Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

Angola Cave-Chat *Xenocopsychus ansorgei*
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Commiphora of the highlands and escarpments of Angola and Namibia

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ABSTRACT

The myrrh genus, *Commiphora* Jacq. (Burseraceae), comprises approximately 190 species of trees and shrubs worldwide that are most commonly encountered in the seasonally dry and arid biomes of sub-Saharan Africa. The diversity of *Commiphora* species in southwestern Africa is notable for its many restricted-range species, including nine that were only discovered within the last two decades. Of the 36 species native to the region, the majority (29 species) are endemic or near-endemic to Angola and/or Namibia and 22 species occur at elevations of 1,000 masl or greater. Molecular phylogenetic data reveal that early divergences within the genus probably involved exchanges between southwestern Africa and Madagascar beginning in the Miocene, and that extant species in southwestern Africa arose from several different evolutionary lineages. Some species divergences within the largest radiation of southwest African endemic species appear to be associated with elevational disjunctions or latitudinal disjunctions between the Kaokoveld and Gariep centres of endemism, some of which are hypothesised to have occurred as recently as the Quaternary. Despite *Commiphora* being renowned for its fragrant oleoresins and ethnobotany, fundamental aspects of *Commiphora*'s systematic biology, ecology and evolution remain understudied. Many species have yet to be included in molecular phylogenetic analyses. Other major avenues for investigation include characterising species' anatomical and physiological abilities to withstand the extreme heat and the water deficit of their natural environment; their reproductive ecology; and the chemical ecological interactions mediated by the diverse secondary chemistry of their oleoresins. Future research priorities include exploratory fieldwork to document the species of *Commiphora* in Angola, collaborative efforts to improve biodiversity informatic resources for the genus and integrative approaches to expand our understanding of *Commiphora*'s ecology and evolution within a comprehensive phylogenomic framework.

Keywords: Angola, *Commiphora*, escarpments, evolution, highlands, Namibia

INTRODUCTION

The myrrh genus, *Commiphora* Jacq., in the Burseraceae family is a group of conspicuous and charismatic tree species that produce fragrant oleoresins of ethnobotanical renown. The genus comprises approximately 190 species, of which around 109 species are native to Africa, with the remaining species being distributed in Madagascar, countries spanning the Arabian Peninsula and eastwards to Bangladesh, and in South America (Figure 1A). Species richness is greatest in tropical East Africa and the Horn of Africa, which contain at least 89 species as well as a biome that is characterised by the presence of the genus, the 1.6 million km^2 *Acacia-Commiphora* woodland (Olson & Dinerstein 2002). Within Africa and across their global range, *Commiphora* species are intolerant of freezing temperatures and fire and are found predominantly in seasonally dry subtropical and tropical forests, arid scrub-thickets, and deserts that are free of these disturbances. Many species are saxicolous and pachycaulescent (Figures 1B and 1C). *Commiphora* species are readily identified in the field by their typically thin bark, aromatic oleoresins, frequently spine-tipped short-shoot branches and drought-deciduous, alternate leaves that are imparipinnate, trifoliolate or unifoliolate (Daly *et al.* 2010). Species are usually dioecious, but all have paniculate or reduced (1–3-flowered) cymose inflorescences that bear small four-parted flowers. The fruits are drupes that dehisce via two or rarely four valves and produce a fleshy, lipid-rich red-to-yellow pseudaril that partially encases the endocarp.

However, the morphological and ecological diversity of *Commiphora* species results in many exceptions to the common diagnosis of the genus. For example, species have a range of habits (from upper canopy trees taller than 20 m, to small scandent trees, to multi-stemmed weeping shrubs), bark characteristics (thickly plated and brown to smooth grey, to paper-thin peels and flakes of translucent red or yellow hue revealing green underbark that is presumably photosynthetic), oleoresin traits (some species produce no apparent oleoresins whereas others produce oleoresins that vary by odour, colour, opacity and viscosity) and edaphic associations (from unconsolidated sands to exposed limestone or granitic outcrops) (Figure 2). Fruit shape and size are highly variable as are pseudarils; some species are entirely non-arillate. Many aspects of morphological and ecological diversity that are readily apparent in the field do not preserve well on herbarium sheets, or are rarely recorded in the literature. This limitation, in combination with *Commiphora*'s drought-deciduous habit and tendency to flower before leaf expansion, means that taxonomic research has been hindered by a lack of high-quality research specimens and observational data from even well-collected areas. The underlying mechanisms of other remarkable biological traits of *Commiphora*, such as its ability to withstand high temperature and extreme water deficit, and its diverse oleoresin chemistry which implicates a complex chemical ecology, remain understudied.

THE EVOLUTIONARY HISTORY AND BIOGEOGRAPHY OF *COMMIPHORA*

Multiple fossil-calibrated molecular phylogenetic studies have shown that *Commiphora* has a complex historical biogeography within Africa and beyond. *Commiphora* is hypothesised to have diverged from a common ancestor with the predominantly American genus, *Bursera*, during the Eocene; mean estimates range from 51.73 to 38.95 mya (Weeks & Simpson 2007, Weeks *et al.* 2014, Gostel *et al.* 2016a, Muellner-Riehl *et al.* 2016, Joyce *et al.* 2023). Early movement of subtribe Burserinae among continents is hypothesised to have been facilitated by boreotropical corridors within Laurasia followed by vicariance (Weeks *et al.* 2005, Weeks *et al.* 2014), based on the age of the lineage and the location in the northern hemisphere of fossils attributable to *Bursera* and *Commiphora*. Long-distance dispersal cannot be ruled out as an important force because the pseudarillate fruits of *Commiphora* are dispersed by birds (van der Walt 1975, Bleher & Böhning-Gaese 2001). Moreover, the distribution of several relatively young, continentally disjunct endemic lineages, such as the sole South American species, *Commiphora leptophloeos* (Mart.) J.B.Gillett, and multiple Madagascan clades of *Commiphora*, can only be attributed to long-distance dispersal via biotic (e.g., bird) or abiotic (e.g., oceanic currents) means because they postdate any possible subdivision of ancestral, contiguous continental populations.

The diversity of *Commiphora* species in southwestern Africa is notable for its many restricted-range species. Of the 36 species native to the region, the majority of species (n = 29) are endemic or near-endemic to Angola and/or Namibia and 22 species may be found at elevations of 1,000 masl or greater (Table 1). The most-densely sampled and fossil-calibrated *Commiphora* phylogeny to date (Gostel *et al.* 2016a) indicates that divergences of all extant species probably began 36.6 ± 9.2 mya and gave rise to six well-supported clades, four of which contain species distributed in continental Africa: the Spinescent clade, the Saxicola clade, the Gariepensis clade and the Arafy + *C. kraeuseliana* Heine clade. Southwest African species of *Commiphora* derive from each of these four clades, although not all species have been evaluated within a phylogenetic framework.

The most recent phylogenetic analysis of *Commiphora* includes 31 of the 36 species native to southwestern Africa as well as 82 other species that occur in sub-Saharan Africa, Socotra, Madagascar, the Arabian Peninsula, India and South America (Figure 3; Gostel *et al.* 2016a, Swanepoel *et al.* 2022). Phylogenetic

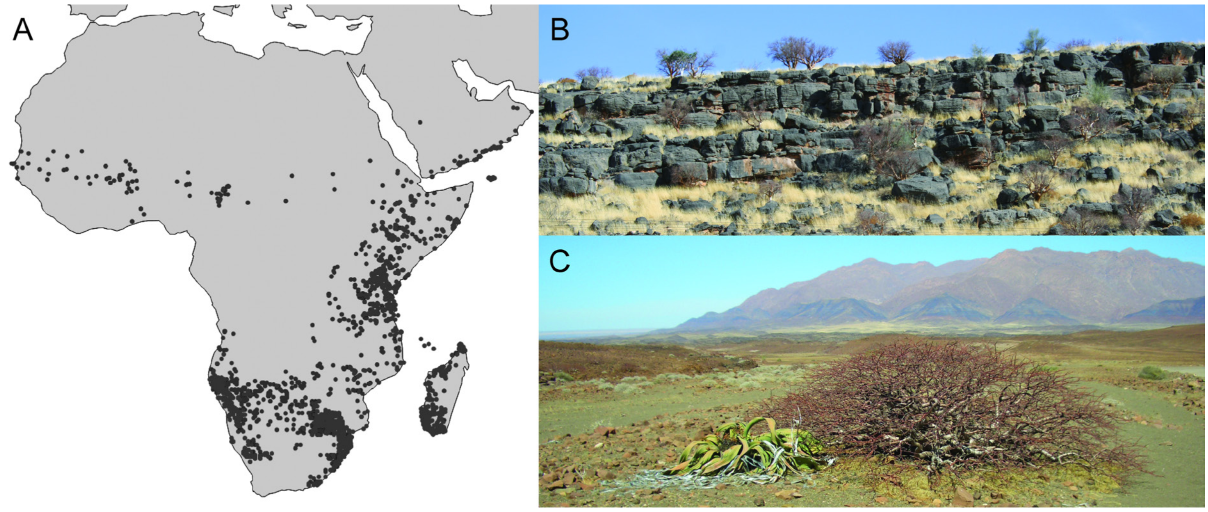

Figure 1: *A) Distribution of* Commiphora *in Africa and the Arabian Peninsula inferred from herbarium specimen records, as analysed by Ringelberg* et al. *(2020; adapted with permission). B)* Commiphora *species may be gregarious in seasonally arid, frost- and fire-free habitats; many are saxicolous. Population of the Angolan–Namibian highland endemic,* C. glaucescens*, along the Tsauchab River in the Naukluft Mountains, Namibia (c. 1,076 masl). Photo: A Weeks. C) Multiple* Commiphora *species are adapted to extremes of water-deficit and have pachycaulescent habit. Angolan–Namibian endemic* C. wildii *with* Welwitschia mirabilis *west of the Brandberg massif, Namibia (c. 429 masl). Photo: A Weeks.*

data comprise 4,379 base pairs of aligned DNA sequence from the nrDNA external transcribed spacer region and three intergenic spacers of the chloroplast genome (*trnH–psbA*, *ndhF–rpl32*, *trnD–trnT*). To preserve visual space in Figure 3, the endemic Madagascan Rhynchocarpa clade and the endemic Madagascan Arafy clade are not shown in full. Resolution of these Madagascan clades is discussed in Gostel *et al.* (2016a, 2016b).

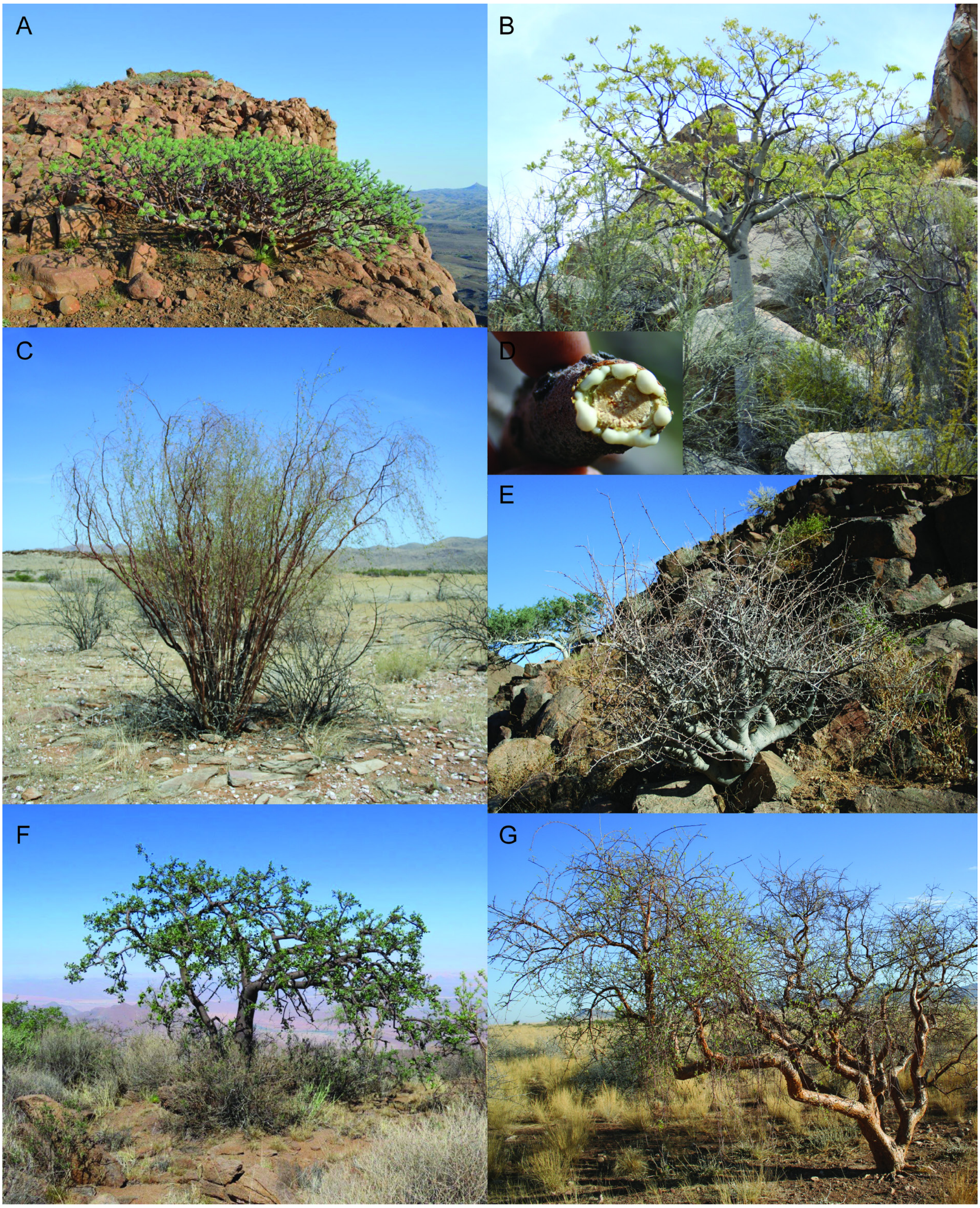

Figure 2: *Examples of* Commiphora *species endemic to the highlands and escarpments of Angola and Namibia showing diversity of substrate and habit. A)* Commiphora kraeuseliana. *Photo: W Swanepoel. B)* C. crenato-serrata. *Photo: A Weeks. C)* C. giessii. *Photo: A Weeks. D) Cut branch of* C. saxicola *showing the opaque white, viscous oleoresins characteristic of its clade. Photo: A Weeks. E)* C. capensis. *Photo: A Weeks. F)* C. otjihipana. *Photo: W Swanepoel. G)* C. glaucescens. *Photo: A Weeks.*

Most of the southwestern African species included in the phylogeny are endemic to Angola, Namibia or both countries (n = 25), of which 19 species can grow at elevations of 1,000 masl or greater. Species native to southwestern Africa but not yet sampled by any phylogeny include *C. antunesii* Engl., *C. glandulosa* Schinz, *C. mossamedensis* Mendes, *C. mulelame* (Hiern) K.Schum. and *C. otjihipana* Swanepoel, all of which are endemic to the region except *C. glandulosa*. Despite incomplete sampling, the currently understood phylogeny of the genus reveals three unanticipated features of *Commiphora*'s evolutionary history and historical biogeography in Africa which are discussed below.

Firstly, phylogenetic relationships of *Commiphora* species suggest that early diversification events within this genus happened outside the centre of its extant species diversity in eastern Africa; this assumes that widespread extinction of ancient lineages have not occurred in this area. The current locus of *Commiphora*'s greatest species richness is in eastern and northeastern Africa (Vollesen 1985, Gillett 1991, Lebrun & Stork 2011), where at least 89 species co-occur. Yet, all species that are native to these areas are members of the Spinescent clade (Figure 3), which probably radiated in the early to middle Miocene, 20.4 mya (28.8–14.0 mya, 95% confidence interval (CI); Gostel *et al.* 2016a). This clade also includes species that have more recently dispersed to South America (*C. leptophloeos*) and regions bordering the Indian Ocean basin (*C. socotrana* Engl., *C. wightii* (Arn.) Bhandari, *C. simplicifolia* H. Perrier), as well as species native

Table 1: Commiphora *species native to the highlands and escarpments of Angola and Namibia and their presence and endemism status in the two countries. X indicates presence.*

Species	**Elevation range (masl)**	**Angola**	**Namibia**	**Endemism status**
C. africana (A.Rich.) Engl.*	300–1,900	X	X	–
C. anacardiifolia Dinter & Engl.*	250–1,400	X	X	Endemic
C. angolensis Engl.*	50–1,800	X	X	–
C. angustefoliolata Mendes*	150–500	X	–	Endemic
C. antunesii Engl.	unknown	X	–	Endemic
C. benguelensis Swanepoel*	50–600	X	–	Endemic
C. buruxa Swanepoel*	200–500	–	X	Near-endemic
C. capensis (Sond.) Engl.*	50–700	–	X	Near-endemic
C. cervifolia J.J.A.van der Walt*	50–700	–	X	Near-endemic
C. crenato-serrata Engl.*	850–1,900	X	X	Endemic
C. dinteri Engl.*	450–1,850	–	X	Endemic
C. discolor Mendes*	400–1,900	X	X	Endemic
C. gariepensis Swanepoel*	300–1,000	–	X	Near-endemic
C. giessii J.J.A.van der Walt*	300–700	X	X	Endemic
C. glandulosa Schinz	500–2,050	X	X	–
C. glaucescens Engl.*	500–2,000	X	X	Endemic
C. gracilifrondosa Dinter ex J.J.A.van der Walt*	100–800	–	X	Near-endemic
C. kaokoensis Swanepoel*	200–1,100	–	X	Endemic
C. kraeuseliana Heine*	450–900	–	X	Endemic
C. kuneneana Swanepoel*	200–1,800	X	X	Endemic
C. mollis (Oliv.) Engl.*	850–1,950	X	X	–
C. mossamedensis Mendes	150–800	X	–	Endemic
C. mulelame (Hiern) K.Schum.	1,400	X	–	Endemic
C. multijuga (Hiern) K.Schum.*	450–1,850	X	X	Endemic
C. namaensis Schinz*	200–900	–	X	Near-endemic
C. namibensis Swanepoel*	20–600	X	–	Endemic
C. oblanceolata Schinz*	140–1,950	X	X	Endemic
C. omundomba Swanepoel & Weeks*	10–1,300	X	X	Endemic
C. otjihipana Swanepoel	1,200–2,050	X	X	Endemic
C. pyracanthoides Engl.*	700–950	–	X	–
C. saxicola Engl.*	300–1,200	–	X	Endemic
C. schimperi Engl.*	1,700–2,050	X	X	–
C. steynii Swanepoel*	800–1,600	X	X	Endemic
C. tenuipetiolata Engl.*	20–1,850	X	X	–
C. virgata Engl.*	200–2,000	X	X	Endemic
C. wildii Merxm.*	50–900	X	X	Endemic

** Species included within the phylogenetic analysis of Figure 3.*

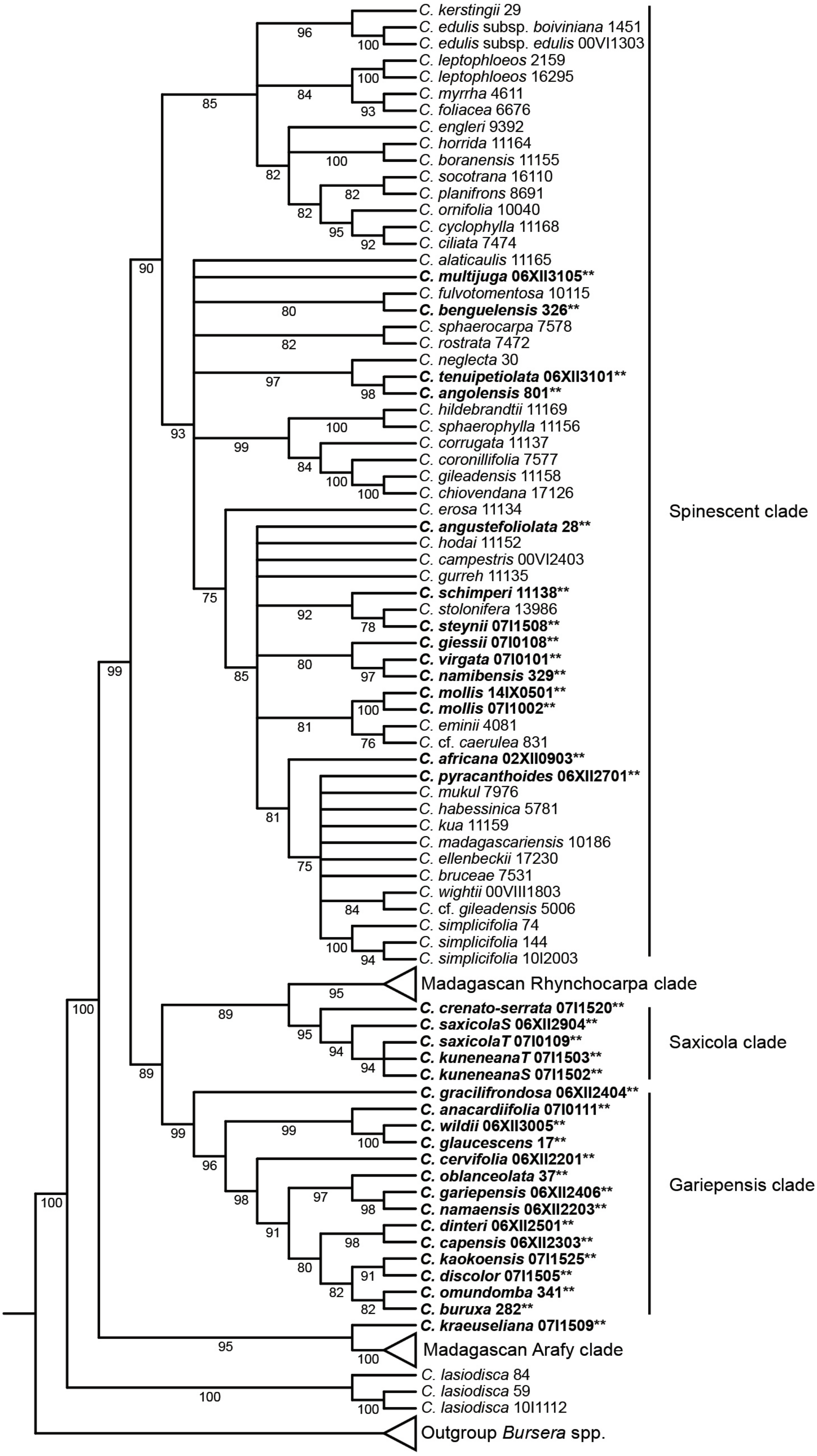

Figure 3: *Phylogeny of* Commiphora *based on the four-gene matrix of Gostel* et al. *(2016a). The topology represents the 75% consensus of 1,000 ultrafast bootstrap replicates using maximum likelihood in IQTREE; bootstrap percentages are shown below branches. To preserve space, the endemic Madagascan Rhynchocarpa clade and the endemic Madagascan Arafy clade are not shown in full but are indicated by small triangles. ** denotes species native to the highlands and escarpments of Angola and Namibia.*

to southwestern Africa (*C. africana* (A.Rich.) Engl., *C. mollis* (Oliv.) Engl., *C. pyracanthoides* Engl., *C. schimperi* Engl., *C. tenuipetiolata* Engl.) or endemic to southwestern Africa (*C. angolensis* Engl., *C. angustefoliolata* Mendes, *C. benguelensis* Swanepoel, *C. giessii* J.J.A.van der Walt, *C. multijuga* (Hiern) K.Schum., *C. namibensis* Swanepoel, *C. steynii* Swanepoel, *C. virgata* Engl.). All other clades stemming from earlier divergence events, including the sister to the Spinescent clade, comprise *Commiphora* species that are currently restricted to either southwest Africa or Madagascar.

Secondly, the close relationships of endemic southwest African and endemic Madagascan lineages reveal an unexpected and repeated biogeographical relationship between these regions during the evolution of *Commiphora*. Cross-continental disjunctions between these regions include the sister relationship of all *Commiphora* species, including early diverging lineages of southwest African species, to the Madagascan endemic, *C. lasiodisca* H. Perrier. Another includes the sister relationship between the southwest African endemic, *C. kraeuseliana,* which is restricted to the Southern Escarpment landscape of the highlands and escarpments of Angola and Namibia (HEAN) *sensu* Mendelsohn and Huntley (2023), and the lineage of 16 Madagascan endemic species of the Arafy clade, which may have diverged in the early Miocene (c. 19 mya; Gostel *et al.* 2016a). The last apparent disjunction includes the sister pair of the endemic southwest African Saxicola clade and the lineage of 26 Madagascan endemic species of the Rhynchocarpa clade, which diverged in the early to middle Miocene, 15.56 mya (23.27–8.55 mya, 95% CI) (Gostel *et al.* 2016a). The Saxicola clade contains three species native to Africa's southwestern highlands, *C. crenato-serrata* Engl. (Southern Escarpment; Central-Western Plains), *C. saxicola* Engl. (Central-Western Plains; Pro-Namib, and *C. kuneneana* Swanepoel (Southern Escarpment), and which radiated 4.03 mya (7.64–1.42 mya, 95% CI). Miocene aridification and uplift of the African continent may have caused vicariance between western and eastern limits of the continent as has been hypothesised for other woody or succulent taxa native to these areas, such as *Thamnosma* Torr. & Frém. (Rutaceae; Thiv *et al.* 2011), *Kleinia* Jacq. (Asteraceae; Pokorny *et al.* 2015) and *Euphorbia* sect. *Aphyllis* Webb & Berthel. (Euphorbiaceae; Pokorny *et al.* 2015). Multiple instances of long-distance dispersal of *Commiphora* across the Mozambique Channel between the African continent and Madagascar also occurred during this period, because this oceanic barrier predates the earliest divergences within the genus.

Lastly, the synthesis of the phylogenetic relationships, ages and extant distributions of endemic or near-endemic southwest African *Commiphora* species provides greater evolutionary context to long-recognised centres of endemism in southern Africa (van Wyk & Smith 2001). Rather than being evolutionary relicts, all extant endemics of *Commiphora* in southwestern Africa are likely to have arisen during the Miocene, Pliocene or more recently during the Quaternary period, as in the case of the sister pairs of *C. namaensis* Schinz – *C. gariepensis* Swanepoel and *C. saxicola* – *C. kuneneana*. Beyond the seven endemic species that derive from the geographically widespread Spinescent clade that began diversifying 20.4 mya (28.8–14.0 mya, 95% CI), most endemic southwest African species are restricted to the lineage containing the Saxicola, Rhynchocarpa and Gariepensis clades. This larger clade is also known as the Granulifera clade because of the granular indumentum that is present on many of its species (Gostel *et al.* 2016a). These relationships suggest that southwestern Africa is likely to have hosted a geographically restricted radiation during the Miocene beginning 19.92 mya (27.76–11.93 mya, 95% CI). The 14 endemic and near-endemic species of the Gariepensis clade, whose phylogenetic resolution is very well supported, began radiating 16.65 mya (24.62–9.73 mya, 95% CI).

Ranges of closely related *Commiphora* species appear to be stratified by elevation and latitude, which suggests that geography and abiotic factors may have been an important factor in driving species divergence, particularly within the Gariepensis clade. Nearly all endemic or near-endemic *Commiphora* species that are found at elevations above 1,000 masl are also found at much lower elevations; the sole exception is *C. mulelame* (Hiern) K.Schum. that occurs only at 1,400 masl or higher. In five of six taxon pairs within the *Commiphora* phylogeny, a high-elevation species is sister to a low-elevation species (*C. virgata* – *C. namibensis*, *C. glaucescens* Engl. – *C. wildii* Merxm., *C. gariepensis* Swanepoel – *C. namaensis* Schinz, *C. dinteri* Engl. – *C. capensis* (Sond.) Engl. and *C. omundomba* Swanepoel & Weeks – *C. buruxa* Swanepoel; Figure 3). Table 2 indicates the distributions within the HEAN of these five pairs of elevationally disjunct sister species. The species in the sixth pair, *C. kaokoensis* Swanepoel – *C. discolor* Mendes, share the ability to grow at high elevation and are both distributed in the Southern Escarpment.

Several latitudinally disjunct species pairs also suggest that allopatric speciation has been an important generative force during *Commiphora*'s evolution in southwestern Africa. Three species pairs span the Kaokoveld and Gariep Centres of endemism, whereas the fourth spans high-elevation areas in northern Namibia. *Commiphora dinteri*, which occurs along the central and southwestern escarpment of central Namibia in the Central-Western Plains and Khomas Hochland, is sister to *C. capensis*, which occurs in the extreme southwest of Namibia in the Cape and Succulent Karoo Floristic Region near the Orange River in the Pro-Namib. *Commiphora oblanceolata*, which ranges from southern Angola into the northern Namib Desert including the Southern Escarpment landscape unit, is sister to the southern Namibian pair, *C. gariepensis* – *C. namaensis*, that are distributed near the central and far eastern Orange River region including the Nama Karoo Basin (only *C. namaensis*) and Pro-Namib landscape units. *Commiphora omundomba*, which is restricted to southern Angola and northern Namibia including the Southern Escarpment landscape unit, is sister to *C. buruxa* that is known only from the central Orange River region of Namibia in the Pro-Namib landscape unit and in the mountains bordering the Orange River Valley further to the east. In the fourth disjunct pair, *C. discolor* is limited to near the Cunene River at the Namibian and Angolan border in the Southern Escarpment landscape unit but its sister, *C. kaokoensis*, is limited to areas further south in, and between, the catchment areas of the Ugab and Hoanib rivers in the same landscape unit. Statistical phylogeographic tests of these apparent geographic correlates would be required to propose probable causality, but phylogenetic data do suggest that genetic isolation imposed by the geography of southwestern Africa drove the diversification of *Commiphora*.

DEFICIENCIES IN KNOWLEDGE AND RESEARCH PRIORITIES

The multiple discoveries of new *Commiphora* species endemic or near-endemic to southwestern Africa in the last two decades highlight that much remains to be discovered about the diversity and evolution of this charismatic lineage of trees (Swanepoel 2005, 2006, 2007, 2008, 2011, 2014, 2015, Swanepoel *et al*. 2022). It is astonishing that such large and immobile terrestrial organisms remained unknown to Western science into the 21st century but is also indicative of the research barriers – both artefactual and biological, as discussed in the introduction – that are particular to the systematic study of *Commiphora*. Field observations combined with the collection of fresh plant material across the growing season and from multiple individuals are critical to capturing all morphological characters and their variation required to recognise and describe new *Commiphora* species. Expeditions to investigate the *Commiphora* of Angola are likely to yield new species, based on the results of recent fieldwork on the group in Namibia.

While herbarium material of *Commiphora* species is often missing key diagnostic features or entirely lacking from floristically underexplored areas, it has been produced in quantity from geographic areas frequented by botanists over the last c. 150 years. *Commiphora* is often one of the few woody taxa encountered by botanists in the arid environments of southwestern Africa and its specimens are relatively easy to collect and press, although they may not be identifiable to the species level if they are lacking reproductive material. Consequently, specimens of *Commiphora* – both identified and unidentified – have accumulated in herbaria around the world. If evaluated en masse these specimens would reveal a more complete picture of the morphological diversity and distribution of species than is appreciated today. However, data on most specimens are not publicly accessible in a digital form, which presents a challenge to synthesising information from all collections of *Commiphora* species. For instance, only 1,116 and 527 herbarium sheets of *Commiphora* from Namibia and Angola, respectively, are available through the Global Biodiversity Informatics Portal (GBIF.org 2022).

Table 2: *Distribution within the highlands and escarpments of Angola and Namibia (HEAN) of five pairs of sister species within the* Commiphora *phylogeny that have elevational disjunctions. The landscape units are described in Mendelsohn and Huntley (2023).*

High-elevation species	**High-elevation species distribution within HEAN**	**Low-elevation species**	**Low-elevation species distribution within HEAN**
C. virgata	Southern Escarpment; Central-Western Plains	*C. namibensis*	Southern Escarpment
C. glaucescens	Southern Escarpment; Karstveld; Central-Western Plains; Pro-Namib	*C. wildii*	Southern Escarpment
C. gariepensis	Not in HEAN but close to it in the mountains bordering the Orange River valley	*C. namaensis*	Nama Karoo Basin; Pro-Namib
C. dinteri	Central-Western Plains; Khomas Hochland	*C. capensis*	Pro-Namib
C. omundomba	Southern Escarpment	*C. buruxa*	Pro-Namib; outside the HEAN but close to it in the mountains bordering the Orange River valley

The holdings of many herbaria within the natural range of *Commiphora* and from countries of the northern hemisphere with a history of collecting in southwestern Africa do not yet serve data through the GBIF portal. Of the herbarium specimen data that are served, just over half (54%) include the latitude and longitude coordinates of the collection locality. These geospatial data are essential for generating accurate distribution maps and robust models of species' environmental niches to assess their past biogeographical movements as well as their future fate in a changing climate (Burke 2004) and in areas with increasing anthropogenic disturbance. Improving the access to herbarium material of *Commiphora* housed globally would improve our ability to conduct informed fieldwork, investigate the systematic biology of the genus and to generate and test phylogeographical and ecological hypotheses.

Uncovering the full complement of *Commiphora* species native to southwestern Africa through expanded fieldwork and herbarium-based research would also enable researchers to reconstruct the evolutionary history of the genus more completely. Current knowledge is frustratingly incomplete because phylogenies of *Commiphora* do not yet include all known extant species. Current phylogenies also lack well-supported resolution within the Spinescent clade that is essential for inferring the evolution and historical biogeography of this wide-ranging group. Several southwest African species are members of this clade, but their closest relatives remain uncertain apart from the well-supported sister pair of *C. virgata* – *C. namibensis*. Genome-scale sequence data (e.g., Khan *et al.* 2019, 2022) would be needed to produce a well-resolved phylogeny of all *Commiphora* species in the future.

As prefaced in the introduction, published research regarding the anatomical, physiological, ecological and life-history traits that may underlie the remarkable ability of *Commiphora* species to withstand extreme environmental conditions in southwestern Africa and elsewhere is lacking. This is notable because the Afrikaans common name for *Commiphora*, *kanniedood*, which translates as 'cannot die' in English, references this ecological resiliency as the most salient and recognisable feature of the genus. Yet, this feature remains largely unstudied. Listed below are three, non-exhaustive categories of key questions, whose answers would extend our understanding of how *Commiphora* managed to diversify within some of the most hostile terrestrial biomes, how it thrives there today and how *Commiphora* might respond to future global climate change.

i. Anatomical: How and where do southwest African *Commiphora* species sequester water in their tissues? To what degree does the structure of water-storing and water-conducting tissues correlate with or directly affect the habit of species (e.g., Olson *et al.* 2013)? Rather than having converged on a similar leaf phenotype in the hot, dry climate of southwestern Africa, *Commiphora* species have a range of leaf morphologies that is extraordinarily diverse compared to that of other woody genera in southern Africa. What is the possible functional and evolutionary developmental explanation of this variation (Nicotra *et al.* 2011)? What are the potential adaptive benefits of exfoliating (i.e., peeling and flaking) versus non-exfoliating bark?

ii. Physiological: What role does photosynthetic bark play in the annual carbon budget of *Commiphora* species that are leafless for much of the year (e.g., Cernusak & Cheesman 2015, Vandegehuchte *et al.* 2015)? Which species conduct photosynthesis in their phelloderm (e.g., Girma *et al.* 2013)? What other benefits might photosynthetic bark confer, such as heat balance or mineral nutrient resource efficiency, compared to non-photosynthetic bark? And if photosynthetic bark does confer any benefit to the plant, why do some species in the same environment lack this trait?

iii. Ecological: What is the annual recruitment and demographic structure of *Commiphora* populations and to what degree are they controlled by interannual precipitation (e.g., Mduma *et al.* 2007, Reddy *et al.* 2012, Tolera *et al.* 2013, Mengich *et al.* 2020)? How long do *Commiphora* species take to reach reproductive maturity and how long do they live? Given the erratic rainfall in southwestern Africa and its concomitant effect on leaf expansion and flowering in *Commiphora*, how does the associated fauna of pollinators (e.g., Farwig *et al.* 2004), herbivores (e.g., Iannella *et al.* 2021) and seed dispersers (e.g., Bleher & Böhning-Gaese 2000) vary from year to year and how does this effect reproductive output? To what extent does the harvesting of oleoresin by humans impact the longevity and reproductive output of *Commiphora* species (e.g., Cunningham *et al.* 2018)?

Finally, a long overdue frontier for research in *Commiphora* includes the integrative exploration of the ecology and evolution of the diverse secondary chemistry present in the oleoresins of its species. The oleoresins, which are best known for their ethnobotanical uses (Langenheim 2003), may be produced in any tissue and are contained within schizogenously formed ducts associated with phloem tissue. These resins comprise 30–60% water-soluble compounds such as polysaccharides and proteins, 3–8% essential oil, and 25–40% alcohol-soluble compounds including terpenes and terpenoids, steroids and sterols (Khalid 1983, Ulrich *et al.* 2022). Some chemical ecological research has focused on its sister genus, the predominantly New World copal genus *Bursera* (e.g., Becerra *et al.* 2009), but very little comparable work on *Commiphora* oleoresins has been conducted beyond the characterisation of more than 300 secondary metabolites from the c. 25 species commonly used in traditional medicine or other cultural practices (Shen *et al.* 2012, Dekebo *et al.* 2022). Reports of the biocidal properties (i.e., antimicrobial, antifungal, acaricidal, anthelminthic and insect antifeedant properties) of the oleoresins from these ethnobotanically important species suggest numerous chemical ecological interactions between the plants and their environment. But most of the research on oleoresins has focused on their pharmacologically active compounds that affect vertebrate physiology or pathogen infection and that could potentially improve human health (i.e., guggulsterones, triterpenes and furanosesquiterpenes; Waterman 1996, Ulrich *et al.* 2022). Characterising the oleoresin chemical profiles of all *Commiphora* species would help us determine the endogenous function of these chemicals within the plants and facilitate chemical ecological experiments required to understand their possible mediation of each species' interaction with its abiotic and biotic environment (e.g., Lwande *et al.* 1992, Assad *et al.* 1997, Chaboo *et al.* 2016, Sommerlatte & van Wyk 2022). Evaluating species' chemical trait data in a phylogenetic context would also reveal how *Commiphora*'s secondary chemistry has evolved over geological time and provide the framework for exploring the functional genomic architecture of these biochemical phenotypes. Interestingly, a major constraint to further advances in natural product chemistry of *Commiphora* has been the inability to obtain accurately identified and properly vouchered plant material that can support replication and expansion of prior experimental findings (Shen *et al.* 2012). Establishing collaborations between systematists, chemical ecologists, ethnobotanists and natural product chemists would be a fruitful way forward in uncovering the biology, ecology and evolution of *Commiphora*'s oleoresin chemistry as well as understanding the sustainability of utilising these oleoresins as natural resources.

CONCLUSIONS

Our knowledge of the systematic biology of *Commiphora* in southwestern Africa has improved considerably within the last two decades, as evidenced by new species descriptions and the advent of expanded molecular phylogenetic analyses that lend insight into the evolution and historical biogeography of the genus. Excellent atlases (e.g., Curtis & Mannheimer 2005) and field handbooks (e.g., Mannheimer & Curtis 2018) have also been produced as aids to further research in Namibia. But as this review has discussed, much remains to be uncovered about *Commiphora* at all levels of organisation: at the ecosystem level, at the species level and at the biochemical level. Exploratory fieldwork on *Commiphora* in Angola, comparable to that which has been conducted to document the Namibian flora, remains to be completed (Goyder & Gonçalves 2019). Readily accessible Angolan plant atlases and field handbooks for *Commiphora* species that can convey information to the non-specialist for education and conservation also remain unwritten. Thus, while the vision for the next two decades of research needs to include fundamental species discovery and integration of expertise from the fields of biodiversity informatics, genomics, anatomy, physiology and ecology to understand the evolutionary biology of *Commiphora* more fully, new partnerships and collaborations across intellectual traditions and international borders will be required to achieve it.

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