Phylogeny of the tribe Phlomideae (Lamioideae: Lamiaceae) with special focus on *Eremostachys* and *Phlomoides*: New insights from nuclear and chloroplast sequences

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Abstract The tribe Phlomideae (Lamiaceae: Lamioideae) is divided into the three genera *Phlomis*, *Phlomoides* (incl. *Pseuderemostachys*, *Lamiophlomis* and *Notochaete*), and *Eremostachys* (incl. *Paraeremostachys*), contains about 278 species and has a distribution range extending from Europe to Mongolia, China, and India. Here, we present a phylogenetic analysis based on nuclear ribosomal (ITS) and cpDNA (partial *trnK*, *rpl32-trnL*, and *trnT-A*) sequence data of 56 accessions representing all genera and major subgeneric taxa of Phlomideae. Taxon sampling covered the genera *Phlomoides* and *Eremostachys* more intensively than previous phylogenetic investigations of the tribe. Parsimony and Bayesian analyses of each marker, as well as the combined plastid datasets, produced nearly congruent trees. Monophyly of *Phlomis* s.str. is confirmed here, although only few representatives of this genus were included. In all obtained trees a core group of *Phlomoides* and *Eremostachys* is strongly supported. In accordance with morphological evidence, molecular data confirm the inclusion of *Eremostachys*, *Notochaete*, and *Paraeremostachys* in *Phlomoides*. In conclusion, the number of recognized genera in Phlomideae is reduced to two: *Phlomis* and *Phlomoides*. The necessary new combinations are proposed.

Keywords *Eremostachys*; Lamiaceae; molecular phylogeny; nr DNA ITS; *Phlomoides*; *rpl32-trnL*; *trnK*; *trnT-A*

Supplementary Material The alignment files are available in the Supplementary Data section of the online version of this article (http://www.ingentaconnect.com/content/iapt/tax).

■ INTRODUCTION

Lamioideae form one of the seven subfamilies currently recognized in Lamiaceae and contain about 1260 species in 63 genera (Harley & al., 2004). Scheen & al. (2010) recently provided a first, general phylogenetic framework for Lamioideae based on chloroplast DNA data, which was updated and expanded by Bendiksby & al. (2011). These new results, gained from analyses of four plastid markers, have elucidated evolutionary relationships of many genera and clades, permitting a preliminary tribal classification system comprising 10 tribes. Most lamioid genera were included, but some important groups were underrepresented and three monotypic genera were left out. Within the subfamily, several major lineages have been studied at infrageneric and/or intergeneric levels (Ryding, 1998; Barber & al., 2002; Lindqvist & Albert, 2002; Lindqvist & al., 2003; Scheen & al., 2008; Scheen & Albert, 2009; Mathiesen & al., 2011).

The tribe Phlomideae Mathiesen, originally suggested to comprise six genera (see Scheen & al., 2010), is a complex group within Lamioideae: *Eremostachys* Bunge, *Lamiophlomis* Kudô, *Notochaete* Benth., *Phlomis* L., *Phlomoides* (L.) Moench, and *Pseuderemostachys* Popov. According to the *World Checklist of Lamiaceae & Verbenaceae* (Govaerts & al., 2010) and the above circumscription, tribe Phlomideae contains 278 species, whereas Kamelin & Makhmedov (1990) recognized about 250 species within the component genera. The species are distributed from Europe to Mongolia, China, and India with the highest number of species found in Central Asia, Afghanistan and Iran (Irano-Turanian and Himalayan regions). They comprise elements of subalpine and alpine vegetation with some species growing in desert conditions. They are mostly non-aromatic herbs, or subshrubs to shrubs and are typical representatives of "Labiatae". The inflorescences are thyrsoid or rarely racemoid, with one- to many-flowered cymes, with a zygomorphic and usually 2-lipped corolla. The morphological features characterizing genera within Phlomideae are summarized in Table 1.

The taxonomy of *Phlomis* and allied genera has been the subject of a long controversy (Table 2). While Linnaeus (1753) included 12 species in the genus, Moench (1794) separated *Phlomis tuberosa* in the monotypic genus *Phlomoides* based on

Table 1. Characteristics of the six genera of tribe Phlomideae (see Scheen & al., 2010) as formerly supposed by Harley & al. (2004, except for *Phlomoides*) with chromosome numbers according to Azizian & Culter (1982).

	Eremostachys[a]	*Phlomoides* s.str.[b]	*Phlomis*	*Pseuderemostachys*	*Notochaete*	*Lamiophlomis*
Type	*E. laciniata*	*Ph. tuberosa*	*P. fruticosa*	*Ps. sewerzovii*	*N. hamosa*	*L. rotata*
Number of species[c]	ca. 65	ca. 95	ca. 90	1	2	1
Growth form	Stout perennial herbs with tuberous rootstock	Tall perennial herbs with woody rhizomes and/or tubers at tip	Perennial herbs or small shrubs	Perennial herbs	Tall perennial (up to 2.5 m), herbaceous with thick rhizomes	Perennial herbs with rhizomes (mostly stemless)
Leaves	Simple or laciniate to bipinnatisect	Simple (entire or toothed)	Simple (entire or toothed)	Simple (entire or toothed)	Simple (broad, toothed)	Simple rosette
Petioles	3–10(–15) cm	2–5(–7) cm	1.5–5.0 cm	2.5–3.0 cm	3.0–7.0 cm	2–8 cm
Flowers per cyme	1–10(–20)	2–10	2–10(–15)	2–4(–5)	15–25(–30)	4–8(–10)
Calyx shape	Campanulate, tubular to broadly funnel-form; apex spiny	Tubular, lobes equal or sometimes unequal (3/2), abruptly narrow to acute apex	Lobes equal, mostly broad at the base (triangular-acuminate)	Tubular, campanulate to funnel-form; narrow to acute apex	Tubular, lobes equal to subequal, spinose with spines mostly subterminal outside lobe, unicinately	Broad at the base and abruptly narrowed to a spinescent apex
Calyx lobe	Straight	Straight	Straight	Straight	Hooked	Straight
Corolla colour	Yellow or white	Purple to pink, rarely yellow or white	Purple to pink, yellow or white	Purple or pink	Purplish	Pink to purplish
Corolla shape	Posterior lip long, hooded, often deeply concave	Posterior lip long, shallowly hooded	Posterior lip long, hooded, often deeply concave	Posterior lip long, shallowly hooded	Posterior lip long, hooded	Posterior lip long, hooded, denticulate
Indumentum on upper corolla lip	Bearded on margins	Bearded with simple hairs at margin	Hardly bearded with simple hairs at margin	Rarely bearded with simple hairs at margin	Densely hairy outside	Densely villous inside
Stamen	Exerted from corolla tube	Exerted from corolla tube	Exerted from corolla tube	Included in corolla tube or only shortly exerted	Exerted from corolla tube	Exerted from corolla tube
Anthers	All similar in size	All similar in size	All similar in size	All similar in size	All similar in size	All similar in size
Style	Lobed unequally	Lobed unequally or sometimes equally	Lobed unequally or sometimes equally	Lobed unequally	Lobed subequally	Lobed equally
Nutlet apex	Densely bearded or rarely glabrous	Stellate hairy or sometimes glabrous	Glabrous, papillose or stellate hairy	Densely bearded	Truncate, glabrous or with branched hairs	Rounded, glabrous
Chromosome number	$2n = 22$	$2n = 22$	$2n = 12, 14, 20, 22, 40, 42$	Unknown	$2n = 22$	Unknown
Distribution	E Europe to Mongolia, W China and NW India	E Mediterranean to Himalaya	E Europe, Mediterranean to Himalaya	Central Asia (Kazakhstan)	Himalaya to China	From Tibet, Nepal and N India to C and S China

[a] *Eremotachys* s.l. is following Harley & al. (2004).
[b] *Phlomoides* s.str. excluding *Eremostachys*, *Notochaete*, and *Lamiophlomis*.
[c] According to Govaerts & al. (2010) after excluding some synonymy according to our unpublished data.

Table 2. Classification history of the tribe Phlomideae.

Genus/genera	Linnaeus (1753)	Moench (1794)	Link (1829)	Bunge (1830, 1873)	Bentham (1832–1836)	Briquet (1895–1897)	Rechinger (1982)	Adylov & al. (1986); Adylov & Makhmedov (1987); Kamelin & Makhmedov (1990)	Scheen & al. (2010)	Mathiesen & al. (2011)
Genera (upper row-bold); sections (lower row, non-bold)				*Eremostachys*	*Eremostachys*	*Eremostachys*	*Eremostachys*	*Eremostachys*	*Eremostachys*	*Eremostachys*
					Notochaete	*Notochaete*		*Paraeremostachys*	*Lamiophlomis*	
			Phlomidopsis						*Notochaete*	
	Phlomis	*Phlomis*	*Phlomis*	*Phlomis*[a]	*Phlomis*[a]	*Phlomis*[a]	*Phlomis*[a]	*Phlomis*	*Phlomis*	*Phlomis*
		Phlomoides						*Phlomoides*	*Phlomoides*	*Phlomoides*
								Pseuderemostachys	*Pseuderemostachys*	
				Eremostachys	***Eremostachys***	***Eremostachys***	***Eremostachys***	***Eremostachys***		
								Anurae		
								Eremostachys		
					Metaxoides	*Metaxoides*	*Metaxoides*			
				Moluccelloides	*Moluccelloides*	*Moluccelloides*	*Moluccelloides*			
				Phlomoides	*Phlomoides*	*Phlomoides*	*Phlomoides*			
							Thyrsiflorae			
							Vulnerantes			
								Paraeremostachys		
								Paraeremostachys		
								Thyrsiflorae		
					Phlomis	***Phlomis***	***Phlomis***	***Phlomis***		
					Euphlomis	*Euphlomis*	*Euphlomis*			
								Gymnophlomis		
								Lychnites		
								Oncophlomis		
								Oxyphlomis		
					Phlomidopsis					
						Phlomoides	*Phlomoides*	*Phlomoides*		
								Phlomis		
								Platyphlomis		
								Phlomoides		
								Filipendula		
								Phlomoides		

[a] *Phlomis* s.l.: including *Phlomidopsis* Link and *Phlomoides* Moench.

differences in corolla shape (having the upper lip of the corolla ciliate and not compressed) and fruit structure (likely referring to the bearded nutlets). The only contemporary botanist sharing his view on the generic distinctness of *P. tuberosa* was Link (1829) who placed it in the illegitimate *Phlomidopsis* Link. Bunge (1830) in contrast kept *P. tuberosa* in *Phlomis* but established the new genus *Eremostachys*. He included four species in *Eremostachys*: two transferred from other genera (*Phlomis laciniata* L., *Moluccella tuberosa* Pall.), and two described as new. Bentham (1832–1836) treated *Eremostachys* and *Notochaete* (with hooked calyx lobes) as separate genera. Though including *P. tuberosa* in *Phlomis*, he placed it in its own section adopting Link's (1829) name at that rank (sect. *Phlomidopsis* Link ex Benth). In a later work Bunge (1873) divided *Eremostachys* into two sections: sect. *Phlomoides* Bunge (based on *E. phlomoides* Bunge, non *Phlomoides tuberosa* (L.) Moench) and sect. *Molucelloides* Bunge. Briquet (1895–1897) mainly followed Bentham's classification but described another new section in *Eremostachys* (sect. *Metaxoides* (Briq.) Rech. f.).

Popov (1940) and Knorring (1954) regarded *Phlomis* as heterogeneous with some species, including *P. tuberosa*, linking the genus to *Eremostachys*. This treatment remained largely unrecognized until Adylov & al. (1986) and Adylov & Makhmedov (1987) who resurrected Moench's *Phlomoides* to accommodate species that have the upper corolla lip ("galea") not laterally compressed and the lateral roots tuberous. They also included *Eremostachys* sect. *Phlomoides* emend. Briq. in the genus *Phlomoides*. Only species with a laterally compressed upper corolla lip remained in *Phlomis* s.str. The species assigned to *Eremostachys* sect. *Metaxoides* by Briquet (1895–1897) were placed in the newly created genus *Paraeremostachys* Adylov & al. (Adylov & al., 1986; Adylov & Makhmedov, 1987), characterized by having tubular to campanulate calyces. *Paraeremostachys phlomoides* (Bunge) Adylov & al. (≡ *E. phlomoides* Bunge) was designated as the type of *Paraeremostachys*. The remnants of *Eremostachys* were characterized by having the upper corolla lip non-compressed, the calyx broadly infundibular and the main root tuberous. The classification of *Phlomis* s.l. as proposed by Adylov & al. (1986) and Adylov & Makhmedov (1987) was not followed by Hedge (1990), Li & Hedge (1994), Harley & al. (2004), and Govaerts & al. (2010). Hedge (1990) also regarded *Paraeremostachys* as a homotypic synonym of *Eremostachys* and consequently as illegitimate. The latter conclusion was based on the assumption that *E. phlomoides* constituted the type of both these genera. However, Sennikov & Lazkov (2010) found that *E. laciniata* had previously been designated as the type of *Eremostachys* (Pfeiffer, 1874). Based on this fact, the generic name *Paraeremostachys* is legitimate. On the other hand, Sennikov & Lazkov (2010) did not resurrect *Paraeremostachys* from synonymy under *Eremostachys*. Among the four genera recognized by Adylov & al. (1986), only *Phlomis* appears to form a distinct group. It differs clearly from *Phlomoides*, *Paraeremostachys*, and *Eremostachys* in having the upper corolla lip laterally compressed. Adylov & al. (1986) claimed that the three genera differ in root thickening, as well as calyx and corolla shape, but these differences are not clear-cut. *Paraeremostachys* was described as being intermediate between *Phlomoides* and *Eremostachys*.

Ryding (2008), who studied the pericarp structure in the *Phlomis* group, agreed that *Phlomoides* should be treated as a separate genus, and that *Lamiophlomis* and *Notochaete* should be included in *Phlomoides*, but did not propose any nomenclatural changes. He disagreed with the very divergent genus classification proposed by Adylov & al. (1986) and Adylov & Makhmedov (1987), and regarded *Eremostachys* (sensu Briquet, 1895–1897 and Rechinger, 1982) as monophyletic. On the basis of similarities in pericarp structure, he also regarded sect. *Metaxoides* (as *Eremostachys*), sect. *Thyrsiflorae* and sect. *Moluccelloides* to be more closely related to each other than to sect. *Phlomoides*.

A recent molecular phylogenetic study of *Phlomis* s.l. clearly supported a split of the lineage into two separate groups, *Phlomis* and *Phlomoides*, the latter also comprising *Lamiophlomis*, *Pseuderemostachys*, and one of the two species of *Notochaete*, *N. hamosa* (Mathiesen & al., 2011). On the basis of these results, Mathiesen & al. (2011) formally resurrected *Phlomoides* as a genus, and included *Pseuderemostachys*, *Notochaete* and *Lamiophlomis* in *Phlomoides*. Since only three *Eremostachys* species (all belonging to the genus *Phlomoides* sensu Adylov & al., 1986) were included in their analysis, *Eremostachys* was retained as a genus, although the data presented suggested that it constitutes a subgroup within *Phlomoides*. Hence, the currently recognized genera of tribe Phlomideae are *Phlomis* s.str., *Phlomoides*, and *Eremostachys*. The new combinations proposed by Mathiesen & al. (2011) are adopted here.

In a molecular analysis of the whole subfamily Lamioidae, Bendiksby & al. (2011) included five species of *Eremostachys*: three of sect. *Phlomoides* (genus *Phlomoides* sensu Adylov & al., 1986), one of sect. *Metaxoides* (genus *Paraeremostachys* sensu Adylov & al., 1986), and one of sect. *Moluccelloides* (genus *Eremostachys* sensu Adylov & al., 1986). However, a much larger sampling is needed in order to evaluate the phylogenetic and taxonomic status of *Eremostachys*.

The aim of the present study is to test current generic classifications against molecular phylogenetic data of tribe Phlomideae by complementing existing molecular data through inclusion of crucial taxa and addition of further nuclear (ITS) as well as plastid (*rpl*32-*trnL*, *trnT-A*, *trnK*) DNA sequence information. Correlating the findings with those of thorough morphological reinvestigations, we hope to infer the phylogeny of Phlomideae and provide nomenclatural stability.

■ MATERIALS AND METHODS

Plant material. — All taxon names in the present study follow the *World Checklist of Lamiaceae & Verbenaceae* (Govaerts & al., 2010) except for species belonging to *Betonica*, *Lamiophlomis*, *Notochaete*, *Paraeremostachys*, *Pseuderemostachys*, and *Phlomoides* for which the checklist has not been updated (see Adylov & al., 1986). A total of 206 DNA sequences were generated from specimens held at the following herbaria: B, E, KUN, LE, M, MSB, MW, TUH, W, and WU, or in several cases

(especially species distributed in Iran) from silica-dried leaves. As the phylogenetic position of *Phlomis* has been clarified already, we focused more intensively on *Eremostachys* including Adylov & al.'s (1986) *Paraeremostachys* and *Phlomoides* p.p. We present a phylogenetic study based on sequence data of three plastid regions (*trnT-A*, *rpl32-trnL*, partial *trnK*) as well as one nuclear ribosomal DNA region (ITS). The sampling strategy was to include the lectotypes (where available) of all generic names allied or attributed once to *Phlomoides* and *Eremostachys*, all five (sensu Rechinger, 1982) recognized sections of *Eremostachys* as well as both sections and seven subsections (out of nine sensu Kamelin & Makhmedov, 1990) of *Phlomoides* along with lectotypes of both sections of *Paraeremostachys*. Only few species representing two subsections of *Phlomoides* have been omitted, because no material was available or attempts to amplify DNA failed. Altogether, 23 accessions representing 21 species of *Eremostachys*, 3 accessions representing 2 species of *Paraeremostachys*, and 13 accessions representing 12 species of *Phlomoides* were analyzed. Several species having transitional morphological states between certain taxonomic groups or showing peculiar morphological features (such as *Phlomoides milkoi* Lazkov, *Ph. ajdarovae* Lazkov, *Eremostachys glabra* Boiss. ex Benth., and *E. lanata* Jamzad) were also added. The sampled taxa of *Eremostachys* and *Phlomoides* represent almost all (morphological) lineages in these two genera. Furthermore, to assess the systematic position of *Notochaete*, we also included an accession of its second species, *N. longiaristata* C.Y. Wu & H.W. Li, which was not included in previous analyses (Mathiesen & al., 2011). Only five representative species of *Phlomis* s.str. were chosen, because this alliance has turned out as the most clearly characterized in previous molecular analyses (Mathiesen & al., 2011). *Paraphlomis* (Prain) Prain (tribe Paraphlomideae Bendiksby, 2 spp.), *Stachys* L. (tribe Stachydeae Dumort., 1 sp.), *Ballota* L. (tribe Marrubieae Vis., 1 sp.) and *Lagochilus* Bunge ex Benth. (tribe Leonureae Dumort., 1 sp.) were selected as outgroups according to Scheen & al. (2010) and Bendiksby & al. (2011). The Appendix lists all taxa included in this study and summarizes sources, voucher specimen data, and GenBank accession numbers of the sequences.

DNA extraction, amplification, and sequencing. — The non-coding region ITS (ITS1, 5.8S rDNA, ITS2) of nuclear DNA and partial *trnK*, *trnT-A*, and *rpl32-trnL* from plastid DNA were analyzed. Total DNA was extracted from dried leaf material using the NucleoSpin Plant Kit (Macherey-Nagel, Düren, Germany). Protocols followed those provided by the manufacturer, except for an additional extraction step with phenol/chloroform to remove potentially interfering secondary compounds as established by Bräuchler & al. (2004). The DNA was dissolved in 30 µl elution buffer (10 mM Tris-HCl) and checked for quality on a 1% agarose-gel. The extracted DNA was resuspended in 50 µl elution buffer (10 mM Tris-HCl), and a standard amount of 1 µl of the solution was used for amplification (higher amounts up to 3 µl in cases where PCR yielded insufficient amounts of product). The markers were amplified from total DNA using *Taq*-polymerase (AGS, Heidelberg, Germany).

Amplification of the ITS region was conducted using the primers Leu1 (Vargas & al., 1998) and ITS4 (White & al., 1990). In some difficult cases ITS2 and ITS3 were used as described by White & al. (1990). The primers used in this study are listed in Table 3.

PCR reactions were performed in volumes of 50 µl containing a dNTP solution of 2.5 mM, *Taq*-polymerase with 1 U/µl, primer solutions with a concentration of 100 pmol/µl, and differing amounts of unquantified genomic DNA. When necessary, an alternative preparation containing 0.05% bovine serum albumin (BSA) and 100% dimethyl sulfoxide (DMSO) was used for ITS. Amplification programs for ITS started with a 5 min initial denaturation step at 94°C; followed by 40 cycles of 30 s denaturation (94°C), 30 s annealing (54°C), and 1 min 15 s extension (72°C); ending with a final extension step of 10 min (72°C).

Partial *trnK* was amplified using the forward primer Sat1200F (Bräuchler & al., 2010) and 16R as the reverse primer (Johnson & Soltis, 1994). In cases where the amplification was not successful, the marker was amplified in two fragments using the primer pairs Sat1200F-1780R and 1780F-16R, with the following cycle profile: an initial denaturation step at 94°C

Table 3. Sequences of primers used for PCR amplification and sequencing.

Region	Primer name	Sequence (5′–3′)	References
ITS	Leu1	GTC CAC TGA ACC TTA TCA TTT AG	Vargas & al. (1998)
	ITS2	GCT GCG TTC TTC ATC GAT GC	White & al. (1990)
	ITS3	GCA TCG ATG AAG AAC GCA GC	White & al. (1990)
	ITS4	TCC TCC GCT TAT TGA TAT GC	White & al. (1990)
trnK	Sat1200F	GAT TCG TAT TCA CAT ACA TGA G	Bräuchler & al. (2010)
	16R	CTA CTC CAT CCG ACT AGT T	Johnson & Soltis (1994)
	1780F	CAG AGG GGT TTG CTT TTA TCC G	Bräuchler & al. (2005)
	1780R	TCT AGA ATT TGA CTC CGT ACC	Bräuchler & al. (2005)
rpl32-trnL	rpl32F	CAG TTC CAA AAA AAC GTA CTT C	Shaw & al. (2007)
	$trnL^{(UAG)}$	CTG CTT CCT AAG AGC AGC GT	Shaw & al. (2007)
trnT-A	$trnL^{(UAA)}$ R (TabB)	TCT ACC GAT TTC GCC ATA TC	Taberlet & al. (1991)
	$trnT^{(UGU)}$F (TabA)	CAT TAC AAA TGC GAT GCT CT	Taberlet & al. (1991)

(2 min 30 s); followed by 40 cycles of 1 min denaturation at 94°C, 1 min annealing at 53°C, 1 min 30 s elongation at 72°C; and a final extension of 10 min at 72°C.

For amplifying the ITS region and partial *trnK* marker from very old herbarium specimens, Phusion polymerase (New England Biolabs, Ipswich, Massachusetts, U.S.A.) was used as described in Bräuchler & al. (2010) following the manufacturer's protocol with an initial denaturation step of 1 min at 98°C; followed by 35 cycles of 30 s at 98°C, 30 s at 53.5°C and 1 min at 72°C; and a final extension step of 10 min at 72°C. All PCR amplifications were carried out in a thermocycler type T-Personal 48 (Biometra, Göttingen, Germany), type Primus 96 plus (MWG-Biotech, Ebersberg, Germany), or type 2720 (Applied Biosystems, Carlsbad, California, U.S.A.).

For amplification of *rpl32-trnL* as one fragment we used the primers rpl32F and trnL$^{(UAG)}$ (Shaw & al., 2007) under following parameters: 80°C, 5 min; 35× (94°C, 30 s; 50°C–55°C, 30 s; 72°C, 1 min); 72°C, 5 min, which were modified from Oxelman & al. (1997).

Likewise, *trnT-A* was amplified either as one fragment using the primer combination trnL$^{(UAA)}$ R (TabB) and trnT$^{(UGU)}$F (TabA) according to Taberlet & al. (1991) and Shaw & al. (2005). The *trnT-A* spacer amplification program started with a 5 min initial denaturation step at 94°C; followed by 40 cycles of 30 s denaturation (94°C), 30 s annealing (53°C), and 1 min 15 s extension (72°C); ending with a final extension step of 10 min (72°C).

Successful PCR reactions were either purified with the NucleoSpin Extract II-Kit (Macherey-Nagel) following the manufacturer's instructions, or were reduced to 25 µl and then purified in 4 µl units with 0.025 µl exonuclease I and 0.25 µl shrimp alkaline phosphatase (Sap) in a 5 µl preparation with 0.0725 µl 10× TP buffer (Scheunert & Heubl, 2011). Cycle Sequencing was carried out using the BigDye Terminator v.3.1 Cycle Sequencing Kit (Applied Biosystems) in a final volume of 20 µl. Runs were performed on an ABI 3730 48 capillary sequencer (Applied Biosystems). In all cases, the markers were sequenced bidirectionally using the same primers as in PCR reactions.

Alignment, indel coding, and phylogenetic reconstruction. — All sequences generated in this study were assembled, edited, and aligned manually using Mesquite v.1.12 (Maddison & Maddison, 2006). Alignment and phylogeny from the present study are available as Supplementary Data to the online version of this article. Ambiguously aligned characters and mononucleotide repeat units were excluded from further analyses. The beginning and end of the alignments where not all of the taxa provided complete data were also excluded. For Bayesian and parsimony analyses, indels resulting from the alignment were coded using the simple indel coding algorithm proposed by Simmons & Ochoterena (2000) as implemented in SeqState (Müller, 2005). The absent/present indel matrix (coded as 0/1) was then added to the end of the alignment. The three plastid markers were analyzed separately as well as in a single combined dataset, while the ITS dataset was analyzed separately. The combined chloroplast matrix as well as a nuclear-chloroplast combined dataset was tested for incongruence between single chloroplast markers as well as nuclear and combined chloroplast datasets, respectively. This was done using the incongruence length difference (ILD) test as a suitable first step (Cunningham, 1997; Hipp & al., 2004). The ILD test was conducted using PAUP* v.4.0b10 (Swofford, 2003), where it is called the partition homogeneity test (PHT), and computed 1000 replicates with MAXTREES option set to 100, without coded indels, and after removing constant characters from the matrix. Phylogenetic reconstruction analyses were performed with a Bayesian inference (BI), and maximum parsimony (MP) approach. An alignment of ITS with 56 accessions and a combined chloroplast concatenated alignment with 50 accessions were analyzed twice, with and without indels coded. Bayesian analyses were conducted using the Markov-chain-Monte-Carlo algorithm of MrBayes v.3.1.4 (Ronquist & Huelsenbeck, 2003) for 10 million generations. The used substitution models were those estimated as optimal using the Akaike information criterion (AIC) in jModelTest v.0.1.1 (Posada, 2008). The general time-reversible model of nucleotide substitution with gamma-shaped rate variation with a proportion of invariable sites (GTR+I+G) was the estimated best-fit model for all markers except partial *trnK* and ITS, for which a simpler model, GTR+G (Rodríguez-Sánchez & al., 1990) was selected. Combined data analysis was run under the GTR+G model. Trees were sampled every 1000th generation with the default of three "heated" and one "cold" chain. Burn-in was set to 2500 in both analyses. The remaining trees were summarized in a 50% majority-rule consensus tree. Maximum parsimony analyses were performed with both datasets (ITS and combined plastid DNA) including coded indels and using PAUP* v.4.0b10 (Swofford, 2003) with the following parameters: all characters unordered and equally weighted, coded indel characters not treated as separate data partition but added at the end of the alignment; heuristic search with random sequence addition, tree-bisection-reconnection branch-swapping, 50 random-addition-sequence replicates, and MAXTREES option set to 300,000. Bootstrapping was done using the following settings: hsearch addseq = random, nchuck = 10, chuckscore = 1, nreps = 50, bootstrap nreps = 5000 (summarized in a 50% majority-rule consensus tree as a cladogram).

■ RESULTS

This is the first inclusive study using nuclear ITS sequences to estimate phylogenetic relationships in the tribe Phlomideae. Detailed information about alignment characteristics and statistics of MP analyses is given in Table 4.

The parsimony and Bayesian analyses of each individual marker, as well as the combined plastid dataset, produced congruent trees without any major difference. Therefore, only the results of the BI are shown and discussed here (Figs. 1–3), and those of MP analyses are summarized in Table 4. The ILD test revealed significant congruence ($P = 0.59$) between the *trnT-A* and *rpl32-trnL* datasets which in turn showed significant congruence ($P = 0.45$) with the partial *trnK* dataset. However, the combined plastid and ITS datasets found no support ($P = 0.001$), so no combined nuclear-chloroplast dataset could be used. The

results from separate analyses of the nuclear and combined chloroplast dataset are shown in Figs. 1–3.

Parts of sequences of the selected plastid markers for the following accessions/taxa are missing: *Eremostachys paropamisica*, *Phlomoides betonicoides*, *Ph. medicinalis*, *Ph. muliensis*; and one accession each of *E. phlomoides*, *Ph. hamosa*, and *Ph. tuberosa*. These taxa had to be omitted from the combined chloroplast analysis. In consequence, the final dataset of ITS included 56 accessions, but the final combined plastid dataset contained only 50 accessions. For *Ballota hirsuta* and *Eremostachys spectabilis*, no partial *trnK* sequence could be obtained. Furthermore, high numbers of ambiguous sites were observed in *trnT-A* and *rpl32-trnL* sequences for *Ph. hamosa* and *Notochaete longiaristata*. In the combined plastid matrix these sequences were treated as missing, and in the respective plastid marker datasets these taxa were excluded.

Indel coding did not affect tree topology but increased support for internal nodes considerably. In terms of percentage of informative characters, the markers show the following decreasing order: *rpL32-trnL*, ITS, *trnT-A*, and *trnK*.

Tree topologies. — In the ITS (Fig. 1) and the combined plastid (Fig. 2) tree topologies, the same monophyletic crown groups were found. Among single plastid phylogenies (data not shown), only minor incongruence was observed in positions of few terminal branches. In the *trnT-A* and *rpl32-trnL* topologies both species of *Notochaete* are nested within *Eremostachys*, while in the partial *trnK* topology they are sister group to *Pseuderemostachys* and *Eremostachys*. Furthermore, more polytomies were observed in a consensus tree gained from the partial *trnK* analysis compared with both other plastid markers.

All trees obtained from plastid and ITS markers were congruent in showing the ingroup, Phlomideae, as monophyletic with relatively high support, although bootstrap support (BS) for the ingroup in the ITS topology was low (BS = 60%; see under Discussion). The monophyly of *Phlomis* s.str. (PP = 1.00, BS = 100%) was confirmed in all analyses even though only few species were included here.

In both the ITS tree and combined plastid tree a core group referred to as the *Phlomoides* s.l. clade (Figs. 1–2, with PP = 1.00, BS = 95% and PP = 1.00, BS = 96%, respectively) containing the species of *Phlomoides*, *Paraeremostachys*, *Notochaete longiaristata*, and *Eremostachys*, was found. Most species of *Phlomoides* including *Phlomoides rotata* (former *Lamiophlomis rotata*) form a paraphyletic assemblage as the most basal groups in this clade. The accession of *Notochaete longiaristata* is a monophyletic group together with *Phlomoides hamosa* (former *Notochaete hamosa*) with high support (PP = 1.00, BS = 100% in both topologies). This branch is followed by *Phlomoides sewerzovii* in the ITS tree (Fig. 1), while it is intermediate between some *Phlomoides* subclades in the combined plastid tree (Fig. 2, Fig 3: box 3E).

The most diverged crown group includes all species of *Eremostachys* along with a few species of *Phlomoides* (PP = 1.00, BS = 94%, in combined plastid topology and PP = 0.99, BS = 75%, in ITS topology). Except for some differences, the topology of the ITS tree is congruent with the combined plastid tree (Fig. 3). The comparison between plastid and ITS trees is shown in Fig. 3. Although few species groups in *Phlomoides* (indicated as B, C, D, and E) have similar species compositions, their positions are different in the two topologies. The most important differences were observed in the following groups: (1)

Table 4. Alignment characteristics and statistics of maximum parsimony analysis for *trnT-A*, *rpl32-trnL*, partial *trnK*, ITS, and combined plastid dataset.

	ITS	Plastid combined	*trnK*	*trnT-A*	*rpl32-trnL*
Number of taxa	56	50	50	53	55
Sequence length [bp]	629–781	1694–2751	757–1163	325–701	612–887
Aligned length [bp]	733	2708	1077	746	892
Excluded characters [bp]	47	180	91	35	36
Constant characters [bp]	384	1848	836	446	380
Parsimony-uninformative characters [bp]	132	372	121	171	205
Parsimony-informative characters [bp]	217	488	120	129	307
Parsimony-informative characters [%]	29.60	20.75	12.51	16.18	34.64
Number of coded indels	81	100	19	37	44
Average G-C content [%]	65.28	31.63	30.73	36.66	35.69
CI of MPTs	0.629	0.763	0.774	0.818	0.777
CI of MPTs (excluding uninformative characters)	0.548	0.667	0.641	0.679	0.690
RI of MPTs	0.779	0.809	0.824	0.802	0.766
Number of MPTs	1988	16858	100,000[a]	100,000[a]	33,071
Length of MPTs	794	1345	377	463	821

CI, consistency index; MPTs, most parsimonious trees; RI, retention index.
[a]Number of MP trees is adjusted on 100,000.

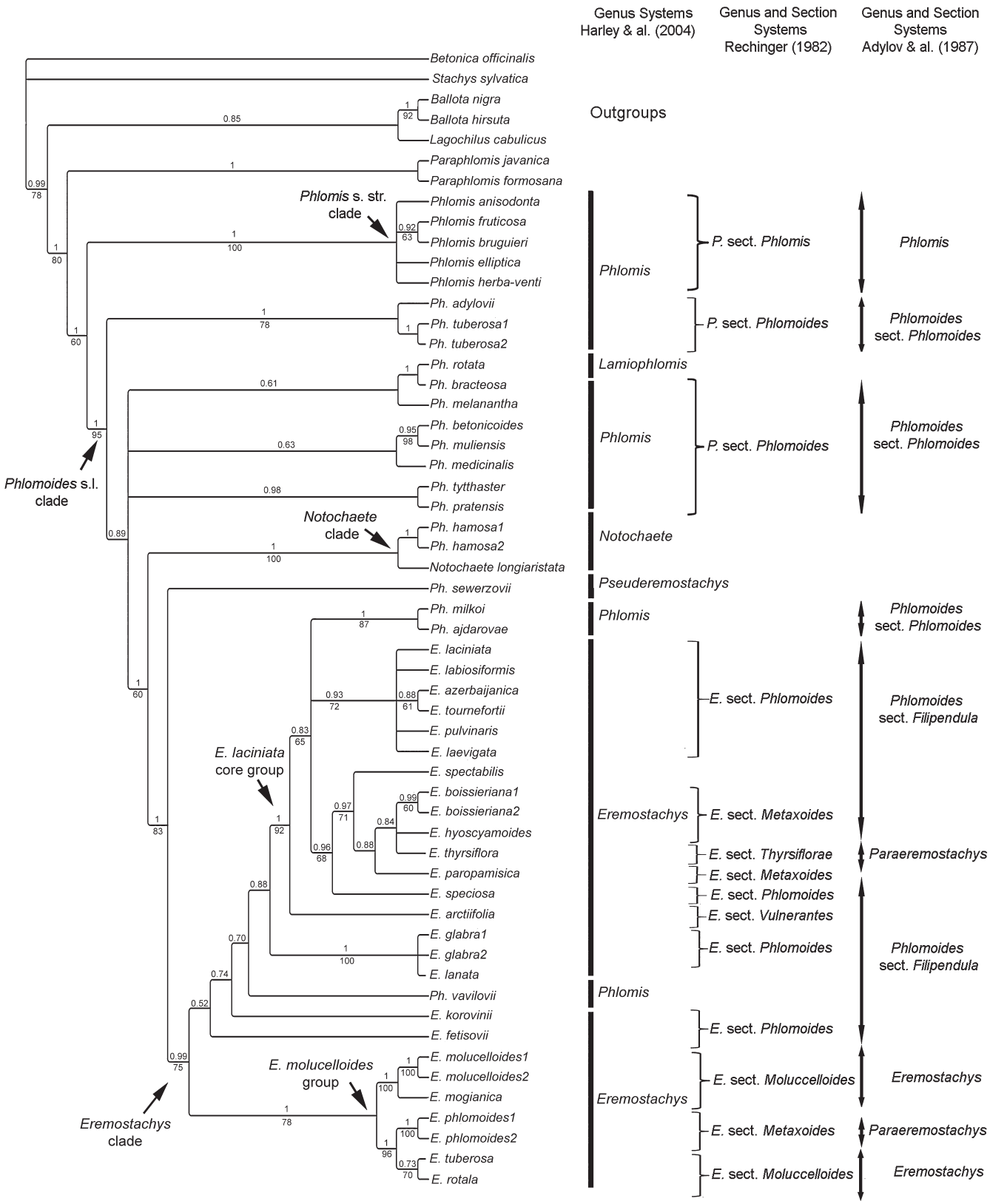

Fig. 1. Strict consensus tree of 8000 trees inferred from Bayesian analysis of the ITS dataset. Posterior probabilities and non-parametric bootstrap values ≥50% from 1000 replicates are indicated below and above branches, respectively. — Abbreviations: *Ph.* = *Phlomoides*, *E.* = *Eremostachys*.

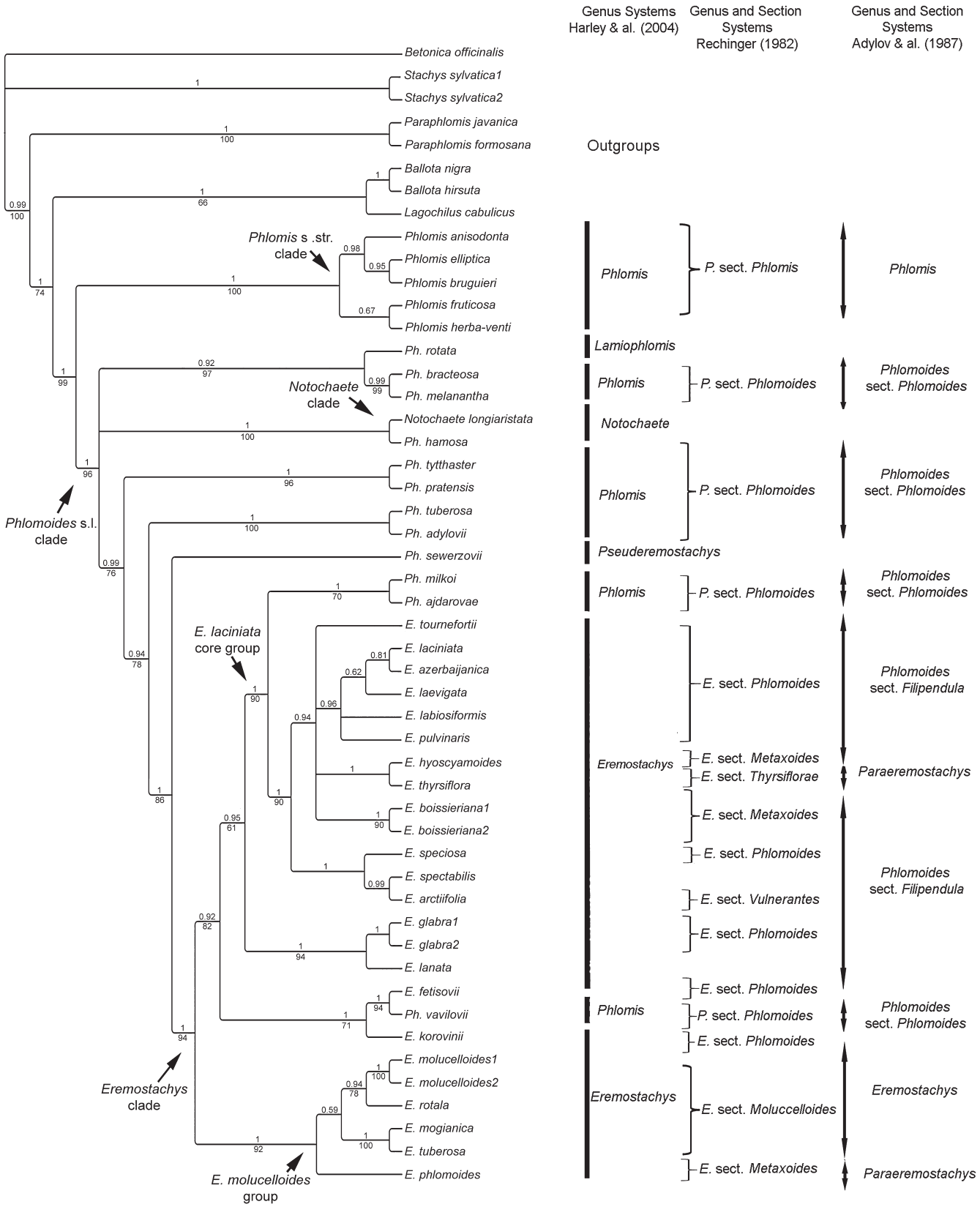

Fig. 2. Strict consensus tree of 8000 trees inferred from Bayesian analysis of the combined cpDNA dataset. Posterior probabilities and non-parametric bootstrap values ≥50% from 1000 replicates are indicated below and above branches, respectively. — Abbreviations: *Ph.* = *Phlomoides*, *E.* = *Eremostachys*.

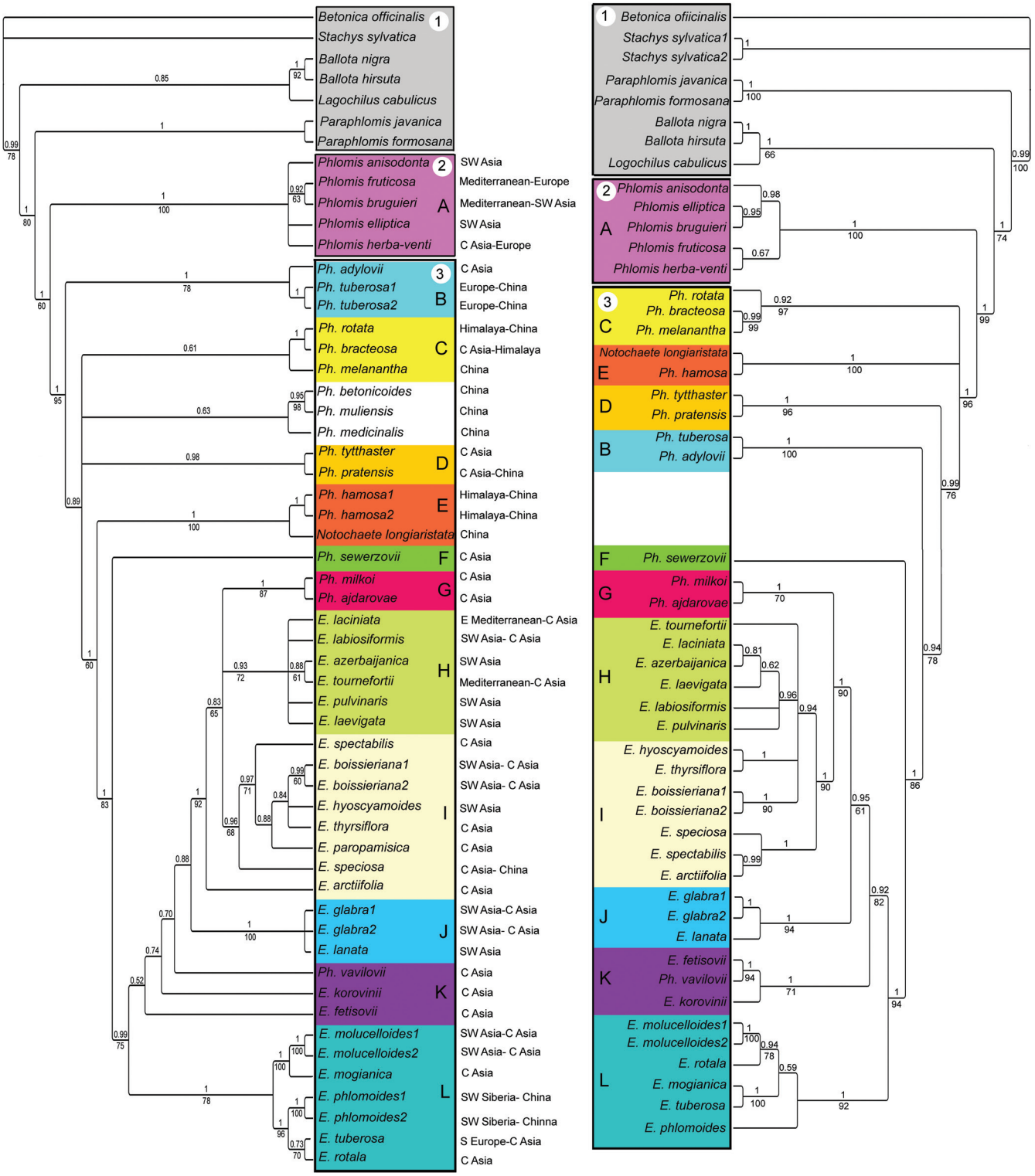

Fig. 3. Bayesian consensus trees from the ITS dataset (left side) compared to the combined chloroplast dataset (*trnT-A*, *rpl32-trnL*, *trnK*; right side). For better comparison of positions of species in the trees, corresponding groups of species are indicated by numbers 1 (outgroups), 2 (genus *Phlomis*), and 3 (genus *Phlomoides* in its wide concept accepted here), and by letters A–L. — Abbreviations: *Ph.* = *Phlomoides*, *E.* = *Eremostachys*.

Phlomoides adylovii–Ph. tuberosa (group B in Fig. 3, PP = 1.00, BS = 100%, in the combined plastid topology and PP = 1.00, BS = 78%, in the ITS topology), which forms the most basal subclade in *Phlomoides* s.l. in the ITS analysis, but is sister to the *Eremostachys* subclade + *Ph. sewerzovii* in the combined plastid tree; (2) a monophyletic subclade including *E. fetisovii*, *E. korovinii* and *Ph. vavilovii* in the combined plastid topology (group K in Fig. 3, PP = 1.00, BS = 71%), which is paraphyletic in the ITS tree; (3) several subclades with relatively low support are found in the *E. laciniata* core group in the ITS tree, but show different positions in the combined plastid tree; (4) the *Notochaete* group as explained in last paragraph; (5) *Eremostachys lanata* and *E. glabra* (PP = 1.00, BS = 94% in the combined plastid topology and PP = 1.00, BS = 100%, in the ITS topology; group J in Fig. 3) make up a sister group to the *E. laciniata* core group (PP = 1.00, BS = 90% in the combined plastid topology and PP = 1.00, BS = 92% in ITS topology). In both the ITS and combined plastid DNA analyses the group of *E. molucelloides* (PP = 1.00, BS = 92% in the combined plastid topology and PP = 1.00, BS = 78%, in the ITS topology) is the most basal monophyletic group in the *Eremostachys* clade.

■ DISCUSSION

Since Bentham (1832–1836), a close relationship between *Phlomis* s.l. and *Eremostachys* has not been questioned fundamentally, although minor changes in segregation and placement of single genera have been suggested from treatment to treatment (e.g., Adylov & al., 1986). Although there is consensus about common ancestry, the generic boundaries have been disputed, and some species are known to be intermediate between genera in morphological characters. Our data show the tribe Phlomideae as an assembly of closely related genera confirming previous assumptions. In the combined plastid trees (Fig. 2) the monophyly of Phlomideae is highly supported, but in the ITS trees (Fig. 1) the bootstrap support for this clade (BS = 60%) is relatively low probably due to higher homoplasy in ITS sequences which makes this sequence of limited use at the rank of tribe in Lamiaceae.

All phylogenetic analyses of both single and combined markers in the present study indicate similar groups of species in each subclade (Fig. 3, letters A–L), but the position of these groups vary to some degree in the combined plastid versus the ITS tree. This variation in topology may be caused either by past hybridization events or extensive incomplete lineage sorting, or likely some combination of these phenomena. There are only few known instances of recent hybridization in *Phlomoides* and *Eremostachys* (Popov, 1940), but several hybrid species are known in the sister genus *Phlomis* (e.g., Aparicio, 1997; Aparicio & al., 2000; Albaladejo & al., 2004; Mathiesen & al., 2011).

The position of *Eremostachys* (incl. *Paraeremostachys*) within Phlomideae has hardly been assessed in recent molecular phylogenetic studies of the tribe because of limited sampling, but a first hint at a close relationship between this genus and *Phlomoides* was given by Mathiesen & al. (2011) based on cpDNA (*trnL* intron, *trnL-F* intergenic spacer, and *rps16* intron) sequence data. The present study corroborates these recent molecular phylogenetic findings (Mathiesen & al., 2011).

The genus *Phlomis* is clearly non-monophyletic as traditionally circumscribed (see for example Harley & al., 2004). Although the splitting of *Phlomis* s.l. into two genera has been rejected on several occasions (Bentham, 1848; Boissier, 1879; Briquet, 1895–1897) and more recently by Harley & al. (2004), it has also been at least equivocally accepted (Makhmedov, 1990; Ryding, 2008; Scheen & al., 2010; Bendiksby & al., 2011; Mathiesen & al., 2011). Along with high support for monophyly of tribe Phlomideae, our data reveal new aspects concerning generic boundaries within the *Phlomoides* group in the tribe.

Generic concept in Phlomideae

***Phlomis*. —** There are about 90 species in *Phlomis* characterized by several synapomorphies (see under Introduction; Fig. 4E; Table 1). In all topologies obtained from the analysis of single plastid markers (*trnT-A*, *rpl*32-*trnL*, partial *trnK*), combined plastid datasets as well as ITS sequences, the few species of *Phlomis* s.str. included here form a strongly supported monophyletic group as also found by Mathiesen & al. (2011). The generic distinctiveness of *Phlomis* s.str. is supported by morphological, anatomical, cytological, and molecular data (Azizian & Culter, 1982; Ryding, 2008; Mathiesen & al., 2011). The laterally compressed and sickle-shaped upper corolla lip (Fig. 4E) can be regarded as synapomorphy for this genus (Table 1). The following characters occur in all species of the genus, while they are variable in the other genera of Phlomideae: basal leaves absent, margin of cauline leaves not deeply lobed (shallowly crenate to entire), indumentum of branched multinodal hairs, upper lip of the corolla smooth at margins and not distinctly bearded, and lateral lobes of corolla lip distinctly smaller than the middle lobes. Furthermore, the species of *Phlomis* s.str. are chemically characterized by the flavon apigenin and the flavonols isorhamnetin and quercetin (Azizian & Culter, 1982) and have a basic chromosome number of $x = 10$ (see for example: Azizian & Culter, 1982; Astanova, 1984; Brullo & al., 1990; Ghaffari, 2006). According to Ryding (2008) most of the species of *Phlomis* have a distinct sclerenchyma region in the pericarp, while this region is lacking in *Phlomoides* and *Eremostachys*.

Although other genera in the tribe can not be distinguished from each other based on morphological characters, *Phlomis* in its narrow circumscription represents a well-defined monophyletic genus. A detailed discussion on the distinctiveness of *Phlomis* s.str. has been presented by Mathiesen & al. (2011). Except for *Phlomis*, all other taxa of the ingroup forming the crown clade of *Phlomoides*, as indicated in Figs. 1–3, are intermingled with regards to morphological characters. An inclusive discussion is presented for each of these genera below. Taxonomic conclusions will be drawn at the end of the discussion.

***Phlomoides*. —** The genus name *Phlomoides* was established by Moench (1794) based on *Phlomoides tuberosa*, but was almost totally ignored until Adylov & al. (1986). In the meantime most species attributed to this genus were included in *Phlomis* and *Eremostachys*. According to Adylov & al.

(1986) the most important morphological characters separating *Phlomoides* from other taxa in Phlomideae are: flowers small in size, petals pink or purple, and corolla non-compressed dome-shaped, with uneven margins densely bearded inside (Fig. 4C; Table 1). However, the differences in corolla size and color are far from consistent. The nutlets are more often hairy in *Phlomoides* than in *Phlomis* s.str. When present, the indumentum on the nutlets consists of short stellate hairs at the apex in *Phlomis*. The hairs sometimes have a small gland on one of their branches (see fig. 4F in Ryding, 2008). The phylogenies presented here show that the genus as defined by Adylov & al. (1986) is paraphyletic, as already pointed out by Mathiesen & al. (2011).

***Notochaete*. —** The genus used to contain two species, and is characterized by having hooked calyx lobes. On the basis of the results of a phylogenetic study Mathiesen & al. (2011) transferred one of these species (*N. hamosa*) to *Phlomoides*, but did not study the other species (*N. longiaristata*). In our study, the two species of *Notochaete* form a strongly supported group nested within *Phlomoides* (Figs. 1–3). Hence, our results suggest that both species of *Notochaete* should be included in *Phlomoides*. This conclusion is also supported by similarities in corolla shape, corolla indumentum, inflorescence structure (composed of remote spherical glomerules shared by several species of *Phlomoides*, Fig. 4D) and pericarp structure (Ryding, 2008). *Notochaete longiaristata* is formally transferred to *Phlomoides* below.

***Lamiophlomis*. —** The genus has been generally accepted as monotypic (Li & Hedge, 1994; Harley & al., 2004) due to several unique features: the plant is monocarpic, stemless and has a basal rosette of leaves having different shapes at the juvenile and the flowering stage (Table 1; Li & Hedge, 1994; Taylor, 1998). Recently, molecular studies based on chloroplast DNA grouped *Lamiophlomis* with species of *Phlomoides* (Mathiesen & al., 2011). Consequently, Mathiesen & al. (2011) transferred *Lamiophlomis* to *Phlomoides*, which is adopted here. The placement of *Phlomoides rotata* (Benth. ex Hook. f.) Mathiesen within *Phlomoides* is also strongly supported here. In both ITS and combined plastid trees it is nested in a group with *Phlomoides melanantha* and *Ph. bracteosa*. The basic chromosome number of *Ph. rotata* is $x = 11$ (Fang & al., 2007). This agrees with reports on the basic chromosome number of *Phlomoides* (Azizian & Culter, 1982; Krasnikov & Schaulo, 1990; Probatova, 2006), and provides further support for the transfer of *Lamiophlomis* to *Phlomoides*.

***Pseuderemostachys*. —** Popov's (1940) monotypic genus is characterized by having petiolate upper leaves and very short stamens included near the mouth of the corolla tube (Table 1). On the basis of its position within the latter genus, Mathiesen & al. (2011) transferred the single species (*Ps. sewerzovii*) to *Phlomoides*. In our trees (Fig. 1–3), both the ITS and combined plastid phylogenies support it as sister to the *Eremostachys* group.

***Eremostachys*. —** The most important result of the present study (Figs. 1–3) is that the genus *Eremostachys* (sensu Harley & al., 2004 but excluding *Paraeremostachys*) forms a group within *Phlomoides* along with three divergent species of *Phlomoides*.

Most species of *Eremostachys* have robust stems, laciniate leaves, large calyces, large corollas of yellow, creamy, or white color, and bearded nutlets (Fig. 4A; Table 1). However, the differences in the leaf and corolla characters are not consistent. The most basal group of *Eremostachys* based on both ITS and plastid DNA phylogenies, here indicated as the *E. molucelloides* group (Figs. 1–2), as well as several other species, have dentate but undivided leaves. Some other species not related to this group such as *E. lanata* and *E. glabra* are characterized by having small creamy flowers and also undivided leaves. Based on both nuclear and plastid markers three species of *Phlomoides* (*Ph. milkoi*, *Ph. vavilovii* (Popov) Adylov & al., *Ph. ajdarovae*) are nested within the *Eremostachys* clade. Morphologically, all these three species show transitional states between *Eremostachys* and *Phlomoides*. They have cordate and undivided leaves similar to some species of *Phlomoides*, but have large flowers similar to those of *Eremostachys*. In general it seems that the leaves in *Phlomoides* and some basal groups of *Eremostachys* are undivided, but become laciniate (or deeply divided) in more advanced groups.

The difference in nutlet indumentum, as described by Knorring (1954) and Rechinger (1982), constitutes the most important difference between the two genera. The nutlet hairs in *Eremostachys* differ from those in *Phlomoides* in being long and all simple instead of short and usually branched (see fig. 4 in Ryding, 2008). However, there are several species of *Phlomoides* and at least one species of *Eremostachys* (*E. nuda* Regel) that have glabrous nutlets. According to Knorring (1954), *Phlomoides vavilovii*, which is nested within *Eremostachys*, conforms to this genus in having the nutlets bearded with long hairs. Unfortunately the data on this character are incomplete as nutlets are lacking in most herbarium specimens. Furthermore, due to the observed homoplasy of this character, it does not provide any clear-cut border between these genera. Palynological information as well as phytochemical, cytological, and anatomical data (Azizian & Culter, 1982; Ryding, 2008) strongly support a close relationship between *Phlomoides* s.str. (*Phlomis* sect. *Phlomoides*) and *Eremostachys*. Azizian & Moore (1982) reported the basic chromosome number of *Eremostachys* to be $x = 11$, similar to what is found in some species of *Phlomoides*, while *Phlomis* s.str. (*Phlomis* sect. *Phlomis*) has a basic chromosome number of $x = 10$ (Azizian & Culter, 1982). According to Ryding (2008), the absence of a sclerenchyma region in the pericarp seems to be a synapomorpy of a clade of *Phlomoides* (incl. *Notochaete*) and *Eremostachys*. Thus, the results of karyology and morphology support the close relationship between *Phlomoides* and *Eremostachys.* Some phytochemical evidence, such as the occurrence of the same glycosides, chrysoeriol and luteolin (Azizian & Culter, 1982), also indicates a close relationship between the two genera.

Even if a few species of *Phlomoides* were transferred to *Eremostachys* rendering the latter genus monophyletic, it would still leave *Phlomoides* a paraphyletic assemblage. Consequently, and for the above-mentioned reasons, we prefer to include *Eremostachys* and *Phlomoides* in one genus. It should be named *Phlomoides* as this name has priority over *Eremostachys*.

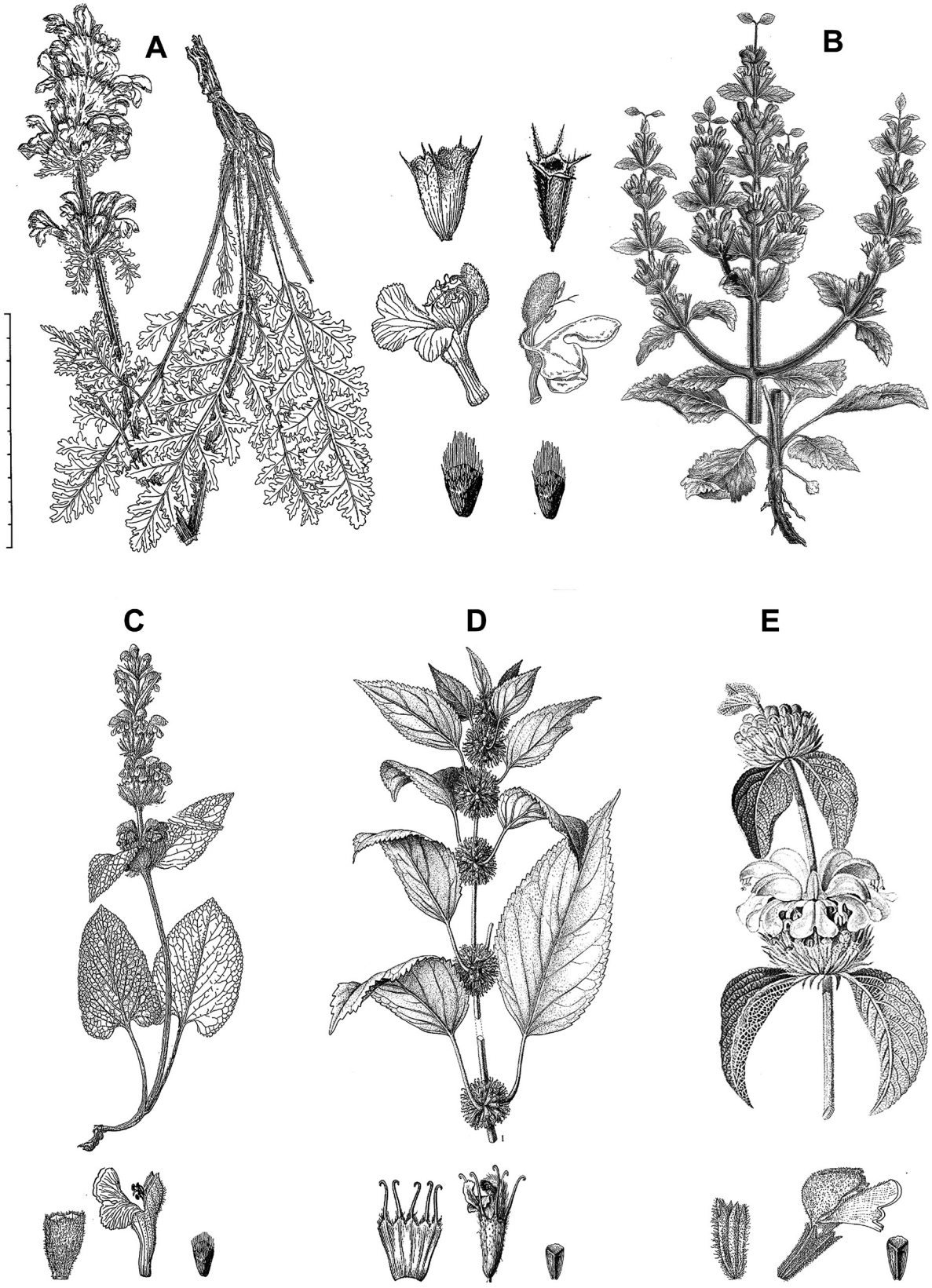

Fig. 4. Representatives of Phlomideae: **A,** *Eremostachys laciniata*; **B,** *Paraeremostachys phlomoides*; **C,** *Phlomoides tuberosa*; **D,** *Phlomoides hamosa* (former *Notochaete hamosa*); **E,** *Phlomis fruticosa*. — Scale bar = 20 cm (A, C), 10 cm (B, D, E). (Fig. 1A: after Rechinger, 1982 and Knorring, 1954; Fig. 1B: after Ledebour, 1830; Fig. 1C: after Konorring, 1954; Fig. 1D: after Li & Hedge, 1994; Fig. 1E: after Turpin, 1829).

***Paraeremostachys*. —** Adylov & al. (1986), who regarded *Eremostachys* and *Phlomoides* as unnatural groups, proposed a more clear-cut separation by transferring several species of *Eremostachys* to the genus *Phlomoides*. The nine species with funnel-shaped calyces were kept in *Eremostachys*, including the widely distributed *E. molucelloides*. Fifteen species were transferred to the newly established genus *Paraeremostachys* that was considered to differ from *Eremostachys* s.str. in having a tubular or campanulate calyx without an expanded apical rim (Fig. 4B). The phylogenetic study presented here shows that the type of *Paraeremostachys* (*Pa. phlomoides*) is nested within the *E. molucelloides* group (Figs. 1–2) and clearly belongs to *Eremostachys* s.str. Moreover, *Paraeremostachys* seems to be polyphyletic as one of its members (*E. thyrsiflora* Benth.) is nested within the *E. laciniata* core group. However, the suggested polyphyly of *Paraeremostachys* disagrees with Ryding's (2008) data on pericarp structure. In *E. thyrsiflora* the pericarp is equally thin in all parts, and crystals in the neighbouring cells of the hairs are present as in *E. molucelloides* and *E. tuberosa* (in the *E. molucelloides* group), while *E. laciniata* and *E. boissieriana* (in the *E. laciniata* core group) differ in lacking crystals and having the pericarp strongly thickened at the nutlet apex. As the condition of having a thin pericarp seems to be plesiomorphic against a pericarp thickened at the apex, the latter may constitute a synapomorphy of a smaller clade within the *E. laciniata* core group that does not include *E. thyrsiflora*. However, the apomorphic condition of having crystals at the hairs obviously conflicts with the new molecular phylogeny (Figs. 1–3). Irrespective of whether *Paraeremostachys* is polyphyletic or not, there are no reasons to recognise the group as a separate genus. The group is vaguely defined, and both *Phlomoides* s.l. and *Eremostachys* will become non-monophyletic if *Paraeremostachys* is treated as a distinct genus.

Biogeography and ecology of genus *Phlomoides*

The implication of our data for the biogeography of the genus is weakened by low sampling density making a biogeographic optimization difficult and prone to error. Therefore, only a preliminary overview is presented here. We roughly estimate the number of species of *Phlomoides* (including *Eremostachys*) to be 150–170. The distribution area of the genus extends from central Europe to the Russian Far East. The major centers of diversity of *Phlomoides* are Central Asia (Fig. 3, box: 3C–G), China (Fig. 3, box: 3C–E), and the Iranian highlands (including Afghanistan, Iran, W Pakistan, SW Turkmenistan, NE Iraq; Fig. 3, box: 3H–L). The group of *Ph. tuberosa* (Fig. 3, box: 3B–E; *Ph.* sect. *Phlomoides* sensu Adylov & al., 1986) is widely represented in China (about 40 species), with a diversity hotspot in Yunnan and Sichuan (22 species; Wu & Li, 1982), but includes a few species extending to Mediterranean Europe. In Central Asia there are 12 species of this group of which four species are shared with China. *Phlomoides* sect. *Filipendula* (sensu Adylov & al., 1986; including *Eremostachys laciniata* core group in the ITS and combined plastid trees; Fig. 3, box: 3H) is absent from China but species-rich (about 65 species) in Central Asia. In the Iranian highlands *Ph*. sect. *Filipendula* with about 30 species is more common than *Ph*. sect. *Phlomoides* (about 15 species). Based on the tree topologies presented here, it is most plausible to assume that *Phlomoides* (including *Eremostachys*) originated in China or Central Asia, as was also suggested by Mathiesen & al. (2011), because the most basal clades are best represented in this area. One or several lineages from these basal groups extend along the Himalayan and Hindu Kush mountain ranges (Fig. 3, box: 3C, E) and could reach high altitudes of above 4000 m. Ecological adaptation might play an important role here, resulting in some taxa or groups of taxa with peculiar morphological characters (such as hooked calyx lobes in *Notochaete*, which might help them to attach to the fur of mammals or feathers of birds and aid in fruit dispersal, or a reduced flowering stem in *Lamiophlomis* (a known morphological response to intensity of UV radiation at high altitudes), which encouraged some botanists to elevate them to generic rank. Among these taxa, *Notochaete* is distributed in south China, Nepal, India, and Burma at an altitude of 1200–2500 m, where it usually is found in the edge of subtropical evergreen forests. The distribution area and ecology of *Notochaete* matches those of several species of *Phlomoides*, although the former prefers slightly lower altitudes. The distribution area of the two genera overlaps considerably in south China, particularly in the provinces Yunnan and Xizang. *Lamiophlomis* shows a similar distribution pattern to *Notochaete* but grows at higher altitudes above the tree line in meadows and grasslands. A habitat at higher altitudes would explain the rosette form of this species.

Most species of the *Eremostachys* clade are distributed in Iran and Afghanistan. *Phlomoides sewerzovii* is sister to this clade and distributed in Central Asia (Kazakhstan). This species is morphologically intermediate between *Phlomoides* and *Eremostachys*, but most similar to the latter. *Phlomoides sewerzovii* is probably the origin of the main westward penetrating line of *Phlomoides*, covering first Afghanistan and then reaching Iran. Few species such as *E. laciniata* and *E. molucelloides* had the chance of expanding their distribution area towards Turkey and the Mediterranean area. The latter area is dominated by the sister group of *Phlomoides*, i.e., *Phlomis*. For a detailed biogeographical history of the latter see Mathiesen & al. (2011).

■ TAXONOMIC TREATMENT

The phylogenetic analyses presented here, as well as other recent investigations, strongly suggest to reduce the number of recognized genera in tribe Phlomideae to two: *Phlomis* L. with about 50–90 species and *Phlomoides* (L.) Moench with about 150–170 species. A widely circumscribed *Phlomoides* (*Phlomoides* s.l.) seems to be unavoidable, particularly due to a high number of transitional species between *Phlomoides* s.str. (which is paraphyletic) and the *Eremostachys* core group. A key to the two recognized genera of Phlomideae according to the results of the present study as well as nomenclatural synonyms and a description of *Phlomoides* in its new circumscription are given below.

Key to genera

1. Plants mostly subshrubs or shrubs, sometimes erect herbs; leaves simple, lanceolate to oblong-lanceolate; verticillasters in a dense scapose capitulum or short spike; upper lip of corolla laterally compressed, flattened, sickle-shaped, not fringed or incised ..... ***Phlomis***
1. Plants herbaceous usually with woody rhizomes and/or tubers on the roots; leaves simple or laciniate to pinnatisect, cordate to triangular-ovate; verticillasters lax or dense; upper corolla lip not compressed laterally, non flattened, arch-shaped, always hairy or fringed-incised ..... ***Phlomoides***

Phlomoides Moench, Methodus: 403. 1794 – Type (only species cited in protologue): *P. tuberosa* (L.) Moench.
= *Notochaete* Benth. in Wallich, Pl. Asiat. Rar. 1: 63. 1830 – Type (only species cited in protologue): *N. hamosa* Benth.
= *Eremostachys* Bunge in Ledebour, Fl. Altaic. 2: 414. 1830, **syn. nov.** – Type (designated by Pfeiffer, 1874): *E. laciniata* (L.) Bunge.
= *Lamiophlomis* Kudô in Mem. Fac. Sci. Taihoku Imp. Univ. 2: 210. 1929 – Type (monotypic): *L. rotata* (Benth. ex Hook. f.) Kudô.
= *Pseuderemostachys* Popov in Novye Mem. Moskovsk. Obshch. Isp. Prir. 19: 148. 1941 ('1940') – Type (monotypic): *P. sewerzowii* (Herder) Popov.
= *Paraeremostachys* Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 112. 1986, **syn. nov.** – Type (designated in protologue): *P. phlomoides* (Bunge) Adylov, Kamelin & Makhm.

Perennial herbs, usually with woody rhizomes and/or tubers on roots, rarely aromatic. Basal leaves simple or laciniate to pinnatisect with toothed margin, mostly petiolate. Cauline leaves similar to basal leaves, but smaller and mostly sessile or shortly petiolate. Inflorescences thyrsoid to sometimes racemose with 2–20 flowers arranged in opposite axillary cymes, forming verticillasters with bracts and frequently bracteoles (sometimes spinose at apex). Calyx 5-lobed, tubular, campanulate or broadly funnel-shaped. Calyx lobes equal to subequal, sometimes broad at base and abruptly narrowed to a short spinose apex, or rarely hooked. Corolla white to yellow, mauve-pink to purple, strongly 2-lipped (1 lobe forming upper, 3 lobes forming lower lip) with the posterior lip hooded (often deeply concave and dome-shaped) and bearded. Corolla tube cylindrical and sometimes hairy at the throat. The four stamens not or only shortly exserted. Style branches unequal or rarely equal (in *P. rotata*). Nutlets truncate or sub-truncate and mostly bearded at apex. Basic chromosome number $x = 11$.

New names and combinations

New combinations are introduced here primarily for those taxa included in our study and those unsampled species of which we were able to investigate representative (where possible type) material. In cases where no material was available at all, we refrained from validating the expanded new combinations at this point.

Phlomoides acaulis (Beck ex Rech. f.) Salmaki, **comb. nov.** ≡ *Eremostachys acaulis* Beck ex Rech. f. in Repert. Spec. Nov. Regni Veg. 48: 161. 1940 – Type: [Afghanistan], Kabul, [without date], *Honigberger* (holotype: W!).

Phlomoides affinis (Schrenk) Salmaki, **comb. nov.** ≡ *Eremostachys affinis* Schrenk in Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersbourg 3: 211. 1844 – Lectotype (designated here by Y. Salmaki): [Songaria] in desertis a sinistra ripa flovii Atasu, medio Majo (florente), *Schrenk* (lectotype: LE!).

Phlomoides ammophila (Rech. f) Salmaki, **comb. nov.** ≡ *Eremostachys ammophila* Rech. f., Fl. Iranica 150: 579. 1982 ≡ *Paraeremostachys ammophila* (Rech. f.) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 114. 1986 – Type: [Afghanistan], SE Kandahar, Alluvions de Dori Rud, 50 km environ SE Kandahar, grande dune de sable rouge mobile dominant la vallée, 15. 04. 1958, *Pabot A-500* (holotype: G!; isotype: W!).

Phlomoides anisochila (Pazij & Vved.) Salmaki, **comb. nov.** ≡ *Eremostachys anisochila* Pazij & Vved., Fl. Uzbekist. 5: 634. 1961 ≡ *Paraeremostachys anisochila* (Pazij & Vved.) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 113. 1986 – Type: [Tajikistan], Pamiralaj in montibus Koj-Tasch, 01. 08. 1931, *Kobranova 137673* (TAD).

Phlomoides aralensis (Bunge) Salmaki, **comb. nov.** ≡ *Eremostachys aralensis* Bunge, Beitr. Fl. Russl.: 266 (= 442). 1852 ('1851') ≡ *Paraeremostachys aralensis* (Bunge) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 113. 1986 – Type: [Uzbekistan, Kazakhstan, Turkmenistan?], in deserto Araneoso Batkak-Kum (Kisil-Kum), 22. 04. 1842, *A. Lehmann* (LE).

Phlomoides badakhshanica (Hedge) Salmaki, **comb. nov.** ≡ *Eremostachys badakhshanica* Hedge in Notes Roy. Bot. Gard. Edinburgh 27: 167. 1967 ≡ *Paraeremostachys badakhshanica* (Hedge) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 113. 1986 – Type: [Afghanistan], Badakhshan, Farizabad, 1500–2100 m, 23. 05. 1964, *Furse 6264* (holotype: K; isotype: M!).

Phlomoides desertorum (Regel) Salmaki, **comb. nov.** ≡ *Eremostachys desertorum* Regel in Trudy Imp. S.-Peterburgsk. Bot. Sada 9: 563. 1886 ≡ *Paraeremostachys desertorum* (Regel) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 113. 1986 – Lectotype (designated here by Y. Salmaki): [Tukmenistan], Saravschanicae deserto inter oppidum, Kermine et pagum Bohistan bucharae occidentalis, 26. 04. 1884, *Regel* (lectotype with illustration: LE!; isotype: LE!).

Phlomoides edelbergii (Rech. f.) Salmaki, **comb. nov.** ≡ *Eremostachys edelbergii* Rech. f. in Biol. Skr. 8(1): 46. 1955 – Type: [Afghanistan], Nuristan, Pashki, 2600 m, 10. 06. 1948, *Edelberg 947* (holotype: C; isotype: W!).

Phlomoides ghorana (Rech. f.) Salmaki, **comb. nov.** ≡ *Eremostachys ghorana* Rech. f. in Anz. Österr. Akad. Wiss., Math.-Naturwiss. Kl. 101: 429. 1964 ≡ *Paraeremostachys ghorana* (Rech. f.) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 114. 1986.– Type: [Afghanistan], Ghorat, Kuh Tscheling-Sefid-Daraq prope Parjuman, 2500 m, 31. 07. – 01. 08. 1962, *Rechinger 19079* (holotype: W!; isotype: M!).

Phlomoides glanduligera (Popov) Salmaki, **comb. nov.** ≡ *Eremostachys glanduligera* Popov in Novye Mem. Moskovsk. Obshch. Isp. Prir. 19: 103. 1941 ('1940') – Syntypes: [Tajikistan], In Asiae Mediae montibus Hissaricis, in eorum baracchiis maxime occidentalibus ad opp. Jakkabagh vergentibus, in monte Chan-tachta prope pagum Kisil-tam, 25. 05. 1913, *Michelson 1943* (LE); Montes Chodsha-Gurgur-ata, ad initia rivuli Turgan-darja, in faucibus Kisil-Saj, 08. 07. 1934, *Butkov 130* (LE).

Phlomoides isochila (Pazij & Vved.) Salmaki, **comb. nov.** ≡ *Eremostachys isochila* Pazij & Vved., Fl. Uzbekist. 5: 636. 1961 – Type: [Uzbekistan], Tian-Schan occidentalis, ad declivia argillosa secus canalem Bos-su prope pag. Niazbek, haud procul ab urbe Taschkent, 02. 05. 1926, *Granitov 1281* (holotype: TAK).

Phlomoides lanata (Jamzad) Salmaki, **comb. nov.** ≡ *Eremostachys lanata* Jamzad in Iran. J. Bot. 3: 112. 1987 – Type: [Iran], Mazandaran, 85 km from Kandavan to Haraz road, Mazid village, 1900–2300 m, 23. 06. 1979, *Assadi & Mozaffarian 33028* (holotype: TARI).

Phlomoides lindbergii (Rech. f) Salmaki, **comb. nov.** ≡ *Eremostachys lindbergii* Rech. f. in Anz. Österr. Akad. Wiss., Math.-Naturwiss. Kl. 101: 428. 1964 ≡ *Paraeremostachys lindbergii* (Rech. f.) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 114. 1986 – Type: [Afghanistan], Orozgan, 1960, *Lindberg 818* (holotype: W!).

Phlomoides longiaristata (C.Y. Wu & H.W. Li) Salmaki, **comb. nov.** ≡ *Notochaete longiaristata* C.Y. Wu & H.W. Li in Acta Phytotax. Sin. 10: 154. 1965 – Type: [China], Yunnan, taron-Taru Divisio, 2300 m, 07. 09. 1938, *T.T. Yü 20995* (HP).

Phlomoides minutigalea Salmaki, **nom. nov.** ≡ *Eremostachys spectabilis* Popov in Novye Mem. Moskovsk. Obshch. Isp. Prir. 19: 117. 1941 ('1941') non *Phlomides spectabilis* (Falc. ex Benth.) Kamelin & Makhm. – Type: in Asiae Mediae montibus Pamiro-Alaicis australioribus, hissaricis, ad flumen Vachsch, 25. 05. 1932, *Gontscharov & Grigorjev 43* (holotype: LE!).

Phlomoides mogianica (Popov) Salmaki, **comb. nov.** ≡ *Eremostachys mogianica* Popov in Novye Mém. Moskovsk. Obshch. Isp. Prir. 19: 132. 1941 ('1940') – Lectotype (designated here by Y. Salmaki): [Seravschan], Mogian, 4500 m, May 1893, *Komarov* (LE!; isotype: LE!).

Phlomoides molucelloides (Bunge) Salmaki, **comb. nov.** ≡ *Eremostachys molucelloides* Bunge in Ledebour, Fl. Altaic. 2: 415. 1830 – Lectotype (designated here by Y. Salmaki): Elegantissima haec stirps non raro in arenosis et siccis deserti Soongoro-Kirghisici, Majo 1829, *Bunge 894* (LE!).

Phlomoides multifurcata Salmaki, **nom. nov.** ≡ *Eremostachys phlomoides* Bunge in Ledebour, Fl. Altaic. 2: 414. 1830 ≡ *Paraeremostachys phlomoides* (Bunge) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 113. 1986 – Lectotype (designated here by Y. Salmaki): [Kirghizistan], Hab. Rarissima in locis subsalsis deserti Soongoro-Kirghisici, montibus Arkaul et Dolen-kara adjacentis, Maio, *A. Ledebour 92* (LE!).

Phlomoides paniculata (Regel) Salmaki, **comb. nov.** ≡ *Eremostachys paniculata* Regel in Trudy Imp. S.-Peterburgsk. Bot. Sada 6: 381. 1879 ≡ *Paraeremostachys paniculata* (Regel) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 113. 1986 – Type: [Turkmenistan], [Kyzyl-Kum], In deserto Kisilkum, 07. 05. 1871, *O. Fedtschenko* (holotype: LE!).

Phlomoides persimilis (Aitch. & Hemsl.) Salmaki, **comb. nov.** ≡ *Eremostachys persimilis* Aitch. & Hemsl. in Trans. Linn. Soc. London, Bot. 3: 98. 1888 ≡ *Paraeremostachys persimilis* (Aitch. & Hemsl.) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 114. 1986. – Type: [Afghanistan], Herat: Badghis, 14. 05. 1835, *Aitchison 464* (holotype: K).

Phlomoides rotala (Schrenk ex Fisch. & C.A. Mey.) Salmaki, **comb. nov.** ≡ *Eremostachys rotala* Schrenk ex Fisch. & C.A. Mey., Index Seminum [St. Petersburg] 9 (Suppl. 3): 11. 1843 – Type: [Kazakhstan], Songaria, Karasu ad Dschussagatsch, May 1840, *Schrenk* (holotype: LE!).

Phlomoides sogdiana (Pazij & Vved.) Salmaki, **comb. nov.** ≡ *Eremostachys sogdiana* Pazij & Vved., Fl. Uzbekist. 5: 635. 1961 ≡ *Paraeremostachys sogdiana* (Pazij & Vved.) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 113. 1986 – Type: [Tajikistan], Pamiralaj, montes sogdiano-transoxani. In schistosis in loco Jang-ogly in montibus Ak-tau (Nura-tau), 08. 06. 1926, *Popov 1291* (TAD).

Phlomoides thyrsiflora (Benth.) Salmaki, **comb. nov.** ≡ *Eremostachys thyrsiflora* Benth. in Candolle, Prodr. 12: 548. 1848 ≡ *Paraeremostachys thyrsiflora* (Benth.) Adylov, Kamelin & Makhm. in Novosti Sist. Vyssh. Rast. 23: 113. 1986 – Type: [Afghanistan], in regno Cabul, [without date], *Griffith 492* (holotype: K).

Phlomoides transoxana (Bunge) Salmaki, **comb. nov.** ≡ *Eremostachys transoxana* Bunge in Mém. Sav. Étrang. Acad. Sci. Petersb. 7: 441. 1851 ≡ *Paraeremostachys transoxana* (Bunge) Adylov, Kamelin & Makhm. in Novosti Sist.

Vyssh. Rast. 23: 113. 1986 – Type: [Uzbekistan, Kazakhstan, Turkmenistan?], in Jaman Kisil-Kum, 22. 04. 1842, *A. Lehmann* (ex herb. Cosson) (type fragment: LE!).

Phlomoides uralensis Salmaki, **nom. nov.** ≡ *Moluccella tuberosa* Pall., Reise Russ. Reich. 3: 738. 1776 ≡ *Eremostachys tuberosa* (Pall.) Bunge in Ledebour, Fl. Altaic. 2: 416. 1830, non *Phlomoides tuberosa* (L.) Moench – Type: Rossia australis, Sibiria uralensis, [without date], *Pallas* (BM).

■ ACKNOWLEDGMENTS

We are grateful to the DAAD ''Deutscher Akademischer Austauschdienst'' for a grant to the first author as well as the ''Alexander-von-Humboldt-Stiftung'' for a grant to the corresponding author. The Research Council, University of Tehran partially provided financial support for this project. The authors thank the curators at E, LE, M, MSB, TUH, W, and WU for permission to sample from herbarium specimens used in this study. Kind assistance from Tanja Ernst (Munich) in Heubl's lab of plant molecular systematics is appreciated. We are grateful also to Alexander Sukhorukov (Moscow) and Chunlei Xiang (Kunming) for providing silica-dried material of *Notochaete*. We would like to thank Prof. Vladimir Dorofeyev as well as other curators of the LE for their helps in various respects. This study was also partially supported by the European Comission (SYNTHESYS grant AT-TAF-610, to C.B. for a visit to W).

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Appendix. Species names and authorities, geographical provenience, and herbarium vouchers for the material included in this study. GenBank accession numbers are given for the four markers sequenced in the order ITS, *trnT-trnA*, partial *trnK*, and *rpl32-trnL*, respectively; an n-dash (–) denotes a missing marker. All sequences were produced here for the first time, except for *trnK* sequence of *Stachys sylvatica* (indicated by an asterisk).

OUTGROUPS: ***Ballota hirsuta*** Benth., Morokko, Goulimine, 17 km E Bou-Izakarn an der Straße (P 30) nach Akka, N Hänge des Djebel Bani 5 km S der Starße (650–1060 m) *Podlech 53328* (M), JN680359, JN680509, –, JN680415; ***Ballota nigra*** L., Iran, E Azarbaijan, Arasbaran protected area, 3 km after bifurcation of Aynalou-Makidi, *Salmaki & al. 39813* (TUH), JN680358, JN680508, JN680462, JN680414; ***Betonica officinalis*** L. Germany, Regierungsbezirk Südbaden, Landkresis Waldshut, Südschwarzwald, Hotzenwald, Urberg, Hügel Südwestlich über der Kirche von Inner-Urberg (990 m), *Schuwerk 09/150* (MSB), JN680360, JN680510, JN680463, JN680416; ***Lagochilus cabulicus*** Benth., Iran, in collibus argilloso-schistosis prope Dorokhsh, ab Assadabad 40 km occidentem versus, ad bifurcationem viae versus Qayen ducentis (1900 m), *Rechinger 56201* (M), JN680362, JN680513, JN680464, JN680419; ***Stachys sylvatica*** L., BM-000954687, –, –, *FJ395437, –; ***Stachys sylvatica*** L., Iran, Gilan, Loshan, on the road from Loshan to Jirandeh, *Salmaki & Zarre 35061* (TUH), –, JN680512, –, JN680418; ***Stachys sylvatica*** L., Iran, E Azarbaijan, Arasbaran protected area, 3 km after bifurcation of Aynalou-Makidi, *Salmaki & al. 39715* (TUH), JN680361, JN680511, –, JN680417; ***Paraphlomis formosana*** (Hayata) T.H. Hsieh & T.C. Huang, Tiwan (China), *Zhong 3676* (E), JN680356, JN680506, JN680460, JN680412; ***Paraphlomis javanica*** (Blume) Prain, Tiwan (China), *Liu & Chen 67* (E), JN680357, JN680507, JN680461, JN680413; ***Eremostachys*** Bunge: ***Eremostachys arctifolia*** Popov., Afghanistan, Takhar, Gebirgsrand 12 km SO ven Eshkamesh, (2000 m), *Podlech 21583* (M), JN680403, JN680546,

Appendix. Continued.

JN680499, JN680452; ***Eremostachys azerbaijanica*** Rech.f., Iran, E Azarbaijan, SW Namin near Ardabil, 23 km to Ardabil, 5 km after bifurcation Namin-Ardabil (1200–1300 m), *Salmaki & Siadati 39147* (TUH), JN680395, JN680548, JN680492, JN680444; ***Eremostachys boissieriana*** Regel, Iran, Shahrud, on the road of Shahrud to Mayamey, ca. 40 km to Mayamey, near the road, *Salmaki & Amini 39145* (TUH), JN680400, JN680542, JN680496, JN680448; ***Eremostachys boissieriana*** Regel, Turkmenistan, Kopetdagh ad declivia argillosa in valle Bogundar prope urb. Kara-Kala, *Popov 6432* (LE), JN680401, JN680543, JN680497, JN680449; ***Eremostachys fetisovii*** Regel, Kazakhstan, rami astro-occidentales jugi Alatau Transiliensis, in fluxu medio fl. Karakunuz, in declivibus australibus lapidosis siccis, *Goloskokov 4487* (M), JN680411, JN680553, JN680505, JN680459; ***Eremostachys glabra*** Boiss. ex Benth., Iran, Tehran, on the road of Chalus to Karaj, at the beginning of the road Arangeh from Chalus-Karaj road, *Salmaki & Zarre 39218* (TUH), JN680389, JN680533, JN680486, JN680438; ***Eremostachys glabra*** Boiss. ex Benth., Tehran, Darakeh, *Assadi & al. 11765* (TUH), JN680390, JN680534, JN680487, JN680439; ***Eremostachys hyoscyamoides*** Boiss. & Buhse, Iran, Shahrud-Bustan (Turan protected area), Jafarabad prope Zamanabad (1200 m), *Rechinger 50914* (M), JN680402, JN680544, JN680498, JN680450; ***Eremostachys korovinii*** Popov, Kazachstan, *Ionkhov 72657* (LE), JN680409, JN680551, JN680503, JN680457; ***Eremostachys labiosiformis*** (Popov) Knorring, Iran, NE Tehran, on the road to Abali, 3 km after Abali factory, *Salmaki & Zarre 39154* (TUH), JN680393, JN680537, JN680490, JN680453; ***Eremostachys laciniata*** (L.) Bunge, Iran, NW Tehran, 5 km on the road to Emamzadeh Davoud, *Salmaki & Zarre 39221* (TUH), JN680392, JN680536, JN680489, JN680441; ***Eremostachys laevigata*** Bunge, Iran, W Azarbaijan, ca 14 km to Oshnaviyeh from Urmia, ca. 45 km after Urmia to Oshnaviyeh, (1780 m), *Salmaki & Siadati 39152* (TUH), JN680397, JN680539, JN680494, JN680443; ***Eremostachys lanata*** Jamzad, Iran, Mazandaran, Haraz to Chalus, on the road Baladeh-Mazid (2 km after Baladeh toward Haraz) 5 km on the deviation of Baladeh to Noor (2550 m), *Salmaki & Zarre 39216* (TUH), JN680391, JN680535, JN680488, JN680440; ***Eremostachys mogianica*** Popov, Saravschan, Mogian, *Smirnova 483* (LE), JN680384, JN680529, JN680482, JN680435; ***Eremostachys molucelloides*** Bunge, Iran, Tehran to Karaj, Vard-Avard station, on the road of Daroupakhsh factory, Dashte mountain, *Salmaki & Zarre 39219* (TUH), JN680382, JN680527, JN680480, JN680433; ***Eremostachys molucelloides*** Bunge, Iran, Markazi, ca. 20 km to Saveh from Zarandiyeh, Rangraz pass (1325 m), *Salmaki & al*., *39960* (TUH), JN680383, JN680528, JN680481, JN680434; ***Eremostachys paropamisica*** Rech.f., Afghanistan, Herat, Kotal-i-Banda Buguchar, ca. 40 km N von Heart an der Straße nach Toraghundi (1300 m), *Podlech & Jarmal 29438* (M), JN680407, –, –, –; ***Eremostachys phlomoides*** Bunge, Kyrgizistan, *Michelson 544* (LE), JN680385, JN680530, JN680483, JN680436; ***Eremostachys phlomoides*** Bunge, Kyrgizistan, *Schischkin* (LE), JN680386, –, –, –; ***Eremostachys pulvinaris*** Jaub. & Spach, Iran, on the road of Kashan toward Esfahan, Meimeh, *Salmaki & Zarre 39220* (TUH), JN680394, JN680538, JN680491, JN680442; ***Eremostachys rotala*** Schrenk ex Fisch. & C.A. Mey., Kazachstan, Heptapotamia austro-orientalis, prope stat. viae ferreae Lepsa, in deserto arenoso, *Ruldugin 4432* (M), JN680388, JN680532, JN680485, JN680437; ***Eremostachys speciosa*** Rupr., Tian-Shan occidentalis, in collibus pr. st. v.f. Dshilga, *Popov & Vvedensky 6295* (M), JN680398, JN680540, JN680495, JN680446; ***Eremostachys spectabilis*** Popov, Tajikistan, *Gontscharov & al*., *420* (LE), JN680399, JN680541, –, JN680447; ***Eremostachys thyrsiflora*** Benth. Afghanistan, Kandahar, bei Kurmohammadkhan, 24 km W Kandahar, (975 m), *Podlech & Jarmal 28869* (M), JN680404, JN680545, JN680500, JN680451; ***Eremostachys tournefortii*** Jaub. & Spach, Iran, W Azarbaijan, ca 98 km to Maku from Khoy, ca 12 km to Hossein-Abad village, *Salmaki & Siadati 39151* (TUH), JN680396, JN680547, JN680493, JN680445; ***Eremostachys tuberosa*** (Pall.) Bunge, Kyrgizistan, *Fyatov & Kuzgechov 259* (LE), JN680387, JN680531, JN680484, JN680456; ***Notochaete*** Benth.: ***Notochaete longiaristata*** C.Y. Wu & H.W. Li, China, Yunnan, Baoshan city, Baihualing National Nature Reserve, (1500–1600 m), *Xiang 041* (KUN), JN680368, –, JN680471, –; ***Phlomis*** L.: ***Phlomis anisodonta*** Boiss., Iran, Mazandaran, Siahkal mountains, from Kalachay-Chaboksar, Javaher-Dasht, (2100–2200 m), *Salmaki & Zarre 39144* (TUH), JN680363, JN680514, JN680465, JN680420; ***Phlomis bruguieri*** Desf., Iran, Kermanshah, *Salmaki & al. 39423* (TUH), JN680366, JN680517, JN680468, JN680423; ***Phlomis elliptica*** Benth., Iran, Fars, Shiraz, Bamu protected area, *Salmaki & al. 36261* (TUH), JN680365, JN680516, JN680467, JN680422; ***Phlomis fruticosa*** L., Montenegro, Hänge über der Küste bei Petrovac, (500 m), *Roessler 6880* (MSB), JN680364, JN680515, JN680466, JN680421; ***Phlomis herba-venti*** L., Iran, E Azarbaijan, on the road of Ahar to Kaleybar, ca 12 km to Kaleybar from Ahar, (1502 m), *Salmaki & al. 39792* (TUH), JN680367, JN680518, JN680469, JN680424; ***Phlomoides*** (L.) Moench: ***Phlomoides adylovii*** Lazkov, Kyrgizistan, *Lazkov s.n.* (LE), JN680374, JN680522, JN680475, JN680428; ***Phlomoides ajdarovae*** Lazkov, Kyrgizistan, *Prod s.n.* (LE), JN680406, JN680550, JN680502, JN680455; ***Phlomoides betonicoides*** (Diels) Kamelin & Makhm., China, Xizang (Tibet), Bomi Xian: E of the city of Bomi (Pome) on highway 318, above Palongzang river (2795 m), *Boufford 22927* (MSB), Jn680378, –, –, –; ***Phlomoides bracteosa*** (Royle ex Benth.) Kamelin & Makhm., Afghanistan, Kunar, Chapadarrah, Suleimanshah Darrah oberhalb Suleimanshah (3000–3500 m), *Anders 11464* (M), JN680373, JN680521, JN680474, JN680427; ***Phlomoides hamosa*** Benth. (former *Notochaete hamosa*), China, Yunnan, Dali city, Nanjian county, Anzhao, Ganjielu (2168 m), *Chang & al. 145* (KUN), JN680369, –, JN680470, –; ***Phlomoides hamosa*** Benth. (former *Notochaete hamosa*), Nepal, Annapurna aseptum publicum, in via (sive potius semita) quae ad Nayapul ducit, inter vicos Ghorepani et Tikhedhunga, in silva juxta semitam (1800 m), *Suchorukov 245* (MW), JN680370, –, –, –; ***Phlomoides medicinalis*** (Diels) Kamelin & Makhm., China, Xizang (Tibet), Baqê Xian, Bada, between the towns of Dêngqên (Tengchen) and Sog Xian along highway 317 (4120 m), *Harvard 29984* (E), JN680408, –, –, –; ***Phlomoides melanantha*** (Diels) Kamelin & Makhm., China, Dali Xian, Diancang Shan mountain range (3050 m), *Bartholomew & al*., *1204* (B), JN680377, JN680524, JN680477, JN680430; ***Phlomoides milkoi*** Lazkov, Kyrgizistan, *Milko 585* (LE), JN680410, JN680552, JN680504, JN680458; ***Phlomoides muliensis*** (C.Y. Wu) Kamelin & Makhm., China, Sichuan, Batang Xian, S of Batang (and S of Zhubalong) on road along the Jinsha Jiang (upper Chang Jiang), and S of bridge and road to Markam (2450–2575 m), *Boufford 35469* (MSB), JN680379, –, –, –; ***Phlomoides pratensis*** (Kar. & Kir.) Adylov, Kamelin & Makhm., Kazakhstan, *Fedtschenko 2172* (LE), JN680380, JN680525, JN680478, JN680431; ***Phlomoides rotata*** (Benth. ex Hook.f.) Kudô (former *Lamiophlomis rotata*), China, Xizang, SE. Tibet, Nyainqentanglha Shan, Yangbajain-Damxung, NW. Of Lhasa. Above base camp (4900 m), *Dikore 3537* (MSB), JN680371, JN680519, JN680472, JN680425; ***Phlomoides sewerzovii*** (Herder) Popov (former *Pseuderemostachys sewerzovii*), Kazakhstan, rami occidentale jugi Alatau Talassici, trajectus Baranschi-Asu, prope stat. Viae ferreae Tjulkubas in parte superiore declivitalis septenterionalis lapidoso-schistosae, (1450 m), *Karmyscheva 4431* (M), JN680372, JN680520, JN680473, JN680426; ***Phlomoides tuberosa*** Moench, Iran, E Azarbaijan, in front of Payam (Yam) village, toward the peak of Mishoudagh mountain, *Salmaki & al*., *39881* (TUH), JN680375, JN680523, JN680476, JN680429; ***Phlomoides tuberosa*** Moench, Armenia, Vayotsdzor, Vajk distr. ca. 2km SE Vajk, gorge at road to Zaritap, (1130 m), *Vitek s.n.* (M), JN680376, –, –, –; ***Phlomoides tytthaster*** (Vved.) Adylov, Kamelin & Makhm., Uzbekistan, *Dessiatoff 786* (LE), JN680381, JN680526, JN680479, JN680432; ***Phlomoides vavilovii*** (Popov) Adylov, Kamelin & Makhm., Kyrgizistan, *Lazkov 553* (LE), JN680405, JN680549, JN680501, JN680454.