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# *Afrosalsola* (Amaranthaceae-Chenopodiaceae), an intermediate $C_3$-$C_4$ lineage from NW Africa and the Canary Islands, and some new combinations in African species of *Caroxylon* and *Soda*

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**Abstract.** The segregation of the polyphyletic genus *Salsola* (Amaranthaceae-Chenopodiaceae) caused enormous nomenclatural changes during the last two decades. A lineage, that is still awaiting to be validated by a new valid name comprises four interesting taxa endemic to the Canary Islands and NW Africa. These are shrubby plants with opposite and alternate branches and leaves, specific leaf-anatomy with a hypodermis and Kranz-like cells performing a $C_3$-$C_4$ intermediate photosynthetic pathway ($C_2$ type). The new genus *Afrosalsola* is described with the inclusion of 2 species [*Afrosalsola divaricata* (Mass. ex Link) Akhani comb. nov., and *A. deschaseauxiana* (Litard. & Maire) Akhani comb. nov.] and three subspecies of the former [*Afrosalsola divaricata* subsp. *divaricata*, *A. divaricata* subsp. *verticillata* (Schousboe) Akhani and *A. divaricata* subsp. *gymnomaschala* (Maire) Akhani]. The synonymy of *Salsola deschaseauxiana* Litard. & Maire with *S. verticillata* Mass. ex Link is rejected based on typical alternate leaves of the former. *Salsola divaricata* is typified based on its original collection in BM. Additional new combinations of African species belonging to *Caroxylon* and *Soda* are provided.

**Keywords**. Caryophyllales, flora of Morocco, halophytes, photosynthetic pathways, western Mediterranean.

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## Introduction

Species of the family Chenopodiaceae in its traditional circumscription —not essentially its inclusion in Amaranthaceae according to APG (Byng *et al.*, 2016)— frequently inhabit arid habitats and saline soils. Despite little specialization in floral morphology, they show a series of highly developed functional adaptations such as habit, shoot and leaf morphology, anatomy and photosynthetic pathways to adapt to their harsh growth conditions ranging from salt marshes to extremely hot deserts and even high-altitude cold peaks and plains (Kühn *et al.*, 1993; Akhani *et al.*, 2007; Voznesenskaya *et al.*, 2013; Rudov *et al.*, 2020).

In the last two decades, intensive phylogenetic, functional and structural studies on chenopods, in particular related to $C_4$ evolution, disclosed many enigmatic aspects of adaptation and evolution of these intriguing desert and halophytic plants (Kadereit *et al.*, 2003; Schütze *et al.*, 2003; Kapralov *et al.*, 2006; Akhani *et al.*, 2007; Kadereit *et al.*, 2010; Fuentes-Bazan *et al.*, 2012; Piirainen *et al.*, 2017). Phylogenetic works provided strong evidences that several groups of chenopods require nomenclatural changes to define monophyletic groups. One of the most critical groups of chenopods belong to the subfamily Salsoloideae and especially to the tribe Salsoleae, which contains the largest number of $C_4$ lineages among eudicots (Akhani *et al.*, 1997; Voznesenskaya *et al.*, 1999; Pyankov *et al.*, 2001; Sage *et al.*, 2011; Rudov *et al.*, 2020).

The monophyly of the genus *Salsola* —as treated in several classical floras e.g. in Flora of Europe, Flora of the USSR and Flora Iranica and the Families and Genera of Vascular Plants (Iljin, 1936; Ball *et al.*, 1993; Kühn *et al.*, 1993; Hedge *et al.*, 1997)— was rejected by several earlier molecular phylogenetic studies (Pyankov *et al.*, 2001; Pyankov *et al.*, 2001; Kadereit *et al.*, 2003; Akhani *et al.*, 2007; Mosyakin *et al.*, 2017, 2023). The first attempt using nuclear and plastid sequences supports reclassification and disintegration of *Salsola* in its traditional use at least into 9 lineages. Some older genera have been resurrected and some new have been described. While we are in the process of providing a comprehensive checklist of the African halophytes (as PhD thesis of the second author) an updated nomenclature of all species of Chenopodiaceae in Africa is required. Four interesting taxa which are endemic to saline soils and coastal parts of NW Africa and the Canaries have been well investigated due to their interesting $C_3$-$C_4$ intermediate photosynthetic pathway

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despite their position in between many $C_4$ lineages. This lineage was informally named "Canarosalsola" (Akhani *et al.*, 2007) and is now formally described as *Afrosalsola* gen. nov. Furthermore, we listed here all species of African *Salsola* s. l. with their new names based on phylogenetic data (Appendix 1).

The main goals of this contribution are: (1) providing a formal nomenclature for an interesting chenopod lineage that lacks a generic name based on the phylogenetic classification of Salsoleae; (2) typification of *Salsola divaricata*; (3) providing a checklist of all names of African flora formerly classified as *Salsola* or related genera with updated phylogenetic nomenclature; and (4) providing new combinations in African *Caroxylon* and *Soda* to update all names based on accepted phylogenies.

## Material and Methods

A population of *Salsola divaricata* has been studied during field work on the Canary Islands (Gran Canaria, western coasts, near Agaete, along the road with some shrubs like *Euphorbia regis-jubae*, *Kleinia neriifolia* and *Pennisetum setaceum*, 23.9.2002, H. Akhani 16469, Hb. Akhani). The collected seeds and leaf material have been studied for molecular phylogenetic studies in Salsoloideae (Akhani *et al.,* 2007), anatomical and physiological studies (Voznesenskaya *et al*., 2013). Additional type and herbarium materials have been studied in the Muséum national d'Histoire naturelle (P) during a herbarium visit in 2023. Further data on typification of various names were collected through contacts with curators of the related herbaria (e.g. Natural History Museum, BM) or virtual specimens available in Jstor Plants (https://plants.jstor.org).

## Results

***Afrosalsola*** Akhani gen. nov.
Type: *Afrosalsola divaricata* (Masson ex Link) Akhani = *"*Canarosalsola*"* lineage in Int. J. Pl. Sci. 168: 947 (2007).
*Description and diagnosis:* The new genus is characterized by a shrubby habit, opposite and subopposite branches, opposite to alternate leaves, whitish and easily pilled and indistinctly papillose stem; leaves subverticillate, succulent, terete, semiterete to subtriangular in cross-section, decurrent, obtuse or indistinctly mucronulate; ovate upper bracts and bracteoles, laterally broadly membranous; flowers solitary in leaf-axile, stamens attached on a circular staminal disk, staminodes absent, anthers non-appendaged, filaments suddenly narrowed below the anthers; spirally recurved stigmata; fruiting perianths winged at the middle, three lower wings much broader and overlapped with the two upper. Leaf anatomy with a presence of a layer of hypodermis and Kranz-like cells around the vascular bundles, plants performing $C_2$ photosynthesis. It differs from *Soda* (Dumort.) Fourr. by exclusively shrubby habit (*Soda* has annual, perennial and shrubby habit), having only one flower per leaf axil (flowers in *Soda* are mostly more than one per leaf axile), leaf anatomy lacking a distinct Kranz layer (leaf anatomy in *Soda* is characterized by Kranz cells performing $C_4$ photosynthesis).

Based on current data and available material two species are to be accepted in the genus *Afrosalsola* by their clear differences in leave position, *A. divaricata* characterized by opposite and *A. deschaseauxiana* by the alternate leaves. Based on available herbarium specimens the minor differences between *Salsola divaricata* from the Canary Islands and *S. verticillata* and *S. gymnomaschala* from the Moroccan coasts are not satisfying to accept them as separate species. They well represent geographical variants, which are also supported by molecular data (Tefarikis *et al.*, 2017). The applied Genotyping-by-Sequencing approach using 3463 markers and 12812 SNPs found three main clusters coinciding three accepted taxa. The cluster of the Canarian populations is further grouped into three subclusters. Our taxonomic decision deviates from Tefarikis *et al.* (2017) considering *S. verticillata* and *S. deschaseauxiana* as close variants. Because the type specimen of *S. deschaseauxiana* clearly differs from that of *S. verticillata* based on the alternate and smaller leaves and upper alternate branches. Probably, in the cited work the distance of the two populations causes misinterpretation of *S. deschaseaxuiana*.

Key to species and infraspecific taxa of *Afrosalsola*:

1. Inflorescence branches and leaves alternate ..... ..... *A. deschaseauxiana*
1. Inflorescence branches and leaves opposite, sometimes alternate along the uppermost leaves ..... ..... 2 (*A. divaricata* s.l.)
2. Leaves acute, style as long as or shorter than the rolled stigma, restricted to Canary Islands ..... ..... *A. divaricata* subsp. *divaricata*
2. Leaves obtuse, style longer than rolled stigma, restricted to the Moroccan's west coasts .....3
3. Leaves linear, bracts linear, longer than the perianth; bracteoles acute, apiculate ..... ..... *A. divaricata* subsp. *verticillata*
3. Leaves obovate-lanceolate, bracts globose or subglobose, equalling or shorter than the perianth; bracteoles retuse at apex ……..... ……..…..……. *A. divaricata* subsp. *gymnomaschala*

***Afrosalsola divaricata*** (Masson ex Link) Akhani **comb. nov.**
Basionym: *Salsola divaricata* Masson ex Link, Phys. Beschr. Canar. Ins. [Buch]:141 (1825).
Lectotype: (**designated here**, selected by H. Freitag 20.7.2001, in sched.): Tenerife, 1778, *F. Masson* (BM00059332, photo!). https://data.nhm.ac.uk/object/ae95cb5a-fa0e-4f31-9b00-5b6a505dfd0b

*Typification*: The type specimen has been collected by Francis Masson in 1778, a plant collector from the Royal Botanic Gardens, Kew who made several botanical expeditions to the Macaronesian Islands from 1776 to 1779

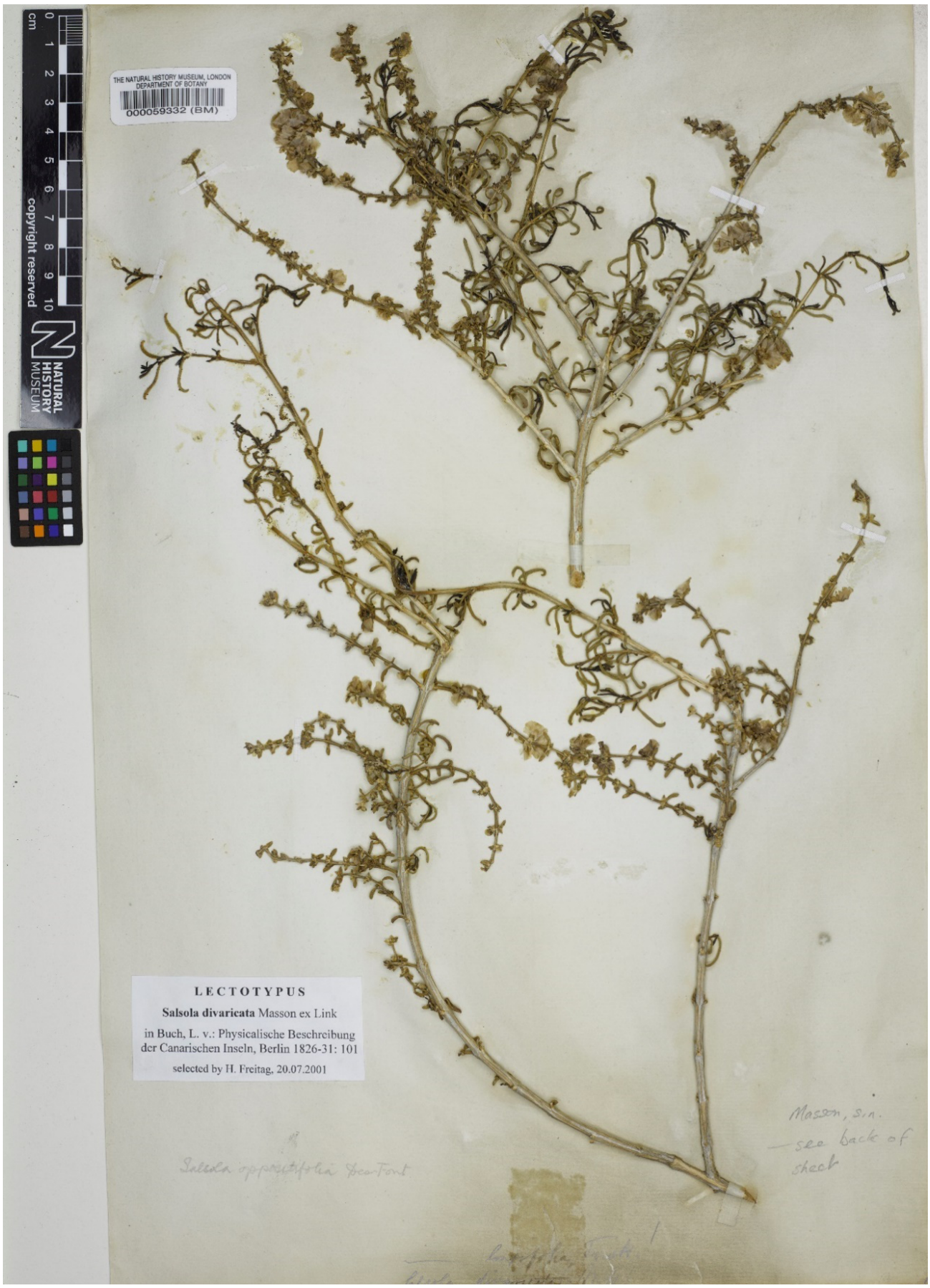


Figure 1. The lectotype of *Salsola divaricata*, courtesy of British Museum (BM).

(Francisco-Ortega *et al.*, 2008). A first comprehensive list of Canarian plants has been published by Johann H. F. Link as an appended list in "Verzeichnis der wildwachsenden Pflanzen, welche bis jetzt auf den canarischen Inseln gefunden worden sind", pages 137-199 (Buch, 1825). *Salsola divaricata* was the only valid new species published in Buch's book. Due to the fact that Link was a botanist in Berlin, it was supposed that the type of *S. divaricata* should have been destroyed during World War II. Castroviejo *et al.* (1992) described *S. marujae*, as a new species of *Salsola* on the Canary Islands. They clearly differentiate the new species from *S. oppositifolia* and *S. longifolia*, but assume that *S. divaricata* described by Link would be in reality a wrongly identified *Suaeda vera* Forssk. ex J.F.Gmel. They suggest it to be a *Suaeda* because the German description has no indication of a species with opposite leaves. However, several other characters in the description refer to a *Salsola* rather than a *Suaeda*. Even the eminent Russian chenopod scientist Victor Petrovitch Botchantsev mentioned the type location of *Salsola divaricata* in Berlin (Botschantzev, 1976). Thanks to Dr. Hans-Walter Lack, we were informed that the type material of *S. divaricata* is kept in the British Museum. As there is only one specimen in BM, there is no complication on its typification (Figure 1).

***Afrosalsola divaricata*** subsp. ***divaricata*** (Figure 2)
= *Salsola marujae* Castrov. & Luceño in Anales Jard. Bot. Madrid 50: 260 (1992).
Type: Islas Canarias, Tenerife, San Juan de Guía, 28RCS2119, cuneta nitrificada, 15.11.1988, S. Castroviejo n.° 10437SC & P. Romero Manrique. Holotype: MA513210a; Isotypes: MA513210-2 (Photo!), G, ORT.
= *Seidlitzia lowei* Iljin in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 90 (1954).
Holotype: Graciosa, Herbarium R. Lowe (LE, isotype K000243928, Photo!).
= *Seidlitzia orotavensis* Iljin in Bot. Gerb. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 88 (1954).
Lectotype (**designated here**): Spain; Canary Islands; Tenerife, ad rupes marit. prope portum Oratavensem, Decemb. 1845, E. Bourgeau 958 (LE00011751, photo!, isolectotype: K000243929, photo!)
Illustrations: Iljin l.c. 91, Fig. 2 (under *Seidlitzia orotavensis*), 92, Fig. 3 (under *Seidlitzia lowei* Iljin).
Distribution: The range of *A. divaricata* subsp. *divaricata* is restricted to the Canary Islands. It is known almost from all the islands, including Gran Canaria, Tenerife, Fuerteventura, La Graciosa and La Gomera.

***Afrosalsola divaricata*** subsp. ***gymnomaschala*** (Maire) Akhani **comb. & stat. nov.**
Basionym: *Salsola gymnomaschala* Maire in Bull. Soc. Hist. Nat. Afrique N. 29: 446 (1938).
Type (Lectotype, designated by Brullo, 1982): Morocco: Aguerguer, Presque'ile du Cap Blanc, fond de labaie du Levrier, 21.1.1937, Murat 1901 (MPU!).
≡ *Darniella gymnomaschala* (Maire) Brullo in Webbia 38: 315 (1984); ≡ *Salsola sieberi* var. *gymnomaschala* (Maire) Maire in Bull. Soc. Hist. Nat. Afrique N. 29: 446 (1939); ≡ *Seidlitzia gymnomaschala* (Maire) Iljin in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 93 (1954).
Distribution: Morocco (Cap Blanc).

***Afrosalsola divaricata*** subsp. ***verticillata*** (Schousboe) Akhani **comb. & stat. nov.**
Basionym: *Salsola verticillata* Schousb. in Iagttag. Vextrig. Marokko: 123 (1800).
≡ *Darniella verticillata* (Schousb.) Brullo in Webbia 38: 308 (1984); ≡ *Salsola longifolia* var. *verticillata* (Schousb.) Ball, Spic. Moroc.: 647 (1878); ≡ *Salsola oppositifolia* var. *verticillata* (Schousb.) Moq. in A.P.de Candolle, Prodr. 13(2): 185 (1849); ≡ *Seidlitzia verticillata* (Schousb.) Iljin in Bot. Mater. Gerb. Bot. Inst. Komarova Akad. Nauk S.S.S.R. 16: 88 (1954).
Type (Holotype): Morocco: In insula ad portum urbis Mogadore, P.K.A. Schousboe *s.n.* (C10000495 Photo! by V. Botschantzev 21.4.1975).
Distribution: Morocco (near Agadir).

***Afrosalsola deschaseauxiana*** (Litard. & Maire) Akhani **comb. nov.**
Basionym: *Salsola deschaseauxiana* Litard. & Maire, Contr. Etude Fl. Grand Atlas 2: 7 (1930); ≡ *Salsola sieberi* subsp. *deschaseauxiana* (Litard. & Maire) Sauvage in Monde Pl. 47: 37 (1952).
≡ *Salsola sieberi* var. *deschaseauxiana* (Litard. & Maire) Maire in Bull. Soc. Hist. Nat. Afrique N. 29: 446 (1939).
Type (Lectotype, designated by Brullo, 1982): Morocco: Agadir-n-Ighir, in rupestribus maritimis, 6.8.1926, R. Maire (MPU); Isotypes: P00083262!, P00083263!, LE00011852 photo!.

*Salsola deschaseauxiana* was synonymized with *S. verticillata* by Brullo (Brullo, 1982, 1984). It was accepted in the Plants of the World Online as *S. verticillata* Schousb. (http://powo.science.kew.org). Botschantzev (1989) has correctly accepted it as a separate species. The type specimen, which was collected from the same region of the type locality of *S. verticillata* (R. Maire, P00083262!, P00083263!) markedly differs from *S. verticillata* by the alternate leaves and branches and terete leaves. The carbon isotope composition of the type specimen (-24.2‰) is a functional evidence of the relationship with *Afrosalsola divaricata*.

## Anatomy, phylogeny and photosynthetic pathways

According to pre-molecular classifications, *Salsola divaricata* and its relatives have been classified into *Salsola* sect. *Caroxylon* subsect. *Coccosalsola* by Botschantzev (Botschantzev, 1976). It has then classified in the genus *Darniella* by Brullo (1984). The first comprehensive morpho-molecular analysis of tribe Salsoleae using nuclear (ITS) and plastid (PspB-PsbH) sequences revealed the unexpected position of *S. divaricata* as sister to a group of $C_4$ genera such as *Haloxylon*, *Hammada*, *Cornulaca* and *Anabasis* (Akhani *et al.*, 2007). The anatomy of *S. divaricata* and its relatives (e.g. *S. verticillata* and

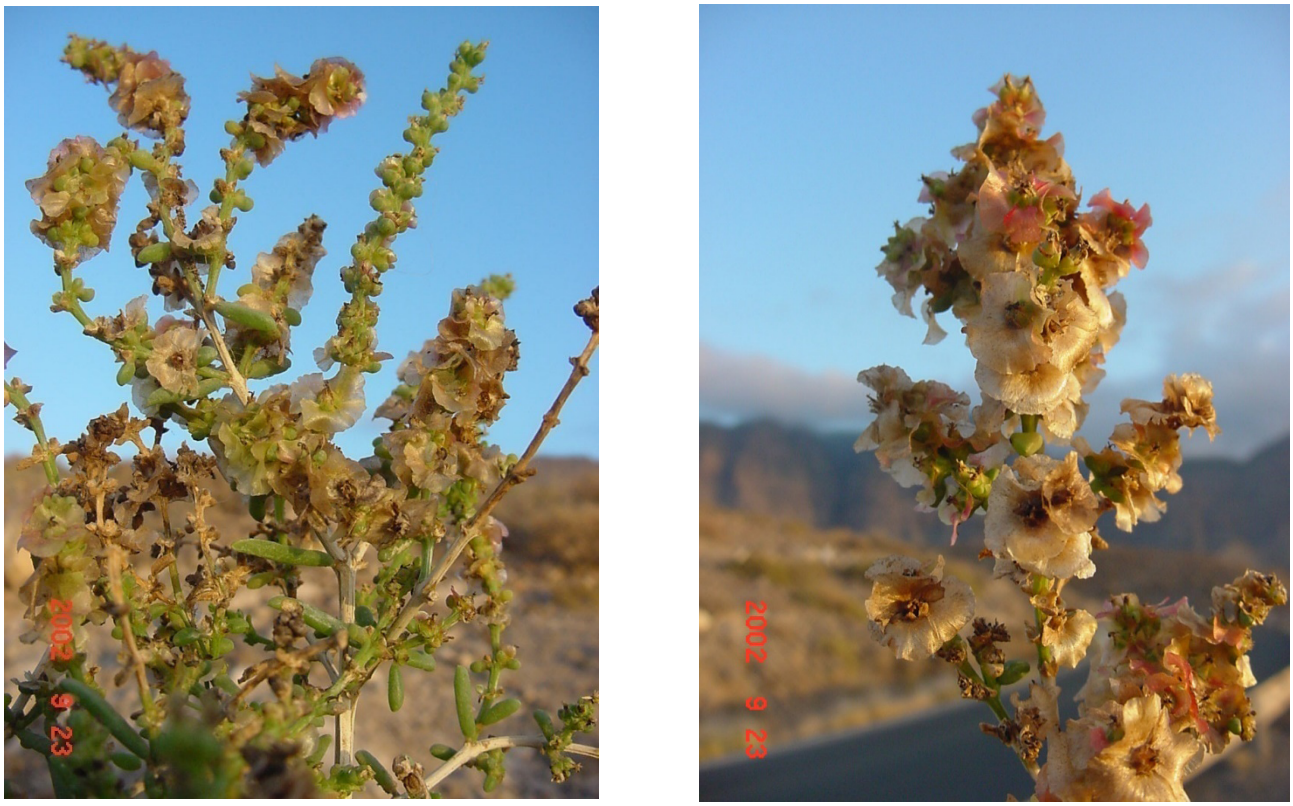


Figure 2. The living fruiting branch of *Afrosalsola divaricata* (Masson ex Link) Akhani subsp. *divaricata* from Gran Canaria, near Agaete, 23.9.2002. Photo credit, H. Akhani.

*S. gymnomaschala*) shows a Kranz-like structure in which a mesophyll layer (M1) similar to a hypodermis followed by the second palisade mesophyll layer and ends finally into a layer of large Kranz-like cells around the vascular tissue (Voznesenskaya *et al.*, 2013). This structure performs $C_2$ photosynthesis in which the photorespiratory $CO_2$ is further recaptured in Kranz-like cells. This structure and further biochemical and gas exchange features (e.g. the $CO_2$ compensation point) suggest that *S. divaricata*, *S. deschaseauxiana* and *S. gymnomaschala* are $C_3$-$C_4$ intermediates ($C_2$) (Schüssler *et al.*, 2017). Further molecular studies using multiple plastid sequences (atpB-rbcL spacer, ndhF-rpl32 spacer, trnQ-rps16) showed that all $C_3$ and $C_3$-$C_4$ intermediate species in Salsoleae belong to a monophyletic clade which consists of three additional subclades. One of them includes all species formerly described under the genus *Oreosalsola* including *Raphidophyton* (Akhani *et al.*, 2016). All four taxa of *Afrosalsola* form one monophyletic clade both in plastid and nuclear trees supporting its generic position.

The stable carbon isotope ratios of all examined specimens in *Afrosalsola* based on the herbarium samples collected in nature and cultivated in greenhouse show a range between -23.7‰ to -29.7‰ (Table 1, Voznesenskaya *et al*., 2013). The value of the type specimens of *A. deschaseauxiana* (-24.2‰) supports the inclusion of this species in the genus *Afrosalsola*.

The conflicting topologies between nuclear and plastid trees suggest hybridization origin and the role of reticulation in several groups of angiosperms. Recent studies using transcriptome data of *Salsola divaricata* aggr. and 12 other Chenopods having $C_3$ and $C_4$ photosynthesis support ancient hybridization between a $C_3$ species and a $C_4$ species as the origin of *S. divariacata* agg. (Tefarikis *et al.*, 2022). The network evidenced an ancient hybridization involving probably a relative of $C_4$ *Soda inermis* (*Salsola soda*) and the ancestor of $C_3$ *Oreosalsola montana*. A second reticulation event involved the ancestor of *Afrosalosla* and *Soda inermis* resulting in a $C_4$ clade that includes *Soda oppositifolia*. Based on the morphological features, *Soda oppositifolia* shows the highest similarity to *Afrosalosla* species.

This lineage is an established $C_2$ lineage well adapted to the saline coasts of the Canaries and north-western African mainland.

## New combinations in *Caroxylon* and *Soda* from Africa

The polyphyly of *Salsola* s.l. required many nomenclatural changes. These have been applied in several publications such as (Akhani *et al.*, 2007, 2016; Mucina, 2017; Rudov *et al.*, 2020; Sukhorukov *et al.*, 2022). The following names have not yet been classified in the new system of phylogenetic classifications. We accept the synonymy of two *Caroxylon* species suggested by Alexander Sukhorukov in Sukhorukov *et al.* (2019). The unexpected change of the type of *Salsola* in the last edition of ICN (Turland *et al.*, 2018) required some nomenclatural changes in affected genera. Most species have already been renamed as *Soda* and accepted in Plants of the World Online (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:7001-1). Mosyakin & Freitag (2023) proposed to conserve the name of *Soda* (Dumort.) Fourr. in Ann. Soc. Linn. Lyon, n.s., 17: 145 (1869) against *Sevada* Moq. in A.P.de Candolle, Prodr. 13(2): 154 (1849).

Table 1. The carbon isotope values of *Afrosalsola divaricata* s.l. and *A. deschaseuxiana.*

| Taxon | Value (‰) | Voucher and reference |
|---|---|---|
| *A. deschaseauxiana* | -24.2 | Morocco: Agadir-n-Ighir, in rupestribus maritimis, 6.8.1926, R. Maire (P00083263) (isotype) |
| *A. deschaseauxiana* | -26.2, -27.0 | W Morocco, H. Freitag, 35.002 (KAS) (Voznesenskaya *et al*., 2013) |
| *A. divaricata* subsp. *divaricata* | -24.5 | Pyankov *et al*. (2001b) |
| *A. divaricata* subsp. *divaricata* | -28.9, -29.7 | Cultivated in green house based on specimens collected from Canary Islands: Gran Canaria, western coasts, near Agaete, along the road with some shrubs like *Euphorbia regis-jubae*, *Kleinia neriifolia* and *Pennisetum setaceum*, 23.9.2002, Akhani 16469 (Voznesenskaya *et al.*, 2013) |
| *A. divaricata* subsp. *divaricata* | -25.7, -25.5 | H. Freitag 10.319 (KAS) (Voznesenskaya *et al.*, 2013) |
| *A. divaricata* subsp. *gymnomaschala* | -27.8, -27.8 | SW Morocco, H. Freitag, 35.019 (KAS) (Voznesenskaya *et al*., 2013) |
| *A. divaricata* subsp. *gymnomaschala* | -25.3, -25.1 | Morocco, R. Maire, 31.03.1937 (LE) (Voznesenskaya *et al*., 2013) |
| *A. divaricata* subsp. *verticillata* | -24.6, -23.7 | Morocco: Agadir and surroundings, H. Humbert, July 1925 (LE) (Voznesenskaya *et al*., 2013) |

***Caroxylon acanthocladum*** (Botsch.) Akhani **comb. nov.**
Basionym: *Salsola acanthoclada* Botsch. in Novosti Sist. Vyssh. Rast. 1968: 233 (1968).
Holotype: Algeria: Algeria, area of Ghardaia city, around Guerrara village, on sandy loam and red clay, 15.2.1965, P. Botschantzev 200, LE00011757 (Photo!), isotype: LE00011758 (Photo!).

***Caroxylon algeriense*** (Botsch.) Akhani & Rudov **comb. nov.**
Basionym: *Salsola algeriensis* Botsch. in Bot. Zhurn. (Moscow & Leningrad) 60(4): 498 (1975).
≡ *Nitrosalsola algeriensis* (Botsch.) Theodorova in Ukrayins'k. Bot. Zhurn. 72(5): 443 (2015).
Holotype: Algeria: Area of Biskra cit. Foum el-Gherza reservoir to the E. of the city, on limestone cliffs, 14.1.1965, V. P. Botschantzev 15 (LE00011769).

***Caroxylon chellalense*** (Botsch.) Akhani **comb. nov.**
Basionym: *Salsola chellalensis* Botsch. in Bot. Zhurn. (Moscow & Leningrad) 60: 499 (1975).
Holotype: Algeria: Chellala area (Reibell), 10 km to the north-west of the village Paul Gazelles, 23.09.1968, V. P. Botschantzev 1418 LE00011841 (isotype LE00011840).

***Caroxylon gypsaceum*** (Botsch.) Akhani **comb. nov.**
Basionym: *Salsola gypsacea* Botsch. in Bot. Zhurn. (Moscow & Leningrad) 60: 500 (1975).
Holotype: Algeria: High plateau, Boghari village area, Djebel Gourine mountains, to the southwest of the village on saline variegated clays, 12.6.1968, V. P. Botschantzev 150 (LE00011864, isotype: LE00011865).

***Caroxylon mairei*** (Botsch.) Akhani **comb. nov.**
Basionym: *Salsola mairei* Botsch. in Bot. Zhurn. (Moscow & Leningrad) 60: 502 (1975).
≡ *Nitrosalsola mairei* (Botsch.) Theodorova in Ukrayins'k. Bot. Zhurn. 72(5): 443 (2015).
Holotype: Algeria: Algeria. High plateau. Zahrez Rharbi salt lake area. Salt marsh at the eastern edge of the lake, 20.09.1968, V. P. Botschantzev 1417 (LE00011883, isotype: LE00011884).

***Caroxylon maroccanum*** (Botsch.) Akhani & Rudov **comb. & stat. nov.**
Basionym: *Salsola gemmascens* Pall. subsp. *maroccana* Botsch. in Novosti Sist. Vyssh. Rast. 6: 50 (1970).
Holotype: Morocco: Safsafat, steppes pierreuses calcaires, 29.6.1921, R. Maire. s.n. (MPU010322).

***Soda cruciata*** (L. Chevall. ex Batt. & Trab.) Akhani **comb. nov.**
Basionym: *Salsola cruciata* L. Chevall. ex Batt. & Trab., Fl. Algérie Tunisie: 288 (1905).
Type (lectotype designated by Brullo, 1982): Algeria: Biskra, in arenosis glareosis necnon in salsuginosis prope Ain Salahin, 20.10.1902, L. Chevallier 499 (P04992778), isolectotypes: P04992777!, P05157616, G00015522 (Photo!), FI000823 (Photo!).
≡ *Salsola zygophylla* Batt. & Trabut var. *vesceritensis* Chevall. in Bull. Herb. Boiss., ser. 2, 9: 777 (1903); ≡ *Salsola longifolia* Forssk. var. *vesceritensis* (Chevall.) Maire in Bull. Soc. Hist. Nat. Afr. Nord 27: 352 (1936); ≡ *Salsola sieberi* C. Presl var. *vesceritensis* (Chevall.) Maire in Bull. Soc. Hist. Nat. Afr. Nord 33: 188 (1942).
= *Salsola tunetana* Brullo in Willdenowia 12: 246 (1982).
Holotype: Tunisie, entre Mareth et Adjina, 10.1951, Labbe s. n. (G00015584, photo!).
Note: The typification of *S. cruciata* follows Brullo (1982) in which No. 499 is selected as type. In P herbarium there is another specimen which is noted as type by Brullo with the label Biskra: à Fontaine chaude, près du marais aux roseaux, October 1902, L. Chevallier (P00487047!). This is a potential isotype.

***Soda cycloptera*** (Stapf) Akhani **comb. nov.**
Basionym: *Salsola cycloptera* Stapf in H.O. Forbes, Nat. Hist. Sokotra: 526 (1903).
≡ *Gyroptera cycloptera* (Stapf) Botsch. in Bot. Zhurn. (Moscow & Leningrad) 52: 809 (1967); ≡ *Lagenantha cycloptera* (Stapf) M.G. Gilbert & Friis in Nordic J. Bot. 11(3): 315 (1991).
Type (lectotype, designated by Boulos *et al.*, 1991): Yemen: Island Aboulkuri, Ogilvie – Grant (K000244000!).
= *Salsola semhahensis* Vierh. in Oesterr. Bot. Z. 53: 434 (1903).
≡ *Choriptera semhahensis* (Vierh.) Botsch. in Bot. Zhurn. (Moscow & Leningrad) 52: 806 (1967).
Holotype: Yemen: Samhah [Semhah], near the harbour, Paulay s.n. (W).
= *Gyroptera somalensis* Botsch. in Bot. Zhurn. (Moscow & Leningrad) 52: 808 (1967).
Holotype: Somalia, Bacino del Nogal, steppes between Budére and Hamùr, 25.6.1924, N. Puccioni & J. Stefanini 918 (FT000983).
= *Lagenantha nogalensis* Chiov., Fl. Somala 1: 293 (1929).
Type (lectotype designated by V. Botschantzev, 17.11.1966): Somalia, Nogal [Nuggal] region, Budére, N. 27.6.1924, Puccioni & J. Stefanini 916 (FT000982).
= *Lagenantha nogalensis* var. *papillosa* Chiov., Fl. Somala 1: 294 (1929).
Lectotype (selected by V. Botschantzev 2.12.1966, Botschantzev 1975): Somalia, Bacino del Nogal: Steppa fra Tur Càhio ed Handurgàb, 27.6.1924, N. Puccioni & J. Stefanini (FT000984).

***Soda gillettii*** (Botsch.) Akhani **comb. nov.**
Basionym: *Gyroptera gillettii* Botsch. in Kew Bull. 30: 369 (1975).
≡ *Lagenantha gillettii* (Botsch.) M.G. Gilbert & Friis in Nordic J. Bot. 11: 315 (1991).
Type (Holotype): Kenya, Isiolo Distr.: Garba Tula-Mado Gashi road, ca. 12 km W. of Mado Gashi, alt. 350 m, 3.6.1970, Gillett & Newbould 19162 (EA000002195). Isotypes: K000243998; FT000985; LE00011748.

***Soda glomerata*** (Maire) Akhani **comb. nov.**
Basionym: *Salsola sieberi* var. *glomerata* Maire in Bull. Soc. Hist. Nat. Afrique N. 33: 188 (1942).
≡ *Salsola glomerata* (Maire) Brullo in Willdenowia 12: 245 (1982).
Hololectotype: Algeria: Sahara central: Oued Djader à l'W de l'Ahnet, 9.12.1940, R. Volkonsky (MPU005489, selected by Brullo 5.9.1982).

***Soda schimperi*** (Moq.) Akhani **comb. nov.**
Basionym: *Sevada schimperi* Moq. in A.P.de Candolle, Prodr. 13(2): 154 (1849).
Type: Saudi Arabia: Prope Dscheddam, in litore maris rubric, 10.1.1837, G. H. Schimper 867 - (P00734046!), P00734045!, P00800955!; E00296921 (photo!), Verified by L.Boulos, 1991/8/12; BM000950590 (photo!), BM000950589 (photo!) Verified by Loutfy Boulos, HAL0072103 (photo!), H. Freitag (KAS), 1994/2/23, LE00011741 (photo!), LE00011743 (photo!); LE00011744 (photo!); LE00011742 (photo!); MPU007244; HBG503407; HBG506283.
The holotype of *Sevada schimperi* is mentioned to be in G herbarium by V. Botschantzev (Botschantzev, 1975). However, we could not find its photo in Geneva Herbaria Catalogue (https://www.ville-ge.ch) and Jstor database (https://plants.jstor.org/).

***Soda subglabra*** (Botsch.) Akhani **comb. nov.**
Basionym: *Salsola subglabra* Botsch. in Bot. Zhurn. (Moscow & Leningrad) 60: 504 (1975).
≡ *Nitrosalsola subglabra* (Botsch.) Theodorova in Ukrayins'k. Bot. Zhurn. 72: 444 (2015).
Holotype: Algeria: Algeria. High plateau. Zahrez Rharbi salt lake area, salt marsh at the eastern edge of the lake,V. P. Botschantyev 1413, LE00011923 (isotype: LE00011924).

***Soda zygophylla*** (Batt.) Akhani & Sukhor. **comb. nov.**
Basionym: *Salsola zygophylla* Batt. in J.A. Battandier & L.C. Trabut, Fl. Algérie, Dicot. (App. 2): 15 (1890).
Holotype: Bords de l'Oued Krebassa près le Chott Chergui, 1890, J.A. Battandier (P00487044, verified by Brullo 18.3.1981). Isotypes: P00083260, BR0000028526131, MPU007910.

***Soda zygophylloides*** (Aellen & C.C. Towns.) Akhani **comb. nov.**
Basionym: *Fadenia zygophylloides* Aellen & C.C.Towns. in Kew Bull. 27: 501 (1972).
Holotype: Kenya: Marsabit district East side of Lake Rudolf, between Koobi Fora and Shin (hill), 30° 57' N, 36°12 'E to 3° 58' N, 36° 20 'E, 400-600m, 01.5.1971, R.B. Faden 71/291 (K000243997!).

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## Conflict of interest

None

## Authorship contribution

H. Ak.: Conceptualization, design, writing; H. Ab.: preparing Appendix, writing; A.R.: translating Russian references used in the paper, writing, critical linguistic improvements. All authors contributed to the critical revision of the text, and approved the final version.

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Appendix 1. Updated checklist of African species of the genus *Salsola* s.l.

| Accepted post molecular phylogenetic name | Pre molecular phylogenetic name |
|---|---|
| *Caroxlon maroccanum* (Botsch.) Akhani & Rudov | *Salsola gemmascens* Pall. subsp. *maroccana* Botsch. |
| *Caroxylon gypsaceum* (Botsch.) Akhani | *Salsola gypsacea* Botsch. |
| *Caroxylon acanthocladum* (Botsch.) Akhani | *Salsola acanthoclada* Botsch. |
| *Caroxylon acocksii* (Botsch.) Mucina | *Salsola acocksii* Botschantzev |
| *Caroxylon adiscum* (Botsch.) Mucina | *Salsola adisca* Botsch. |
| *Caroxylon adversariifolium* (Botsch.) Mucina | *Salsola adversariifolia* Botsch. |
| *Caroxylon aellenii* (Botsch.) Mucina | *Salsola aellenii* Botsch. |
| *Caroxylon albidum* (Botsch.) Theodorova | *Salsola albida* Botsch. |
| *Caroxylon albisepalum* (Aellen) Mucina | *Salsola albisepala* Aellen |
| *Caroxylon algeriense* (Botsch.) Akhani & Rudov | *Salsola algeriensis* Botsch. |
| *Caroxylon aphyllum* (L.f.) Tzvelev | *Salsola aphylla* L.f. |
| *Caroxylon apiciflorum* (Botsch.) Mucina | *Salsola apiciflora* Botsch. |
| *Caroxylon apterygeum* (Botsch.) Mucina | *Salsola apterygea* Botsch. |
| *Caroxylon araneosum* (Botsch.) Akhani & E.H.Roalson | *Salsola araneosa* Botsch. |
| *Caroxylon arboreum* (C.A.Sm. ex Aellen) Mucina | *Salsola arborea* C.A.Sm. ex Aellen |
| *Caroxylon armatum* (C.A.Sm. ex Aellen) Mucina | *Salsola armata* C.A.Sm. ex Aellen |
| *Caroxylon aroabicum* (Botsch.) Mucina | *Salsola aroabica* Botsch. |
| *Caroxylon atratum* (Botsch.) Mucina | *Salsola atrata* Botsch. |
| *Caroxylon barbatum* (Aellen) Mucina | *Salsola barbata* Aellen |
| *Caroxylon caffrum* (Sparrman) Mucina | *Salsola caffra* Sparrman |
| *Caroxylon callunum* (Drège ex C.H.Wright) Theodorova ex Mucina | *Salsola calluna* Drège ex C.H.Wright |
| *Caroxylon campylopterum* (Botsch.) Mucina | *Salsola campyloptera* Botsch. |
| *Caroxylon cauliflorum* (Botsch.) Mucina | *Salsola cauliflora* Botsch. |
| *Caroxylon ceresicum* (Botsch.) Mucina | *Salsola ceresica* Botsch. |
| *Caroxylon chellalense* (Botsch.) Akhani | *Salsola chellalensis* Botsch. |
| *Caroxylon columnare* (Botsch.) Theodorova | *Salsola columnaris* Botsch. |
| *Caroxylon contrariifolium* (Botsch.) Mucina | *Salsola contrariifolia* Botsch. |
| *Caroxylon cryptopterum* (Aellen) Mucina | *Salsola cryptoptera* Aellen |
| *Caroxylon cyclophyllum* (Baker) Akhani & Roalson | *Salsola cyclophylla* Baker |
| *Caroxylon dealatum* (Botsch.) Mucina | *Salsola dealata* Botsch. |
| *Caroxylon decussatum* (C.A.Sm. ex Botsch.) Mucina | *Salsola decussata* C.A.Sm. ex Botsch. |
| *Caroxylon denudatum* (Botsch.) Mucina | *Salsola denudata* Botsch. |
| *Caroxylon dinteri* (Botsch.) Mucina | *Salsola dinteri* Botsch. |
| *Caroxylon divaricatum* Moq. | *Salsola divaricata* (Moq.) Moq. ex Ulbr. nom. illeg. (= *S. capensis* Botsch.) |
| *Caroxylon dolichostigmum* (Botsch.) Mucina | *Salsola dolichostigma* Botsch. |
| *Caroxylon esterhuyseniae* (Botsch.) Mucina | *Salsola esterhuyseniae* Botsch. |
| *Caroxylon etoshense* (Botsch.) Mucina | *Salsola etoshensis* Botsch. |
| *Caroxylon exalatum* (Botsch.) Mucina | *Salsola exalata* Botsch. |
| *Caroxylon gaetulum* (Maire) Akhani & Roalson | *Salsola gaetula* (Maire) Botsch. |
| *Caroxylon garubicum* (Botsch.) Mucina | *Salsola garubica* Botsch. |
| *Caroxylon geminiflorum* (Fenzl ex C.H.Wright) Mucina | *Salsola geminiflora* Fenzl ex C.H.Wright |
| *Caroxylon gemmatum* (Botsch.) Mucina | *Salsola gemmata* Botsch. |

| Accepted post molecular phylogenetic name | Pre molecular phylogenetic name |
|---|---|
| *Caroxylon gemmiferum* (Botsch.) Mucina | *Salsola gemmifera* Botsch. |
| *Caroxylon gemmiparum* (Botsch.) Mucina | *Salsola gemmipara* Botsch. |
| *Caroxylon giessii* (Botsch.) Mucina | *Salsola giessii* Botsch. |
| *Caroxylon glabrescens* (Burtt Davy) Akhani & E.H.Roalson | *Salsola glabrescens* Burtt Davy |
| *Caroxylon glabrescens* var. *apiculatum* (C.A.Sm. ex Botsch.) Mucina | *Salsola glabrescens* var. *apiculata* C.A.Sm. ex Botsch. |
| *Caroxylon glabrum* (Botsch.) Mucina | *Salsola glabra* Botsch. |
| *Caroxylon henriciae* (I.Verd.) Mucina | *Salsola henriciae* I.Verd. |
| *Caroxylon hoanibicum* (Botsch.) Mucina | *Salsola hoanibica* Botsch. |
| *Caroxylon hottentotticum* (Botsch.) Mucina | *Salsola hottentottica* Botsch. |
| *Caroxylon huabicum* (Botsch.) Mucina | *Salsola huabica* Botsch. |
| *Caroxylon humifusum* (C.A.Sm. ex A.Brückn.) Theodorova | *Salsola humifusa* C.A.Sm. ex A.Brückn. |
| *Caroxylon imbricatum* (Forssk.) Moq. | *Salsola imbricata* Forssk. |
| *Caroxylon inapertum* (Botsch.) Mucina | *Salsola inaperta* Botsch. |
| *Caroxylon kalaharicum* (Botsch.) Mucina | *Salsola kalaharica* Botsch. |
| *Caroxylon kleinfonteini* (Botsch.) Mucina | *Salsola kleinfonteini* Botsch. |
| *Caroxylon koichabicum* (Botsch.) Mucina | *Salsola koichabica* Botsch. |
| *Caroxylon littorale* (Moq.) Akhani & E.H.Roalson | *Salsola littoralis* Moq. |
| *Caroxylon marginatum* (Botsch.) Mucina | *Salsola marginata* Botsch. |
| *Caroxylon melananthum* (Botsch.) Mucina | *Salsola melanantha* Botsch. |
| *Caroxylon merxmuelleri* (Aellen) Mucina | *Salsola merxmuelleri* Aellen |
| *Caroxylon microtrichum* (Botsch.) Mucina | *Salsola microtricha* Botsch. |
| *Caroxylon minutifolium* (Botsch.) Mucina | *Salsola minutifolia* Botsch. |
| *Caroxylon mirabile* (Botsch.) Mucina | *Salsola mirabilis* Botsch. |
| *Caroxylon namaqualandicum* (Botsch.) Mucina | *Salsola namaqualandica* Botsch. |
| *Caroxylon namibicum* (Botsch.) Mucina | *Salsola namibica* Botsch. |
| *Caroxylon nigrescens* (C.A.Sm. ex I.Verd.) Mucina | *Salsola nigrescens* C.A.Sm. ex I.Verd. |
| *Caroxylon nollothense* (Aellen) Mucina (=*C. angolense* (Botsch.) Mucina, *C. luederitzense* (Botsch.) Mucina) | *Salsola nollothensis* Aellen (=*Salsola angolensis* Botsch., *S. luederitzensis* Botsch.) |
| *Caroxylon okaukuejense* (Botsch.) Mucina | *Salsola okaukuejensis* Botsch. |
| *Caroxylon omaruruense* (Botsch.) Mucina | *Salsola omaruruensis* Botsch. |
| *Caroxylon parviflorum* (Botsch.) Mucina | *Salsola parviflora* Botsch. |
| *Caroxylon patentipilosum* (Botsch.) Mucina | *Salsola patentipilosa* Botsch. |
| *Caroxylon pearsonii* (Botsch.) Mucina | *Salsola pearsonii* Botsch. |
| *Caroxylon phillipsii* (Botsch.) Mucina | *Salsola phillipsii* Botsch. |
| *Caroxylon pillansii* (Botsch.) Mucina | *Salsola pillansii* Botsch. |
| *Caroxylon procerum* (Botsch.) Mucina | *Salsola procera* Botsch. |
| *Caroxylon ptilopterum* (Botsch.) Mucina | *Salsola ptiloptera* Botsch. |
| *Caroxylon rabieanum* (I.Verd.) Mucina | *Salsola rabieana* I.Verd. |
| *Caroxylon robinsonii* (Botsch.) Mucina | *Salsola robinsonii* Botsch. |
| *Caroxylon ruschii* (Aellen) Mucina | *Salsola ruschii* Aellen |
| *Caroxylon mairei* (Botsch.) Akhani | *Salsola mairei* Botsch. |
| *Caroxylon schreiberae* (Botsch.) Mucina | *Salsola schreiberae* Botsch. |
| *Caroxylon scopiforme* (Botsch.) Mucina | *Salsola scopiformis* Botsch. |
| *Caroxylon seminudum* (Botsch.) Mucina | *Salsola seminuda* Botsch. |

| Accepted post molecular phylogenetic name | Pre molecular phylogenetic name |
|---|---|
| *Caroxylon sericatum* (Botsch.) Mucina | *Salsola sericata* Botsch. |
| *Caroxylon seydelii* (Botsch.) Mucina | *Salsola seydelii* Botsch. |
| *Caroxylon smithii* (Botsch.) Mucina | *Salsola smithii* Botsch. |
| *Caroxylon spenceri* (Botsch.) Mucina | *Salsola spenceri* Botsch. |
| *Caroxylon spinescens* (Moq.) Akhani & Roalson | *Salsola spinescens* Moq. |
| *Caroxylon squarrosulum* (Botsch.) Mucina | *Salsola squarrosula* Botsch. |
| *Caroxylon swakopmundense* (Botsch.) Mucina | *Salsola swakopmundensis* Botsch. |
| *Caroxylon tetragonum* (Delile) Moq. | *Salsola tetragona* Delile |
| *Caroxylon tetramerum* (Botsch.) Mucina | *Salsola tetramera* Botsch. |
| *Caroxylon tetrandrum* (Forssk.) Akhani & Roalson | *Salsola tetrandra* Forssk. |
| *Caroxylon tuberculatiforme* (Botsch.) Mucina | *Salsola tuberculatiformis* Botsch. |
| *Caroxylon tuberculatum* Moq. | *Salsola tuberculata* (Moq.) Fenzl ex Drège |
| *Caroxylon ugabicum* (Botsch.) Mucina | *Salsola ugabica* Botsch. |
| *Caroxylon unjabicum* (Botsch.) Mucina | *Salsola unjabica* Botsch. |
| *Caroxylon verdoorniae* (Toelken) Mucina | *Salsola verdoorniae* Toelken |
| *Caroxylon vermiculatum* (L.) Akhani & Roalson | *Salsola vermiculata* L. |
| *Caroxylon villosum* (Schult.) Akhani & Roalson | *Salsola villosa* Schult. |
| *Caroxylon warmbadicum* (Botsch.) Mucina | *Salsola warmbadica* Botsch. |
| *Caroxylon zeyheri* Moq. | *Salsola zeyheri* (Moq.) Bunge |
| *Kaviria rubescens* (Franch.) Akhani | *Salsola rubescens* Franch. |
| *Salsola kali* L. | *Salsola kali* L. |
| *Soda cruciata* (L.Chevall. ex Batt. & Trab.) Akhani | *Salsola cruciata* L.Chevall. ex Batt. & Trab. |
| *Soda cycloptera* (Stapf) Akhani | *Lagenantha cycloptera* (Stapf) M.G. Gilbert & Friis |
| *Soda gillettii* (Botsch.) Akhani | *Lagenantha gillettii* (Botsch.) M.G.Gilbert & Friis |
| *Soda cyrenaica* (Maire & Weiller) Akhani | *Salsola cyrenaica* (Maire & Weiller) Brullo |
| *Soda glomerata* (Maire) Akhani | *Salsola glomerata* (Maire) Brullo |
| *Soda inermis* Fourr. | *Salsola soda* L. |
| *Soda longifolia* (Forssk.) Akhani | *Salsola longifolia* Forssk. |
| *Soda oppositifolia* (Desf.) Akhani | *Salsola oppositifolia* Desf. |
| *Soda rosmarinus* (Bunge ex Boiss.) Akhani | *Seidlitzia rosmarinus* Bunge ex Boiss. |
| *Soda schweinfurthii* (Solms) Akhani | *Salsola schweinfurthii* Solms |
| *Soda schimperi* (Moq.) Akhani | *Sevada schimperi* Moq. |
| *Soda subglabra (*Botsch.) Akhani | *Salsola subglabra* Botsch. |
| *Soda zygophylla* (Batt.) Akhani & Sukhor. | *Salsola zygophylla* Batt. |
| *Soda zygophylloides* (Aellen & C.C.Towns.) Akhani | *Fadenia zygophylloides* Aellen & C.C.Towns. |