

# TAXON

International Journal of Taxonomy, Phylogeny and Evolution

Electronic Supplement to

## **Phylogeny and systematics of the tribe Thlaspideae (Brassicaceae) and the recognition of two new genera**

**Shokouh Esmailbegi, Ihsan A. Al-Shehbaz, Milan Pouch, Terezie Mandáková,  
Klaus Mummenhoff, Mohammad Reza Rahiminejad, Mansour Mirtadzadini &  
Martin A. Lysak**

*Taxon* 67: 324–340 (<https://doi.org/10.12705/672.4>)

**Table S1.** ITS and *trnL-F* primers used in phylogenetic study.

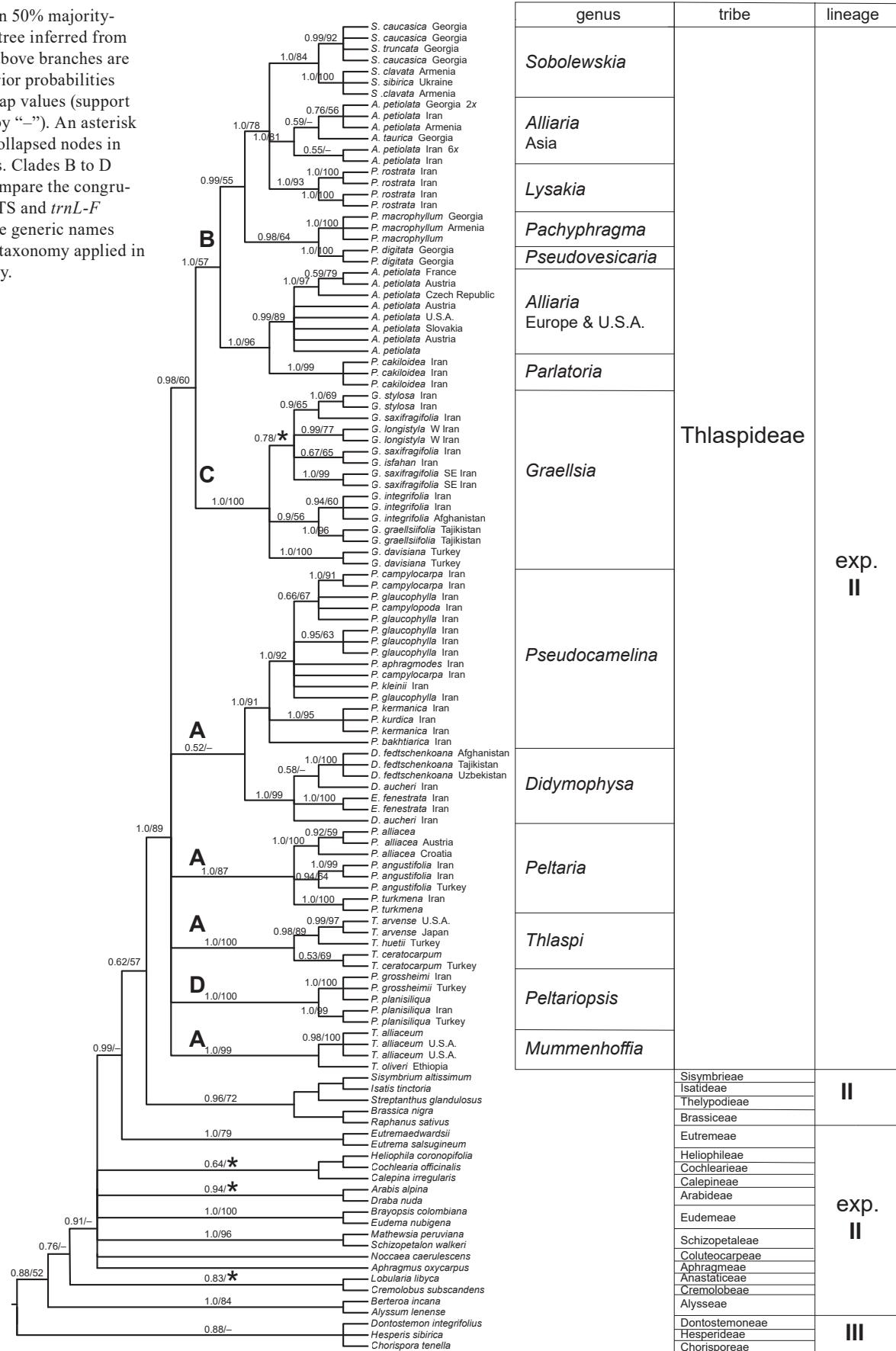
Gene	Primer	Sequence	Reference
ITS	ITS1	TCC GTA GGT GAA CCT GCG G	White & al., 1990
	ITS4	TCC TCC GCT TAT TGA TAT GC	White & al., 1990
	ITS-18F	GGA AGG AGA AGT CGT AAC AAG G	Mummenhoff & al., 1997
<i>trnL-F</i>	tabC	CGA AAT CGG TAG ACG CTA CG	Shaw & al., 2005
	tabF	ATT TGA ACT GGT GAC ACG AG	Shaw & al., 2005

- White, T.J., Bruns, T., Lee, S. & Taylor, J.** 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (eds.), *PCR protocols: A guide to methods and applications*. San Diego: Academic Press.
- Mummenhoff, K., Franzke, A. & Koch, M.** 1997. Molecular data reveal convergence in fruit characters used in the classification of *Thlaspi* s.l. (Brassicaceae). *Bot. J. Linn. Soc.* 125: 183–199. <https://doi.org/10.1111/j.1095-8339.1997.tb02253.x>
- Shaw, J., Lickey, E., Beck, J.T., Farmer, S.B., Liu, W., Miller, J., Siripun, K.C., Winder, C.T., Schilling, E.E. & Small, R.L.** 2005. The tortoise and the hare II: Relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *Amer. J. Bot.* 92: 142–166. <https://doi.org/10.3732/ajb.92.1.142>

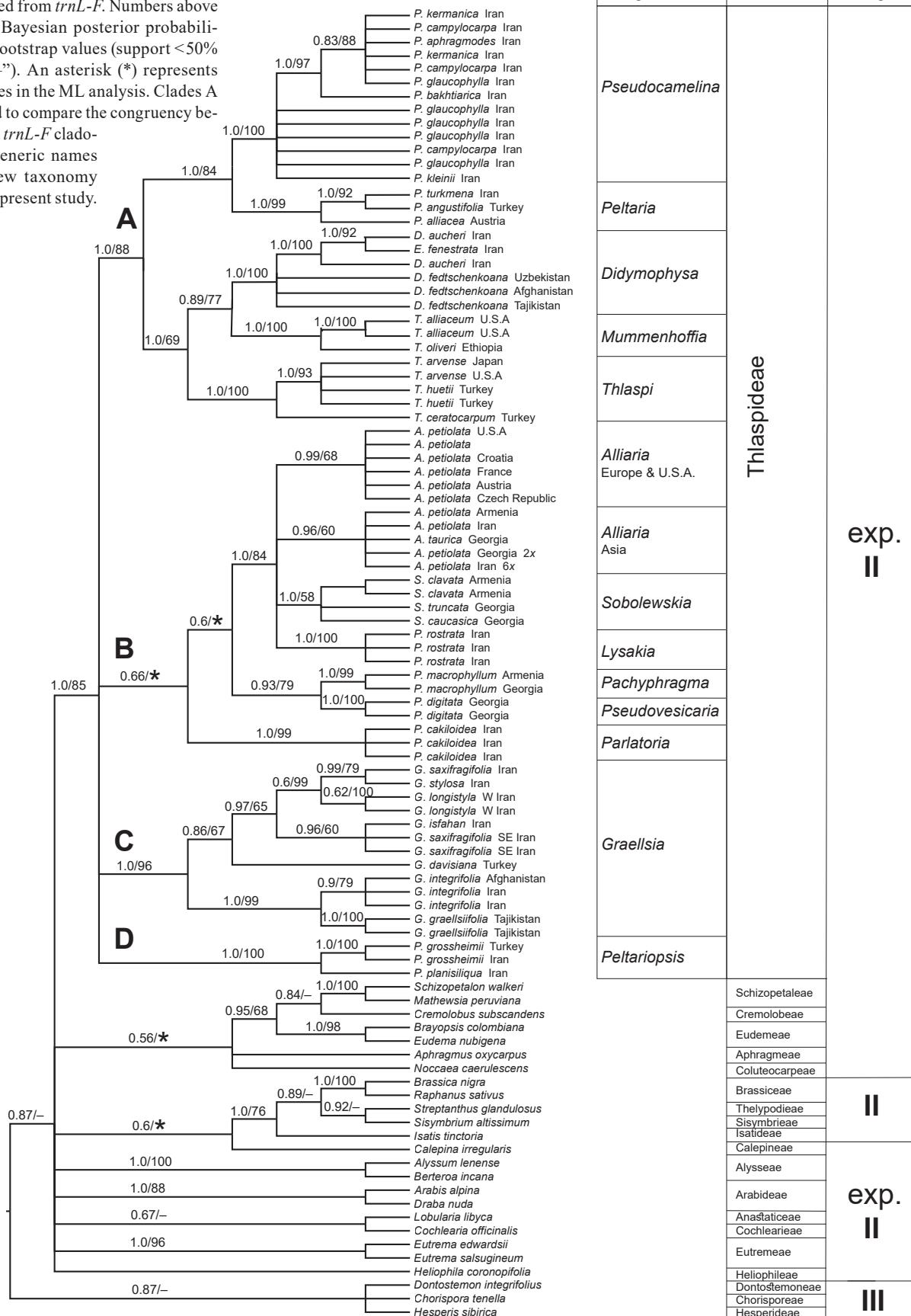
**Table S2.** List of accessions with chromosome counts.

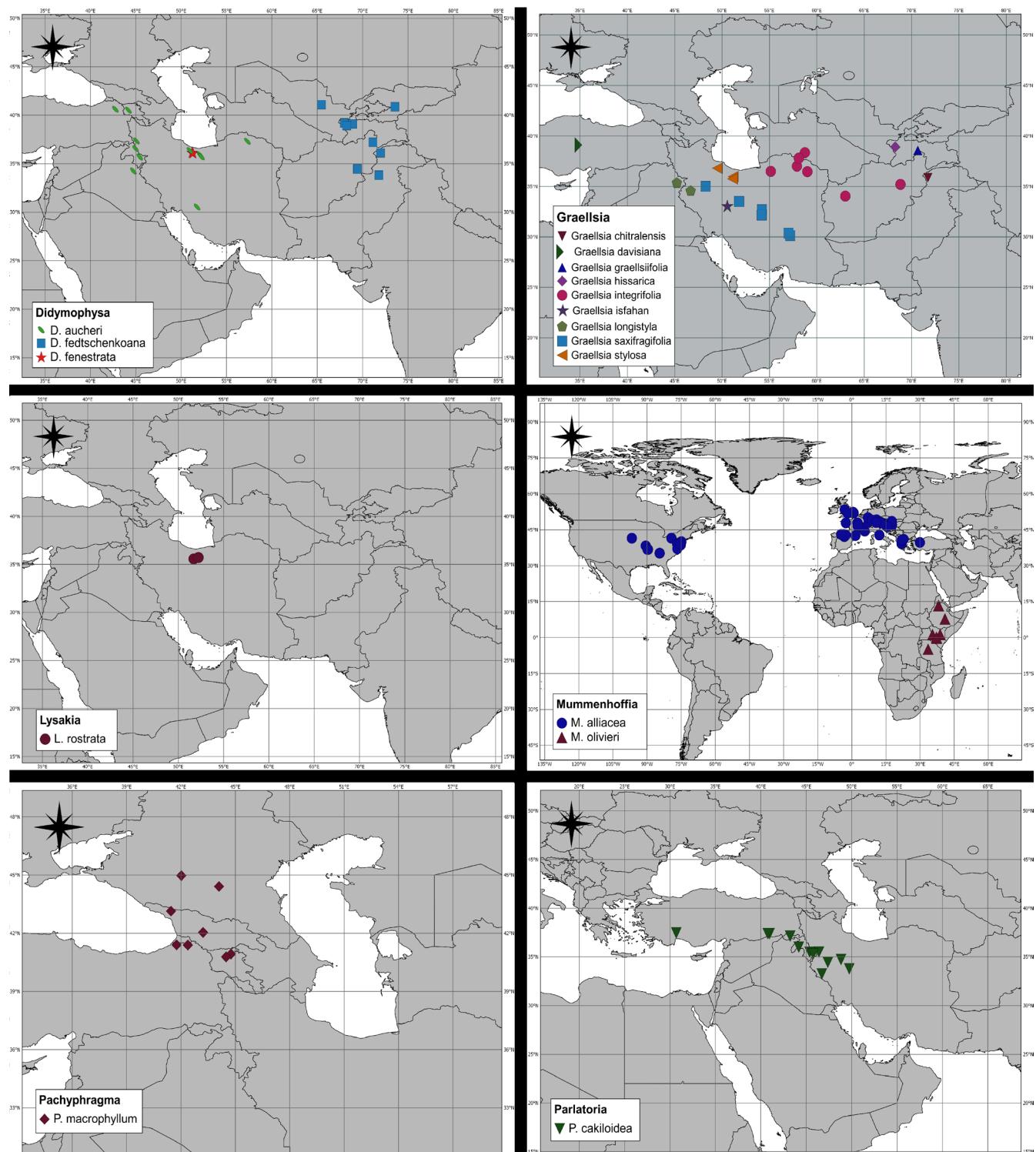
Species	Collector, number (herbarium)	Origin	Chromosome number
<i>Alliaria petiolata</i>	Esmailbegi 2092 (MIR)	Austria, Vienna, Lainzer Tiergarten	2n = 42
<i>Alliaria petiolata</i>	Esmailbegi 2093 (MIR)	Czech Republic, Brno, near the Lesni bus stop	2n = 42
<i>Alliaria petiolata</i>	Esmailbegi & Al-Shehbaz 2091 (MIR)	France, Paris, Jardin Botanique	2n = 42
<i>Alliaria petiolata</i>	Doostmohammadi 2090 (MIR)	Iran, Tehran, Darband	2n = 42
<i>Didymophysa aucheri</i>	Mirtadzadini 1759 (MIR)	Iran, NW of Tar lake	2n = 14
<i>Elburzia fenestrata</i>	Mirtadzadini 1758a (MIR)	Iran, 5 km W of Gachsar	2n = 14
<i>Graellsia saxifragifolia</i>	Mirtadzadini 1780c (MIR)	Iran, Kerman, Rabor	2n = 14
<i>Graellsia stylosa</i>	Esmailbegi 1744 (MIR)	Iran, Darband	2n = 14
<i>Parlatoria cakiloidea</i>	Lysak & al. s.n. (Lysak)	Turkey, Antalya, Gazipaşa, Sugözü village, Atçıl hill	2n = 14
<i>Parlatoria cakiloidea</i>	Ahmad & al. 17_1107 (MIR)	Iraq, Sulaimani Province, Qaiwan mt.	2n = 14
<i>Peltaria turkmena</i>	Joharchi 45111 (FUMH)	Iran, NW of Neyshabur, Bar waterfall	2n = 14
<i>Peltaria angustifolia</i>	Lysak & al. s.n. (Lysak)	Turkey, Antalya, Gazipaşa, Sugözü village	2n = 14
<i>Peltariopsis grossheimii</i>	Mirtadzadini 1827e (MIR)	Iran, Azarbaijan, 15 km S of Tshaldoran	2n = 14
<i>Peltariopsis planisiliqua</i>	Mirtadzadini 1777e (MIR)	Iran, between Sufian and Marand, SW of Yam village	2n = 14
<i>Pseudocamelina aphragmodes</i>	Mirtadzadini 1787 (MIR)	Iran, between Sisakht and Padena	2n = 14
<i>Pseudocamelina campylocarpa</i>	Mirtadzadini 1754 (MIR)	Iran, Kerman, Khane-Sorkh neck	2n = 14
<i>Pseudocamelina glaucophylla</i>	Maroofi 12763 (Sanandaj)	Iran, Kurdistan	2n = 14
<i>Pseudocamelina kermanica</i>	Mirtadzadini 1784 (MIR)	Iran, Kerman, Shahrbabak, Meymand	2n = 14
<i>Thlaspi arvense</i>	Lysak & al. s.n. (Lysak)	Czech Republic, Brno	2n = 14
<i>Thlaspi ceratocarpum</i>	Özüdoğru 3661 (HUB)	Turkey, Erzincan, Refahiye, SW of Sağlık village	2n = 14

**Fig. S1.** Bayesian 50% majority-rule consensus tree inferred from ITS. Numbers above branches are Bayesian posterior probabilities and ML bootstrap values (support <50% marked by “–”). An asterisk (\*) represents collapsed nodes in the ML analysis. Clades B to D were used to compare the congruency between ITS and *trnL-F* cladograms. The generic names reflect the new taxonomy applied in the present study.

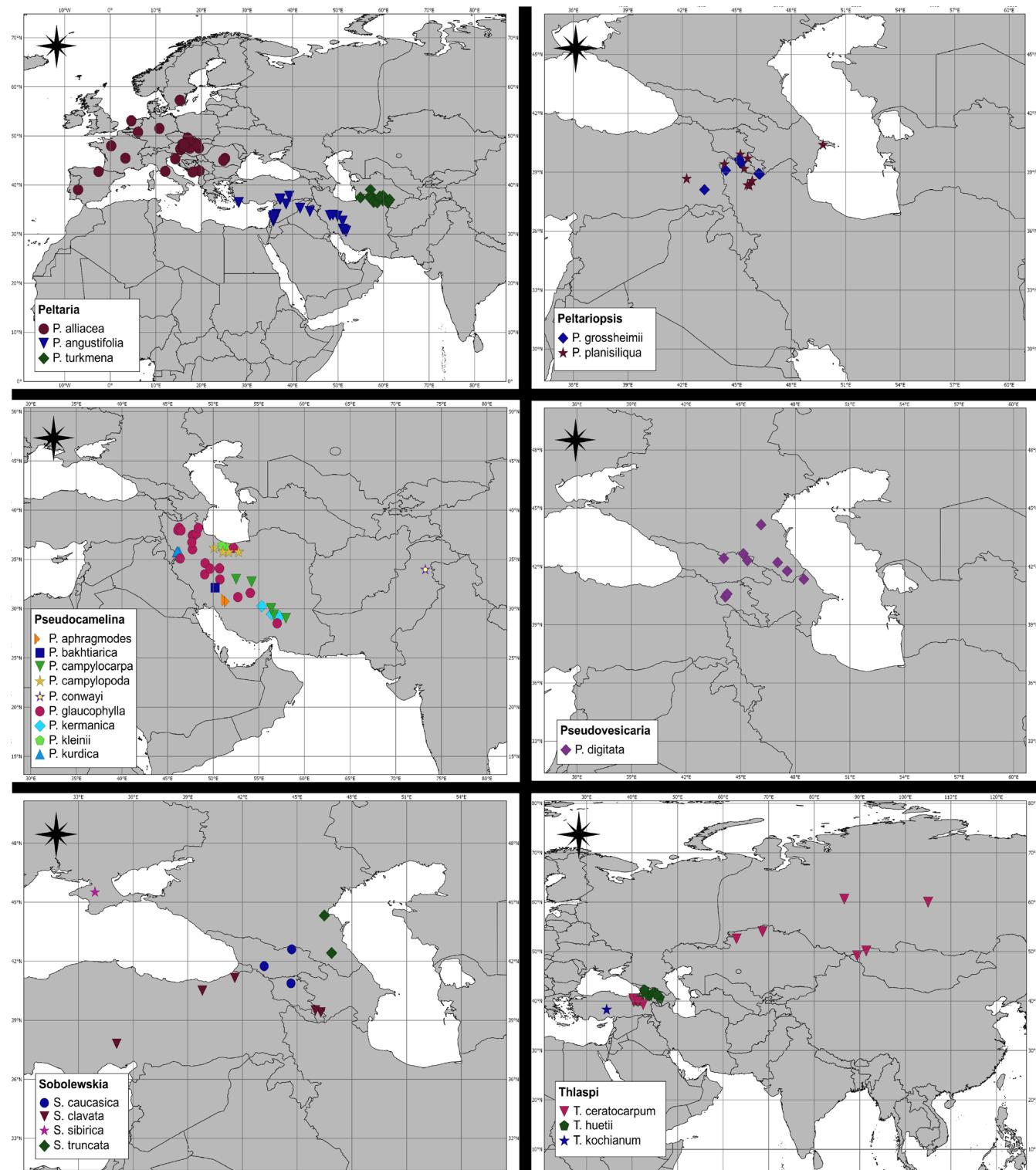


**Fig. S2.** Bayesian 50% majority-rule consensus tree inferred from *trnL-F*. Numbers above branches are Bayesian posterior probabilities and ML bootstrap values (support <50% marked by “–”). An asterisk (\*) represents collapsed nodes in the ML analysis. Clades A to D were used to compare the congruency between ITS and *trnL-F* cladograms. The generic names reflect the new taxonomy applied in the present study.





**Fig. S3A.** Distribution of Thlaspidae genera except *Alliaria petiolata*, *A. taurica*, and *Thlaspi arvense*. *Alliaria taurica* is restricted to the Caucasus, while *A. petiolata* and *T. arvense* are cosmopolitan weeds not mapped here. *Peltariopsis grossheimii* is presented here as a new record for Iran.

**Fig. S3B.** Continued from Fig. S3A.

## ■ APPENDIX S1. TAXONOMIC CONSIDERATIONS

As delimited here, the Thlaspidae consists of 13 genera and 42 species distributed primarily in SW Asia and S and C Europe, and representative taxa are shown in Fig. 5 (see main paper). Of these, 39 species (93%) are native to SW Asia, 22 (52%) to Iran, and 13 (31%) to the Caucasus. Therefore, it is safe to consider a SW Asian origin and/or diversification center for the tribe (see Fig. S3).

Except for the addition of several new taxa and the generic rearrangements proposed here the limits, description, and distinguishing features of the tribe Thlaspidae have not changed since it was resurrected (Al-Shehbaz & al., 2006) and expanded (Al-Shehbaz, 2012), and therefore, these aspects are not repeated here. The taxonomic adjustments and novelties in *Graellsia* and *Pseudocamelina* have already been addressed in Esmailbegi & al. (2017a, b). The recognition of *Lysakia* and *Mummenhoffia* as new genera, as well as the reduction of *Elburzia* to synonymy of *Didymophysa*, necessitated drafting the following key to the Thlaspidae genera.

### Key to genera of Thlaspidae

- 1 Fruit winged at least apically, often strongly keeled .... 2
- 1 Fruit wingless, not keeled ..... 4
- 2 Plants rhizomatous perennial; caudine leaves petiolate, not auriculate; seeds up to 4 per fruit ..... *Pachyphragma*
- 2 Plants annual or biennial; caudine leaves sessile, auriculate or sagittate; seeds 5–16 per fruit ..... 3
- 3 Seeds reticulate-foveolate; fruit minutely winged apically ..... *Mummenhoffia*
- 3 Seeds longitudinally striate; fruit winged all around or with distinct apical wing-like horns ..... *Thlaspi*
- 4 Racemes with strongly flexuous rachis.. *Pseudocamelina*
- 4 Racemes with straight rachis ..... 5
- 5 Fruit didymous, strongly inflated, bladder-like ..... *Didymophysa*
- 5 Fruit neither didymous nor inflated, variously shaped .. 6
- 6 Fruit indehiscent; seeds 1 or 2, rarely 4 ..... 7
- 6 Fruit dehiscent; seeds 4–20 ..... 10
- 7 Fruit orbicular, elliptic or obovate samara, strongly latiseptate; cotyledon accumbent ..... 8
- 7 Fruit oblong or clavate siliques, terete or slightly 4-angled; cotyledon incumbent ..... 9
- 8 Leaves pinnately veined ..... *Peltaria*
- 8 Leaves palmately veined ..... *Graellsia*
- 9 Plants annual; anthers not apiculate; seeds 1; pedicels articulate ..... *Parlatoria*
- 9 Plants perennial; anthers apiculate; seeds 2–4; pedicels not articulate ..... *Sobolewskia*
- 10 Fruit linear, terete or 4-angled; seeds striate ..... 11
- 10 Fruit elliptic, oblong or obovate, latiseptate or angustiseptate; seeds reticulate ..... 12
- 11 Fruit beaked, often curved and indehiscent distally, dehiscent proximally; ovules 6–8 per ovary; seeds minutely striate ..... *Lysakia*

- 11 Fruit not beaked, straight apically, dehiscent throughout; ovules 14–20 per ovary; seeds coarsely striate .. *Alliaria*
- 12 Leaves pinnately veined, entire ..... *Peltariopsis*
- 12 Leaves palmately veined; dentate or 3–6 lobed ..... 13
- 13 Biennials; seeds biserrate ..... *Pseudovesicaria*
- 13 Perennials; seeds uniseriate ..... 14
- 14 Basal leaves not rosulate, 3-lobed, short petiolate; fruit valves not veined ..... *Didymophysa*
- 14 Basal leaves rosulate, dentate or entire, long petiolate; fruit valves prominently veined ..... *Graellsia*

### *Didymophysa*

As shown in the prior and present molecular phylogenetic studies, *Elburzia* is nested within *Didymophysa*, and the recognition of one genus necessitated expanding the limits of *Didymophysa*.

***Didymophysa*** Boiss. in Ann. Sci. Nat., Bot., sér. 2, 16: 379. 1841 – Type: *D. aucheri* Boiss.

= *Elburzia* Hedge in Notes Roy. Bot. Gard. Edinburgh 29: 181. 1969, **syn. nov.** – Type: *E. fenestrata* (Boiss. & Hohen.) Hedge (≡ *Petrocallis fenestrata* Boiss. & Hohen.).

Herbs perennial, suffruticose or surculose. Trichomes absent. Stems erect to ascending, simple from ultimate caudex branches, leafy. Basal leaves petiolate or sessile, not rosulate, simple, entire or palmately 3- to 5-lobed; caudine leaves petiolate or sessile, cuneate, not auriculate at base, entire or 3- to 5-lobed. Racemes few- to many-flowered, ebracteate, corymbose, slightly elongated or not in fruit; rachis straight; fruiting pedicels ascending to divaricate, persistent. Sepals ovate to oblong, free, deciduous, ascending, equal, base of lateral pair not saccate; petals white to purple, erect to ascending at base with flaring blade, longer than sepals; blade obovate to orbicular, apex rounded; claw differentiated from blade, subequal or shorter than sepals, glabrous, unappendaged, entire; stamens 6, exserted, erect, tetrodynamous; filaments wingless, unappendaged, glabrous, free; anthers ovate to oblong, apiculate or not; nectar glands lateral, 2, or 4 and 1 on each side of lateral stamens; median glands absent; ovules 4 per ovary; placentation parietal. Fruit unsegmented, dehiscent, slightly inflated, subterete-latiseptate, ellipsoid to obovoid-globose, or indehiscent and bladder-like, strongly inflated-didymous, angustiseptate, with terete halves enclosing 2 seeds; valves membranous to thin papery, veinless, glabrous, not keeled, smooth, wingless, unappendaged; gynophore absent; replum rounded, visible; septum membranous, complete or perforated, veinless; style obsolete or 0.3–1.5 mm long, persistent; stigma capitate, entire, unappendaged. Seeds aseriate, wingless, ovate to oblong, flattened; seed coat smooth or minutely reticulate, not mucilaginous when wetted; cotyledons accumbent.

The placement of *Elburzia* in the tribe Thlaspidae was firmly established by Warwick & al. (2010). However, that study did not include *Didymophysa*, and it showed *Elburzia* sister to a clade containing *Peltaria*, *Peltariopsis*, and *Thlaspi*. By contrast, Couvreur & al. (2010) demonstrated that *Elburzia* and *Didymophysa* form a single clade with a strong support.

The reduction of *Elburzia* to synonymy of the earlier-published *Didymophysa* is based on Couvreur & al. (2010) and the present molecular phylogenetic studies, where the former is nested within the latter. In establishing the genus *Elburzia*, Hedge (1969) compared it with the European *Petrocallis* W.T.Aiton, a genus not yet assigned to a tribe, and to the Caucasian *Pseudovesicaria*, and he separated it based on differences in habit, lack of indumentum, non-saccate sepals, and clawed petals. Except for having woody (vs. surculose) caudex and subterete, ovoid-globose, and slightly inflated fruit (vs. angustiseptate, didymous, and profoundly inflated), *Elburzia* is indistinguishable from *Didymophysa* in every other morphological aspect. Plants of both genera are glabrous with petiolate, non-auriculate, usually lobed leaves, ebracteate racemes hardly elongated in fruit, obovate to orbicular petals differentiated into blade and claw, lateral nectar glands, 4 ovules per ovary, thin and veinless valves, wingless seeds not mucilaginous when wetted, and accumbent cotyledons. The differences between the two genera in habit and type of caudex (woody vs. surculose) are found in various other Brassicaceae genera, including small genera such as *Pseudocamelina* (see Esmailbegi & al., 2017b) and larger ones such as *Draba* L. and *Lepidium* L. Furthermore, the occurrence of latiseptate and angustiseptate fruits within a single genus is found in many genera, including *Graellsia* (see Esmailbegi & al., 2017a), *Erysimum* L., *Eutrema* R.Br., and *Physaria* (Nutt. ex Torr. & A.Gray) A.Gray, to name a few. In our opinion, whereas the differences between *Elburzia* and *Didymophysa* are rather trivial, their similarities, together with the molecular data, strongly advocate their merger (Fig. 1).

#### Key to the species of *Didymophysa*

- 1 Fruit dehiscent, slightly inflated, subterete-latiseptate, ellipsoid to obovoid-globose; valves thin papery; plants suffruticose; Iran ..... *D. fenestrata*
- 1 Fruit indehiscent, bladder-like, strongly inflated, angustiseptate, didymous; valves membranous; plants surculose ..... 2
- 2 Leaves flabellate, deeply 3–5-fid into linear lobes; petals 4–6 mm; Armenia, Azerbaijan, Iran, Iraq, Turkey ..... *D. aucheri*
- 2 Leaves spatulate to oblanceolate, entire, rarely apically 1- to 3-toothed; petals 2–2.5 mm; Afghanistan, Kyrgyzstan, Pakistan, Tajikistan, Uzbekistan .... *D. fedtschenkoana*

***Didymophysa fenestrata*** (Boiss. & Hohen.) Esmailbegi, D.A.German & Al-Shehbaz, **comb. nov.** ≡ *Petrocallis fenestrata* Boiss. & Hohen. in Boissier, Diagn. Pl. Orient., ser. 1, 8: 27. 1849 ≡ *Elburzia fenestrata* (Boiss. & Hohen.) Hedge in Notes Roy. Bot. Gard. Edinburgh 28: 181. 1969. – Lectotype (designated by Hedge in Rechinger, Fl. Iranica 57: 175. 1968): as No. 493: Iran, “In saxosis meidan Abdullah in valle Loura m. Elbrus. 12 Jul. 1843. [T. Kotschy] 493. A. 795.” (G-BOIS barcode G00332464!; isolectotypes: P barcode P02272395!, W No. W 0053489!). Distribution: endemic to Iran.

#### *Lysakia*

The present molecular phylogenetic data clearly show that this new monospecific genus forms a well-supported clade sister to *Sobolewskaia* and is only remotely related to *Parlatoria* in which it was originally described. *Lysakia* can easily be separated from related genera by having long-beaked fruits strongly curved and indehiscent distally and dehiscent proximally (see key to genera).

***Lysakia*** Esmailbegi & Al-Shehbaz, **gen. nov.** – Type: *L. rostrata* (Boiss. & Hohen.) Esmailbegi & Al-Shehbaz (≡ *Parlatoria rostrata* Boiss. & Hohen.).

**Diagnosis.** – Differs from *Parlatoria* by having persistent, non-articulate (vs. deciduous and articulate) fruiting pedicels, basally dehiscent and distally indehiscent, long-beaked, and linear (vs. indehiscent, beakless, oblong-lanceolate) fruits, basally bracteate (vs. ebracteate) racemes, striate (vs. reticulate) seeds, and 6–8 (vs. 1 or 2) ovules per ovary.

**Description.** – Herbs annual or biennial. Trichomes simple. Stems erect to ascending, simple or few-branched distally, leafy. Basal leaves petiolate, rosulate, simple, dentate or crenate, palmately veined; cauline leaves petiolate, cuneate or cordate at base, not auriculate, dentate or crenate. Racemes several- to many-flowered, bracteate along lowermost few flowers, ebracteate above, corymbose, elongated considerably in fruit; rachis straight; fruiting pedicels divaricate to horizontal, persistent, not articulate. Sepals oblong, free, deciduous, ascending, equal, base of lateral pair not saccate; petals white, erect at base with flaring blade, longer than sepals; blade oblanceolate, apex obtuse; claw shorter than sepals, glabrous, unappendaged, entire; stamens 6, exserted, erect, strongly tetrodynamous; filaments wingless, unappendaged, glabrous, free; anthers ovate, not apiculate; nectar glands confluent, subtending bases of median stamens, surrounding those of lateral stamens; ovules 6–8 per ovary; placentation parietal. Fruit capsular siliques, dehiscent proximally, indehiscent distally, linear, terete, not inflated, attenuate into curved beak, unsegmented; valves papery, with a distinct midvein, sparsely pilose to puberulent or glabrous, not keeled, smooth, wingless, unappendaged; gynophore obsolete or to 0.5 mm long; replum rounded, visible; septum complete, membranous, veinless; style to 1 mm long, stout, persistent; stigma capitate, entire, unappendaged. Seeds uniseriate, wingless, narrowly oblong, plump; seed coat minutely striate, not mucilaginous when wetted; cotyledons obliquely incumbent.

**Distribution.** – A monospecific genus endemic to northern Iran (Fig. S3).

**Etymology.** – The genus is named in honor of Dr. Martin A. Lysak (30 March 1973–) in recognition of his major contributions to the cytogenetics, genome evolution, and phylogenetics of the Brassicaceae.

The type of *Lysakia* was originally described by Boissier (1849) in *Parlatoria*, and it remained in that genus for the past 168 years. However, the molecular phylogenetic studies presented here clearly demonstrated that the generic types *Lysakia rostrata* and *Parlatoria cakiloidea* fall into well-supported but remotely related clades. Both species are remarkably similar

in their vegetative and floral morphology, and they share the cordate, palmately veined, and crenate to dentate basal and lower caudine leaves, non-auriculate caudine leaves, horizontal to divaricate fruiting pedicels nearly as thick as fruit, white flowers, oblanceolate petals, strongly tetrodynamous stamens, unisexual, narrowly oblong seeds, and incumbent cotyledons. However, *Lysakia* is readily distinguished from *Parlatoria* by having long-beaked, linear, distally indehiscent and basally dehiscent fruit, non-articulate fruiting pedicels, basally bracteate racemes, 6–8 ovules per ovary, and minutely striate seeds. By contrast, *Parlatoria* has beakless, oblong-lanceolate, indehiscent fruit, fruiting pedicels articulate at both ends, ebracteate racemes, 1 or 2 ovules per ovary, and minutely reticulate seeds. Because the fruiting pedicels in *P. cakiloidea* are articulate at both ends, the fruit is readily detached upon maturity. By contrast, the non-articulate fruiting pedicels in *L. rostrata* allow the fruit to remain persistently attached to the plant. In our opinion, the morphological and molecular differences are substantial to support the placement of the two species in separate genera.

***Lysakia rostrata* (Boiss. & Hohen.) Esmailbegi & Al-Shehbaz, comb. nov. = *Parlatoria rostrata* Boiss. & Hohen. in Diagn. Pl. Orient., ser. 1, 8: 22. 1849 – Lectotype (first-step designated by Hedge in Rechinger, Fl. Iranica 57: 311. 1968), second step (designated here): Iran, “In valle Wesbach m. Elbrus pr. Derbend. D. 3. Jun. 1843”, T. Kotschy 236 (G-BOIS barcode G00332257!; isolectotypes: BM barcodes BM001254051! & BM001254073!, FI barcode FI005715!, G barcodes G00446112!, G00446113! & G00446114!, P barcodes P00741766! & P00741767!, W Nos. W 0075971! & W 0075972!).**

Hedge (1968) did not specify which one of the four duplicates in the combined Geneva herbaria is the lectotype. For this reason, a second-step lectotypification became necessary.

### Mummenhoffia

The two species of *Mummenhoffia* have long been recognized both morphologically and phylogenetically as distinct from *Thlaspi*, no matter how narrowly or broadly delimited, though they remained in that genus to the present study (see below). *Mummenhoffia* is easily distinguished from *Thlaspi* and the other Thlaspideae genera by having narrowly winged fruits apically and coarsely reticulate seeds.

***Mummenhoffia* Esmailbegi & Al-Shehbaz, gen. nov.** – Type: *M. alliacea* (L.) Esmailbegi & Al-Shehbaz (= *Thlaspi alliaceum* L.).

*Diagnosis.* – *Mummenhoffia* is readily distinguished from *Thlaspi* by having rudimentary (vs. well-developed) fruit wing and reticulate-foveolate (vs. longitudinally striate) seeds.

*Description.* – Herbs annual. Trichomes simple. Stems erect to ascending or decumbent, simple or branched basally and/or apically, leafy. Basal leaves petiolate, not rosulate, simple, entire, repand, or dentate; caudine leaves sessile, auriculate to sagittate at base, entire or dentate. Racemes several to many flowered, ebracteate, corymbose, slightly to considerably elongated in

fruit; rachis straight; fruiting pedicels divaricate, persistent. Sepals ovate or oblong, free, deciduous, suberect, equal, base of lateral pair not saccate; petals white, ascending, longer than sepals; blade spatulate, apex obtuse; claw obscurely differentiated from blade, shorter than sepals, glabrous, unappendaged, entire; stamens 6, included, erect, slightly tetrodynamous; filaments wingless, unappendaged, glabrous, free; anthers ovate, not apiculate; nectar glands 2, lateral, minute, toothlike, subtending bases of lateral stamens; ovules 6–10 per ovary; placentation parietal. Fruit dehiscent, capsular silicles, obovate, angustiseptate, not inflated, unsegmented; valves papery, with an obscure midvein, glabrous, keeled, smooth, apically narrowly winged, unappendaged; gynophore obsolete; replum rounded, visible; septum complete, membranous, veinless; style to 0.5 mm long, cylindric; stigma capitate, entire, unappendaged. Seeds unisexual, wingless, ovoid, plump; seed coat reticulate-foveolate, not mucilaginous when wetted; cotyledons incumbent, entire.

*Distribution.* – A genus of two species, of which one is a naturalized weed originally native to central and southern Europe and the other is an Afro-alpine plant (Fig. S3).

*Etymology.* – The genus is named in honor of Dr. Klaus Mummenhoff (12 November 1956–) for his major contributions to phylogenetics of the Brassicaceae, including three papers (Koch & Mummenhoff, 2001; Mummenhoff & al., 2001; Khosravi & al., 2009) showing that *Thlaspi alliaceum* did not fall from a monophyletic clade with *T. arvense*, the type of the genus name.

Meyer (1973, 2001) placed both *Thlaspi alliaceum* and *T. oliveri* in sect. *Chaunothlaspi*, a section that Schulz (1933) distinguished from the rest of the genus by having reticulate-foveolate seeds and rudimentary fruit wing. The remaining four species of *Thlaspi* s.str. have longitudinally concentric striate seed sculpture and a well-developed fruit wing. Indeed, these characters strongly support the molecular data presented here and are in full agreement with the conclusion of Koch & Mummenhoff (2001) that solving the limits of *Thlaspi* s.str. would depend on resolving the position of *T. alliaceum* together with *Alliaria* and *Peltaria*.

### Key to the species of *Mummenhoffia*

- Stems (22–)30–75(–90) cm tall, erect to ascending; racemes with numerous flowers; fruiting pedicels (6–)9–14(–17) mm long; petals 2.5–4 mm long; style 0.1–0.3 mm long; C & S Europe, naturalized in E & C U.S.A. .... *M. alliacea*
- Stems 3–12 cm tall, several from base, decumbent, rarely erect when single; racemes with few to several flowers; fruiting pedicels 2–4.5 mm long; petals 2–2.5 mm long; style 0.3–0.5 mm long; Ethiopia, Kenya, Tanzania ..... *M. oliveri*

***Mummenhoffia alliacea* (L.) Esmailbegi & Al-Shehbaz, comb. nov. = *Thlaspi alliaceum* L., Sp. Pl.: 646. 1753 – Lectotype (designated by Marhold & Mártonfi in Novon 11: 189. 2001): “Habitat in Europa australi”; [illustration] “SCORODOTHLASPI ULYSSIS Aldroandi” in Bauhin & al., Hist. Pl. 2: 932. 1651.**

*Note.* – Meyer (2001) designated a collection by Van Royen in Leiden (L-901.257-174) as the lectotype, but his lectotypification was predated by that of Marhold & Mártonfi (2001).

*Distribution.* – Native of S and C Europe from N Spain into Hungary, Romania, and European Turkey; naturalized elsewhere in Europe and E and C U.S.A. (Greuter & al., 1986; Jalas & al., 1996; Al-Shehbaz, 2010).

**Mummenhoffia oliveri** (Engl.) Esmailbegi & Al-Shehbaz, comb. nov. ≡ *Thlaspi oliveri* Engl., Hochgebirgsfl. Afr.: 223. 1892 – Lectotype (designated by Jonsell in Polhill, Fl. Trop. East Africa: 27. 1982): Ethiopia, Begemdir, 4500 m, 1850, W. Schimper 216 (P barcode P00486650!; isolectotype: B barcode B 10 0154915!).

*Distribution.* – E African mountains at 3050–4600 m in Ethiopia, Kenya, and Tanzania.

*Notes.* – Although Warwick & Al-Shehbaz (2006) did not list a chromosome number of the species, the label Hedberg & Aweke 5427 (MO) indicated that the chromosome count  $2n = 14$  was made from that collection. Both Jonsell (1982) and Meyer (2001) lectotypified *Thlaspi oliveri* based on the same herbarium sheet, though Jonesll's typification predates that of Meyer and ought to be followed. Following Hedberg (1957), Jonsell (1982, 2000) also misidentifyied the Ethiopian and other afro-alpine plants as the European native *Thlaspi alliaceum* instead of *T. oliveri*, listed the latter in the synonymy of the former, and provided a species description that covers both taxa. However, Meyer (2001) was the first to point out that error and distinguished the two species based on branching habit, style length, and petal size. Although the last two features differ in fractions of millimeters, and thus are unreliable as the other characters provided in the key above.

## ■ LITERATURE CITED

- Al-Shehbaz, I.A. 2012. A generic and tribal synopsis of the Brassicaceae (Cruciferae). *Taxon* 61: 931–954.
- Al-Shehbaz, I.A., Beilstein, M.A. & Kellogg, E.A. 2006. Systematics and phylogeny of the Brassicaceae: An overview. *Pl. Syst. Evol.* 259: 89–120.
- Bioissier, E. 1849. *Diagnoses plantarum orientalium novarum*, ser. 1, no. 8. Parisiis [Paris]: typis Marci Ducloux et Cons.
- Couvreur, T.L.P., Franzke, A., Al-Shehbaz, I.A., Bakker, F., Koch, M.A. & Mummenhoff, K. 2010. Molecular phylogenetics, temporal diversification and principles of evolution in the mustard family (Brassicaceae). *Molec. Biol. Evol.* 27: 55–71. <https://doi.org/10.1093/molbev/msp202>
- Esmailbegi, S., Lysak, M.A., Rahiminejad, M.R., Mirtadzadini, M., Mummenhoff, K. & Al-Shehbaz, I.A. 2017a. A taxonomic revision of the genus *Graellsia* (Brassicaceae, tribe Thlaspideae). *Phytotaxa* 313: 105–116. <https://doi.org/10.11646/phytotaxa.313.1.7>
- Esmailbegi, S., Lysak, M.A., Rahiminejad, M.R., Mirtadzadini, M., Mummenhoff, K. & Al-Shehbaz, I.A. 2017b. A taxonomic revision of the genus *Pseudocamelina* (Brassicaceae, tribe Thlaspideae). *Phytotaxa* 313: 117–129. <https://doi.org/10.11646/phytotaxa.313.1.8>
- Hedberg, O. 1957. *Afroalpine vascular plants: A taxonomic revision*. Symbolae Botanicae Upsalienses 15(1). Uppsala: Acta Universitatis Upsaliensis.
- Hedge, I.C. 1968. Sisymbrieae. Pp. 309–342 in: Rechinger, K.H. (ed.), *Flora Iranica*, vol. 57. Graz: Akademische Druck- u. Verlagsanstalt.
- Hedge, I.C. 1969. *Elburzia*: A new genus of Cruciferae from Iran. *Notes Roy. Bot. Gard. Edinburgh* 29: 181–185.
- Jonsell, B. 1982. Cruciferae. Pp. 1–73 in: Polhill, R.M. (ed.), *Flora of tropical East Africa*. Rotterdam: Balkema.
- Jonsell, B. 2000. Brassicaceae. Pp. 121–158 in: Edwards, S., Mesfin Tadesse, Sebsebe Demissew & Hedberg, I. (eds.), *Flora of Ethiopia and Eritrea*, vol. 2(1). Addis Ababa: National Herbarium; Uppsala: Uppsala University.
- Khosravi, A.R., Mohsenzadeh, S. & Mummenhoff, K. 2009. Phylogenetic relationships of Old World Brassicaceae from Iran based on nuclear ribosomal DNA sequences. *Biochem. Syst. Ecol.* 37: 106–115. <https://doi.org/10.1016/j.bse.2009.01.010>
- Koch, M. & Mummenhoff, K. 2001. *Thlaspi* s.str. (Brassicaceae) versus *Thlaspi* s.l.: Morphological and anatomical characters in the light of ITS nrDNA sequence data. *Pl. Syst. Evol.* 227: 209–225. <https://link.springer.com/content/pdf/10.1007/s006060170049.pdf>
- Meyer, F.K. 1973. Conspectus der “*Thlaspi*”-Arten Europas, Afrikas und Vorderasiens. *Feddes Repert.* 84: 449–470. <https://doi.org/10.1002/fdr.19730840503>
- Meyer, F.K. 2001. Kritische Revision der “*Thlaspi*”-Arten Europas, Afrikas und Vorderasiens, Spezieller Tiel, II. *Thlaspi* L. *Haussknechtia* 8: 3–42.
- Mummenhoff, K., Coja, U. & Brüggemann, H. 2001. *Pachyphragma* and *Gagria* (Brassicaceae) revisited: Molecular data indicate close relationship to *Thlaspi* s.str. *Folia Geobot. Phytotax.* 36: 293–302.
- Schulz, O.E. 1933. Kurze Notizen über neue Gattungen, Sektionen und Arten der Cruciferen. *Bot. Jahrb. Syst.* 66: 91–102.
- Warwick, S.I. & Al-Shehbaz, I.A. 2006. Brassicaceae: Chromosome number index and database on CD-Rom. *Pl. Syst. Evol.* 259: 237–248. <https://doi.org/10.1007/s00606-006-0421-1>
- Warwick, S.I., Mummenhoff, K., Sauder, C.A., Koch, M.A. & Al-Shehbaz, I.A. 2010. Closing the gaps: Phylogenetic relationships in the Brassicaceae based on DNA sequence data of nuclear ribosomal ITS. *Pl. Syst. Evol.* 285: 209–232. <https://doi.org/10.1007/s00606-010-0271-8>