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Guillaume Besnard, Cynthia Hong-Wa, Frédéric Médail. On the taxonomic subdivision of the Brown Olive from Africa and Asia through the reinstatement of *Olea europaea* subsp. *africana* (Mill.) P.S. Green. *Botany Letters*, 2024, 171 (1), pp.80-83. 10.1080/23818107.2023.2248234 . hal-04201639

HAL Id: hal-04201639

<https://hal.science/hal-04201639v1>

Submitted on 11 Sep 2023

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On the taxonomic subdivision of the Brown Olive from Africa and Asia through the reinstatement of *Olea europaea* subsp. *africana* (Mill.) P.S. Green

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ABSTRACT: The classification of the Olive tree complex (*Olea europaea* L.) underwent numerous taxonomic changes before a consensus was seemingly reached two decades ago through the combination of morphological, chemical, cytological and molecular evidence that supported the identification of six subspecies in the Old World. While several authors claimed that Brown Olive populations from Africa and Asia were differentiated, there was no attempt to recognize two taxa due to the difficulty to distinguish them based on phenotypic characters and the possibility of a large secondary contact zone between differentiated taxa in NE Africa and the SW Arabian Peninsula. All genetic and phylogenomic studies, however, sufficiently distinguished the Asian Brown Olive, recognized here as *Olea europaea* L. subsp. *cuspidata* (Wall. ex G. Don) Cif., from the African Brown Olive, which is here reinstated as *Olea europaea* L. subsp. *africana* (Mill.) P.S. Green.

KEY-WORDS: Africa, Asia, Olive complex, Synonymy, Taxonomy, Nomenclature.

Background and context

The Olive tree (*Olea europaea* L.) is well known as one of the most iconic crops of the Mediterranean Basin, but the native distribution of its wild forms in the Old World goes far beyond the borders of this region from Macaronesian archipelagos in the West, southern Africa in the South, to the foothills of Himalayan mountains in the East (Green and Wickens 1989; Médail et al. 2001; Green 2002; Figure 1). In the last two decades, six wild Olive subspecies were recognized in the so-called olive complex (Green 2002), through the combination of morphological, chemical, cytological and molecular evidence: subsp. *europaea* in the Mediterranean Basin, *cerasiformis* (Webb & Berth.) Kunkel & Sunding in Madeira, *guanchica* P. Vargas et al. in the Canary Islands, *maroccana* (Greuter & Burdet) P. Vargas et al. in southern Morocco, subsp. *laperrinei* (Batt. & Trab.) Cif. in the Saharan mountains, and subsp. *cuspidata* (Wall. ex G. Don) Cif., also known as the Brown Olive, from southern Africa to China. These olives are usually diploid ($2n = 2x = 46$), except for the narrow endemics *maroccana* and *cerasiformis* that are polyploid (6x and 4x, respectively; Besnard et al. 2008). Natural or artificial hybridizations have been mainly reported between diploids but may also happen between diploids and polyploids (Díaz-Rueda et al. 2020). These taxa are, thus, usually considered to be primary genetic resources for cultivated olive breeding (Zohary 1994; Besnard et al. 2018).

The subspecies *cuspidata* has the largest distribution, and the distinction between African and Asian Brown Olives is not obvious based on phenotypic characters according to Green and Wickens (1989). Yet, genetic data showed a marked differentiation between the populations of the two continents with some evidence of admixture in eastern Africa and the Arabian Peninsula (Angiolillo et al. 1999; Lumaret et al. 2000; Besnard et al. 2001, 2007; Rubio de Casas et al. 2006; Besnard and El Bakkali 2014; Kassa et al. 2019; Julca et al. 2023). The complex orogenesis of mountain ranges in eastern Africa and southwestern Asia coupled with climatic oscillations have likely contributed to

increased habitat fragmentation and recurrent disruption of gene flow between distant populations of most species with a wide distribution in this region (e.g. Linder 2017). Olive populations from Tropical Africa and Asia may have thus been temporarily disconnected during long dry periods leading to their current genetic divergence. Considering this pattern, Julca et al. (2023) recently proposed a geographic partition to recognize two taxa within the Brown Olive, i.e., subsp. *cuspidata* in Africa and subsp. *ferruginea* in Asia. The latter subspecies, however, is not validly published (Art. 38.1, 40.1, 41.1, 41.5; Turland et al. 2018) and the epithet *ferruginea* has also already been used for a European variety of olive (*Olea europaea* var. *ferruginea* Aiton) and cannot be used within the same taxon (Art. 24 Note 2, 53.3; Turland et al. 2018).

Reinstatement of subspecies *africana*

Numerous names have been given to wild Olive populations leading to a long list of synonyms (Green 2002). The first distinction of Olive subspecies was made by Ciferri (1942), where subsp. *cuspidata* was proposed for the Asian Brown Olive. Under pressure to produce a name for the eastern and southern African representative for *Flora Zambesiaca*, Green and Kupicha (1979) gave the name *Olea europaea* subsp. *africana* (Mill.) P.S. Green to the African Brown Olive. Yet, when considering the difficulty to taxonomically distinguish the African and Asian Brown Olives, Green opted for a broadly defined taxon subsequently placed in *O. e.* subsp. *cuspidata* (Green and Wickens 1989) due to the priority of this subspecific epithet at the rank established by Ciferri (1942).

Given both the genetic differentiation and the geographic partition between the African and Asian Brown Olives (Angiolillo et al. 1999; Lumaret et al. 2000; Besnard et al. 2001, 2007; Rubio de Casas et al. 2006; Besnard and El Bakkali 2014; Kassa et al. 2019; Julca et al. 2023), it seems reasonable to recognize them as two distinct subspecies, and to reinstate subsp. *africana*. In addition, all occurrences found in the GBIF database (www.gbif.org) for *Olea africana* and *Olea europaea* subsp. *africana* correspond to the African Olive (including non-native olives introduced in Australasia and the USA), and this is another practical aspect to consider when revising nomenclature in historical and living collections.

Therefore, we here recognize the African Brown Olive as *Olea europaea* L. subsp. *africana* (Mill.) P.S. Green and the Asian Brown Olive as *Olea europaea* L. subsp. *cuspidata* (Wall. ex G. Don) Cif.

***Olea europaea* L. subsp. *africana* (Mill.) P.S. Green, Kew Bull. 34(1):69 (1979)**

Homotypic synonym: *Olea africana* Mill., Gard. Dict. ed. 8, *Olea* 4 (1768). Type: Cult. Hort. Chelsea (holotype BM).

Vernacular name: African Brown Olive.

Distribution: Native from the Cap Peninsula (South Africa) in the South, to Gebel Elba (Egypt) in the North. Recent colonization in the Mascarene Islands, possibly allochthonous. Invasive in Australasia (from eastern Australia to northern New Zealand), Hawaii and Saint Helena.

***Olea europaea* L. subsp. *cuspidata* (Wall. ex G. Don) Cif., L'Olivicoltore 19(5):96 (1942)**

Homotypic synonyms: *O. cuspidata* Wall. ex G. Don, Gen. Syst. 4:49 (1838). Type: India, Kumoan, Wallich 2817 (holotype K-Wallich). *O. chrysophylla* var. *cuspidata* (Wall. ex G. Don) A. Chev., Rev. Int. Bot. Appl. Agric. Trop. 28:18 (1948).

Vernacular name: Asian Brown Olive.

Distribution: Native from the Arabian Peninsula to Southern China. Frequently cultivated as an ornamental plant outside its natural habitat in SE Asia (e.g. Guangdong, China).

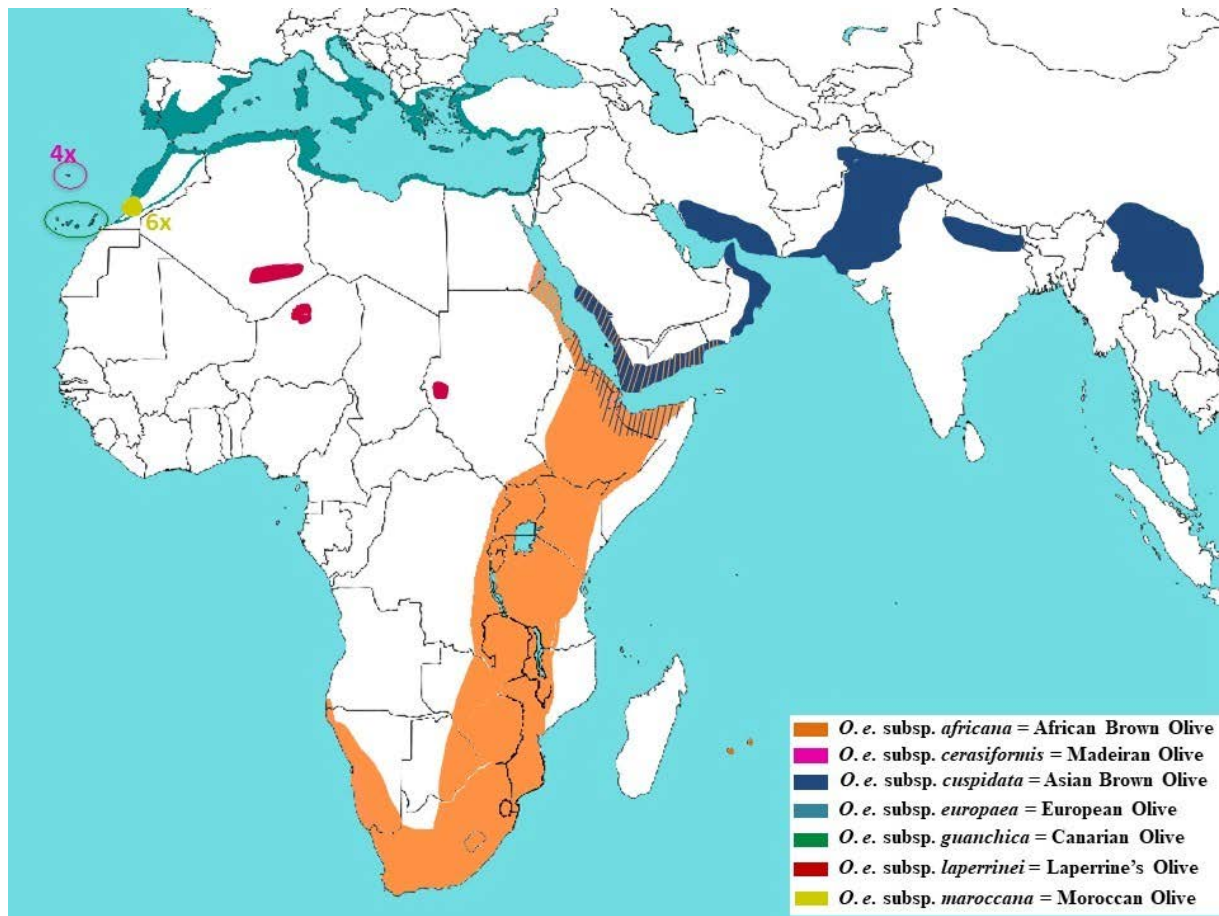


Figure 1. Native distribution of the olive complex, adapted from Green & Wickens (1989) and Rubio de Casas et al. (2006). Seven subspecies are now recognized, with a supposedly wide area of admixture between subspecies *africana* and *cuspidata* straddling the Horn of Africa and southwestern Arabia (hatched areas); there is also evidence of admixture between subspecies *europaea* and *africana* in southern Egypt and NE Sudan (Besnard et al. 2007; Besnard and El Bakkali 2014). More studies are still necessary to depict the genetic structure among olive populations from these regions. See also Besnard et al. (2018) for the distribution of matrilineages in the olive complex. Two Macaronesian subspecies are polyploid (6x for *maroccana*; 4x for *cerasiformis*).

Finally, genetic data have suggested that Arabian Olives are on a large contact zone between African and Asian Olives (Besnard et al. 2007; Besnard and El Bakkali 2014), and may thus be considered as admixed populations (Figure 1). Additional investigations are still necessary to depict the genetic structure among olive populations from these regions (e.g. Kassa et al. 2019).

Acknowledgements We thank V. Depierre and R. Ward (CBN Bailleul) for providing a bibliographic reference and L. Civeyrel for discussions on rules in plant taxonomy. We dedicate this article to Pierre Villemur, who shared with some of us his passion for the olive tree.

Disclosure statement No potential conflict of interest was reported by the authors.

Funding G.B. is supported by the H2020 project Gen4Olive (H2020-SFS-2020-1; G.A. No. 101000427) and by LabEx TULIP (ANR-10-LABX-0041) and CEBA (ANR-10-LABX-25-01) both managed by the French Agence Nationale de la Recherche.

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