

Towards a new classification of *Salvia* s.l.: (re)establishing the genus *Pleudia* Raf.

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Abstract: *Salvia* L. in its traditional circumscription is the largest genus within the mint family. To date, the magnitude of the task has rendered it difficult to provide a genus-wide revision based on morphological data. Current molecular investigations based on a dense taxon sampling representing the whole phenotypic diversity and distribution range of *Salvia* confirmed that the genus is polyphyletic. *Salvia* species fall in 4 distinct clades, although all of them, except Clade IV, also include non-*Salvia* genera. A taxonomic revision is thus urgently needed with two different approaches that have to be considered: (1) to include the 5 morphologically distinct non-*Salvia* genera in *Salvia* or (2) to split *Salvia* s.l. into *Salvia* s.s. and several additional genera. Since *Salvia* is already highly heterogeneous in species distribution, morphology, and chromosome number, we prefer to split the genus into molecularly well-supported clades. This new concept may facilitate monographic studies and more focused analyses of character evolution within or between the clades. Species representing *Salvia* sect. *Eremosphace* Bunge (subclade III-A) were chosen exemplarily to provide arguments for elevating this particular group to the level of genus (*Pleudia* Raf.).

Key words: *Pleudia* Raf., *Salvia aegyptiaca*-group, *Salvia* sects. *Notiosphace* Benth. and *Eremosphace* Bunge, phylogeny, North Africa, Southwest Asia

1. Introduction

The approximately 945 species placed in *Salvia* L. are highly diverse in distribution, ecology, life form, morphology, and karyology (Will, 2013). This is reflected by molecular studies revealing that *Salvia* is nonmonophyletic (Walker et al., 2004; Walker and Sytsma, 2007) and showing that its phenotypic diversity largely reflects parallel evolution (Will and Claßen-Bockhoff, 2014). An example of parallel evolution is the presence of a unique modification of the androecium leading to the formation of lever-like stamens. The lever was traditionally regarded as a synapomorphic character supporting the genus and was assumed to reflect various degrees of diversification (primitive vs. derived types) in certain subgeneric or geographical groups (Himmelbaur and Stibal, 1932, 1933, 1934; Claßen-Bockhoff et al., 2004; Walker and Sytsma, 2007). Interestingly, staminal levers are also known from two Australian genera, *Hemigenia* R.Br. and *Microcorys* R.Br. (Guerin, 2005), reflecting more apparent examples of parallel stamen evolution within the Lamiaceae.

Salvia s.l. contains 4 distinct lineages (Clades I–IV) that include all *Salvia* species as well as the genera *Dorystaechas* Boiss. & Heldr., *Meriandra* Benth., *Perovskia* Kar., *Rosmarinus* L., and *Zhumeria* Rech.f. & Wendelbo

(Figure 1) (Walker et al., 2004; Walker and Sytsma, 2007; Will and Claßen-Bockhoff, 2014). One might argue that the small genera nested within *Salvia* s.l. represent derived lineages, and probably emerged from obscured evolutionary processes such as budding or a progenitor-derivate relationship as reviewed by Hörandl (2006) or addressed by Hörandl and Stuessy (2010). Consequently, one might expect that the corresponding genera evolved and/or diverged more recently than the *Salvia* lineages, a pattern that might be reflected in a calibrated phylogeny. However, recently published estimates for divergence times in *Salvia* s.l. (see Figure 2 in Drew and Sytsma, 2012) rather seem to support the relict hypothesis. According to current data, the most recent common ancestor (MRCA) of *Rosmarinus* and *Perovskia* is not found to be younger than the one of the two species representing Clade I. This approach is a first approximation towards the putative origin of the major lineages within *Salvia* s.l. and might change when *Salvia* s.l. is represented with more species. Today, in view of the preliminary calibration and morphological data (e.g., primitive stamen morphology) the relict hypothesis appears to be sufficiently supported. We thus consider *Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, and *Zhumeria* to be most probably ‘satellite’

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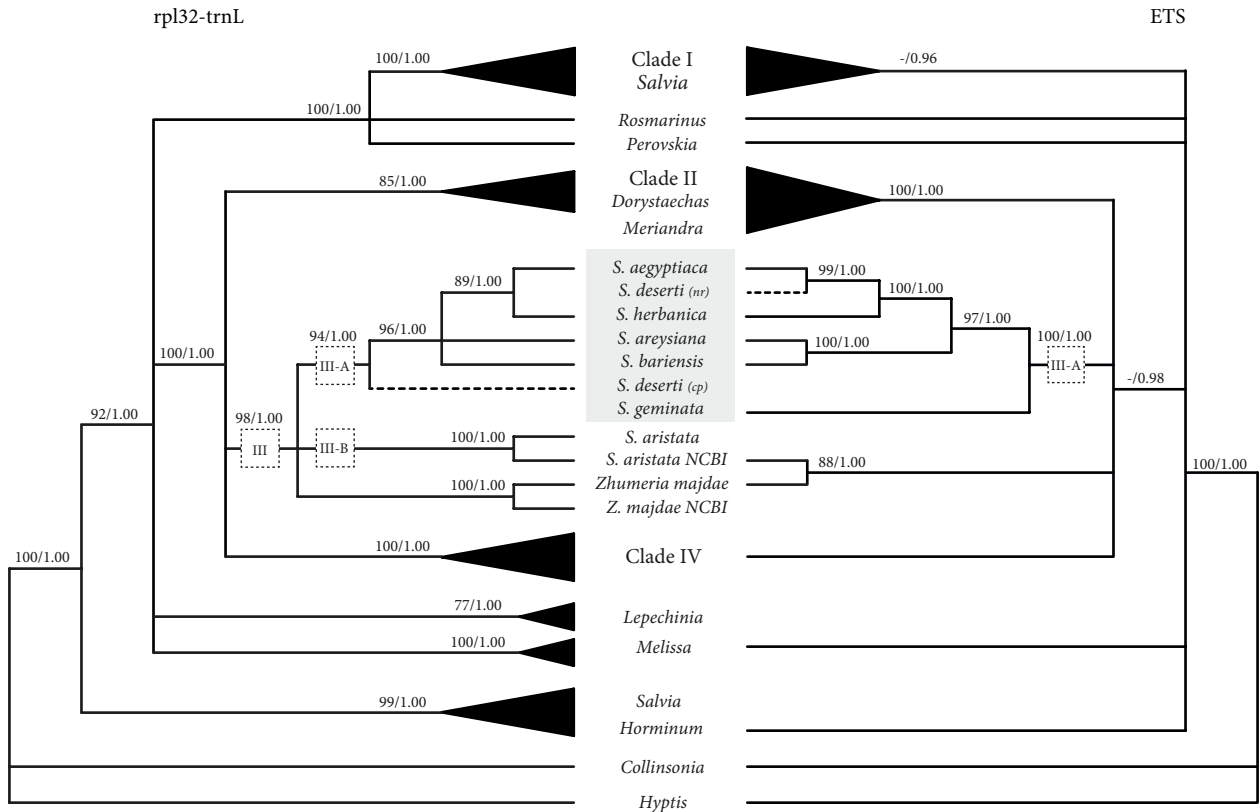


Figure 1. Simplified phylogenetic tree of *Salvia* s.l. (Will and Claßen-Bockhoff, 2014; modified). Molecular phylogeny based on chloroplast data (left) compared to nuclear data (ETS) (right) with focus on SW Asian taxa nesting in subclade III-A (highlighted: gray box). A highly supported incongruence within this clade is identified for the placement of *S. deserti* (dotted line).

genera in the sense of Frodin (2004), who argued that a single larger taxon would be accompanied by several, often quite small ‘satellite’ taxa. The supposed relict status is also supported by the comparably narrow distribution of, for example, *Dorystaechas hastata* in the Mediterranean region of southern Turkey.

These findings demand taxonomic consequences that should not be taken lightly. Maintaining *Salvia* in its traditional circumscription would require the inclusion of the 5 distinct genera and consequently lead to a morphologically and karyologically more heterogeneous group. This of course would involve fewer taxonomic changes than the alternative approach, but morphological characters have not been found that support all of the major clades including, for example, Clade III (*Salvia*-species plus *Zhumeria*). In contrast, splitting *Salvia* s.l. into a narrowly defined *Salvia* s.s. plus several molecularly highly supported clades might appear unpopular in terms of the long taxonomic tradition and the use of *Salvia* in horticulture or medicine. One might also argue that a new classification should not be done before an exhaustive taxonomic revision of *Salvia* s.l., which would probably take decades.

So far, several genera of comparable size or with similar horticultural importance as *Salvia* (e.g., orchids; Whitten et al., 2007) have already been the subject of molecular studies, which often result in generic re-circumscriptions, partial generic revisions, or at least proposals to split polyphyletic genera (e.g., Frodin, 2004; Mansion, 2004; Kress et al., 2005; Whitten et al., 2007; Kučera et al., 2013; Dillenberger and Kadereit, 2014).

We are convinced that splitting *Salvia* will contribute to comparably small, and thus manageable, genera and a natural classification (see Frodin, 2004). Novel circumscriptions are needed for the new genera, while *Dorystaechas*, *Meriandra*, *Perovskia*, *Rosmarinus*, and *Zhumeria* are accepted with their previous circumscriptions. Since the type species of *Salvia*, *S. officinalis* L. (Jarvis, 2007), is placed in a derived position within Clade I, this lineage represents *Salvia* s.s.

As part of the ongoing revision of the polyphyletic *Salvia* s.l., we suggest that well-supported clades that can additionally be supported by distribution, morphology, karyology, and/or ecology be recognized at generic level. One of them is subclade III-A (*Salvia aegyptiaca*-group; Will and Claßen-Bockhoff, 2014), as already proposed by Rafinesque (1837; gen. *Pleudia* Raf.).

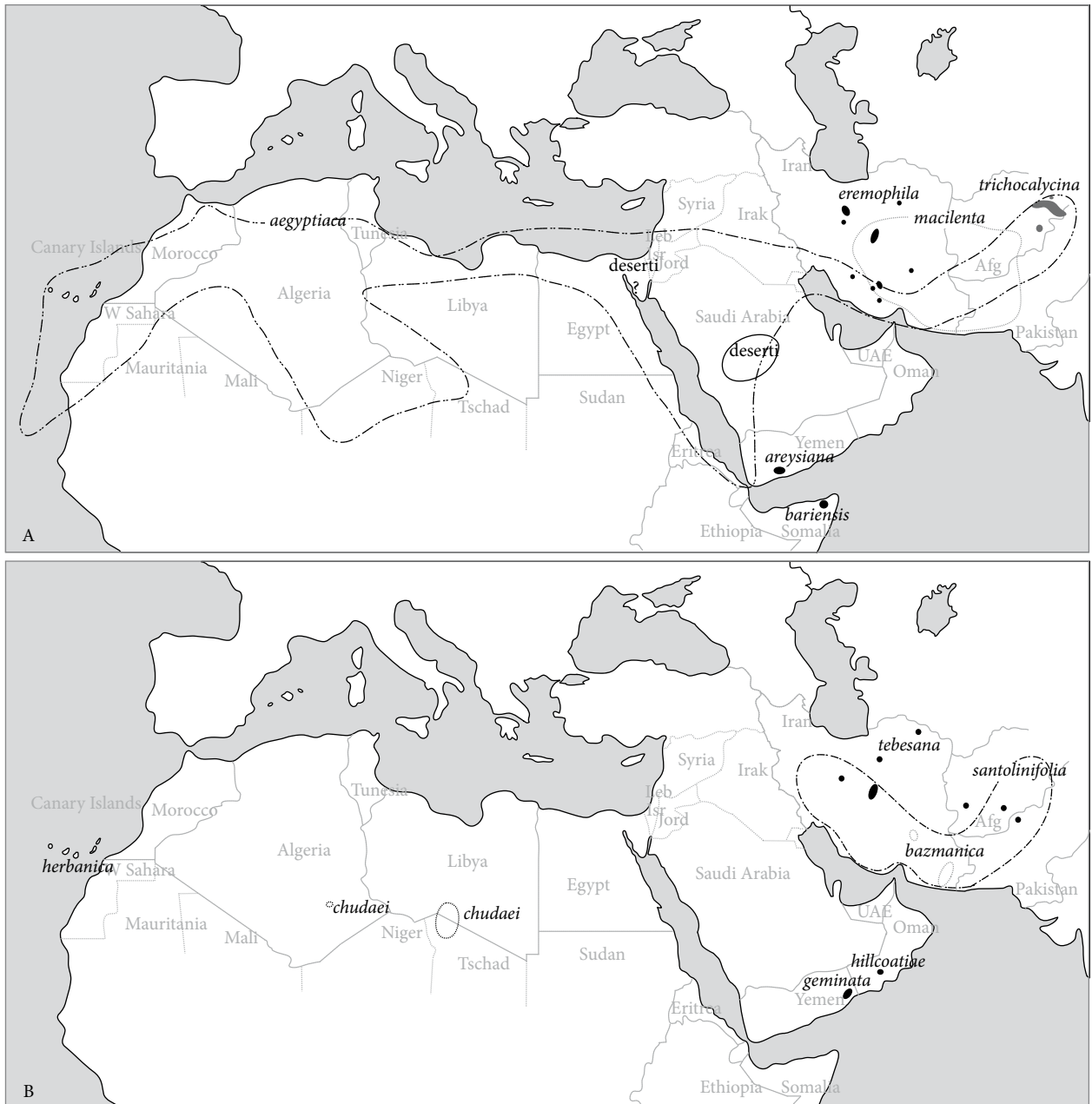


Figure 2. Distribution of *Pleudia* (*S. aegyptiaca*-group). Based on Hedge (1968, 1974a, 1982b, 1982c), Bokhari and Hedge (1977), Santos and Fernández, (1986), and Thulin (1993, 2009). Afg = Afghanistan, Isr = Israel, Jord = Jordan, Leb = Lebanon, UAE = United Arab Emirates. A: Overlapping distribution of *S. aegyptiaca*, *S. deserti*, *S. macilenta*, *S. eremophila*, and *S. trichocalycina* vs. locally restricted species on the Arabian Peninsula and in East Africa. B: Disjunct or scattered distribution of *S. chudaei* (Libya/Chad, Algeria) and *S. tebesana* in contrast to locally restricted species, i.e. *S. geminata*, *S. hillcoatiae*, and *S. herbanica* (Fuerteventura, Canary Islands).

2. Materials and methods

Molecular data, distribution, and morphology were used to circumscribe the highly supported *Salvia aegyptiaca*-group (Will and Claßen-Bockhoff, 2014) as a genus. For the taxonomic treatment, morphological data and information about species distribution were mainly obtained from the literature (Hedge, 1966, 1974a; Bokhari and Hedge, 1977;

Hedge, 1982a, 1982b, 1982c; Santos and Fernández, 1986; Hedge 1990; Scholz, 1993; Thulin, 1993, 2009). Molecular data are available for 8 of the 14 species (66.7%) (Table) (Will and Claßen-Bockhoff, 2014). Chromosome numbers for Clade III species are based on literature research and the Index to Plant Chromosome Numbers (IPCN). The incomplete taxon sampling for molecular studies is due to

Table. Species placed in *Pleudia* with some distinctive characters. Species highlighted (bold) were originally placed in *Salvia* sect. *Eremosphace* Bunge (Bunge, 1873). Molecular data: based on Walker and Sytsma (2007), Will (2013), Will and Claßen-Bockhoff (2014); leaf anatomy: Bokhari and Hedge (1977); distribution and morphology: Hedge (1966, 1974a, 1982b, 1982c), Santos and Fernández (1986); Thulin (1993, 2009); Afg = Afghanistan; Afr = Africa; C = Central; CI = Canary Islands; Co = Corolla, upper lip; E = East; N = North/Northern; Pak = Pakistan; S = South/Southern; SE = Southeast; SW = Southwest; (×) = imperfect; ! = different, lower thecae fertile (Bokhari and Hedge, 1977) or sterile (Hedge, 1982b); – = no data available; ^P leaf margin lobed to pinnatifid; * the maximal length of the pedicel is generally based on a slight enlargement of the pedicel after flowering. We point to different descriptions of growth forms in various floras, e.g., for *S. aegyptiaca*. While Hedge (1974a) refers to this species as ‘much branched suffruticose herb, 10–20(–40 cm)’, it is described as dwarf shrub in a later work by the same author (Sales et al., 2010).

Species [distribution]	Morphology					Phylogeny				
	Height [in cm]	Simple leaves	Xeromorphic leaves	Co size [in mm]	Pedicel [in mm] *	Lower thecae fertile	ITS	ETS	rp132-trnL	trnL-F
<i>Salvia</i> species recognized in <i>Pleudia</i>										
<i>aegyptiaca</i> L. [CI, E & N Afr to Pak, India]	6-20(40)	×	×	5-8	2-3.5 (-5)	×	×	×	×	×
<i>areysiana</i> Deflers [S Yemen]	20-40(50)	×	–	16	–	×	–	×	×	–
<i>bariensis</i> Thulin [Somalia, E Afr]	20-40	×	–	14-17	4	×	–	×	×	–
<i>bazmanica</i> Rech.f. & Esfand. [S Iran]	20-30	×	–	10	1.5-4	×	–	–	–	–
<i>chudaei</i> Batt. & Trab. [S Sahara]	30-60	×	–	7	1.5	×	–	–	–	–
<i>deserti</i> Decne. [Sinai, Israel, Jordan, Arabia]	≤ 30	×	×	6	0.6	×	–	×	×	–
<i>eremophila</i> Boiss. [C & S Iran]	10-30	×	×	4-5	1.5-5	!	–	–	–	–
<i>geminata</i> Thulin [Yemen]	≤ 10	×	–	10	3	×	–	×	–	–
<i>herbanica</i> A.Santos & M.Fernández [Fuerteventura, CI]	12-15	×	–	14-16	–	(×)	×	×	×	–
<i>hillcoatiae</i> Hedge [Oman]	15	×	–	5-8	2	×	–	–	–	–
<i>macilenta</i> Boiss. [Oman, S Iran, SW Afg]	15-50	×	×	5-6	2-3.5	×	–	–	–	–
<i>santolinifolia</i> Boiss. [S Iran, Pak, SE Afg, India]	10-30	× ^P	×	5-6	1.5-2.5	×	–	–	–	×
<i>tebesana</i> Bunge [SW Iran]	18-24	×	×	5-6	1.5-3	×	–	–	–	–
<i>trichocalycina</i> Benth. [E Afg, Pak]	10-25	× ^P	×	10-12	1.5-5	×	×	–	–	×

difficulties in collecting the species in their natural habitats in Northern Africa and Southwest Asia (Figure 2) and the restricted number of specimens available in collections (herbaria and botanical gardens) for destructive sampling.

3. Results and discussion

3.1. Molecular data concerning the taxonomy of *Salvia* L. Preliminary molecular investigations revealed that *Salvia* is nonmonophyletic (Walker et al., 2004; Walker and Sytsma, 2007). Bräuchler et al. (2010) assumed that the genus was paraphyletic ‘with regard to at least *Dorystoechas* [sic] and *Perovskia*’ (Bräuchler et al., 2010; p. 502). Drew and Sytsma (2012) also considered *Salvia* as paraphyletic but did not specify which of the five non-*Salvia* genera were nested within it. Our data (Will, 2013; Will and

Claßen-Bockhoff, 2014) similarly suggest that *Salvia* is polyphyletic and therefore in need of revision. The strong geographical signal detected in the ‘genus-wide’ study in combination with morphological characters provides a pragmatic approach to circumscribe monophyletic groups that can be revised separately.

Major clades and subclades of *Salvia* s.l. supported in phylogenetic studies are only partly in accordance with the existing concepts of subgeneric classification (Will, 2013). Although the clades are not resolved at the species level, it is reasonable to draw taxonomic conclusions at this point, as new molecular data are only likely to resolve relationships within the major clades, and are therefore unlikely to lead to further taxonomic changes in the future. As a first example, we elevate *S. aegyptiaca* and its

allies, the former *Salvia* sect. *Eremosphace* Bunge, to the level of genus, re-establishing the name *Pleudia* Raf. (see taxonomic treatment; Table).

3.2. Taxonomic history of the species group centered on *Salvia aegyptiaca*

Linnaeus (1753) already included *S. aegyptiaca* L. in his *Species Plantarum*. Since then, various taxonomical treatments have placed the species and its allies in different sections (Bentham, 1832–1836, 1848; Bunge, 1873; Bentham, 1876; Briquet, 1897) and species groups (Hedge, 1974, 1982b) or recognized it as its own genus (Rafinesque, 1837).

3.2.1. *Pleudia* Raf.

Rafinesque (1837) provided one of the earliest concepts for a taxonomic treatment of *Salvia* s.l. He suggested that *Salvia* L. should be split into several small genera (Rafinesque, 1837; Appendix), among them *Pleudia*, which he described as follows: ‘12. *Pleudia*, Galea brevissima emarg. labio concavo ut Nepeta, stam. plerumque 4 [sic!] fertilis ! *S. egyptiaca* [sic!] & c.’ (Rafinesque, 1837; p. 94). It is thus the oldest name proposed at the generic rank for *Salvia aegyptiaca* and its relatives.

3.2.2. *Salvia* sect. *Notiosphace* Benth.

Bentham (1832–1836) established 14 sections in *Salvia*, among them *Salvia* sect. *Notiosphace* Benth. According to his circumscription, *S. aegyptiaca* and the other species placed in this section are perennial herbs with either fertile or sterile thecae at the lower lever arm. The section contains exclusively small-flowered species (Figure 3). Except for the widespread species *S. plebeia* R.Br. (Southwest to East Asia and Northern Australia), all other representatives of the section are restricted to Southwest (SW) Asia and Northern Africa. Bentham maintained *Salvia* sect. *Notiosphace* in his later treatments (Bentham 1848, 1876) and placed it in subg. *Leonia* Benth. The name *Notiosphace* is derived from the Greek ‘notio’ (south) and ‘sphace’ (sage) (Sales et al., 2010).

3.2.3. *Salvia* sect. *Eremosphace* Bunge

Paying special attention to species distribution, Bunge (1873) split *Salvia* sect. *Notiosphace* Benth. into *Salvia* sects. *Eremosphace* Bunge and *Notiosphace* Benth. p.p. The former contained only *Salvia* species restricted to SW Asia, i.e. *S. aegyptiaca* (also occurring on the Arabian Peninsula, in Northern Africa, and on the Canary Islands), *S. santolinifolia*, *S. eremophila*, and the newly described species *S. tebesana*. These species were characterized by having fertile lower thecae (except *S. eremophila*; Hedge, 1982b; see Table), and were separated from species with completely sterile lower thecae, which were maintained in *Salvia* sect. *Notiosphace*. Briquet (1897) followed this classification and added *S. deserti*, *S. trichocalycina*, and *S. macilenta* to *Salvia* sect. *Eremosphace*.

The sectional name *Eremosphace* is derived from the Greek ‘eremos’ (ερεμος) referring to lonely, desolate, and uninhabited places, and the Latin ‘sphaceo’, which comes from the Greek ‘elelispacos’ (ἐλελίσφακος referring to *S. triloba*) and ‘sphacos’ (σφακος describing *S. calycina*, the so-called sage-apple) used by Pliny the Elder (Carvahlo, 1850).

3.2.4. Species groups sensu Hedge

Not aiming to provide a new subgeneric classification, but instead contributing to a more natural system for the genus, Hedge (e.g., 1974a) introduced informal ‘species groups’ in his treatments of Old World *Salvia*. These groups were largely defined by distribution and morphology (Hedge, 1974a, 1982a, 1982b). Thereby, problems arose from the lack of comparability between local floras (Hedge, 1974a, 1982a, 1982b). In his revision of African *Salvia*, Hedge (1974a) placed *S. aegyptiaca* in ‘species group F’ together with the African species *S. chudaei* and *S. deserti*. In the *Flora Iranica* (Hedge 1982b), *S. aegyptiaca* was part of a species group with 8 SW Asian species (‘Grex A’), among them *S. viridis* L. and *S. plebeia* R.Br. These two species are morphologically clearly distinct from the *S. aegyptiaca*-group. They also have minute to small flowers but are the only annuals placed in the group (Hedge, 1982b). Molecular data highly support the placements of *S. plebeia* in Clade IV (Will, 2013) and *S. viridis* in Clade I (Walker et al., 2004). All species previously placed in *Salvia* sect. *Eremosphace* are highly supported as members of Clade III (Figure 1).

Bokhari and Hedge (1977) conducted a comparative anatomical study of *S. aegyptiaca* and its relatives (Table). They recognized 11 species but argued that some of them might be conspecific with one another, e.g., *S. gabrieli* Rech.f. and *S. aegyptiaca* L. or *S. tebesana* Bunge and *S. santolinifolia* Boiss. Since this study, 4 species fitting morphologically into the *S. aegyptiaca*-group sensu Bokhari and Hedge (1977) have been described (Hedge, 1982c; Santos and Fernández, 1986; Thulin, 1993, 2009). Today, 14 species clearly belong to this species group (Table) (Hedge, 1966, 1974a; Bokhari and Hedge, 1977; Hedge, 1982a, 1982b, 1982c; Santos and Fernández, 1986; Hedge, 1990; Scholz, 1993; Thulin, 1993; Walker and Sytsma, 2007; Thulin, 2009; Will and Claßen-Bockhoff, 2014). Another taxon, *S. halaensis* Vicary (Vicary, 1847), is also assumed to belong to this group, but further studies are needed to confirm this placement (Hedge, 1982b, 1990).

3.3. Circumscription of *Pleudia* Raf. based on molecular data

As we provide nomenclatural changes at the end of this article and in order to facilitate comparisons with previously published phylogenies, we retain the names (*Salvia* spp.) as provided in the corresponding studies.

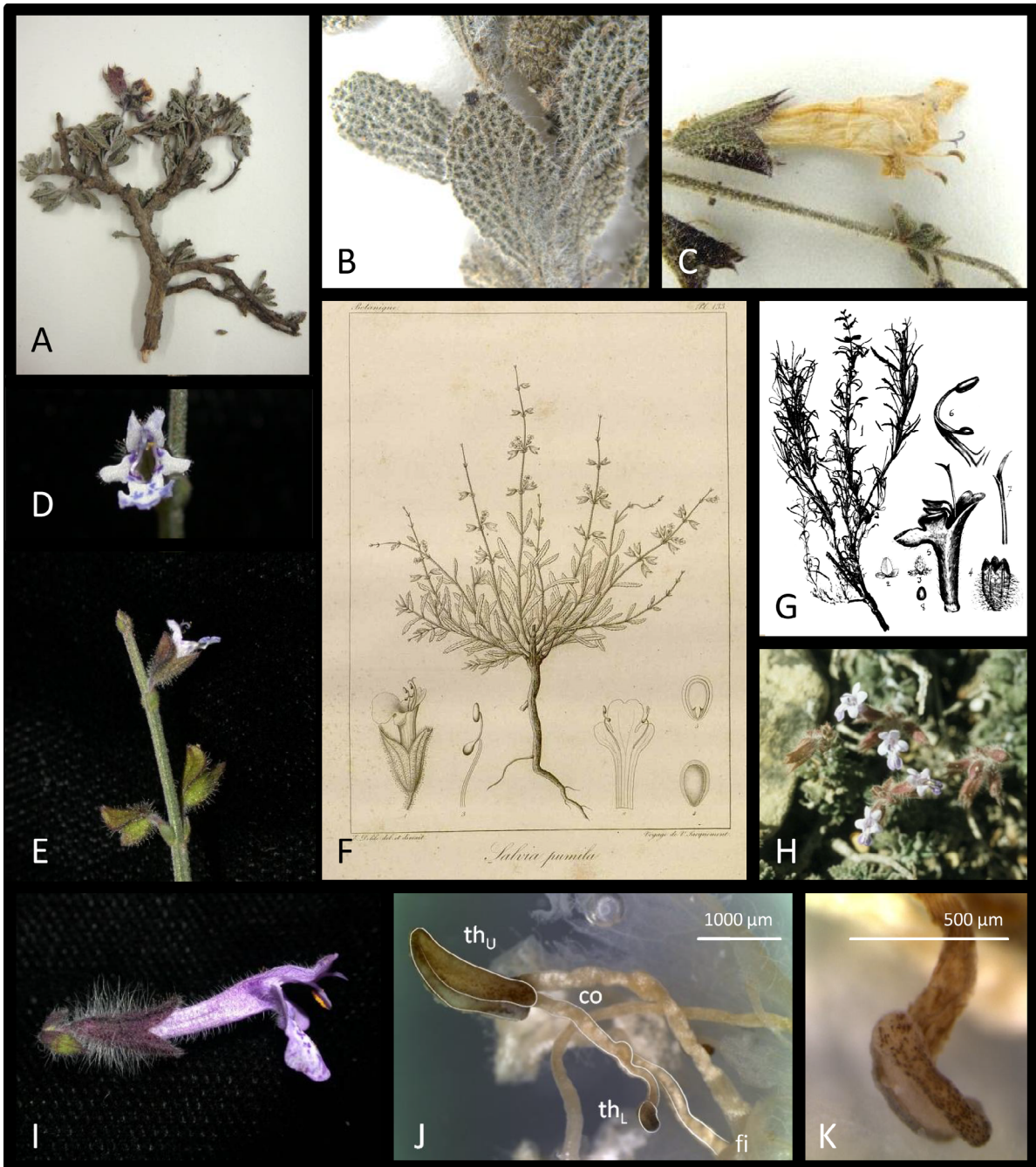


Figure 3. Habit and morphology of *Pleudia* Raf. (*Salvia aegyptiaca*-group). (A) *S. geminata*; dwarf shrub approx. 10 cm in height; specimen: M. Thulin, A. Beier & Mohammed A. Hussein no. 9629; K00248959; isotype, (B-C) *S. areysiana*; specimen: Thulin, Erikson, Gifri & Långstöm no. 8472; V64083 (Kew); (B) simple, revolute leaves from below with dense indumentum; (C) flower: approx. 17 mm excluding pedicel; (D-F) *S. aegyptiaca*, minute to small flowers; (D) frontal view; (E) lateral view, (F) drawing of *S. aegyptiaca* L. (as *S. pumila* Benth.) (Jacquemont, 1844); (G) *S. chudaei* (Battandier and Trabut 1907), with straight upper lip and exposed stamens; (H) habit of *S. geminata*, a much-branched dwarf shrub up to 10 cm (photo: M. Thulin); (I-K) *S. herbanica* from a natural population on Fuerteventura; (I) flower, lateral view; (J) dissected flower (MJG 009888); stamen with upper and lower lever arm; (K) close-up of the lower lever arm; fertile thecae with pollen grains; 16 flowers (2 populations) from Fuerteventura were dissected; size and shape of the thecae of the lower lever arm largely vary (fertile and sterile thecae).

Eight (57%) of the 14 species recognized in *Pleudia* are represented in molecular studies (Walker and Sytsma, 2007; Will, 2013; Will and Claßen-Bockhoff, 2014). According to plastid and nuclear data (*trnL-F*, *psbA-trnH*, *rpl32-trnL-F*, ITS, ETS) (Figures 1 and 4), they are well supported as members of Clade III (subclade III-A, C; Figures 1 and 4). According to ETS data, 6 of these species are placed in subclade III-A (1.00 PP/100% BS) (Figure 1) (Will and Claßen-Bockhoff, 2014). Walker and Sytsma (2007) included only three *Pleudia* species, *S. santolinifolia*, *S. trichocalycina*, and *S. aegyptiaca*, which were supported in a polytomy (Figures 4A–4C). The former were placed in (Bunge, 1873; Briquet, 1897) or near (Hedge, 1966, 1974a, 1982a, 1982c) *Salvia* sect. *Eremosphace*. Since morphological and molecular data are not conflicting, we also include species that were not sampled in molecular studies in the new genus.

Chloroplast data show *Pleudia* (subclade III-A) to be part of a trichotomy with *Zhumeria* and subclade III-B (Figure 4D). Within the latter, *S. aristata* Aucher (Northeast Iran; Southeast Turkey), *S. pterocalyx* Hedge (Northeast Afghanistan), *S. vvedenskii* Nikitina, and *S. margaritae* Botsch. (both Central Asia) are highly supported. Nuclear data support a slightly different position for *S. margaritae* as sister species to *Zhumeria* (Figure 4B). However, this relationship is only moderately supported (78% BS).

Based on molecular data, one might recognize the whole Clade III including *Zhumeria majdae* (Rechinger and Wendelbo, 1967) as one genus. Bokhari and Hedge (1976) investigated the anatomy, taxonomy, and affinities of *Zhumeria*. The authors described the genus as ‘most isolated genus [...] with some links with the genera of the tribe Meriandreae’. This particular tribe was already recognized as an artificial assemblage of isolated relict genera, i.e. *Dorystaechas*, *Meriandra*, and *Perovskia* (Bokhari and Hedge, 1971, 1976; Henderson et al., 1986).

Indeed, molecular, morphological (e.g., pollen; Jamzad et al., 2006), and anatomical (Bokhari and Hedge, 1971) data support the hypothesis that these genera are neither closely related to *Zhumeria* nor to each other, except probably *Dorystaechas* and *Meriandra*.

To recognize Clade III as one genus requires the acceptance of a quite heterogeneous taxon. Although some characters are shared by all *Salvia* representatives nesting in Clade III, i.e. clearly bilabiate corollas bearing 2 fertile stamens with significantly enlarged connectives and 2 staminodes, characters to support the inclusion of *Zhumeria* have as yet not been identified (Bokhari and Hedge, 1976; Harley et al., 2004). This monospecific genus rather differs from all other species nesting in Clade III in: (1) the lack of an enlarged connective tissue separating both thecae (the latter are only somewhat separated and do not form a lever; see Figure 1 in Bokhari and Hedge, 1976), (2) staminodes exerted from the corolla (Harley et al., 2004), (3) an indistinctly bilabiate corolla with subequal lips, (4) few flowers borne singly in the uppermost leaf axils, and (5) an extraordinary diversity of trichomes not recorded for any other genus of the family (for details see Bokhari and Hedge, 1976). Considering morphology and the previously discussed relict status of *Zhumeria*, it seems most parsimonious that this genus is a basally branching lineage within Clade III. Species with lever-like stamens are most probably derived, although the underlying evolutionary processes leading to their development and radiation remain unclear based on current data.

Molecular data clearly distinguish *Pleudia* (subclade III-A) from the remainder of Clade III, which have their westernmost distribution in SW Asia (Figure 2). Species nesting in subclade III-B also occur in dry habitats, but were traditionally separated from *Pleudia* based on morphology and distribution (Bunge, 1873; Briquet, 1897; Pobedimova, 1954). More broadly sampled molecular

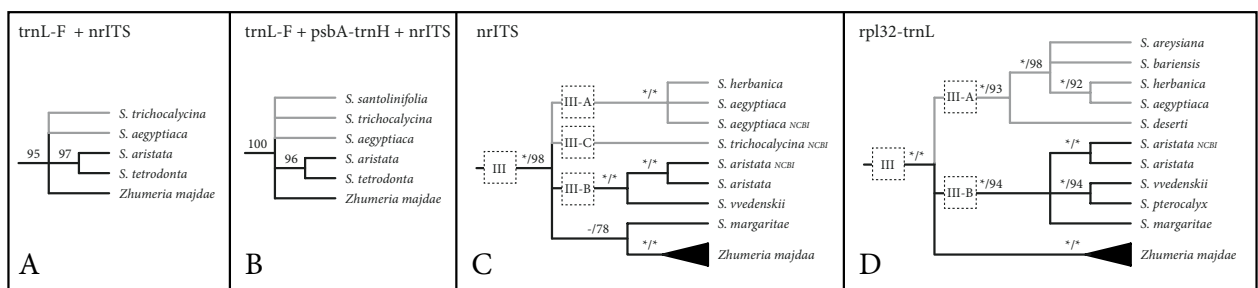


Figure 4. Placement of species representing *Pleudia* (*S. aegyptiaca*-group) based on various molecular markers in previous molecular studies. Asterisks above branches indicate maximal support values (100% BS, 1.00 PP); species representing *Pleudia* are highlighted by light gray branches; A and C: strict consensus trees, based on maximum parsimony analysis of combined datasets (plastid and nuclear markers) (Walker and Sytsma, 2007; modified); B and D: topology of Clade III; based on nuclear (*nrITS*; B) and plastid data (*rpl32-trnL*; D); maximum likelihood analysis and bayesian inference (Will, 2013; modified). The placement of *S. santolinifolia* and *S. trichocalycina* in a basal polytomy within Clade III (Figures 4A–4C) is not in conflict with the recognition/circumscription of *Pleudia*.

studies of Old World *Salvia*-species support *S. aristata*, *S. pterocalyx*, *S. vvedenskii*, and *S. margaritae* as one highly supported clade (subclade III-B; Figure 4D; Will, 2013). Based on similar morphology and distribution, 16 species from Central (former USSR) and SW Asia are expected to belong to this group representing sect. *Physosphace* Bunge and subg. *Macrosphace* Pobed. (Pobedimova, 1954). Although this group needs to be studied in more detail, some supporting characters might be corolla (≥ 25 mm) and calyx (rarely < 15 mm) size; relatively long pedicels (≥ 5 mm up to 20 mm); large, occasionally lobed or even compound leaves; and large seeds (Pobedimova, 1954; Hedge, 1960; Nikitina, 1962; Hedge, 1974b, 1982b; Behçet and Avlamaz, 2009). Concerning the proposed split of Clade III, the name *Polakia* Stapf (1885) has to be considered for the subclade III-B species. Briquet (1897) adopted this genus distinct from *Salvia* based on *Polakia paradoxa* Stapf (syn. *Salvia aristata* Aucher ex Benth.; WCSP, 2014). If subclade III-B is shown to form a monophyletic group with *Pleudia*, the latter name would have priority at the generic rank. Thus, accepting *Pleudia* for the members of subclade III-A would not entail further nomenclatural changes if they are found to be congeneric with the members of subclade III-B. Further hypotheses on the relationships of these large-flowered relatives of *Pleudia* are discussed in more detail by Hedge (1960, 1974b).

3.4. Genetic diversity vs. morphological uniformity

Though *Pleudia* is well-supported and characterized, morphological characters separating the species from each other are largely lacking. According to Bokhari and Hedge (1977), leaf shape, degree of revolution of the leaf margin, calyx shape, and indumentum are the most suitable characters for species delimitation. However, character states vary even within taxa. Hedge (1974a) observed a slightly changed ratio of leaf length to width as a function of distribution, with the leaves of *S. aegyptiaca* being generally narrower in North African specimens. In addition, plants collected in the easternmost distribution range have more glandular hairs than those from N Africa and on the Canary Islands (Bokhari and Hedge, 1977). As a consequence, the indumentum might reflect adaptation to microclimatic differences (locally more mesic conditions; Hedge 1974a), instead of being a suitable character for species delimitation (see also Bokhari and Hedge, 1977).

3.5. Local endemics vs. widespread species

Within the new genus, the distribution area of *S. aegyptiaca* (Figure 2A) almost completely overlaps with the distribution areas of taxa restricted to Africa and Saudi Arabia (Figure 2). The latter are geographically well isolated from each other. A general trend in the new genus seems to be a locally restricted distribution except for *S. aegyptiaca*. It would be worthwhile to investigate whether the corresponding species are adapted to certain

edaphic conditions. *Salvia herbanica* for example is restricted to only a few populations growing on basaltic cliffs on Fuerteventura (Canary Islands). A decline of their populations in size was observed and is most likely explained by the restricted number of suitable, geological often instable habitats, land use (grazing goats and sheep), and an infection/consumption of the fruits by parasitic insects (Scholz, 1993). Today, *S. herbanica* is critically endangered (Scholz, 1993; Gobierno de Canarias, 2004; Scholz and Santos Guerra, 2004; Gangoso et al., 2006; Moreno, 2008; Scholz and Santos Guerra, 2011; Rodríguez González et al., 2013). Such detailed information is not available for further *Pleudia* species (IUCN, 2014) and thus the conservation status of these taxa is not easy to evaluate.

3.6. Nuclear vs. chloroplast sequence data—hybridization discovered

Plastid and nuclear data suggest the hybrid origin of one species nesting in subclade III-A, i.e. *S. deserti*. The finding is based on the highly supported conflict observed between nuclear and chloroplast data (Figure 1, dotted branches). In the plastid dataset, *S. deserti* is found in a basally branching position, sister to the remainder of subclade III-A (Figure 1, left). This molecular marker is inherited maternally. Therefore, the seed parent was expected to be the sister species to *S. deserti*. Since no sister species was found, we conclude that the maternal parent was not sampled or is an extinct species. In contrast, ETS data support *S. deserti* as a sister species to *S. aegyptiaca* (Figure 1, right). According to this bi-parentally inherited marker, we assume *S. aegyptiaca* is most likely the pollen parent of *S. deserti*.

Hybridization is an important factor triggering speciation (Arnold, 1992; Abbott et al., 2013 and literature cited therein). Several aspects such as intermediate morphological characters, aberrant chromosome numbers, and the lack of isolation mechanisms to avoid hybridization have been repeatedly discussed for *Salvia* s.l. (Hrubý, 1933, 1935; Epling, 1938; Steward, 1939; Hrubý, 1941; Epling, 1947; Grant and Grant, 1964; Emboden, 1971; Wu and Huang, 1975; Hedge, 1982a; Meyn and Emboden, 1987; Fernández Alonso, 1991; Reisfield, 1993; Hihara et al., 2001; Van Jaarsveld, 2002; Reales et al., 2004; Zhiyun et al., 2004; Wester and Claßen-Bockhoff, 2006; Wood, 2007; Wester and Pauw, 2009; Bercu et al., 2012). However, the hypothesis of a hybrid origin has only been tested for a limited number of taxa and has not yet been confirmed by molecular studies (Sudarmono, 2007; Jenks, 2008; Will and Claßen-Bockhoff, 2014; P. Wester, pers. comm.).

Hybrids might become isolated from the parental species by geographic isolation or by establishing effective barriers to avoid back-crossing. For sympatric species,

the latter is possible via polyploidization. Interestingly, the chromosome number of *S. deserti* is relatively high ($2n = 48$; Al-Turki et al., 2000). Several chromosome numbers for *S. aegyptiaca* have been reported in the literature, most frequently $2n = 26$ or 28 (Hedge, 1974a; Borgen, 1980; Haque and Ghoshal, 1980; Haque, 1981; Siddiqi, 1985; Dalgaard, 1986; Al-Turki et al., 2000), but different studies have found $2n = 12$ (Díaz Lifante et al., 1992), $2n = 38$ (Löve, 1971), and $2n = 42$ (Humphries et al., 1978). Except for *S. chudaei* ($2n = 28$; Haifa and Joumena, 1991), other chromosome numbers have not been reported for *Pleudia* or for subclade III-B and *Zhumeria*.

We cannot exclude the possibility that the observed incongruence reflects incomplete lineage sorting (Joly et al., 2009), but based on an overlapping distribution (Figure 2A) and the relatively high chromosome number of *S. deserti* ($2n = 48$; Al-Turki et al., 2000), we prefer the hybrid hypothesis and assume that *S. deserti* arose via allopolyploidization. Further chromosome counts in the new genus could support our hypothesis.

4. Taxonomic and nomenclatural consequences

Pleudia Raf.

Basionym: *Pleudia* Raf., Fl Tell 3:94 (1837).

Synonym: *Salvia* sect. *Notiosphace* Benth. p.p. (Labiata. Gen. Spec. p. 309 (1832–36); A. De Candolle Prodr. 12 p. 354 (1848); Gen. Pl. 2, p. 1167 (1876); non Bentham 1833 Hook. Bot. Misc. 3 p. 374); *Salvia* sect. *Eremosphace* Bunge (Bunge 1873, Lab. Pers. in Mém. Acad. St. Petersburg., ser. 7, XXI, Nr. 1, 51 (1873); species group F (Hedge, 1974a; Notes Roy. Bot. Gard. Edinburgh 33(1): 1–121).

Type: *S. aegyptiaca* L.

Low growing shrubs or suffruticose herbs, often appearing as dwarf shrubs, usually <40 cm, rarely up to 50 or 60 cm (Table); stems much branched. Leaves small, simple, narrow linear-elliptic, rarely obovate-oblong (*P. bariensis*, occasionally in *P. aegyptiaca*) and pinnatifid, leaf margins usually revolute, thick textured. Flowers small, up to 16 mm, usually less than 10 mm. Verticillasters up to 10, few-flowered [(1)–2(–8)], with short-lived flowers. Calyces somewhat enlarging in fruit, slightly reflexed upper lip. Corolla upper lip \pm straight, occasionally shorter than or equal to lower lip; white, pale violet to pink; tube with annulus, subannulate (*P. macilenta*) or exannulate (*P. tebesana*). Stamens at least partly exposed; connective very short; lower thecae fertile, sometimes reduced (very small or even sterile), e.g., in *P. eremophila*; within *P. herbanica* both fertile and sterile lower thecae appear. Nutlets small (up to 2×1.4 mm), black, mucilaginous on wetting.

Distribution and ecology: typical elements of the Saharo-Sindian phytogeographical region, usually locally restricted to arid habitats on the Canary Islands, in North

Africa, on the Arabian Peninsula (Oman, Saudi Arabia, Yemen), and in SW Asia (Syria, Lebanon, Israel, Jordan, Palestine, Iran, Afghanistan, Pakistan); generally on sandy soil, gravel wadi beds and basalt rocks; on open limestone (*P. bariensis*) and basaltic slopes (*P. herbanica*); well-adapted to intense sunlight and water deficiency during the summer, e.g., by reduced number and size of leaves, small, \pm linear leaves with revolute margin; xeromorphic features (well-developed cuticula, lower surface of the leaves with stomatal grooves, mesophyll of the leaves composed of palisade parenchyma only, well-developed chlorenchyma in the wings and flanks of petioles and cortex of the stems); indumentum variable with trichomes of different types: simple, eglandular, retrorse hairs and oil globules; short spiky eglandular hairs; very short to long spreading eglandular hairs; stalked glands; 1- to 5-celled trichomes.

Referring to the characteristic growth form of *Pleudia* (e.g., Figure 3A), we propose the vernacular name ‘dwarf-sage’ for the new genus. The trivial name ‘desert-sage’, used for different representatives of *Salvia* s.l. that are also restricted to dry or desert-like habitats, is not advised. It refers to a group of species molecularly and morphologically clearly distinct from *Pleudia*, i.e. *S. dorrii* (Kell.) Abrams, *S. eremostachya* Jeps., *S. pachyphylla* Epl. ex Munz (all restricted to America; Clade II), and *S. deserta* Schang (Eurasia; Clade I) (Quattrocchi, 1999).

A taxonomic revision of *Pleudia* based on fieldwork is still needed to clarify species delimitations. Due to the lack of comprehensive studies on morphology, anatomy, karyology, and ecology, we do not provide a key to the species here.

Pleudia aegyptiaca (L.) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia aegyptiaca* L., Sp. Pl. 1: 23 (1753). non *S. aegyptiaca* L. Mant. Pl. 26 (1767).

Type: ‘Habitat in Aegypto’; Herb. Clifford 13, *Salvia* 17 (BM-000557609) (photo!); lectotype defined by Hedge in Notes Roy. Bot. Gard. Edinburgh 33(1): 89 (1974a).

Icon.: Hedge in: Rechinger, Fl Iranica (Tabulae), Vol. 150; Tab. 468 (1982).

Synon.: = *Pleudia aegyptiaca* (L.) Raf., Fl. Tellur. 3: 94 (1837).

= *Melissa perennis* Forssk., Fl Aegyptiaca: LXVIII no. 296; Descriptiones plantarum: 108; Cent. IV no. 30 (1775).

Type: syn. C; C10002589 (photo!), C10002590 (photo!); C10002591 (photo!); Fl. Aeg. Arab. no. 296, p. 108 Cent. 30; Herb. Forskål no. 341, ‘in desertis Kahirinis’ C10002592 (photo!)

= *Salvia arida* Salisb., Prodr. Stirp. Chap. Allerton: 73 (1796).

= *Thymus hirtus* Viv., Fl. Libyc. Spec.: 30 (1824), nom. illeg.

Type: Africae-borealis, in collibus arenosis Magnae Syrteos, 1817; *P. Della Cella* s.n.

Icon.: Viviani, Fl. Libyc. Spec., Tab. XIV, fig. 1 (1824).

≡ *Thymus syrticus* Spreng., Syst. Veg. 2: 697 (1825). nom. nov. for *Th. hirtus* Viv.

= *Salvia pumila* Benth., Labiat. Gen. Spec.: 726 (1835).

Type: caulibus erecti, floribus diluti violaceis, violaceo punctatis, odore teucii botrydis, herb. V. Jacquemont 74 K0090121 (photo!); 'Hab. in collib. gypsosis et salinis juxta PindadenKhan 6. Apr.' P00714654 (photo!); MPU (!).

Icon.: Jacquemont, Descriptions des collections botanique, t. 133, (1844). ≡ *Salvia aegyptiaca* var. *pumila* (Benth.) J.D. Hook., Fl. Br. Ind. Vol. IV: 656 (1885) p.p. ≡ *Salvia aegyptiaca* var. *pumila* (Benth.) Aschers. & Schweinf. ex I.Löw Sitzungsber. Kaiserl. Akad. Wiss., Phil. Hist. Cl. Vol. 161(3), p. 28 (1909).

= *Salvia aegyptiaca* var. *glandulosissima* Bornm. & Kneuck., Allg. Bot. Z. Syst. 22(1-4): 4 (1916).

Type: Sinaihalbinsel, im NW der Halbinsel, im Wädi Firan, 25. März 1904, *Hans Guyot* s.n.; Sinaihalbinsel, 'zw. den Tälern Sahâra, es-Sahîr, Cscheib ect. im SW. am 24. April 1904 und im SO. zw. den Tälern ab-Orta und Chreise am 2. Mai 1904 gesammelt'; A. Kneucker s.n.

Salvia aegyptiaca f. *colorata* Maire, Bull. Soc. Hist. Nat. Afrique N. 23: 205 (1932).

Type: 'rocaïlles calcaïres à Agadir-n-Ighir'

= *Salvia aegyptiaca* var. *intermedia* E.Peter, Repert. Spec. Nov. Regni Veg. 39: 182 (1936).

Type: Punjab; Drummond 14429

= *Salvia gabrieli* Rech.f., Bot. Jahrb. Syst. 71: 538 (1941).

Type: Iranisch-Baločistan: Bashakird, Paß Pohki zwischen Anguhran und Ispand, 1635 m; a 1928, A. Gabriel no. 57; (holo. W)

= *Salvia aegyptiaca* f. *albiflora* Sauvage, Mém. Off. Nat. Anti-Acrïdien 2: 34 (1947).

Type: Mauritanie septentrionale; Zemmour, Bir Moghreïn, Kedia Kheneijât; 5. Nov. 1942, 'fl. entièrement blanches', coll. Ch. Runge & Sauvage, R.S. no. 30; MPU005370 (photo!)

Pleudia areysiana (Deflers) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia areysiana* Deflers, Bull. Soc. Bot. France 43: 229 (1896).

Type: P.D.R.Y. (People's Democratic Republic of Yemen; South Yemen), 'Bilad Fodhil, ad fauces australes montis el-Areys, prope Serreya, 27. April 1893', Deflers 1041; (holo. P)

holo.: P00714656 (photo!), P00714657 (photo!), P00714658 (photo!)

iso.: MPU (!)

Pleudia bariensis (Thulin) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia bariensis* Thulin, Opera Bot. 121: 145 (1993).

Type: Somalia, Bari Region, Al Miskat Mts, Bahaya; Hab.: stony limestone slope; shrublet, 0.2–0.4 m; flowers blue; 11°18'N, 49°49'E; 26. Nov. 1986, Thulin & Warfa 6059; (holo. UPS)

holo.: UPS:BOT:V-041526 (photo !)

iso.: K, MOG

Icon.: Thulin, Opera Bot. 121: 146, fig. 1 (1993).

Pleudia bazmanica (Rech.f. & Esfand.) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia bazmanica* Rech.f. & Esfand., Oesterr. Bot. Z. 99: 61 (1952).

Type: Persiae prov. Balučistan (Makran): Bazman, 11. March 1949, Sharif 1150 E, (holo. W).

Icon.: Rechinger, Oesterr. Bot. Z. 99: 61, fig. 10a (1952); Hedge in: Rechinger, Fl Iranica (Tabulae), Vol. 150; Tab. 469 (1982).

Placement of this species in *Pleudia* is based on distribution and habitat preferences, growth form, and the combination of different morphological characters, such as flower morphology; it was not sampled in a molecular study.

Pleudia chudaei (Batt. & Trab.) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia chudaei* Batt. & Trab., Bull. Soc. Bot. France 53 (Sess. extrao.): XXX (1906 publ. 1907).

Type: Sahara Central; Algeria: Ahaggar mts., Tit, 6. Aug. 1909, Chudeau; (holo. MPU) holo.: MPU010317!

Icon.: Bull. Soc. Bot. France 53 (Sess. extrao.): t. 10 (1906 publ. 1907).

Synon.: = *Salvia chudaei* var. *typica* Bull. Soc. Hist. Nat. Afrique N. 23: 205 (1932).

= *Salvia chudaei* Batt & Trab. var. *lanuginosa* Maire. Bull. Soc. Hist. Nat. Afrique N. 34(6): 138 (1943)

Type: Sahara méridional, Tibesti, Sommet du mont Toussidé, 3000 m, coll. 1939-1940, Th. Monod s.n.

= *Salvia tibestiensis* A.Chev., Bull. Soc. Bot. France 78: 322 (1931).

Type: Plantes du Borkou. Tibesti récoltées par M. Jean Tarrieux s.n., Nov. 1930; Tibesti, station dans les Oueds, endroits hum., renseignements divers-Hauteur P00541281 (photo!), P00541282 (photo!); = *Salvia chudaei* var. *tibestiensis* (A.Chev.) Maire, Bull. Soc. Bot. France 78: 322 (1931).

= *Salvia chudaei* var. *tefedestica* Maire, Bull. Soc. Hist. Nat. Afrique N. 23: 205 (1932).

Type: Algeria; Hab.: in arenosis ad radices montium Tefedest Saharæ centralis: Tehi-n-Beidigen inter montes Tefedest & Ahaggar-n-Deren; ad alt. c. 1200 m; 12. Apr. 1928; Maire 953; (holo. MPU)

holo.: MPU002988 (photo!)

Placement of this species in *Pleudia* is based on distribution and habitat preferences, growth form, and the combination of different morphological characters, such as flower morphology; it was not sampled in a molecular study.

Pleudia deserti (Decne.) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia deserti* Decne., Ann. Sc. Nat. Paris sér. 2, 2: 248 (1834).

Type: Rabeja Arab. désert du Sinaï, June 1832, *N. Bové* s.n.; (holo. P)

holo.: P00714698 (photo!)

Pleudia eremophila (Boiss.) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia eremophila* Boiss., Diagn. Pl. Orient. Ser. 1, 5: 12 (1844).

Type: In desertis Persiae australis, *P.M.R. Aucher-Eloy* 5194; (holo. G, iso. K, G);

holo.: G00156032 (photo!)

iso.: G00098506 (photo!); G00098507 (photo!); K000479419 (photo!); P00714729 (photo!); P00714730 (photo!)

Icon.: Hedge in: Rechinger Fl Iranica (Tabulae), Vol. 150; Tab. 467 (1982).

Placement of this species in *Pleudia* is based on distribution and habitat preferences, growth form, the combination of different morphological characters, such as flower morphology, and leaf anatomy; it was not sampled in a molecular study.

Pleudia geminata (Thulin) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia geminata* Thulin, Nordic J. Bot. 27: 336 (2009).

Type: Yemen, Al Mahrah Region, Ras Fartak, above Al Wadi, 15°40'N, 52°11'E; Hab. rocky slope; 7. Nov. 1998, *M. Thulin, B.-A. Beier & Mohammed A. Hussein* 9629; (holo. UPS, iso. K, para. K, UPS)

holo.: UPS:BOT:V-095774 (photo !)

iso.: K00248959 !

para.: Yemen, Al Mahrah Region: 35 km northeast of Itab along road to Qishn; Hab. Rocky hillside; plant forming small cushions; flowers pale blue; 15°24'N, 51°35'E, 5. Nov. 1998, *M. Thulin, B.-A. Beier & Mohammed A. Hussein* 9569, UPS:BOT:V-095713

Icon.: Thulin, Nordic J. Bot. 27: 337, fig. 1 (2009).

Pleudia herbanica (A.Santos & M.Fernández) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia herbanica* A.Santos & M.Fernández, Lazaroa 9: 52 (1986 publ. 1988).

Type: Fuerteventura; circa Vigán, 350 m s.m. 22. Febr. 1985, *F. de la Roche* n°. 29239; Rarissima; (holo. ORT).

Icon.: Santos and Fernández, Lazaroa 9: 53, fig. a–f (1986).

Pleudia hillcoatiae (Hedge) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia hillcoatiae* Hedge, Notes Roy. Bot. Gard. Edinburgh 40(1): 69 (1982). Type: Sultanate of Oman; Dhofar, Wadi Shibun, 'Ramaida', 11. Febr. 1947, *Thesinger* s.n.; (holo. BM)

Icon.: Hedge, Notes Roy. Bot. Gard. Edinburgh 40(1): 70, fig. 3 (1982).

Placement of this species in *Pleudia* is based on distribution and habitat preferences, growth form, and morphology; it was not sampled in a molecular study.

Pleudia macilenta (Boiss.) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia macilenta* Boiss., Diagn. Pl. Orient. Ser. 1, 5: 13 (1844).

Type: Oman, ad radices montium regni Mascatensis, *P.M.R. Aucher-Eloy* 5210, s.d. (holo. G, iso. W)

holo.: G00156030 (photo!)

iso.: G00098509 (photo!); P00714705 (photo!); P00714706 (photo!); MO-149605 (photo!)

syn.: BM001125654 (photo!)

Placement of this species in *Pleudia* is based on distribution and habitat preferences, growth form, leaf anatomy, and the combination of different morphological characters, such as flower morphology; it was not sampled in a molecular study.

Pleudia santolinifolia (Boiss.) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia santolinifolia* Boiss., Diagn. Pl. Orient. Ser. 1, 5: 13 (1844).

Type: Persia, in desertis ad sinum Persicum, *P.M.R. Aucher-Eloy* 5214 s.d. (holo. G, iso. W, G, P).

holo.: 'desert ad sin. Persicum' G00156029 (photo!)

iso.: G00098510 (photo!); P00714786 (photo!); 'Salvia aff. *S. deserti*, 931, desert ad sin. Persicum' P00714787 (photo!); P00714788 (photo!); MO-149608 (photo!)

Icon.: Hedge in: Rechinger Fl Iranica (Tabulae), Vol. 150; Tab. 462, 463 (1982).; Hedge in: Ali & Nasir Fl. Pakistan, Vol. 192 (1990), accessed online: Tropicos.org. Missouri Botanical Garden. 5. March 2014; <http://www.tropicos.org/Image/100165672>.

Pleudia tebesana (Bunge) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia tebesana* Bunge, Labiat. Persic.: 52 (1873) in: Mém. Acad. Scienc. Petersbg. Sér. 7, 21: 52 (1873).

Type (syn.): [Iran] in praeruptis calcareis supra Tebbes et prope Meibut inter Jezd et Isfahan, Mai 1859, *Bunge & Bienert*; (syn. G, P); nec non in rupe Tacht-i Rustam prope Isfahan Bode (G)

A.A. von Bunge s.n., 30. April 1859 G00098508 (photo!); inter Jezd et Isfahan, Mai 1859, A.A. von Bunge s.n. G00156031 (photo!); syn.: inter Jezd et Isfahan, Maj 1859, A.A. von Bunge s.n. P00714813 (photo!)

Icon.: Hedge in: Rechinger Fl Iranica (Tabulae), Vol. 150; Tab. 466 (1982).

Synon.: = *S. lacei* Mukerjee, Notes Roy. Bot. Gard. Edinburgh 19: 304 (1938).

Typus: Baluchistan, Chappar Rift, Lace No. 3976; in Cal et co-typus in E;

Iso.: E00301998 (photo !), E00301999 (photo !)

Placement of this species in *Pleudia* is based on distribution and habitat preferences, growth form, leaf anatomy, and the combination of different morphological characters, such as flower morphology; it was not sampled in a molecular study.

Pleudia trichocalycina (Benth.) M.Will, N.Schmalz & Class.-Bockh., comb. nov.

Basionym: *Salvia trichocalycina* Benth., in: de Candolle A, Prodr. 12: 356 (1848).

Type: Herb. Late East India Comp. 3984, Griffith 791 (holo. K); K000929791 (photo!); K000929792 (photo!)

Icon.: Hedge in: Rechinger Fl Iranica (Tabulae), Vol. 150; Tab. 464, 465 (1982).

Taxon of uncertain status probably belonging to *Pleudia*:

Salvia halaensis Vicary, Journ. As. Soc. Bengal 16: 1165 (1847).

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