/10.1046/j.1469-8137.2003.00944.x

Rivas-Martínez, S. (1975) La vegetación de la clase Quercetea ilicis en España y Portugal. *Annales del Instituto Botanico de A.J. Cavanilles* 31: 205–259.

Rivas-Martinez S., Aguiar C., Aguilella A., Alonso R., Alvarez M., Amich F., Arnaiz C., Baccheta G., Barbero M., Barbour M.G., Bartolome C., Barreno Eva, Belmonte D., Benabid A., Luis Benito J., Bermejo E., Biondi E., Biurrun I., Blasi C., Bohn U., Boira H., de_Bolos O., Box E.O., Brullo S., Bueno A., Cabezudo B., Capelo J., Carrillo E., Carlos Costa J., Crespo A., Crespo M.B., Deil

U., Dias E., Duarte C., Escudero A. & Espirito-Santo D. (2011a) Map of series, geoseries and geopermaseries of vegetation in Spain. PART I. *Itinera Geobotanica* 18: 1–424.

Rivas-Martínez, S., González-Días, T.E., González, F.F., Loidi, J.J., Lousã, M.F. & Merino, Á.P. (2002) Vascular plant communities of Spain and Portugal: addenda to the syntaxonomical checklist of 2001. Part II. *Itinera Geobotanica* 15 (2): 433–922.

Rivas-Martínez, S., Lousa, M., Diaz, T.E., Fernández-González, F. & Costa, J.C. (1990) La vegetación del sur de Portugal (Sado, Alentejo y Algarve). *Itinera Geobotanica* 3: 5–126.

Rivas-Martínez, S., Rivas-Sáenz, S., Penas, A., Alcaraz, F., Amigo, J. & Asensi, A. (2011b) World bioclimatic classification system. *Global Geobotany* 1: 1–634.
https://doi.org/10.5616/gg110001

Rivas-Martínez, S. & Saénz, C. (1991) Enumeración de los Quercus de la Península Ibérica. *Rivasgodaya* 6: 101–110.

Sampaio, G. (1910) *Manual da Flora Portugueza*. Porto: Universidade do Porto.

Schwarz, O. (1936) Sobre los Quercus catalanes del subgénero Lepidobalanus Oerst. *Cavanillesia* 8: 65–100.

Schwarz, O. (1964) Quercus L. *In:* Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (Eds.) *Flora Europaea*. Cambridge University Press, Cambridge, pp. 61–64.

Vázquez, F.M., R., S. & Ruiz, T. (2000) Hybridisation processes in Mediterranean oaks from South Spain. *International Oaks Journal* 12: 108–117.

Vázquez, F.M. (1995) Híbridos de Quercus faginea subsp. broteroi (Coutinho) A.Camus en el suroeste de la Península Ibérica. *Annales del Jardín Botânico De Madrid* 53: 247–251.

Vázquez, F.M., Coombes, A.J., García, D., Márquez, F., Meireles, C., Barrena, M.J. & Vila-Viçosa, C. (2018) Anotaciones a la nomenclatura del género Quercus L., (FAGACEAE) en la Península Ibérica y NW de África. *Folia Botánica Extremadurensis* 12: 5–79.

Vázquez, F.M., Ramos, S., Doncel, E., Coombes, A.J. & Rodríguez, M. (2003) New oak hybrids from Spain. *International Oaks Journal* 14: 49–60.

Vázquez, F.M., Ramos, S. & Garcia, S. (2004) Diversity of Iberian oaks. *International Oaks Journal* 15: 31–43.

Vázquez, F.M., Sánchez Gullón, E., Pinto-Gomes, C., Pineda, M.A., García Alonso, D., Marquez García, F., Guerra Barrena, M.J., Blanco Salas, J. & Villaviçosa, C. (2015) Three New Oak Hybrids from Southwest Iberia (Spain and Portugal). *International Oaks Journal* 26: 43–56.

Vicioso, C. (1942) Materiales para el estudio de la flora soriana. *Anales del Jardín Botânico De Madrid* 2: 188–235.

Vicioso, C. (1950) *Revisión del género Quercus en España*. Madrid: Tipografía Artítica.

Vila-Viçosa, C. (2023) Natural History, Biogeography and Evolution of the Iberian white oak Syngameon (Quercus L. Sect. Quercus). University of Porto, Porto, 346 pp.

Vila-Viçosa, C., Arenas-Castro, S., Marcos, B., Honrado, J., García, C., Vázquez, F.M., Almeida, R. & Gonçalves, J. (2020a) Combining Satellite Remote Sensing and Climate Data in Species Distribution Models to Improve the Conservation of Iberian White Oaks (Quercus L.). *ISPRS International Journal of Geo-Information* 9: 735.
https://doi.org/10.3390/ijgi9120735

Vila-Viçosa, C. & Arsénio, P. (2021) Vegetação do Sudoeste Português. *In:* Capelo, J. & Aguiar, C. (Eds.) *A vegetação de Portugal*. ENCM, Lisbon, pp. 110–121.

Vila-Viçosa, C., Capelo, J., Alves, P., Almeida, R. & Vázquez, F.M. (2023) New annotated checklist of the Portuguese oaks. *Mediterranean Botany* 44: 1–32.
https://doi.org/10.5209/mbot.79286

Vila-Viçosa, C., Gonçalves, J., Honrado, J., Lomba, Â., Almeida, R.S., Vázquez, F.M. & Garcia, C. (2020b) Late Quaternary range shifts of marcescent oaks unveil the dynamics of a major biogeographic transition in southern Europe. *Scientific reports* 10: 1–12.
https://doi.org/10.1038/s41598-020-78576-9

Vila-Viçosa, C., Vázquez, F.M., Meireles, C. & Pinto-Gomes, C. (2014) Taxonomic peculiarities of marcescent oaks (Quercus, Fagaceae) in southern Portugal. *Lazaroa* 35: 139–153.
https://doi.org/10.5209/rev_LAZA.2014.v35.42555

Vila-Viçosa, C., Vázquez, F.M., Mendes, P., Del Rio, S., Musarella, C., Cano-Ortiz, A. & Meireles, C. (2015) Syntaxonomic update on the relict groves of Mirbeck's oak (Quercus canariensis Willd. and Q. marianica C. Vicioso) in southern Iberia. *Plant Biosystems* 149: 512–526.
https://doi.org/10.1080/11263504.2015.1040484

Willdenow, C.L. (1809) *Enumeratio plantarum Horti Regii Berolinensis*. Berlin: Taberna libraria Scholae Realis.