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ORIGINAL ARTICLE

AlyBase: database of names, chromosome numbers, and ploidy levels of Alysseae (Brassicaceae), with a new generic concept of the tribe

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Abstract Database of published chromosome numbers and ploidy-level estimates of the tribe Alysseae is presented, together with the revised generic concept and the list of accepted names, to reflect the most recent taxonomic and phylogenetic studies in Alysseae. It is available on-line at www.alysseae.sav.sk. The tribe encompasses 24 genera and 277 species. Chromosome numbers and/or ploidy levels are known for 171 out of 297 recognized taxa. Of these, 95 (55.6 %) taxa are diploids, 43 (25.1 %) are polyploids, and 33 (19.3 %) involve both diploids and polyploids. The most common base chromosome number in the tribe is $x = 8$ and less frequent is $x = 7$. The highest variation in base chromosome numbers ($x = 7, 8, 11, 15$) is found in the genus *Hormathophylla*. A key to all genera and descriptions of the two new genera *Cuprella* and *Resetnikia* are presented. Many new nomenclatural combinations, mainly in the re-established *Odontarrhena* (77), are proposed.

Keywords Chromosome counts · Cruciferae · Generic concept · Nomenclature · Polyploidy

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Introduction

Alysseae DC. is the third largest tribe of the family Brassicaceae (Cruciferae). Its native range is Eurasia and North Africa, and the center of its greatest diversity is the Mediterranean and Irano-Turanian regions. Members of the Alysseae are annual or perennial herbs or subshrubs morphologically characterized by having stellate trichomes, yellow or white (rarely pink) petals, appendaged filaments, and latiseptate or terete (rarely angustiseptate) few-seeded silicles (Al-Shehbaz 1987; Warwick et al. 2008).

Phylogenetic relationships in the Alysseae have been poorly explored until a recent series of molecular studies (Beilstein et al. 2008, *ndh*F, *phy*A; Warwick et al. 2008, 2010, ITS; Cecchi et al. 2010, ITS; German et al. 2009, ITS; Khosravi et al. 2009, ITS; Rešetnik et al. 2013, ITS, *ndh*F, *trn*L-F; Li et al. 2014, ITS) have demonstrated that the traditional morphology-based taxonomic concept of the tribe (Schulz 1936; Janchen 1942; Dorofeyev 2004) was artificial. In a treatment adopted in the most recent synopsis of the family Brassicaceae (Al-Shehbaz 2012), the tribe

Alysseae comprised 262 species classified in 17 genera. This novel approach included several important changes in the delimitation of Alysseae based on molecular evidence, such as the transfer of *Alyssum klimesii* Al-Shehbaz [now *Ladakiella klimesii* (Al-Shehbaz) D.A.German & Al-Shehbaz] to Crucihimalayeae D.A.German & Al-Shehbaz (German et al. 2009; German and Al-Shehbaz 2010), transfer of *Athysanus* Greene and return of *Botschantzevia* Nabiev to Arabideae DC. (Warwick et al. 2008), the assignment of *Farsetia* Turra and *Lobularia* Desv. at first to Malcolmieae Al-Shehbaz & Warwick (Warwick et al. 2008) and later to Anastaticeae DC. (Warwick et al. 2010; Al-Shehbaz 2012), transfer of *Leptoplax* O.E.Schulz from Thlaspideae DC. to Alysseae (Cecchi et al. 2010), exclusion of *Ptilotrichum* C.A.Mey. (Warwick et al. 2008) and its placement in Stevenieae Al-Shehbaz et al. (Al-Shehbaz et al. 2011), the assignment of previously unplaced *Physocardamum* Hedge to Alysseae (Warwick et al. 2010), and the segregation of previously unrecognized genera *Lepidotrichum* Velen. & Bornm. and *Phyllolepidum* Trinajstić from *Aurinia* Desv. (Cecchi 2011). A recent comprehensive phylogenetic study by Rešetnik et al. (2013) supported the above-mentioned separation of *Phyllolepidum* and *Lepidotrichum*, suggested the placement of *Leptoplax* and *Physocardamum* in *Bornmuellera* Hausskn. (relevant combinations were published by Rešetnik et al. 2014), and demonstrated that several genera (*Alyssoides* Mill., *Alyssum* L., *Fibigia* Medik.) are para- or polyphyletic.

During the last decade, many genus- and species-level studies of the Alysseae dealt with (micro) evolution, origin of polyploids, phylogeography, population genetics, taxonomic diversity or nomenclature (Iljinska 2005; Ortiz and Rodríguez Oubiña 2005; Ančev and Goranova 2006; Orcan 2006; Wesche et al. 2006; Çelik et al. 2007; Iljinska et al. 2007; Avetisian 2009; Orcan and Binzet 2009; German 2010, 2011, 2012b, 2014a, b, c; German and Al-Shehbaz 2010; Cecchi 2011; Knjasev 2011; Marhold et al. 2011; Meyer 2011; Pakravan et al. 2011; Španiel et al. 2011a, b, 2012a, b; Çetin et al. 2012; Rusterholz et al. 2012; Yılmaz 2012; Al-Shehbaz 2013; Cecchi et al. 2013; Kavousi et al. 2014; Magauer et al. 2014; Ranjbar et al. 2014; Rešetnik et al. 2014; Zozomová-Lihová et al. 2014). Other studies in Alysseae focused on heavy-metals tolerance and uptake and potential for phytoremediation and phytomining applications (e.g., Cecchi et al. 2013; Adamidis et al. 2014; Bani et al. 2015; Ghaderian et al. 2015; Morais et al. 2015; and references therein).

The growing interest in the Alysseae and the increasing amount of molecular and other data contributed considerably to our understanding of the phylogenetic relationships in the tribe and emphasized the need to carry out necessary changes in circumscriptions and nomenclature of taxa. Although several phylogenetic incongruencies still remain to be addressed, the available data enable us to make substantial taxonomic re-arrangements among the most controversial genera of the Alysseae.

The Brassicaceae family is well known for the common occurrence of polyploids and considerable variation in chromosome numbers (Marhold and Lihová 2006). Three ancient whole-genome duplication events, named γ, β, α, were probably experienced by all core Brassicaceae, of which the most recent *At*-α event might have triggered extensive radiation and diversification of the family. In addition, several independent mesopolyploidizations have been assumed or revealed in specific lineages (reviewed by Franzke et al. 2011). It was estimated that approximately 37 % of the species may be polyploid (Warwick and Al-Shehbaz 2006) but this figure most likely represents an underestimation (Franzke et al. 2011). From the available data, it appears that chromosome and ploidy variation is substantial also in the Alysseae, and the most frequent base chromosome number is $x = 8$, but $x = 7$, 11, 15 were also reported (Warwick and Al-Shehbaz 2006). Although the majority of small genera are diploid, genera such as *Alyssum*, *Hormathophylla* Cullen & T.R.Dudley, and *Clypeola* L. (as circumscribed by Al-Shehbaz 2012) include diploid, polyploid, or diploid–polyploid species. The origin of polyploids and various base chromosome numbers in the Alysseae, as well as their evolutionary significance, have not yet been sufficiently understood. To address these questions, a detailed summary of the current knowledge on karyological variation of the tribe across all genera and the whole distribution area is an essential starting point. For this purpose, chromosome number and ploidy-level database is the most convenient information tool.

Our goals in this Alysseae paper are to: (1) provide an updated generic concept, an identification key to genera, and a list of accepted species and infraspecific names that should represent the taxonomic backbone for further studies; (2) present a research platform for Alysseae taxa consisting of the database of accepted species and infraspecific names and their synonyms, and published chromosome number/ploidy-level data; (3) present new names and combinations reflecting the revised generic concept and the current state of knowledge.

Materials and methods

Generic and species concepts

The generic and species concepts of the tribe Alysseae adopted in the present paper reflect the most recent phylogenetic, taxonomic, and nomenclatural studies at the levels of tribe and above (Warwick et al. 2008; Jaén-

Molina et al. 2009; Al-Shehbaz 2012; Rešetnik et al. 2013), as well as at the levels of genera and species (German 2010, 2011, 2012a, b, 2014a, b, c; German and Al-Shehbaz 2010; Cecchi 2011; Marhold et al. 2011; Španiel et al. 2011a, b, 2012a, b; Cecchi et al. 2013; Magauer et al. 2014; Rešetnik et al. 2014; Zozomová-Lihová et al. 2014). Part of the decisions was also made based on our yet-to-be-published studies focusing on *Hormathophylla* (E. Salmerón Sánchez et al., unpublished data) and *Alyssum montanum–A. repens* Baumg. complex in the Balkan Peninsula (S. Španiel et al., unpublished data).

List of accepted species and infraspecific names and synonyms

An initial list of published species and infraspecific names of the Alysseae was assembled based on the existing nomenclatural databases of vascular plants (The International Plant Names Index, www.ipni.org; The Plant List, www.theplantlist.org; Tropicos, www.tropicos.org), and the Brassicaceae species checklist (Warwick et al. 2006). All names were classified into the following categories: accepted names, provisionally accepted names, synonyms, doubtful synonyms, and unresolved names. Additionally, basionyms, illegitimate, and replaced names were identified. The effort was made to consult original publications, protologues, and original material of all controversial names of taxa before classifying them into the above-mentioned categories. The final list of accepted and provisionally accepted species and infraspecific names is available in the printed version of this paper. Furthermore, an extended version containing also synonyms, doubtful synonyms, and unresolved names is available online at AlyBase web (www.alysseae.sav.sk). It also lists designations that were not validly published but have been registered in some of the above-mentioned databases. The online version will be continuously updated, including the less frequently cited synonyms that perhaps were overlooked in the present version.

Chromosome numbers and ploidy-level data

Published data on chromosome numbers and flow cytometry (FCM)-based ploidy-level estimates of the tribe Alysseae were gathered using the dataset by Warwick and Al-Shehbaz (2006), IPCN database by Goldblatt and Johnson (1979 onwards), printed volumes of Index of plant chromosome numbers (for references see Goldblatt and Lowry 2011), IAPT/IOPB Chromosome Data reports (Marhold 2006 onwards), Mediterranean chromosome number reports (Kamari et al. 1991 onwards), and several chromosome number atlases (e.g., Bolkhovskikh et al. 1969; Agapova et al. 1990; Dobeš and Vitek 2000). In addition, more recent papers with chromosome number records were searched primarily via portal Web of Science. References to all sources of the chromosome numbers and/or FCM ploidy-level estimates are displayed in the presented AlyBase database.

The primary sources of all chromosome number records and FCM ploidy-level estimates were checked, and additional relevant information was obtained and stored in the database. Taxonomic identity of the analyzed material was ascertained according to the localities of origin and/or voucher specimens (if available).

For each record, the following data were stored (some optionally, depending on their availability in the original source):

1. Taxon name: name with authorship as published in the original source (including typographical errors), standardized name of the taxon (corrected spelling of the name and its authorship), and currently accepted name of taxon after taxonomic revision of the record, taking into account the voucher specimens (if available) and/or the collection place (following the checklist of accepted and provisionally accepted names presented in this article).
2. Chromosome data: mitotic and/or meiotic chromosome number, ploidy level, name of the person who counted chromosomes, number of analyzed plants, presence or absence of karyotype, idiogram, and photograph of chromosomes or their drawing in the original publication.
3. Genome-size data: ploidy-level estimate, chromosome number estimate, flow-cytometric method using fluorochromes 4′,6-diamidino-2-phenylindole (DAPI) or propidium iodide (PI), number of analyzed plants.
4. Locality: details on locality from which material was collected, including geographical coordinates (if coordinates are lacking in the original publication, locality was geo-referenced, but the exactness of coordinates depends on the accuracy of locality description in the original source), and classification of the locality according to the World geographical scheme for recording plant distributions (Brummitt 2001).
5. Voucher specimen: collector(s) name(s), collection number, date of collection, specimen number, and the herbarium in which the collection is deposited (herbarium acronyms follow Thiers 2014; when no acronym is available, full name of the institution, city, and country are provided).
6. Place of publication: the authorship and title of the paper, name of the journal, volume and pages (including exact page(s) and year in which records were published); for books, the corresponding information is provided as well.

Local geographical names, titles of papers and their author names in Cyrillic were transliterated following British standard for transliteration of Cyrillic and Greek characters (BS 2979 1958).

Technical solution of the AlyBase database

The production version of entire project is deployed on a server that runs Debian Linux 2.6, "lenny" distribution. The database platform used is PostgreSQL 8.3. In the near future, it will be migrated to Ubuntu Linux 14.04 with PostgreSQL 9.3. The web server installation is Apache 2.2 HTTP with support of PHP. Client side uses CakePHP framework with HTML5, CSS, and JavaScript with the usage of jQuery 1.10 and jQueryUI 1.11 libraries. Visualization of geographic data is done by Google Maps API v3. Database is available at www.alysseae.sav.sk.

The final product contains 17 database tables. The detailed list of fields in tables is given in Online Resource 1. We have generally followed the model suggested by Berendsohn et al. (1997) in the construction of the database structure for chromosome number and ploidy-level data. Presentation interface is in the form of a website with pages offering to search accepted names and synonyms and chromosome and ploidy-level data (including references) (Figs. 1, 2). Each of these pages offers search fields that allow users to narrow down search results.

Chromosome and ploidy-level data search results in a list of taxa that have properties specified by search terms. Then, a list of chromosome records associated with a given taxon appears, including chromosome count or FCM ploidy-level estimate and publication place of the record. Furthermore, it is possible to display respective records on a map. Single chromosome-record display provides detailed information about the particular record. Data are grouped into chromosome number and/or ploidy-level estimates according to the genome size, locality, material, and reference sections for clarity. This page also contains a map showing the locality, provided it has associated geographic coordinates (either published in original source or determined by the authors of the database). Taxon name of the record is linked to the nomenclature part of the website. The connected reference page offers a list of sources of the chromosome data.

Nomenclatural data are arranged in a list of names with their places of publication and status. For synonyms, column status contains a reference to its accepted name expressed by formulation "synonym of" or "doubtful synonym of". The page of particular name contains details of the name, including its publication place, basionym (if available), and a list of other synonyms. For all synonyms, the accepted names are given.

The detailed pages of chromosome records and nomenclatural data offer possibility to add an annotation to specific records. Annotations are revised before their publication on the web.

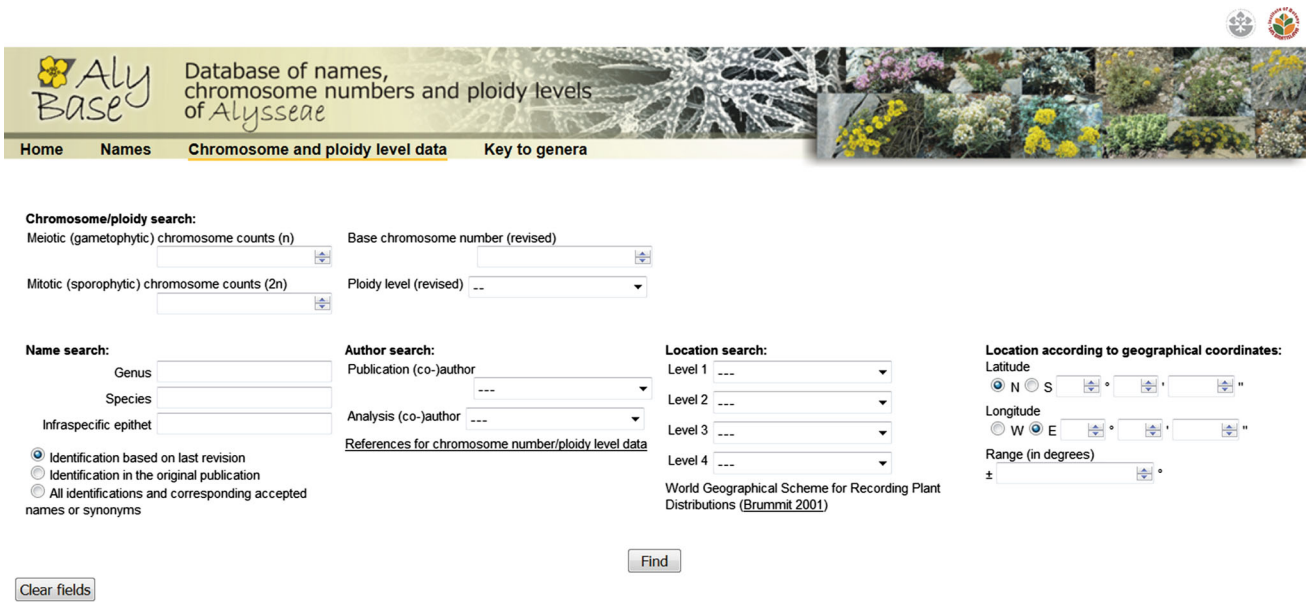

Fig. 1 Presentation interface of AlyBase for chromosome and ploidy-level data search (including references). Search fields allow users to narrow down search results. Search results in a list of taxa that have specified properties. Clicking on the particular name brings a list of chromosome records associated with this taxon. At the top of the list, it is possible to click on a Map tab that shows respective records on a map. One can click the pin on the map to show chromosome count of the record and further obtain the detailed page of the record

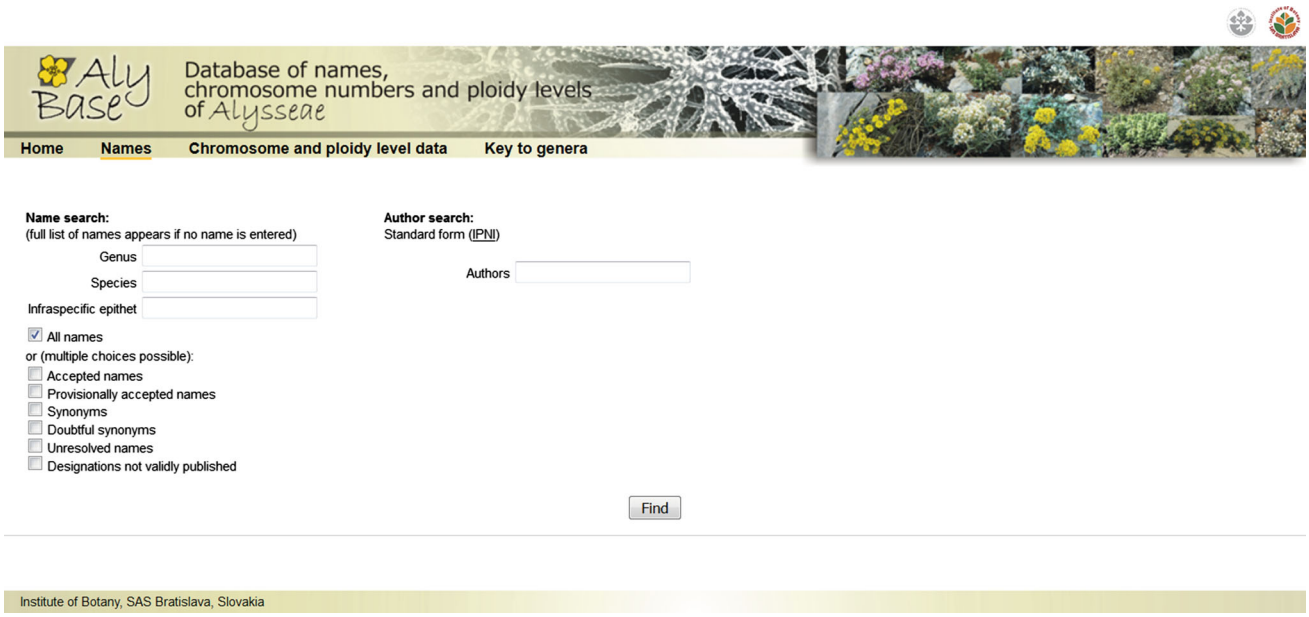

Fig. 2 Presentation interface of AlyBase for accepted names and synonyms search. Search results are compiled in a list of names with their places of publication and status. Clicking on the particular name takes the user to the page containing details of the name

In order to make the process of data insertion quick and distributable, a custom administration interface was created. It allows the logged user to insert all necessary data into respective fields. Moreover, it offers the possibility to update inserted data, as well as to manage checklist of names of taxa, person names, and literature references. This interface allows more project members to insert data simultaneously without accessing the database directly at its lowest level or without any knowledge of SQL language. The server side is written in PHP5 with usage of Medoo library. Client side does not implement any framework. We used PHP5, XHTML, CSS, and JavaScript.

Results and discussion

Revised generic concept

Although the treatment of the tribe Alysseae has recently undergone a number of changes in the circumscription and internal division into genera, as already reflected in the treatment by Al-Shehbaz (2012) and its adjustments by Rešetnik et al. (2014), polyphyly of the genera *Alyssoides*, *Alyssum,* and *Fibigia* and the relatedness of *Clypeola* to *Alyssum* (Rešetnik et al. 2013) are still major sources of controversy in the generic treatment of the tribe. Here we summarize the necessary changes in the generic concept of Alysseae, reflecting the current knowledge on its phylogeny (Fig. 3).

Polyphyly of the genus *Alyssoides*, which resulted from inclusion of the two unrelated species, *A. cretica* (L.) Medik. and *A. utriculata* (L.) Medik. (the type of the genus) (Warwick et al. 2008; Rešetnik et al. 2013), should be resolved by the transfer of *A. cretica* to *Lutzia* Gand., as suggested by Rešetnik et al. (2013). As a result, both *Alyssoides* and *Lutzia* become monotypic. Indeed, Rešetnik et al. (2013) argued that such treatment was already adopted by some authors (Greuter and Raus 1983; Kit Tan 2002; Cecchi 2011).

Rešetnik et al. (2013), confirming the findings of Warwick et al. (2008) and Khosravi et al. (2009), have further revealed that *Fibigia*, as delimited by Al-Shehbaz (2012), is polyphyletic. In order to achieve monophyly and more balanced taxonomic treatment, it should be either (1) split into genera *Acuston* Raf. [*F. lunarioides* (Willd.) Sweet], *Brachypus* Ledeb. [*F. suffruticosa* (Vent.) Sweet], *Fibigia*, *Irania* Hadač & Chrtek (comprising all the members of *Fibigia* sect. *Edmondia* Bunge ex Boiss.), *Pterygostemon* V.V.Botschantz. [*F. spathulata* (Kar. & Kir.) B.Fedtsch.], and here described monotypic genus *Resetnikia* [*F. triquetra* (DC.) Boiss. ex Prantl] (see "Taxonomic treatment" below), or (2) merged with *Alyssoides*, *Clastopus* Bunge ex Boiss., *Degenia* Hayek, and *Physoptychis* Boiss. to form a very broadly conceived, but still monophyletic genus *Alyssoides*. Because the second option would make *Alyssoides* extremely heterogeneous morphologically, we prefer to split from *Fibigia* the above-mentioned five genera. None of these were accepted in the most recent generic synopsis of Al-Shehbaz (2012), and we changed the broad

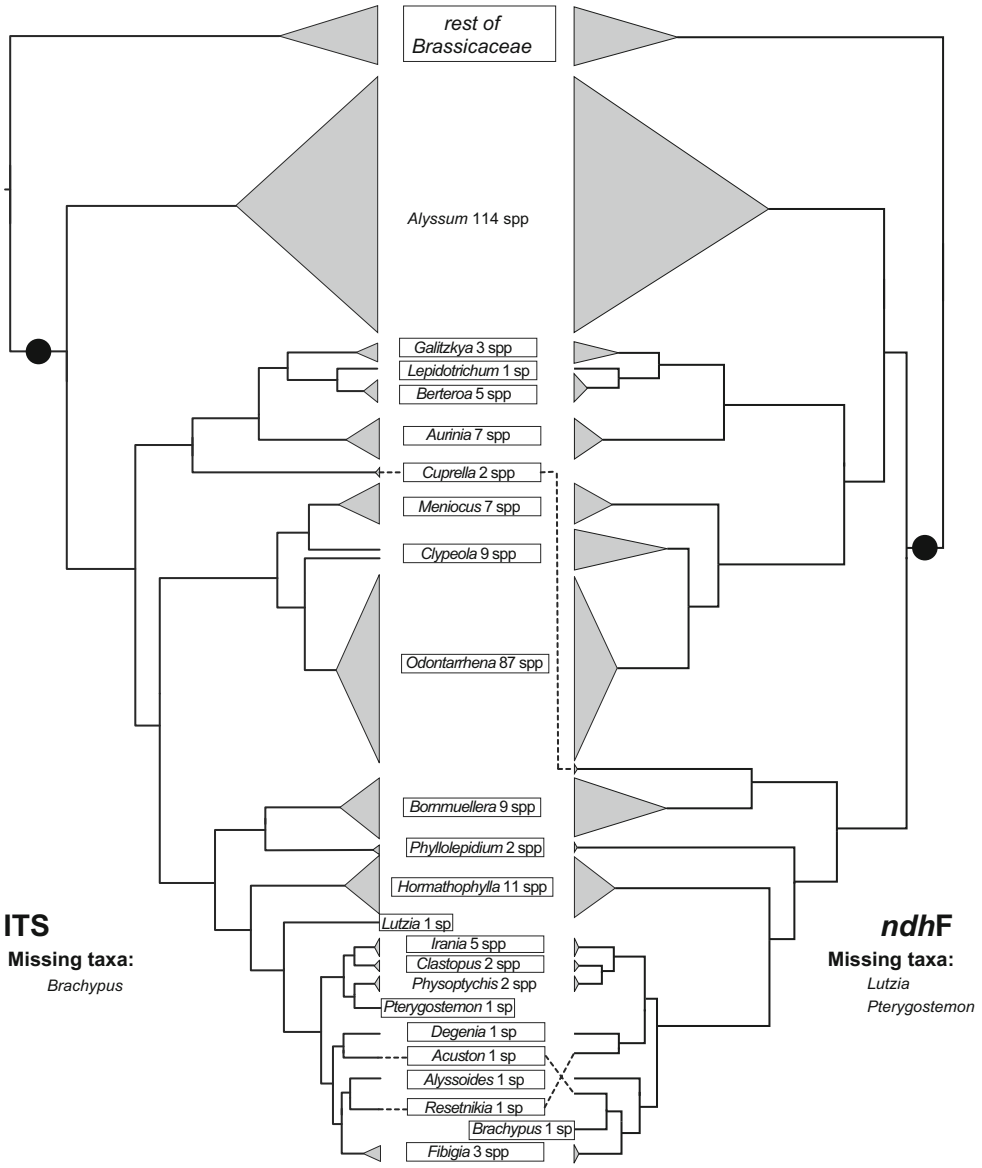

Fig. 3 Phylogenetic relationships within the tribe Alysseae (indicated by *black circle*) based on ITS (nuclear) and *ndh*F (plastid) (redrawn from Rešetnik et al. (2013), Fig. 2 and Fig. S4) adapted to the new generic rearrangement accepted here. Topological incongruences between the *markers* are shown

concept of *Fibigia* following Rafinesque (1838), Dorofeyev (2012), Hadač and Chrtek (1973), and Boczantzeva (1976, 1977), respectively.

The polyphyletic *Alyssum* currently comprises three clades (Warwick et al. 2008; Rešetnik et al. 2013; E. Salmerón Sánchez et al., unpublished data): (1) "*Alyssum s.str.* clade" consisting of *A.* sect. *Alyssum*, *A.* sect. *Gamosepalum* (Hausskn.) T.R.Dudley, and *A.* sect. *Psilonema* (C.A.Mey.) Hook.f. (except "*A. homalocarpum-A. antiatlanticum* clade"), (2) "*A. homalocarpum-A. antiatlanticum* clade", and (3) "*Clypeola* clade", comprising *A.* sect. *Odontarrhena* (C.A.Mey. ex Ledeb.) W.D.J.Koch, *A.* sect. *Meniocus* (Desv.) Hook.f., and *Clypeola*.

While preparing a phylogenetic study of the genus *Hormathophylla* (E. Salmerón-Sánchez et al., unpublished data), we included in our analyses *Alyssum antiatlanticum* Emb. & Maire and *A. homalocarpum* (Fisch. & C.A.Mey.) Boiss. because of their uncertain generic affinities and their possible relationship to *Hormathophylla.* Our cpDNA and nuclear ITS sequence data showed that both species are neither related to *Hormathophylla* nor to most members of *A.* sect. *Psilonema*, into which they were previously classified. Our phylogenetic analyses revealed that these two *Alyssum* species form an isolated, well-supported lineage outside of the genus *Alyssum* (Fig. 4), from which it is also biogeographically distinct (contiguous vicariant). Treatment of this lineage as a separate taxonomic entity is also supported by morphological data. *Alyssum* sect. *Psilonema*, as circumscribed by Dudley (1964a), differed from the other five sections of the genus by having wingless, toothless, and unappendaged staminal filaments plus petals scarcely longer than sepals. In addition, Maire (1967)

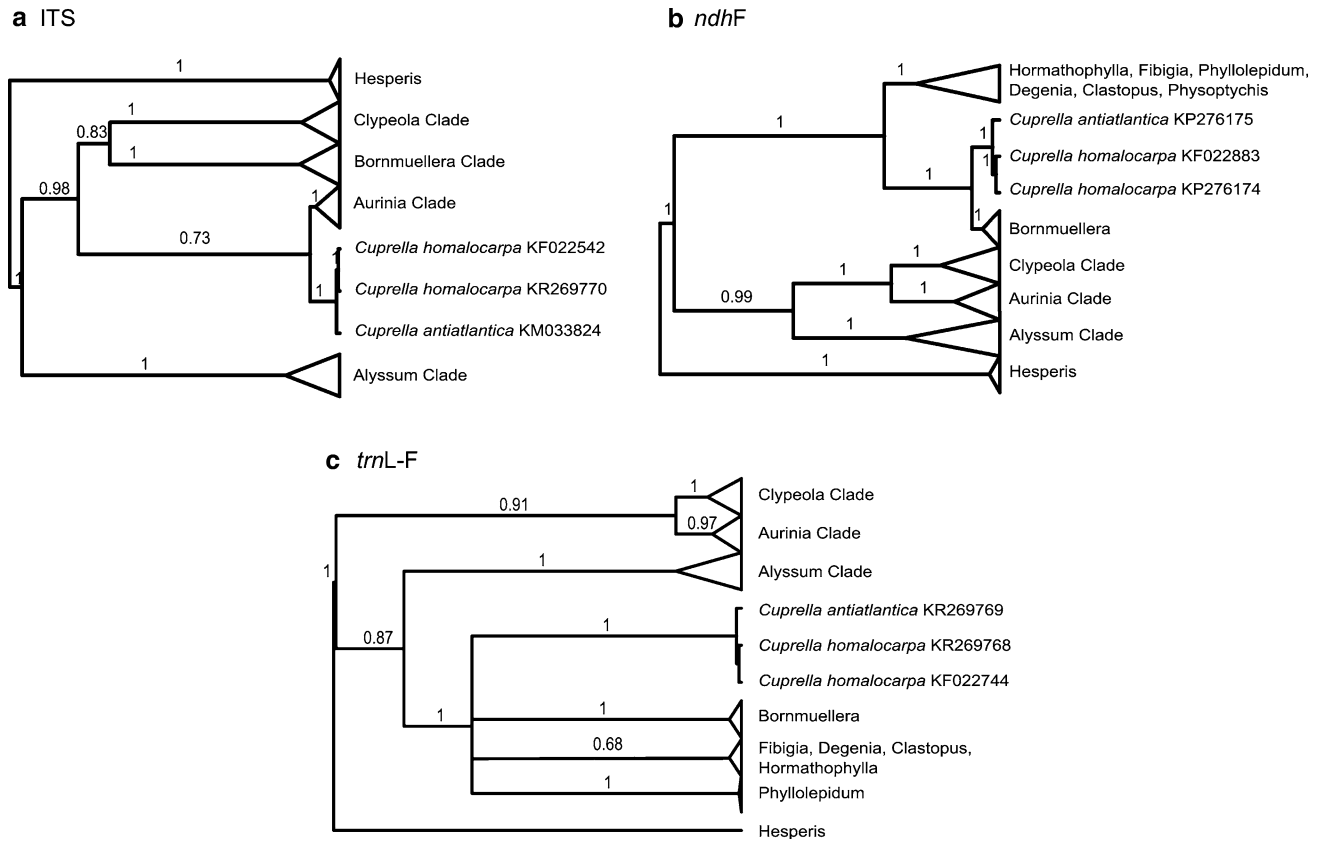

Fig. 4 Phylogenetic analyses revealing that *Cuprella antiatlantica* and *C. homalocarpa* form an isolated, well-supported lineage outside of the genus *Alyssum. Schematic* Bayesian-inference phylogenetic trees showing *Cuprella* relationships within Alysseae based on ITS (**a**), *ndh*F (**b**), and *trn*L-F (**c**) sequences

concluded that members of this section had elongated cylindrical nectaries. The section sensu Dudley (1964a) and Maire (1967) included *A. antiatlanticum*, *A. homalocarpum*, *A. alyssoides* (L.) L., *A. damascenum* Boiss. & Gaill., *A. dasycarpum* Stephan ex Willd., and *A. granatense* Boiss. & Reut. The inclusion of the first two species, however, was not unequivocal. *Alyssum homalocarpum* differs from the rest of the section by its broadly obovate, truncate, glabrous fruits with papillate margins, deciduous sepals, and leaves minutely denticulate at apex (unique in *Alyssum*; Dudley 1968; I. A. Al-Shehbaz personal observation). According to Maire (1967), *A. antiatlanticum* is the most isolated species in the genus, but he assigned it to *A.* sect. *Psilonema* due to its elongated cylindrical nectaries. On the other hand, the putative assignment of *A. antiatlanticum* to *Hormathophylla* was informally proposed by Philippe Küpfer on some annotated specimens (e.g., MA 121991), as well as by Maire who highlighted its morphological proximity to *H. cochleata* (Coss. & Durieu) P.Küpfer and *Alyssum* sect. *Ptilotrichum* (C.A.Mey.) Hook.f. (Maire 1967; Küpfer 1974). For the above-mentioned phylogenetic and morphological reasons, we propose here *Cuprella* Salmerón-Sánchez et al. as a new genus in the tribe Alysseae, comprising two species, *C. antiatlantica* (Emb. & Maire) Salmerón-Sánchez et al. and *C. homalocarpa* (Fisch. & C.A.Mey.) Salmerón-Sánchez et al. (see "Taxonomic treatment" below).

Due to incongruences among the results obtained from different molecular markers, the relationships within the *Clypeola* clade are not yet sufficiently resolved. While *Alyssum* sect. *Odontarrhena* appears to be monophyletic, *Clypeola* is not consistently separated from *A.* sect. *Meniocus* and is mostly paraphyletic in relation to *A.* sect. *Odontarrhena* (Rešetnik et al. 2013). To achieve monophyly of *Alyssum*, apart from the recognition of *Cuprella*, the *Clypeola* clade would have to be either split into three hitherto weakly phylogenetically supported genera (*Odontarrhena* C.A.Mey., *Meniocus* Desv., and *Clypeola*), or kept as one monophyletic, but morphologically heterogeneous genus *Clypeola* (the oldest available generic name for this group). The latter solution would require numerous new nomenclatural combinations that we presently want to avoid. Therefore, we prefer to treat these three genera separately, in agreement with their morphology, until their phylogenetic relationships are fully resolved by additional molecular markers.

For the genus *Meniocus*, we adopted here the traditional and morphology-based treatment despite the fact that its type, *M. serpyllifolius* (Desf.) Desv., the only species mentioned in the protologue of the genus (Desvaux 1815), unambiguously belongs to the genus *Odontarrhena*. While *Odontarrhena* encompasses 87 perennial species with uniovulate locules, *Meniocus* traditionally includes seven annual species with 2–4(−8)-ovuled locules (Dudley 1964a). The silicles with many seeds are also mentioned in the original description of the genus *Meniocus*. Because *Odontarrhena serpyllifolia* (Desf.) Jord. & Fourr. [≡ *Alyssum serpyllifolium* Desf.] is a perennial with uniovulate locules, as all other taxa of *Odontarrhena*, a conservation of the name *Meniocus* with a more appropriate type is necessary to resolve this inconsistency.

After the exclusion of *Alyssum* sect. *Odontarrhena*, *A.* sect. *Meniocus*, *A. homalocarpum*, and *A. antiatlanticum*, *Alyssum* s.str. consists of two clades (Rešetnik et al. 2013; E. Salmerón Sánchez et al., unpublished data): (1) most of the annual and perennial taxa of *A.* sect. *Alyssum*, (2) *A.* sect. *Gamosepalum*, few perennials of *A.* sect. *Alyssum,* and annual *A. dasycarpum*. In order to resolve the sectional classification of *Alyssum*, future phylogenetic studies should include more species that would also help in the identification of morphological synapomorphies for its infrageneric clades.

The name *Alyssum montanum*, which is the lectotype of the genus *Alyssum* (see Green 1925), was recently proposed to be conserved with a conserved type (Marhold et al. 2011). The original lectotype of *A. montanum* designated by Dudley (1964a) contradicted the widespread usage of the name, as it belongs to *Odontarrhena obovata* C.A.Mey. Therefore, the name *A. montanum* should be conserved with a conserved type, which is in agreement with the protologue and the traditional use of the name and which does not disrupt the well-established usage of the names *A.* sect. *Alyssum* and *A.* sect. *Odontarrhena* (Marhold et al. 2011).

The monotypic genus *Takhtajaniella* V.E.Avet. (Avetisian 1980, 2013), classified in synonymy of *Alyssum* by Al-Shehbaz (2012), was not sampled in the published phylogenetic studies of the Alysseae, and its status will be addressed in the future. In fact, *Takhtajaniella* with its white petals, 2–6-rayed trichomes, and globose fruits might be close to *Bornmuellera* (I. A. Al-Shehbaz and D. A. German, personal observation).

It seems that there are no morphological grounds for keeping *Clastopus* and *Straussiella* Hausskn. as separate genera, as was done by Al-Shehbaz (2012). The single available sequence for *Straussiella purpurea* (Bunge ex Boiss.) Hausskn. (Jaén-Molina et al. 2009), which is part of ITS2, is closer to that of *Clastopus vestitus* (Desv.) Boiss. (96.8 % identity) than to any other sampled Alysseae.

To summarize, compared with the generic treatment of the Alysseae adopted in the most recent synopsis of the family (Al-Shehbaz 2012), we suggest reassignment of *Alyssoides cretica* to *Lutzia*, exclusion of *Alyssum* sect. *Odontarrhena* and *A.* sect. *Meniocus* from *Alyssum* and resurrection of the genera *Odontarrhena* and *Meniocus*, transfer of *Alyssum antiatlanticum* and *A. homalocarpum* into the newly described genus *Cuprella*, reassignment of *Alyssum globosum* Grossh. to *Takhtajaniella*, placement of *Physocardamum davisii* Hedge and *Leptoplax emarginata* (Boiss.) O.E.Schulz into *Bornmuellera*, transfer of *Fibigia suffruticosa* into resurrected *Brachypus*, reassignment of *Fibigia* sect. *Edmondia* into *Irania*, reassignment of *Fibigia lunarioides* into *Acuston*, transfer of *Fibigia spathulata* into resurrected *Pterygostemon*, transfer of *Fibigia triquetra* into the newly described genus *Resetnikia*, and uniting *Straussiella* with *Clastopus*.

We recognize here the following 24 genera in the tribe Alysseae (the number of species is in parentheses, accepted and provisionally accepted species are included, unresolved cases are not taken into consideration; see also Fig. 5b): *Acuston* (1), *Alyssoides* (1), *Alyssum* (114), *Aurinia* (7), *Berteroa* DC. (5), *Bornmuellera* (9), *Brachypus* (1), *Clastopus* (2), *Clypeola* (9), *Cuprella* (2), *Degenia* (1), *Fibigia* (3), *Galitzkya* V.V.Botschantz. (3), *Hormathophylla* (11), *Irania* (5), *Lepidotrichum* (1), *Lutzia* (1), *Meniocus* (7), *Odontarrhena* (87), *Phyllolepidum* (2), *Physoptychis* (2), *Pterygostemon* (1), *Resetnikia* (1) and *Takhtajaniella* (1).

An identification key to the genera of the tribe is in the Taxonomic treatment below. An online interactive identification key is available at the AlyBase web.

Accepted species and infraspecific names and synonyms

The nomenclature checklist of Alysseae currently available in the AlyBase database comprises a total of 281 accepted taxa, 16 provisionally accepted taxa, and 774 synonyms. In addition, there are 53 doubtful synonyms and 70 unresolved names that require further attention (Table 1). Full list of accepted and provisionally accepted taxa, including nomenclatural novelties (new combinations), is provided in the Taxonomic treatment below. The information presented in the AlyBase checklist is coordinated with the BrassiBase database (Koch et al. 2012; Kiefer et al. 2014), nevertheless, concentration on a single tribe gave us possibility to provide much more extensive synonymy compared with BrassiBase, apart from new generic concept presented here.

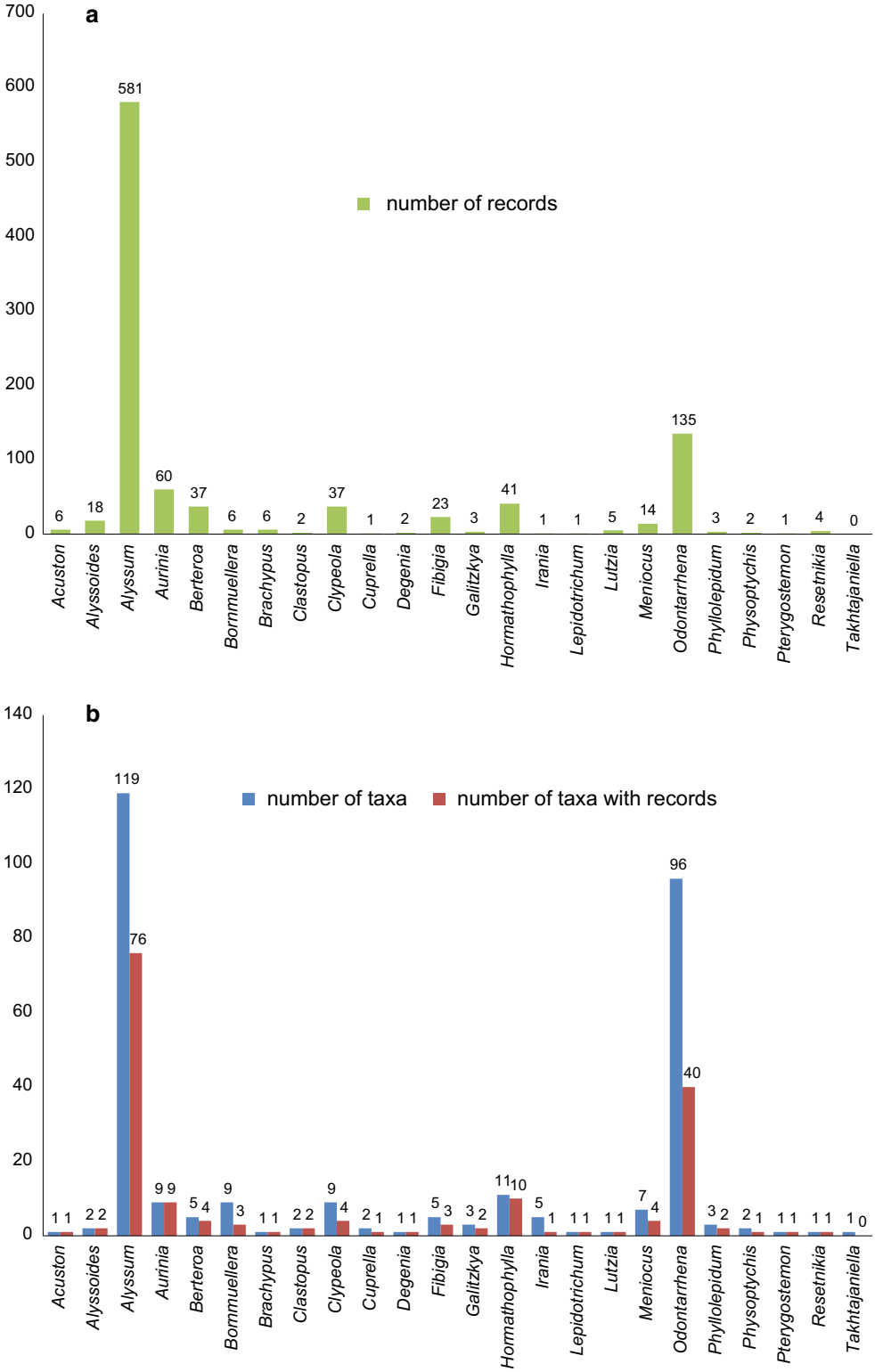

Fig. 5 **a** Distribution of the chromosome number reports and ploidy-level estimates among the genera of the tribe Alysseae. **b** Number of accepted taxa (species, subspecies, varieties, autonyms excluded) and number of the taxa with the chromosome number records and/or ploidy-level estimates in the genera of the tribe Alysseae

Chromosome numbers and ploidy-level data

Chromosome numbers and/or ploidy-level estimates presented in the database cover all genera currently placed in the tribe Alysseae (Fig. 5) except for *Takhtajaniella*. Out of the total number of currently accepted species, subspecies and varieties (297, excluding nominal taxa), chromosome number data and/or ploidy-level estimates are

Table 1 Statistics on the accepted species and infraspecific names, provisionally accepted names, synonyms, doubtful synonyms and unresolved names of accepted genera of the tribus Alysseae

Genus	Accepted names	Provisionally accepted names	Synonyms	Doubtful synonyms	Unresolved names
Acuston	1		3		
Alyssoides	2		8	1	
Alyssum	105	14	254	28	66
*Anodontea**					1
Aurinia	9		31	5	
Berteroa	5		12		1
Bornmuellera	9		15		
Brachypus	1		4		
Clastopus	2		8		
Clypeola	9		31	3	
Cuprella	2		6		
Degenia	1		3		
Fibigia	5		11		
Galitzkya	3		8		
Hormathophylla	10	1	37	1	
Irania	5		9		
Lepidotrichum	1		2		
Lutzia	1		18		
Meniocus	7		21		
Odontarrhena	95	1	272	15	2
Phyllolepidum	3		8		
Physoptychis	2		6		
Pterygostemon	1		3		
Resetnikia	1		3		
Takhtajaniella	1		1		
Total	281	16	774	53	70

* For the genus *Anodontea*, not recognized here, there is one unresolved name of uncertain generic placement

Autonyms are not taken into account

available for 171 taxa (57.6 %). Sole ploidy-level estimates are known for four taxa. In total, the database comprises 780 records of chromosome numbers and 209 of ploidy-level estimates based on genome-size studies that were published in 213 papers.

In terms of geographical coverage (according to the level 2 of the World geographical scheme for recording plant distributions; Brummitt 2001), the highest number of records is from southeastern Europe (386), followed by western Asia (155), southwestern Europe (143), and central Europe (105). Details are shown in Fig. 6 (unassigned records on this diagram are those based on material from botanical gardens, from old literature, or from experimental papers, where the localities of origin were not given).

The most frequently registered ploidy level is diploid (593 records). Out of polyploids (395 records), the most often recorded ploidy level is tetraploid (341 records) and

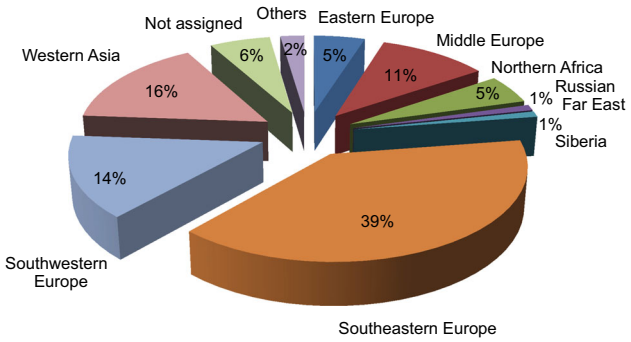

Fig. 6 Geographical distribution of the chromosome number and ploidy-level records for the tribe Alysseae. The geographical division of the world follows level 2 of the World geographical scheme for recording plant distributions (Brummitt 2001). Only areas gathering at least 1 % of the chromosome number records are marked

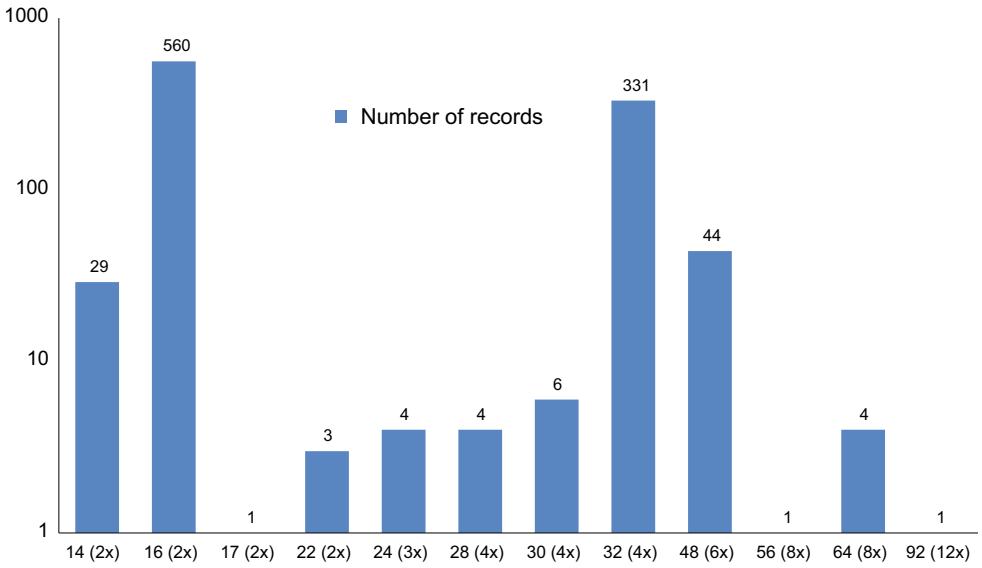

Fig. 7 Distribution of chromosome numbers and ploidy levels in the tribe Alysseae. For the construction of this histogram, haploid chromosome numbers were multiplied by two and ploidy-level estimates were assigned to the relevant chromosome numbers. Differences among diploids ($2x$) and polyploids are due to $x = 7, 8, 11, 15$

hexaploid (44 records) (Fig. 7; for the distribution details of ploidy levels in the genera *Alyssum*, *Clypeola*, *Hormathophylla*, and *Odontarrhena* see Online Resource 2).

From the accepted taxa of the tribe for which we have chromosome number reports and/or ploidy-level estimates, 95 (55.6 %) taxa are diploid, 43 (25.1 %) polyploid, and 33 (19.3 %) with both diploids and polyploids. Based on Warwick and Al-Shehbaz (2006), the corresponding percentages for larger genera of other Brassicaceae tribes are as follows: *Cardamine* L.—32 % taxa diploid, 10 % both diploid and polyploid, and 58 % entirely polyploid (see also Kučera et al. 2005); *Draba* L.—25 % taxa diploid, 7 % both diploid and polyploid, and 68 % entirely polyploid; *Lepidium* L.—34 % taxa diploid, 14 % both diploid and polyploid, and 52 % entirely polyploid; *Rorippa* Scop.—48 % taxa diploid, 39 % both diploid and polyploid, and 13 % entirely polyploid. Such numbers underline the importance of polyploidy in the speciation and evolution of taxa of this family.

The most common base chromosome number reported for Alysseae is $x = 8$, less frequent is $x = 7$ (given for some *Clypeola*, *Hormathophylla*, and *Meniocus* species and for *Alyssum umbellatum* Desv.; for references see AlyBase). The highest variation in base chromosome numbers ($x = 7, 8, 11, 15$) is reported for *Hormathophylla*. Out of 11 species of this genus, chromosome or ploidy-level records are not available only for *H. baetica* P.Küpfer. Among the rest of *Hormathophylla*, $x = 8$ is reported for six species, five of them are tetraploid [*H. ligustica* (Breistr.) Španiel et al., *H. purpurea* (Lag. & Rodr.) P.Küpfer, *H. pyrenaica* (Lapeyr.) Cullen & T.R.Dudley, *H. saxigena* (Jord. & Fourn.) D.A.German & Govaerts] and one is diploid–tetraploid [*H. spinosa* (L.) P.Küpfer]. Base chromosome number $x = 7$ was recorded for three species, including the tetraploids *H. cadevalliana* (Pau) T.R.Dudley and *H. reverchonii* (Degen & Hervier) Cullen & T.R.Dudley and the octoploid *H. longicaulis* (Boiss.) Cullen & T.R.Dudley. Base chromosome number $x = 11$ is known only in *H. cochleata* (Coss. & Durieu) P. Küpfer and $x = 15$ in *H. lapeyrouseana* (Jord.) P. Küpfer. The taxa with $2n = 22$ and $2n = 30$ might be classified as secondarily diploid. The exact nature and origin of these chromosome numbers in *Hormathophylla* has not yet been explored. There are several taxa of Alysseae for which two different base chromosome numbers, $x = 7$ and $x = 8$, have been reported (references in AlyBase). In three such species [*Alyssum szovitsianum* Fisch. & C.A.Mey., *Fibigia macrocarpa* (Boiss.) Boiss., and *Odontarrhena corsica* (Duby) Španiel et al.] the chromosome counts corresponding to $x = 8$ are likely correct, while those corresponding to $x = 7$ are most probably erroneous. In *Alyssum umbellatum*, *Meniocus linifolius* (Stephan ex Willd.) DC., and *M. meniocoides* (Boiss.) Hadač & Chrtek, counts corresponding to $x = 7$ and $x = 8$ were reported with equal frequency, and none of them are treated here as likely incorrect. Further attention should be particularly paid to taxa of the genera *Clypeola*, *Hormathophylla*, and *Meniocus* to clarify the reported base chromosome number variation.

Aneuploidy was rarely reported in the Alysseae, and only eight cases are found in literature that might be considered as such (references in AlyBase). Three of them seem plausible [$2n = 16$, 18 in *Alyssum contemptum* Schott & Kotschy and *A. erosulum* Gennar. & Pestal.,

$2n = 17$ in *Galitzkya macrocarpa* (Ikonn.-Gal.) V.V.Botschantz.], while two are likely erroneous ($2n = 30$ in *Odontarrhena obovata* C.A.Mey. and $2n = 36$ in *Alyssum simplex* Rudolphi). Another three likely aneuploid chromosome numbers have been recorded repeatedly and thus appear plausible, but they deserve verification in future studies [$2n = 46$ in *Alyssum hirsutum* M.Bieb.; $2n = 24$ and $2n = 26$ in *Clypeola aspera* (Grauer) Turrill]. The highest polyploid recorded in Alysseae is the assumed hypododecaploid ($2n = 92$, in *Alyssum harputicum* T.R.Dudley), whose exact chromosome number needs verification. B-chromosomes were reported in Alysseae only three times [in *Alyssum fastigiatum* Heywood, *Lutzia cretica* (L.) Greuter & Burdet, and *Odontarrhena tortuosa* subsp. *caliacrae* (Nyár.) Španiel et al.; see AlyBase].

The currently available online resources on chromosome numbers mostly cover only some periods of time, certain areas, or taxonomic groups. The database of Index of Plant Chromosome Numbers (IPCN, Goldblatt and Johnson 1979 onwards), which is part of more complex Tropicos database by the Missouri Botanical Garden, is currently limited from years 1979 to 2006 (Goldblatt 2007; Goldblatt and Lowry 2011). However, final steps are being made to renew the collection of data for this database under auspices of the International Association for Plant Taxonomy (K. Marhold, unpublished data). Most recently, Chromosome Counts Database (CCDB, version 1.11) was made public (Rice et al. 2015) to represent a global and unlimited information source on chromosome numbers.

Other chromosome number databases are regionally or taxonomically restricted. These include CHROBASE—Chromosome Numbers for the Italian Flora (Bedini et al. 2010 onwards), Chromosome Number Survey of the Ferns and Flowering Plants of Slovakia (Marhold et al. 2007), Chromosome Number Database of Polish Plants (Góralski et al. 2009 onwards), BSBI Cytology Database (Botanical Society of the British Isles 2014), Chilean Plants Cytogenetic Database (Jara-Seguel and Urrutia 2011), and ChromoPar—Paraguay Chromosome Counts Database (Simon et al. 2000). Examples of taxonomically restricted databases include Index to Chromosome Numbers in Asteraceae (Watanabe 2002), Chromosome Counts in *Hieracium* L. (Schuhwerk 1996), BrassiBase (Koch et al. 2012; Kiefer et al. 2014), and Karyological Database of the Genus *Cardamine* (Kučera et al. 2005).

Unlike global sources, such as IPCN and CCDB, or widely conceived specialized BrassiBase database, which present very simple data (mostly just taxon names, chromosome numbers, and place of publication), AlyBase provides more complete information on the origin of analyzed material, voucher specimens and revision of the identification of plant material according to the collection place or voucher specimens (if available). Our aim is also to point to the records that are unequivocally erroneous or doubtful either with respect to the identity of analyzed material or chromosome count. In some cases, we suspected that meiotic counts were likely confused with mitotic ones (e.g., $2n = 8$ in *Alyssoides utriculata*, Pogliani 1971 and Gagnidze 1983; $2n = 8$ in *Alyssum strictum* Willd., Ghaffari 1987).

Another innovative feature of our database is that we register both the chromosome number counts and ploidy-level estimates based on flow-cytometric measurements. Flow cytometry has considerably changed the practice of studies of plant polyploids during the past two decades. Detailed studies at the population level enabled the discovery of cases of the occurrence of minority cytotypes that were not revealed using classical chromosome counting (Kron et al. 2007; Vrána et al. 2014). Such minority cytotypes are usually missing in standard-reference sources that refer solely to the chromosome number counts. The presentation of ploidy-level estimates based on flow-cytometric measurements is a practice applied recently also in the column IAPT/IOPB Chromosome Data published in Taxon (Marhold 2006 onwards).

Taxononomic treatment

Key to the genera of Alysseae

The number of ovules per ovary is an important character in distinguishing genera of the tribe. It can easily be obtained from the fruit by counting the number of seeds plus aborted ovules, or by counting the number of funicles or their scars from fruit that shed all of its seeds.

For an interactive key to the genera, see the AlyBase web.

1a. Ovules 1 or 2 per ovary.

2a. Annual herbs; septum absent or reduced to a rim; fruit indehiscent, samaroid, usually with setose, barbed, or hooked trichomes; ovules 1 per ovary ..... 9. ***Clypeola***

2b. Perennial herbs or subshrubs; septum complete; fruit dehiscent, rarely samaroid, without setose, barbed, or hooked trichomes; ovules 2 per ovary (rarely 1 in some *Bornmuellera*).

3a. At least some trichomes malpighiaceous (2-rayed, medifixed), other trichomes 3–6-rayed; fruit inflated or rarely latiseptate ..... 6. ***Bornmuellera***

3b. All trichomes stellate, (6–)8–24-rayed; fruit latiseptate.

4a. Filaments toothless, unappendaged; petals white; style to 0.7 mm ..... 16. ***Lepidotrichum***

4b. Filaments usually toothed, appendaged; petals yellow, rarely creamy white; style usually 1–3 mm ..... 19. ***Odontarrhena***

1b. Ovules 4–16 per ovary.

5a. Sepals persistent well after fruit maturity, accrescent; fruit indehiscent or tardily dehiscent; seeds rugose or verrucose, wingless ..... 8. ***Clastopus***

5b. Sepals usually caducous well before fruit maturity, not accrescent; fruit dehiscent; seeds smooth or reticulate, winged, margined, or rarely wingless.

6a. Petals deeply bifid to about middle.

7a. Trichomes a mixture of simple and 2–8-rayed; lateral sepals not saccate at base; Mediterranean region, one cosmopolitan annual weed ..... 5. ***Berteroa***

7b. Trichomes exclusively 8–12-rayed; lateral sepals saccate at base; China, Mongolia ..... 13. ***Galitzkya***

6b. Petals obtuse, rounded, truncate, retuse, or emarginate.

8a. Style (5–)6–10 mm long.

9a. Petals purple or crimson red ..... 7. ***Brachypus***

9b. Petals yellow or white, if pinkish then plants subshrubs.

10a. Filaments minutely appendaged at base; anthers apiculate; cotyledons oblique incumbent; at least some cauline leaves sinuate or dentate; lateral sepals not saccate at base ..... 4. ***Aurinia***

10b. Filaments unappendaged at base; anthers not apiculate; cotyledons accumbent; cauline leaves entire; lateral sepals saccate at base.

11a. Fruit inflated.

12a. Fruit valves thickened, leathery to subwoody, glabrous outside and inside; ovules 8–12 per ovary; at least some trichomes malpighiaceous, 2-rayed ..... 2. ***Alyssoides***

12b. Fruit valves papery, pubescent outside and inside; ovules 4 per ovary; all trichomes stellate, 12–20-rayed ..... 11. ***Degenia***

11b. Fruit strongly latiseptate.

13a. Petals white or rarely pink; ovules 4–8 per ovary; fruit obovate, orbicular, elliptic, or cochleariform; style rarely to 5 mm, persistent ..... 14. ***Hormathophylla***

13b. Petals yellow; ovules 12–16 per ovary; fruit oblong to narrowly elliptic; style 7–10 mm, caducous ..... 23. ***Resetnikia***

8b. Style 0.1–3(–4) mm long.

14a. Annual herbs.

15a. Leaves distally denticulate; fruit margin papillate ..... 10. ***Cuprella***
15b. Leaves entire; fruit margin entire.

16a. Ovules 4–8(–16) per ovary; fruit latiseptate, valves glabrous or with simple trichomes and/or papillae ..... 18. ***Meniocus***
16b. Ovules 4 per ovary; fruit fully or unilaterally inflated, valve glabrous or with stellate trichomes.

17a. Petals yellow; infructescene distinctly elongated; fruit slightly inflated unilaterally, variously shaped ..... 3. ***Alyssum***
17b. Petals white; infructescene subcapitate; fruit fully inflated, globose ..... 24. ***Takhtajaniella***

14b. Perennial herbs, subshrubs, or shrubs.

18a. Trichomes malpighiaceous or mixed with 3–6-rayed ones, simple trichomes absent ..... 6. ***Bornmuellera***
18b. Trichomes (6–)8–24-rayed, sessile or stalked, simple ones present or absent.

19a. All filaments unappendaged, toothless, and wingless.

20a. Fruit ovoid to globose-ovoid, strongly inflated; ovules 8–16 per ovary; cotyledons incumbent ..... 17. ***Lutzia***
20b. Fruit obovate, orbicular, elliptic, or cochleariform, strongly latiseptate; ovules 4–8 per ovary; cotyledons accumbent.

21a. Petals yellow, shorter than or subequaling sepals, claw undifferentiated from blade ..... 10. ***Cuprella***
21b. Petals white or pink, distinctly longer than sepals, claw differentiated from blade.

22a. Fruit replum concealed by valve margins; ovules 4 per ovary; nectar glands 1, confluent, median glands present ..... 20. ***Phyllolepidum***
22b. Fruit replum visible; ovules 4–8 per ovary; nectar glands 4, 1 on each side of lateral stamen, median glands absent ..... 14. ***Hormathophylla***

19b. At least median or lateral filaments appendaged, winged, or toothed.

23a. Stigma strongly 2-lobed, lobes connivent, decurrent ..... 1. ***Acuston***
23b. Stigma entire, rarely slightly 2-lobed, lobes neither connivent nor decurrent.

24a. Replum visible, not concealed by distinct valves margin; anthers apiculate (except for *Alyssum*).

25a. Ovules 4–8(–16) per ovary; leaves dentate, sinuate, or pinnatifid, very rarely entire; cotyledons obliquely incumbent ..... 4. ***Aurinia***
25b. Ovules 4 per ovary; leaves entire; cotyledons accumbent.

26a. Anthers not apiculate; fruit usually dehiscent, 2–4-seeded; seeds usually winged; valves not veined; style 0.5–3 mm long ..... 3. ***Alyssum***

26b. Anthers apiculate; fruit tardily dehiscent, 1-seeded; seeds wingless; valves reticulate veined; style 2.5–4 mm long ..... 15. ***Irania***

24b. Replum not visible, concealed by connate valves margin; anthers not apiculate.

27a. Fruit indehiscent, globose or ovoid, inflated and bladder-like ..... 21. ***Physoptychis***

27b. Fruits dehiscent, oblong, orbicular to ovate, not inflated.

28a. Ovules 12–16 per ovary; racemes elongated considerably in fruit, bracteate or ebracteate; style persistent; trichomes 6–8-rayed ..... 12. ***Fibigia***

28b. Ovules 4–8 per ovary; racemes slightly elongated in fruit, ebracteate; style caducous; trichomes 12–20-rayed ..... 22. ***Pterygostemon***

List of names

The list contains the names of genera (numbered and in bold; with synonymy and distribution) and accepted and provisionally accepted (marked by #) names of species and infraspecific taxa in Alysseae, including nomenclatural novelties (in bold) and descriptions of new genera *Cuprella* and *Resetnikia*.

1. ***Acuston*** Raf., Sylva Tell. 131. 1838. [Oct–Dec 1838]–[1 sp.]. —TYPE: *Acuston lunarioides* (Willd.) Raf.
≡ *Pevalekia* Trinajstić
Distribution area: Greece (Crete, Cyclades, Dodecanese).
Acuston lunarioides (Willd.) Raf., Sylva Tellur. 131. 1838.

2. ***Alyssoides*** Mill., Gard. Dict. Abr., ed. 4. 1754. [28 Jan 1754]–[1 sp.]. —TYPE: *Alyssum utriculatum* L. [≡ *Alyssoides utriculata* (L.) Medik.].
≡ *Cistocarpium* Spach; = *Vesicaria* Adans.
Distribution area: Albania, Bosnia and Herzegovina, Bulgaria, Croatia, France, Greece, Gruziya, Italy, Macedonia, Montenegro, Romania, Russia, Serbia, Switzerland, Turkey.
Alyssoides utriculata (L.) Medik., Philos. Bot. 1: 189. 1789.
Alyssoides utriculata (L.) Medik. subsp. *utriculata*
Alyssoides utriculata subsp. *bulgarica* (Sagorski) Hartvig in Strid, Mount. Fl. Greece 1: 277. 1986.

3. ***Alyssum*** L., Sp. Pl.: 650. 1753. [1 Mai 1753]–[114 spp.]. —LECTOTYPE: *Alyssum montanum* L. (designated by Green 1925: 52).
= *Gamosepalum* Hausskn.; = *Psilonema* C.A.Mey.
Distribution area: throughout North Africa, Asia, and Europe; several species naturalized in North and South America, South Africa, and Australia.
Alyssum aizoides Boiss., Ann. Sci. Nat., Bot. sér. 2, 17: 153. 1842.
Alyssum alyssoides (L.) L., Amoen. Acad. 4 (Fl. Monsp.): 487. 1759; Reg. Veg. Syst. Nat., ed. 10, 2: 1130. 1759.
Alyssum andinum Rupr., Mém. Acad. Imp. Sci. Saint-Pétersbourg, sér. 7, 15(2) (Fl. Cauc.): 103. 1869.
Alyssum argyrophyllum Schott & Kotschy, Oesterr. Bot. Wochenbl 7: 229. 1857.
Alyssum armenum Boiss., Fl. Orient. 1: 278. 1867.
Alyssum artwinense N.Busch, Fl. Cauc. Crit. 3(4): 566. 1909.
Alyssum atlanticum Desf., Fl. Atlant. 2: 71, tab 149. 1798.
Alyssum aurantiacum Boiss., Fl. Orient. 1: 276. 1867.
Alyssum austrodalmaticum Trinajstić, Suppl. Fl. Anal. Jugosl. 8: 7. 1982.
#*Alyssum bargalense* Micevski, Fragm. Bot. Mus. Maced. Sci. Natur. 12(10): 105. 1985.
Alyssum baumgartnerianum Bornm. ex Jos.Baumgartner, Jahresber. Kais.-Franz-Jos. Oberrealschule Baden b. Wien 48: 16. 1911.

Alyssum blancheanum Gomb., Bull. Soc. Bot. France 112: 320. 1966.
Alyssum bornmuelleri Hausskn. ex Degen, Oesterr. Bot. Z. 48: 108. 1898.
Alyssum bosniacum Beck, Glasn. Zem. Mus. Bosn. i Hercegov. 28: 122. 1916, nom. alt.
Alyssum bulbotrichum Hausskn. & Bornm., Mitt. Thüring. Bot. Vereins 20: 3. 1905.
Alyssum cacuminum Španiel, Marhold & Lihová, Taxon 63: 585. 2014.
Alyssum caespitosum Jos.Baumgartner, Jahresber. Nieder-Österr. Landes-Lehrersem. Wiener-Neustadt 36: 26. 1909.
#*Alyssum calycocarpum* Rupr., Mém. Acad. Imp. Sci. St.-Pétersbourg, sér. 7, 15(2): 103. 1869.
Alyssum cephalotes Boiss., Diagn. Pl. Orient. Nov., ser. 2, 3(1): 34. 1854.
#*Alyssum clausonis* Pomel, Nouv. Mat. Fl. Atl.: 236. 1874.
Alyssum contemptum Schott & Kotschy, Österr. Bot. Wochenbl. 4: 177. 1854.
Alyssum corningii T.R.Dudley, J. Arnold Arbor. 45: 72. 1964.
Alyssum cuneifolium Ten., Flora Napol. 1: XXXVII. 1812.
Alyssum dagestanicum Rupr., Mém. Acad. Imp. Sci. Saint-Pétersbourg, sér. 7, 15(2) (Fl. Cauc.): 104. 1869.
Alyssum damascenum Boiss. & Gaill., Diagn. Pl. Orient. Nov., ser. 2, 3(6): 18. 1859.
Alyssum dasycarpum Stephan ex Willd., Sp. Pl., ed. 4, 3(1): 469. 1800.
#*Alyssum decoloratum* Pomel, Nouv. Mat. Fl. Atl.: 236. 1874.
Alyssum diffusum Ten., Flora Napol. 1: XXXVII. 1812.
Alyssum diffusum Ten. subsp. *diffusum*
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Alyssum strigosum subsp. *cedrorum* (Schott & Kotschy) T.R.Dudley, J. Arnold Arbor. 45: 67. 1964.
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Alyssum szovitsianum Fisch. & C.A.Mey., Index Sem. Horti Petropol. 4: 31. 1838.
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Alyssum tetrastemon Boiss., Ann. Sci. Nat. Bot., sér. 2, 17: 153. 1842.
Alyssum thymops (Hub.-Mor. & Reese) T.R.Dudley, J. Arnold Arbor. 45: 71. 1964.
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Alyssum vernale Kit. ex Hornem., Hort. Bot. Hafn. 2: 601. 1815.
Alyssum wierzbickii Heuff., Flora (Regensburg) 18: 242. 1835.
Alyssum wulfenianum Willd., Enum. Pl. Hort. Berol. Suppl.: 44. 1813 [publ. Jul.–Dec. 1814].
Alyssum wulfenianum Willd. subsp. *wulfenianum*
Alyssum wulfenianum subsp. *ovirense* (A.Kern.) Magauer, Schönswetter & Frajman, Bot. J. Linn. Soc. 176: 500. 2014.
Alyssum xanthocarpum Boiss., Ann. Sci. Nat., Bot., ser. 2, 17: 154. 1842.

4. ***Aurinia*** Desv., J. Bot. Agric. 3: 162. 1815.–[7 spp.]. —LECTOTYPE: *Aurinia saxatilis* (L.) Desv. (designated by Dudley 1964b: 391).
= *Anodontea* (DC.) Sweet

Distribution area: Albania, Austria, Bosnia and Herzegovina, Bulgaria, Croatia, Czech Republic, Germany, Greece, Gruziya, Hungary, Italy, Macedonia, Moldavia, Montenegro, Poland, Romania, Russia, Serbia, Slovakia, Slovenia, Turkey, Ukraine.

Aurinia corymbosa Griseb., Spicil. Fl. Rumel. 1: 271. 1843.
Aurinia gionae (Quézel & Contandr.) Greuter & Burdet, Willdenowia 13: 86. 1983.
Aurinia leucadea (Guss.) K.Koch, Hort. Dendrol.: 23. 1853.
Aurinia moreana Tzanoud. & Iatroú, Bot. Chronika 1: 22. 1981.
Aurinia petraea (Ard.) Schur, Enum. Pl. Transsilv.: 61. 1866.
Aurinia saxatilis (L.) Desv., J. Bot. Agric. 3: 162. 1815.
Aurinia saxatilis (L.) Desv. subsp. *saxatilis*
Aurinia saxatilis subsp. *megalocarpa* (Hausskn.) T.R.Dudley, J. Arnold Arbor. 45: 397. 1964.
Aurinia saxatilis subsp. *orientalis* (Ard.) T.R.Dudley, J. Arnold Arbor. 45: 394. 1964.
Aurinia sinuata (L.) Griseb., Spicil. Fl. Rumel. 1: 271. 1843.

5. ***Berteroa*** DC., Mém. Mus. Hist. Nat. 7: 232. 1821.–[5 spp.]. —LECTOTYPE: *Berteroa incana* (L.) DC. (designated by Pfeiffer 1871–1873: 397).
≡ *Myopteron* Spreng.

Distribution area: Albania, Armenia, Austria, Azerbaijan, Bosnia & Herzegovina, Bulgaria, China, Croatia, Czech Republic, Estonia, France, Greece, Gruziya, Hungary, Italy, Kazakhstan, Kyrgyzstan, Latvia, Lithuania, Macedonia, Moldavia, Mongolia, Montenegro, Poland, Romania, Russia, Serbia, Slovakia, Slovenia, Tajikistan, Turkey, Ukraine, Uzbekistan; *B. incana* is naturalized throughout much of Europe, Asia, and North America.

Berteroa gintlii Rohlena, Magyar Bot. Lapok 3: 232. 1904.
Berteroa incana (L.) DC., Reg. Veg. Syst. Nat. 2: 291. 1821.
Berteroa mutabilis (Vent.) DC., Reg. Veg. Syst. Nat. 2: 292. 1821.
Berteroa obliqua (Sm.) DC., Reg. Veg. Syst. Nat. 2: 292. 1821.
Berteroa orbiculata DC., Reg. Veg. Syst. Nat. 2: 293. 1821.

6. ***Bornmuellera*** Hausskn., Mitth. Thüring. Bot. Vereins, ser. 2, 11: 71. 1897.–[9 spp.]. —TYPE: *Bornmuellera tymphaea* (Hausskn.) Hausskn.
= *Leptoplax* O.E.Schulz; = *Physocardamum* Hedge

Distribution area: Albania, Greece, Serbia, Turkey.

Bornmuellera angustifolia (Hausskn. ex Bornm.) Cullen & T.R.Dudley, Feddes Repert. 71: 228. 1965.
Bornmuellera baldaccii (Degen) Heywood, Feddes Repert. 69: 61. 1964.
Bornmuellera cappadocica (Willd.) Cullen & T.R.Dudley, Feddes Repert. 71: 228. 1965.
Bornmuellera davisii (Hedge) Rešetnik, Phytotaxa 159: 299. 2014 [18 Feb 2014].
Bornmuellera dieckii Degen, Oesterr. Bot. Z. 50: 313. 1900.
Bornmuellera emarginata (Boiss.) Rešetnik, Phytotaxa 159: 299. 2014 [18 Feb 2014].
Bornmuellera glabrescens (Boiss. & Balansa) Cullen & T.R.Dudley, Feddes Repert. 71: 228. 1965.
Bornmuellera kiyakii Aytaç & A.Aksoy, Bot. J. Linn. Soc. 134: 487. 2000.
Bornmuellera tymphaea (Hausskn.) Hausskn., Mitt. Thüring. Bot. Vereins 11: 72. 1897.

7. ***Brachypus*** Ledeb., Fl. Rossica 1: 133. 1841.–[1 sp.]. —TYPE: *Brachypus asper* Ledeb. [= *Brachypus suffruticosus* (Vent.) V.I.Dorof.].

Distribution area: Armenia, Azerbaijan, Iran, Iraq, Turkmenistan, Turkey.

Brachypus suffruticosus (Vent.) V.I.Dorof., Consp. Fl. Cauc. 3(2): 411. 2012.

8. ***Clastopus*** Bunge ex Boiss., Fl. Orient. 1: 261. 1867.–[2 spp.]. —LECTOTYPE: *Clastopus vestitus* (Desv.) Boiss. (designated by Al-Shehbaz 2012: 933).

= *Straussiella* Hauskn.

Distribution area: Iran, Iraq, Turkey.

Clastopus purpureus Bunge ex Boiss., Fl. Orient. 1: 261. 1867.

Clastopus vestitus (Desv.) Boiss., Fl. Orient. 1: 261. 1867.

9. ***Clypeola*** L., Sp. Pl.: 652. 1753.–[9 spp.]. —LECTOTYPE: *Clypeola jonthlaspi* L. (designated by Green 1925: 55).

≡ *Fosselinia* Scop.; = *Bergeretia* Desv. (1815), non Bubani (1901); = *Orium* Desv.; = *Pseudoanastatica* (Boiss.) Grossh.

Distribution area: Afghanistan, Albania, Algeria, Armenia, Azerbaijan, Bulgaria, Croatia, Cyprus, France, Greece, Gruziya, Iran, Iraq, Israel, Italy, Jordan, Kazakhstan, Kyrgyzstan, Lebanon, Libya, Macedonia, Morocco, Oman, Pakistan, Romania, Russia, Serbia, Saudi Arabia, Spain, Switzerland, Syria, Ukraine, Tajikistan, Tunisia, Turkmenistan, Turkey, Uzbekistan.

Clypeola aspera (Grauer) Turrill, J. Bot. (London) 60: 269. 1922.

Clypeola ciliata Boiss., Fl. Orient. 1: 309. 1867.

Clypeola cyclodontea Delile, Bull. Soc. Centr. Agric. Dép. Hérault 23: 258. 1830.

Clypeola dichotoma Boiss., Ann. Sci. Nat. Bot., sér. 2, 17: 175. 1842.

Clypeola elegans Boiss. & A.Huet, Diagn. Pl. Orient. Nov., ser. 2, 3(5): 38. 1856.

Clypeola eriocarpa Cav., Descr. Pl.: 401. 1802.

Clypeola jonthlaspi L., Sp. Pl.: 652. 1753.

Clypeola lappacea Boiss., Ann. Sci. Nat. Bot., sér. 2, 17: 174. 1842.

Clypeola raddeana Albov, Bull. Herb. Boissier, sér. 1, 2: 448. 1894.

10. ***Cuprella*** Salmerón-Sánchez, Mota & Fuertes, **gen. nov.**–[2 spp.]. —TYPE: *Cuprella antiatlantica* (Emb. & Maire) Salmerón-Sánchez, Mota & Fuertes

Description: Herbs annual or perennial with woody base. Trichomes sessile, 10–18-rayed stellate, without webbing between slender rays, those on leaves not umbonate, simple trichomes present or absent. Multicellular glands absent. Stems erect to ascending, sometimes prostrate, simple, leafy, not spiny. Basal and lowermost stem leaves short petiolate, not rosulate, simple, entire or distally denticulate; cauline leaves subsessile, cuneate to attenuate, not auriculate at base, entire or denticulate. Racemes many-flowered, ebracteate, corymbose, elongated in fruit; rachis straight; fruiting pedicels divaricate or recurved, sometimes straight, pubescent, persistent. Sepals ovate, free, deciduous, erect, pubescent, equal, base of lateral pair not saccate; petals yellow, erect, shorter than or subequaling sepals; blade obovate to oblanceolate, glabrous, apex retuse; claw hardly differentiated from blade, glabrous, unappendaged, entire; stamens 6, included, erect, subequal; filaments wingless, toothless, unappendaged, glabrous, free; anthers ovate or oblong, not apiculate; nectar glands 4, lateral, cylindrical, 1 on each side of lateral stamen; ovules 4 per ovary; placentation subapical. Fruit dehiscent, capsular silicles, obovate, latiseptate, not inflated, unsegmented; valves papery, veinless or with an obscure midvein, pubescent outside or glabrous with papillate margin, not keeled, smooth, wingless, unappendaged; gynophore absent; replum rounded, visible; septum complete, membranous, veinless; style 0.5–1 mm long, cylindric, persistent; stigma capitate, entire, unappendaged. Seeds aseriate, usually 1 per locule, narrowly winged, ovate, flattened; seed coat smooth, not mucilaginous when wetted; cotyledons accumbent.

Diagnosis: *Cuprella* is readily distinguished from *Alyssum* sect. *Psilonema*, within which its two species were formerly placed, by having deciduous sepals longer than or subequaling the petals and by the broadly obovate silicles truncate at apex. One of its species (*C. antiatlantica*) is woody at base, and the other (*C. homalocarpa*) has denticulate leaves and papillate fruit margin. The four species of *A.* sect. *Psilonema* are annuals with orbicular or ovate fruits emarginate or rarely subobtuse at apex and have persistent sepals slightly shorter than petals.

Cuprella is defined by forming a well-supported phylogenetic lineage within the tribe Alysseae quite isolated from other lineages of *Alyssum* and *Clypeola.* The GenBank accession numbers for *Cuprella homalocarpa* and *C. antiatlantica* are KR269770, KM033824 for ITS, KR269768, KR269769 for *trn*L, *trn*L-F, and KP276174, KP276175 for *ndh*F, respectively.

Distribution area: *Cuprella antiatlantica* is a narrow endemic to Morocco, whereas *C. homalocarpa* is widely distributed from Egypt eastward into Israel, Jordan, Syria, Saudi Arabia, Iraq, Kuwait, Iran, and Pakistan.

Habitats: The species of *Cuprella* occupy xeric environments on limestone (*C. antiatlantica*) or basaltic and siliceous substrates (*C. homalocarpa*).

Etymology: The name of the genus honors Phillipe Küpfer (1924-), a Swiss professor emeritus at the University of Neuchâtel, where he focused on the study of the tribe Alysseae. The root is formed by late Latin *cuprum*, after his family name, which means copper trader or artisan in German, and the suffix "*–ella*" indicating the minute habit of the two species included in the genus.

Key to the species of *Cuprella*:

1a. Perennials with woody base; fruit stellate pubescent, not papillate; leaves entire ..... ***C. antiatlantica***

1b. Annuals; fruit glabrous, papillate at margin; leaves denticulate ..... ***C. homalocarpa***

Cuprella antiatlantica (Emb. & Maire) Salmerón-Sánchez, Mota & Fuertes, **comb. nov.** ≡ *Alyssum antiatlanticum* Emb. & Maire, Bull. Soc. Hist. Nat. Afrique N. 23: 165. 1932. Described from: "in rupestribus siliceis editis Anti-Atlasis: prope castellum Igherm, et in monte Fidoust, ad alt. 1700–2200 m, april florens (Emberger, Jahandiez, Maire et Weiller)." —LECTOTYPE (**here designated**): In Anti-Atlante: in rupestris arenaceis prope castellum Igherm, 1700–1800 m, 21 Apr 1931, *R. Maire s.n.* (lectotype: MPU! MPU002814, http://plants.jstor.org/stable/10.5555/al.ap.specimen.MPU002814); isolectotype: MA49591).

Cuprella homalocarpa (Fisch. & C.A.Mey.) Salmerón-Sánchez, Mota & Fuertes, **comb. nov.** ≡ *Psilonema homalocarpum* Fisch. & C.A.Mey., Index Seminum [St.Petersburg (Petropolitanus)] 6: 63. 1840. Described from: "Semina in Arabia petraea legit Dr. Schimper [cultivated in Hortus Botanicus Imperialis Petropolitanus]." —LECTOTYPE vel HOLOTYPE (designated as "holotype" by Dudley in: 1965: 210): Semina in Arabia petraea legit Dr Schimper, Cult[a] in hb. [horto botanico] Petropolit. 1839, *Meyer s.n.* (LE!).

11. ***Degenia*** Hayek, Oesterr. Bot. Z. 60: 93. 1910.–[1 sp.]. —TYPE: *Degenia velebitica* (Degen) Hayek

Distribution area: Croatia (Velebit and Velika Kapela Mts).

Degenia velebitica (Degen) Hayek, Oesterr. Bot. Z. 60: 93. 1910.

12. ***Fibigia*** Medik., Pfl.-Gatt.: 90. 1792.–[3 spp.]. —TYPE: *Fibigia clypeata* (L.) Medik.

Distribution area: Afghanistan, Albania, Armenia, Azerbaijan, Bulgaria, Cyprus, Egypt, Greece, Gruziya, Iran, Iraq, Israel, Italy, Jordan, Lebanon, Macedonia, Serbia, Syria, Turkey, Ukraine.

Fibigia clypeata (L.) Medik., Pfl.-Gatt. 1: 90. 1792.

Fibigia clypeata (L.) Medik. subsp. *clypeata*

Fibigia clypeata subsp. *anatolica* A.Duran & Tuştaş, Afr. J. Biotech. 11: 112. 2012.

Fibigia clypeata subsp. *eriocarpa* (DC.) Greuter, Bocconea 25: 50. 2012.

Fibigia heterophylla Rech.f., Ark. Bot., ser. 2, 5: 166. 1960.

Fibigia macrocarpa (Boiss.) Boiss., Fl. Orient. 1: 258. 1867.

13. ***Galitzkya*** V.V.Botschantz., Bot. Zhurn. (Moscow & Leningrad) 64: 1440. 1979.–[3 spp.]. —TYPE: *Galitzkya spathulata* (Stephan ex Willd.) V.V.Botschantz.

Distribution area: NW China, Kazakhstan, SW Mongolia, Russia (SE of European part, SW Siberia).

Galitzkya macrocarpa (Ikonn.-Gal.) V.V.Botschantz., Bot. Zhurn. (Moscow & Leningrad) 64: 1442. 1979.

Galitzkya potaninii (Maxim) V.V.Botschantz., Bot. Zhurn. (Moscow & Leningrad) 64: 1442. 1979.

Galitzkya spathulata (Stephan ex Willd.) V.V.Botschantz., Bot. Zhurn. (Moscow & Leningrad) 64: 1442. 1979.

14. ***Hormathophylla*** Cullen & T.R.Dudley, Feddes Repert. 71: 225. 1965.–[11 spp.]. —TYPE: *Hormathophylla reverchonii* (Degen & Hervier) Cullen & T.R.Dudley.

= *Nevadensia* Rivas Mart.

Distribution area: Algeria, France, Italy, Morocco, Spain.

#*Hormathophylla baetica* P.Küpfer, Anales Inst. Bot. Cavanilles 35: 123. 1978.

Hormathophylla cadevalliana (Pau) T.R.Dudley, Feddes Repert. 71: 226. 1965.

Hormathophylla cochleata (Coss. & Durieu) P. Küpfer, Boissiera 23: 215. 1974.
Hormathophylla lapeyrouseana (Jord.) P. Küpfer, Boissiera 23: 213. 1974.
Hormathophylla ligustica (Breistr.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum ligusticum* Breistr., Bull. Soc. Sci. Dauph. 61: 616. 1947.
Hormathophylla longicaulis (Boiss.) Cullen & T.R.Dudley, Feddes Repert. 71: 226. 1965.
Hormathophylla purpurea (Lag. & Rodr.) P. Küpfer, Fl. Iberica 4: 193. 1993.
Hormathophylla pyrenaica (Lapeyr.) Cullen & T.R.Dudley, Feddes Repert. 71: 226. 1965.
Hormathophylla reverchonii (Degen & Hervier) Cullen & T.R.Dudley, Feddes Repert. 71: 225. 1965.
Hormathophylla saxigena (Jord. & Fourn.) D.A.German & Govaerts, **comb. nov.** ≡ *Ptilotrichum saxigenum* Jord. & Fourr., Brev. Pl. Nov. 2: 13. 1868.
Hormathophylla spinosa (L.) P. Küpfer, Boissiera 23: 208. 1974.

15. ***Irania*** Hadač & Chrtek, Acta Univ. Carol., Biol. 1971(4): 248. 1973 [Sep 1973].–[5 spp.]. —TYPE: *Irania umbellata* (Boiss.) Hadač & Chrtek

Distribution area: Afghanistan, Iran, Iraq.
Irania compacta (Rech.f.) Hadač & Chrtek, Acta Univ. Carol., Biol. 1971 (4): 248. 1973.
Irania membranacea (Rech.f.) Hadač & Chrtek, Acta Univ. Carol., Biol. 1971 (4): 248. 1973.
Irania multicaulis (Boiss. & Hohen.) Hadač & Chrtek, Acta Univ. Carol., Biol. 1971 (4): 248. 1973.
Irania pendula (Boiss.) Hadač & Chrtek, Acta Univ. Carol., Biol. 1971 (4): 248. 1973.
Irania umbellata (Boiss.) Hadač & Chrtek, Acta Univ. Carol., Biol. 1971 (4): 248. 1973.

16. ***Lepidotrichum*** Velen. & Bornm., Oesterr. Bot. Z. 39: 323. 1889.–[1 sp.]. —TYPE: *Lepidotrichum uechtritzianum* (Bornm.) Velen. & Bornm.

Distribution area: Black Sea coast of Bulgaria and Turkey.
Lepidotrichum uechtritzianum (Bornm.) Velen. & Bornm., Oesterr. Bot. Z. 39: 324. 1889.

17. ***Lutzia*** Gand., Bull. Soc. Bot. France 67 Sess. Extraord.: viii. 1923.–[1 sp.]. —LECTOTYPE (**designated here**): *Lutzia fruticosa* Gand., Bull. Soc. Bot. France 67, Sess. Extr.: viii (1920) [1923], nom. illeg. (Art. 52) [≡ *Lutzia cretica* (L.) Greuter & Burdet].

Distribution area: Greece (Astipalea, Crete, Karpathos, Kasos).
Lutzia cretica (L.) Greuter & Burdet, Willdenowia 13: 94. 1983.

18. ***Meniocus*** Desv., J. Bot. Agric. 3: 173. 1815.–[7 spp.]. —TYPE: *Meniocus serpyllifolius* (Desf.) Desv. [= *Odontarrhena serpyllifolia* (Desf.) Jord. & Fourr.].

Distribution area: Afghanistan, Algeria, Armenia, Azerbaijan, Bulgaria, China, Gruziya, Iran, Iraq, Israel, Jordan, Kazakhstan, Kuwait, Kyrgyzstan, Lebanon, Macedonia, Moldavia, Mongolia, Morocco, Pakistan, Romania, Russia, Saudi Arabia, Spain, Syria, Tajikistan, Turkmenistan, Turkey, Ukraine, Uzbekistan. Introduced in Australia.
Meniocus aureus Fenzl, Pugillus Pl. Nov. Syr.: 13. 1842.
Meniocus blepharocarpus (T.R.Dudley & Hub.-Mor.) Hadač & Chrtek, Acta Univ. Carol., Biol. 1971 (4): 260. 1973.
Meniocus heterotrichus (Boiss.) Hadač & Chrtek, Acta Univ. Carol., Biol. 1971 (4): 260. 1973.
Meniocus huetii (Boiss.) Hadač & Chrtek, Acta Univ. Carol., Biol. 1971 (4): 260. 1973.
Meniocus linifolius (Stephan ex Willd.) DC., Reg. Veg. Syst. Nat. 2: 325. 1821.
Meniocus meniocoides (Boiss.) Hadač & Chrtek, Acta Univ. Carol., Biol. 1971 (4): 260. 1973.
Meniocus stylaris Boiss. & Balansa, Diagn. Pl. Orient. Nov., ser. 2, 1(6): 16. 1859.

19. ***Odontarrhena*** C.A.Mey. ex Ledeb., Icon. Pl. Nov. 2: 15. 1830.–[87 spp.]. —TYPE: *Odontarrhena microphylla* Ledeb. (= *Odontarrhena obovata* C.A.Mey.).
= *Triplopetalum* Nyár.

Distribution area: Predominantly mountainous areas of Palaeoarctics (one native species in north-west N America) with the center of diversity in Mediterranean region, Balkans, and SW Asia.
Odontarrhena akamasica (B.L.Burtt) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum akamasicum* B.L.Burtt, Kew Bulletin 4: 100. 1949.
Odontarrhena albiflora (F.K.Mey.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum albiflorum* F.K.Mey., Haussknechtia Beih. 15: 63, Fig. 9. 2011.

Odontarrhena alpestris (L.) Ledeb., Fl. Ross. 1: 142. 1841.
Odontarrhena anatolica (Hausskn. ex Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum anatolicum* Hausskn. ex Nyár., Bul. Grăd. Bot. Univ. Cluj 9: 40. 1929.
Odontarrhena argentea (All.) Ledeb., Fl. Ross. 1: 141, 751. 1841.
Odontarrhena bertolonii (Desv.) Jord. & Fourr., Brev. Pl. Nov. 2: 6. 1868.
Odontarrhena bertolonii (Desv.) Jord. & Fourr. subsp. *bertolonii*
Odontarrhena bertolonii **subsp.** ***scutarina*** (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum bertolonii* subsp. *scutarinum* Nyár., Bul. Grăd. Bot. Univ. Cluj 7: 101. 1927 [1928].
Odontarrhena borzaeana (Nyár.) D.A.German, Turczaninowia 17(4): 30. 2014.
Odontarrhena bracteata (Boiss. & Buhse) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum bracteatum* Boiss. & Buhse, Nouv. Mém. Soc. Imp. Naturalistes Moscou 12 (Aufzähl.): 18. 1860.
Odontarrhena callichroa (Boiss. & Balansa) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum callichroum* Boiss. & Balansa, Diagn. Pl. Orient. Nov., ser. 2, 3(5): 34. 1856.
Odontarrhena carica (T.R.Dudley & Hub.-Mor.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum caricum* T.R.Dudley & Hub.-Mor., J. Arnold Arbor. 45: 89. 1964.
Odontarrhena cassia (Boiss.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum cassium* Boiss., Diagn. Pl. Orient. Nov., ser. 1, 2(8): 34. 1849.
Odontarrhena chalcidica (Janka) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum chalcidicum* Janka, Oesterr. Bot. Z. 22: 175. 1872.
Odontarrhena chondrogyna (B.L.Burtt) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum chondrogynum* B.L.Burtt, Kew Bulletin 4: 101. 1949.
Odontarrhena cilicica (Boiss. & Balansa) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum cilicicum* Boiss. & Balansa, Diagn. Pl. Orient. Nov., ser. 2, 3(5): 34. 1856.
Odontarrhena condensata (Boiss. & Hausskn.) Jord. & Fourr., Brev. Pl. Nov. 2: 4. 1868.
Odontarrhena condensata (Boiss. & Hausskn.) Jord. & Fourr. subsp. *condensata*
Odontarrhena condensata **subsp.** ***flexibilis*** (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum flexibile* Nyár., Bul. Grăd. Bot. Univ. Cluj 7: 157. 1927 [1928].
Odontarrhena constellata (Boiss.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum constellatum* Boiss., Ann. Sci. Nat. Bot., sér. 4, 2: 244. 1854.
Odontarrhena corsica (Duby) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum corsicum* Duby, Bot. Gall. 1: 34. 1828.
Odontarrhena corymbosoidea (Formánek) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum corymbosoides* Formánek, Verh. Naturf. Vereins Brünn 34: 329. 1896.
Odontarrhena crenulata (Boiss. & Heldr.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum crenulatum* Boiss. & Heldr., Diagn. Pl. Orient. Nov., ser. 1, 2(8): 33. 1849.
Odontarrhena cyprica (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum cypricum* Nyár., Bul. Grăd. Bot. Univ. Cluj 7: 156. 1927 [1928].
Odontarrhena davisiana (T.R.Dudley) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum davisianum* T.R.Dudley, J. Arnold Arbor. 45: 81. 1964.
Odontarrhena debarensis (Micevski) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum debarense* Micevski, Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 15: 50. 1994.
Odontarrhena diffusa Jord. & Fourr., Brev. Pl. Nov. 2: 5. 1868.
Odontarrhena discolor (T.R.Dudley & Hub.-Mor.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum discolor* T.R.Dudley & Hub.-Mor., J. Arnold Arbor. 45: 80. 1964.
Odontarrhena dubertretii (Gomb.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum dubertretii* Gomb., Mém. Soc. Bot. France 1952: 4. 1952.
Odontarrhena dudleyi (Adıgüzel & R.D.Reeves) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum dudleyi* Adıgüzel & R.D.Reeves, Edinburgh J. Bot. 59: 216. 2002.
Odontarrhena elatius (F.K.Mey.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum elatius* F.K.Mey., Haussknechtia Beih., 15: 64. 2011.
Odontarrhena eriophylla (Boiss. & Hausskn.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum eriophyllum* Boiss. & Hausskn., Fl. Orient. 1: 273. 1867.

Odontarrhena euboea (Halácsy) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum euboeum* Halácsy, Consp. Fl. Graec. 1: 93. 1900.
Odontarrhena fallacina (Hausskn.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum fallacinum* Hausskn., Mitth. Thüring. Bot. Vereins, n.f., 3–4: 114. 1893.
Odontarrhena fedtschenkoana (N.Busch) D.A.German, Komarovia 6(2): 85. 2008 [19 May 2010].
Odontarrhena filiformis (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum filiforme* Nyár., Bul. Grăd. Bot. Univ. Cluj 9: 35. 1929.
Odontarrhena floribunda (Boiss. & Balansa) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum floribundum* Boiss. & Balansa, Diagn. Pl. Orient. Nov., ser. 2, 3(5): 33. 1856.
Odontarrhena fragillima (Bald.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum alpestre* var. *fragillimum* Bald., Malpighia 9: 58. 1895.
Odontarrhena gehamensis (Fed.) D.A.German, Turczaninowia 17(4): 30. 2014.
Odontarrhena gevgelicensis (Micevski) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum gevgelicense* Micevski, Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 15: 55. 1994.
Odontarrhena giosnana (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum giosnanum* Nyár., Bul. Grăd. Bot. Univ. Cluj 7: 127. 1927 [1928].
Odontarrhena haradjianii (Rech.f.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum haradjianii* Rech.f., Ark. Bot., ser. 2, 5: 172. 1960.
Odontarrhena haussknechtii (Boiss.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum haussknechtii* Boiss., Fl. Orient. 1: 269. 1867.
Odontarrhena heldreichii (Hausskn.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum heldreichii* Hausskn., Mitt. Thüring. Bot. Vereins 3-4: 113. 1893.
Odontarrhena huber-morathii (T.R.Dudley) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum huber-morathii* T.R.Dudley, J. Arnold Arbor. 45: 83. 1964.
Odontarrhena inflata (Nyár.) D.A.German, Turczaninowia 17(4): 31. 2014.
Odontarrhena kavadarcensis (Micevski) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum kavadarcense* Micevski, Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 15: 52. 1994.
Odontarrhena kurdica (Boiss.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum oxycarpum* var. *kurdicum* Boiss., Fl. Orient. 1: 269. 1867.
Odontarrhena lanigera (DC.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum lanigerum* DC., Reg. Veg. Syst. Nat. 2: 308. 1821.
Odontarrhena lesbiaca P.Candargy, Bull. Soc. Bot. France 44: 151. 1897.
Odontarrhena libanotica (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum libanoticum* Nyár., Bul. Grăd. Bot. Univ. Cluj 18: 83. 1938 [1939].
Odontarrhena litvinovii (Knjaz.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum litvinovii* Knjaz., Novosti Sist. Vyssh. Rast. 42: 143 (-145; Fig. 3). 2011 [13 Jul 2011].
Odontarrhena lurensis (F.K.Mey.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum lurense* F.K.Mey., Haussknechtia Beih., 15: 64. 2011.
Odontarrhena markgrafii (O.E.Schulz) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum markgrafii* O.E.Schulz, Ber. Deutsch. Bot. Ges. 44: 422. 1926.
Odontarrhena masmenaea (Boiss.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum masmenaeum* Boiss., Diagn. Pl. Orient. Nov., ser. 2, 3(5): 36. 1856.
Odontarrhena metajnae (Plazibat) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. et stat. nov.** ≡ *Alyssum serpyllifolium* var. *metajnae* Plazibat, Nat. Croatica 18: 413. 2009.
Odontarrhena mughlaei (Orcan) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum mughlaei* Orcan, Nordic J. Bot. 23: 703. 2006.
Odontarrhena muralis (Waldst. & Kit.) Endl., Cat. Horti Vindob. 2: 245. 1841 [Nov–Dec 1842].
Odontarrhena nebrodensis (Tineo) L.Cecchi & Selvi, Inform. Bot. Ital. 45: 308. 2013 [11 Dec 2013].
Odontarrhena nebrodensis (Tineo) L.Cecchi & Selvi subsp. *nebrodensis*
Odontarrhena nebrodensis* subsp. *tenuicaulis (Hartvig) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum nebrodense* subsp. *tenuicaule* Hartvig, Mount. Fl. Greece 1: 300. 1986.
Odontarrhena obovata C.A.Mey. in Ledebour, Fl. Alt. 1: 61. 1831 [Jul.-Dec. 1831].

Odontarrhena obtusifolia (Steven ex DC.) C.A.Mey., Verz. Pfl. Casp. Meer (C.A. von Meyer). 181. 1831 [Nov-Dec 1831].
Odontarrhena orbelica (Ančev & Uzunov) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum orbelicum* Ančev & Uzunov, Phytol. Balcan. 8: 26. 2002.
Odontarrhena oxycarpa (Boiss. & Balansa) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum oxycarpum* Boiss. & Balansa, Diagn. Pl. Orient. Nov., ser. 2, 3(5): 35. 1856.
Odontarrhena pateri (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum pateri* Nyár., Bul. Grăd. Bot. Univ. Cluj 9: 33. 1929.
Odontarrhena pateri (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold subsp. *pateri*
Odontarrhena pateri* subsp. *prostrata (Boiss. & A.Huet ex Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum prostratum* Boiss. & A.Huet ex Nyár., Bul. Grăd. Bot. Univ. Cluj 18: 98. 1939.
Odontarrhena peltarioidea (Boiss.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum peltarioides* Boiss., Ann. Sci. Nat. Bot., sér. 2, 17: 158. 1842.
Odontarrhena peltarioidea (Boiss.) Španiel, Al-Shehbaz, D.A.German & Marhold subsp. *peltarioidea*
Odontarrhena peltarioidea* subsp. *virgatiformis (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum peltarioides* var. *virgatiforme* Nyár., Anal. Acad. Rep. Pop. Române, Biol. ser. A, mem. 3, 1: 84. 1949.
Odontarrhena penjwinensis (T.R.Dudley) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum penjwinense* T.R.Dudley, Notes Roy. Bot. Gard. Edinburgh 24: 162. 1962.
Odontarrhena pinifolia (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Triplopetalum pinifolium* Nyár., Magyar Bot. Lapok 24: 97. 1925 [1926].
Odontarrhena polyclada (Rech.f.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum polycladum* Rech.f., Phyton (Horn, Austria) 3: 55. 1951.
Odontarrhena pterocarpa (T.R.Dudley) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum pterocarpum* T.R.Dudley, J. Arnold Arbor. 45: 370. 1964.
Odontarrhena pugiostyla (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum pugiostylum* Nyár., Bul. Grăd. Bot. Univ. Cluj 18: 89. 1938 [1939].
Odontarrhena robertiana (Bernard ex Gren. & Godr.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum robertianum* Bernard ex Gren. & Godr., Fl. France 1: 117. 1847.
Odontarrhena samarifera (Boiss. & Hausskn.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum samariferum* Boiss. & Hausskn., Fl. Orient. 1: 272. 1867.
Odontarrhena samia (T.R.Dudley & Christod.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum samium* T.R.Dudley & Christod., Notes Roy. Bot. Gard. Edinburgh 45: 433. 1988.
Odontarrhena serpentina (Micevski) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum serpentinum* Micevski, Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 15: 46. 1994.
Odontarrhena serpentinicola (F.K.Mey.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum serpentinicola* F.K.Mey., Haussknechtia Beih. 15: 65. 2011.
Odontarrhena serpyllifolia (Desf.) Jord. & Fourr., Brev. Pl. Nov. 2: 1. 1868.
Odontarrhena sibirica (Willd.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum sibiricum* Willd., Sp. Pl., ed. 4, 3(1): 465. 1800.
Odontarrhena singarensis (Boiss. & Hausskn.) Španiel, Al-Shehbaz, D.A.German & Marhold**, comb. nov.** ≡ *Alyssum singarense* Boiss. & Hausskn., Fl. Orient. Suppl.: 49. 1888.
Odontarrhena skopjensis (Micevski) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum skopjense* Micevski, Prilozi Oddel. Biol. Med. Nauki Makedonska Akad. Nauk. Umet. 15: 43. 1994.
Odontarrhena smolikana (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum smolikanum* Nyár., Bul. Grăd. Bot. Univ. Cluj 9: 43. 1929.
Odontarrhena stipitata (Kavousi & T.R.Dudley) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum stipitatum* Kavousi & T.R.Dudley, Iran J. Bot. 9: 48. 2001.
Odontarrhena subspinosa (T.R.Dudley) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum subspinosum* T.R.Dudley, Notes Roy. Bot. Gard. Edinburgh 24: 160. 1962.
Odontarrhena syriaca (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum syriacum* Nyár., Bul. Grăd. Bot. Univ. Cluj 18: 84. 1938 [1939].
Odontarrhena szarabiaca (Nyár.) D.A.German, Komarovia 6(2): 85. 2008 [19 May 2010].
#Odontarrhena subalpina (M.Bieb.) D.A.German, Turczaninowia 17(4): 30. 2014.

Odontarrhena tavolarae (Briq.) L.Cecchi & Selvi, Inform. Bot. Ital. 45: 308. 2013 [31 Dec 2013].
Odontarrhena tortuosa (Waldst. & Kit. ex Willd.) C.A.Mey. in Ledebour, Fl. Alt. 1: 60. 1831 [Jul.-Dec. 1831].
Odontarrhena tortuosa (Waldst. & Kit. ex Willd.) C.A.Mey. subsp. *tortuosa*
Odontarrhena tortuosa* subsp. *caliacrae (Nyár.) Španiel, Al-Shehbaz & Marhold, **comb. nov.** ≡ *Alyssum caliacrae* Nyár., Bul. Grăd. Bot. Univ. Cluj 6: 92. 1926.
Odontarrhena tortuosa* subsp. *cretacea (Kotov) Španiel, Al-Shehbaz & Marhold, **comb. nov.** ≡ *Alyssum tortuosum* subsp. *cretaceum* Kotov, Zhurn. Inst. Bot. Vseukraïns'k. Akad. Nauk 21–22: 238. 1939.
Odontarrhena tortuosa* subsp. *heterophylla (Nyár.) Španiel, Al-Shehbaz & Marhold, **comb. nov.** ≡ *Alyssum tortuosum* subsp. *heterophyllum* Nyár., Bul. Grăd. Bot. Univ. Cluj 7: 132. 1928 [sep. ed. Vorst. Alyssum: 118. 1929.].
Odontarrhena tortuosa* subsp. *savranica (Andrz.) Španiel, Al-Shehbaz & Marhold, **comb. nov.** ≡ *Alyssum savranicum* Andrz., in Besser, Enum. Pl. Volhyn., ed. 2: 82. 1822.
Odontarrhena trapeziformis (Bornm. ex Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum trapeziforme* Bornm. ex Nyár., Anal. Acad. Rep. Pop. Române, Biol. ser. A, mem. 3, 1: 83. 1949.
Odontarrhena troodi (Boiss.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum troodi* Boiss., Fl. Orient. Suppl.: 49. 1888.
Odontarrhena turgida (T.R.Dudley) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum turgidum* T.R.Dudley, Great Basin Naturalist 24: 7. 1964.
Odontarrhena virgata (Nyár.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Alyssum virgatum* Nyár., Bul. Grăd. Bot. Univ. Cluj 7: 115. 1927 [1928].

20. ***Phyllolepidum*** Trinajstić, Razpr. Slov. Akad. Znan. Umetn. 31: 362. 1990.–[2 spp.]. —TYPE: *Phyllolepidum rupestre* (Sweet) Trinajstić.
≡ *Lepidophyllum* Trinajstić (1980), non Cass. (1816), nec Brongn. (1828).
Distribution area: Albania, Greece, Italy, Macedonia, Montenegro, Serbia, Turkey.
Phyllolepidum cyclocarpum (Boiss.) L.Cecchi, Pl. Biosystems 145: 828. 2011.
Phyllolepidum cyclocarpum (Boiss.) L.Cecchi subsp. *cyclocarpum*
Phyllolepidum cyclocarpum subsp. *pindicum* (Hartvig) L.Cecchi, Pl. Biosystems 145: 828. 2011.
Phyllolepidum rupestre (Sweet) Trinajstić, Razpr. Slov. Akad. Znan. Umet. 31: 363. 1990.

21. ***Physoptychis*** Boiss., Fl. Orient. 1: 260. 1867.–[2 spp.]. —TYPE: *P. gnaphalodes* (DC.) Boiss. (= *Physoptychis caspica* (Hablitz) V.V.Botschantz.).
Distribution area: Armenia, Azerbaijan, Iran, Iraq, Turkey.
Physoptychis caspica (Hablitz) V.V.Botschantz., Bot. Zhurn. (Moscow & Leningrad) 61: 1440. 1976.
Physoptychis haussknechtii Bornm., Mitt. Thüring. Bot. Vereins 13–14: 1. 1899.

22. ***Pterygostemon*** V.V.Botschantz., Bot. Zhurn. (Moscow & Leningrad) 62: 1504. 1977 [6–31 Oct 1977].–[1 sp.]. —TYPE: *Pterygostemon spathulatus* (Kar. & Kir.) V.V.Botschantz.
≡ *Asterotricha* V.V.Botschantz. (1976), non Kuntze (1903), nec *Astrotricha* DC. (1829).
Distribution area: NW China, E Kazakhstan.
Pterygostemon spathulatus (Kar. & Kir.) V.V.Botschantz., Bot. Zhurn. (Moscow & Leningrad) 62: 1504. 1977.

23. ***Resetnikia*** Španiel, Al-Shehbaz, D.A.German & Marhold, **gen. nov.**–[1 sp.]. —TYPE: *Resetnikia triquetra* (DC.) Španiel, Al-Shehbaz, D.A.German & Marhold.
Description: Herbs perennial, canescent throughout, with simple caudex terminated in a central rosette and covered with leaf or petiole remains of previous seasons. Trichomes sessile, 12–20-rayed, stellate, without webbing between rigid rays, at least those on leaves often umbonate, simple trichomes absent. Multicellular glands absent. Stems erect to ascending, originating laterally from below central rosette, leafy, not spiny. Basal leaves petiolate, rosulate, simple, entire, with a distinct midvein abaxially; cauline leaves petiolate, not auriculate at base, entire. Racemes several- to many-flowered, ebracteate, corymbose, slightly elongated in fruit; rachis straight; fruiting pedicels ascending to divaricate, straight, densely pubescent, persistent. Sepals oblong, free, deciduous, erect, pubescent, unequal, base of lateral pair saccate; petals yellow, erect at base with flaring blade, much longer than sepals; blade obovate, glabrous, apex obtuse; claw strongly differentiated from blade, longer than sepals, glabrous, unappendaged, entire; stamens 6, distinctly exserted, erect, tetradynamous; filaments narrowly winged, unappendaged or lateral pair sometimes minutely toothed, glabrous, free; anthers oblong, not apiculate; nectar glands 2, lateral, ring-like, surrounding base of lateral stamen, or U-shaped and subtending it, median glands absent; ovules 12–16

per ovary; placentation parietal. Fruit dehiscent, capsular broad siliques or narrow silicles, oblong to elliptic or narrowly so, strongly latiseptate, not inflated, unsegmented; valves thin leathery, veinless, densely pubescent outside, very sparsely pubescent inside, not keeled, smooth, wingless, unappendaged; gynophore absent; replum rounded concealed by connate valve margins; septum complete, membranous, veinless; style 7–10 mm long, filiform, pubescent along proximal half, caducous; stigma capitate entire, unappendaged. Seeds biseriate, winged all around, ovate or broadly so, strongly flattened; seed coat not mucilaginous when wetted; cotyledons accumbent.

Diagnosis: *Resetnikia* is readily distinguished from *Fibigia,* in which its single species was formerly placed, by having 12–20-rayed (vs. 6–8-rayed) stellate trichomes, fruiting style 7–10 (vs. 1–2) mm long, unequal (vs. equal) sepals the lateral pair of which saccate (vs. not saccate) at base, fruit valves sparsely pubescent (vs. glabrous) inside, and ebracteate racemes slightly elongated in fruit (vs. at least basally bracteate or rarely ebracteate racemes elongated considerably in fruit).

Distribution area: *Resetnikia triquetra* is a narrow endemic to Croatian Adriatic coast.

Habitats: vertical fissures of calcareous rocks.

Etymology: the name of the genus honors Ivana Rešetnik (University of Zagreb, Croatia) in recognition for her work (and other collaborators) on the phylogenetic relationships of the tribe Alysseae.

Resetnikia triquetra (DC.) Španiel, Al-Shehbaz, D.A.German & Marhold, **comb. nov.** ≡ *Farsetia triquetra* DC. Reg. Veg. Syst. Nat. 2: 290. 1821. Described from: "in Dalmatiâ ad rupes arcis Clissa". —HOLOTYPE: [Croatia] In Dalmat: ad rupes arcis Clissa, *misit* 1820, *Portenschlag s.n.* (G-DC! G00205396, http://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.g00205396).

24. ***Takhtajaniella*** V.E.Avet., Sist. Evol. Vyssh. Rast.: 54. 1980.–[1 sp.]. —TYPE: *Takhtajaniella globosa* V.E.Avet.

Distribution area: Azerbaijan (Karabakh).

Takhtajaniella globosa V.E.Avet., Sist. Evol. Vyssh. Rast.: 54. 1980.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Online Resource 1. List of tables and fields in the AlyBase database

Table 1 – List of names of species and infraspecific taxa (list_of_names)

id_list_of_names – identification number
ntype – status of the name: accepted / provisionally accepted / doubtful / synonym / hybrid
hybrid – hybrid status of the name (YES/NO)
genus – genus name
species – species epithet
subsp – subspecies epithet
var – variety epithet
subvar – subvariety epithet
forma – forma epithet
authors – authorship of the name
genus_h (hybrid) – nothogenus name
species_h – nothospecies epithet
subsp_h – nothosubspecies epithet
var_h – nothovariety epithet
subvar_h – nothosubvariety epithet
forma_h – nothoforma epithet
authors_h – authorship of the name of hybrid
id_accepted_name – reference to the corresponding accepted name in this table
publication – place of the valid publication of the name of taxon
tribus – name of tribus
ntype_order – order of the display of the name (accepted name, synonyms ...)
id_basionym – reference to the corresponding basionym in this table
id_nomen_novum – reference to the corresponding replacement name in this table
syn_type – type of synonym: nomenclatural synonym / taxonomic synonym
is_isonym – isonym status of the name (YES/NO)
is_basionym – basionym status of the name (YES/NO)
id_replaced - reference to the corresponding replaced name in this table

Table 2 – Annotations to the list of names of species and infraspecific taxa (names_comments)

id_ names_comments – identification number
id_list_of_names – reference to the Table 1 – List of names of species and infraspecific taxa (list_of_names)
author – author of the annotation (name, city, country, and, optionally, institution)

annotation – text of the annotation to the list of names of species and infraspecific taxa
date_posted – date of the posting of the annotation
parent_id – identification number of the previous comment to the same name of species or infraspecific taxon
approved – annotation approved by the database management or not (YES/NO)

Table 3 – Chromosome number data (chrom_data)

id_ chrom_data – identification number
id_material – reference to the Table 8 – Origin of plant material from which chromosome number, ploidy level or genome size record was acquired and corresponding vouchers (material)
n – meiotic chromosome number published in original source
dn – 2n / mitotic chromosome number published in the original source
x – base chromosome number published in the original source
counted_by – chromosome number counted by, according to the original source / reference to the Table 16 – Person names (persons)
drawing – drawing of chromosomes published in the original source (YES/NO)
photo – photograph of chromosomes published in the original source (YES/NO)
idiogram – idiogram of chromosomes published in the original source (YES/NO)
karyotype – karyotype as published in the original source
ploidy_level – ploidy level as published in the original source (2x/3x/4x/5x/6x ...)
number_of_analysed_plants – number of analysed plants according to the original source
note – note by the database authors on the chromosome number record
id_list_of_names – standardised version of the name of taxon as published in the original source (spelling and authorship corrected), reference to the Table 1 – List of names of species and infraspecific taxa (list_of_names)
erroneous_record – unequivocally erroneus record (YES/NO)
erroneous_note – note explaining why this record is unequivocally erroneus
erroneous_marked_by – name of the person who marked this record as unequivocally erroneus, reference to the Table 16 – Person names (persons)
erroneous_marked_by_date – date when this record was marked as unequivocally erroneus
erroneous_input_by – name of the person who input the evidence on this record as unequivocally erroneus into the database, reference to the Table 16 – Person names (persons)
erroneous_input_by_date – date of the input of the evidence on this record as unequivocally erroneus into the database
doubtful_record – doubtful record (YES/NO)
doubtful_note – note explaining why this record is doubtful
doubtful_marked_by – name of the person who marked this record as doubtful, reference to the Table 16 – Person names (persons)
doubtful_marked_by_date – date when this record was marked as doubtful
doubtful_input_by – name of the person who input the evidence on this record as doubtful, reference to the Table 16 – Person names (persons)

doubtful_input_by_date – date of the input of the evidence on this record as doubtful into the database
duplicate_data – record already published at some other place (YES/NO)
duplicate_data_prob – record probably already published at some other place (YES/NO)
hoc_loco – record published for the first time in the cited source (YES/NO)
id_gs_data – reference to the Table 4 – Data on ploidy levels and genome size based on flow cytometric measurements (gs_data)
ploidy_level_revised – ploidy level revised by the database authors (2x/3x/4x/5x/6x ...)
exclude_from_statistics – whether record should be excluded from statistics (erroneous or doubtful records) (YES/NO)
public_note – text of the note that appears in the public output of the database

Table 4 – Data on ploidy levels and genome size based on flow cytometric measurements (gs_data)

id_gs_data – identification number
method – DAPI/PI/other - flow-cytometric method using 4′,6-diamidino-2-phenylindole (DAPI), propidium iodide (PI), or other fluorochrome
ploidy – estimated ploidy level as published in the original source
ch_number – estimated chromosome number as published in the original source
size_c – expression of the genome size (Cx/1C/2C)
size_from – value of the genome size or lower value of the genome size in the case that interval of values was provided in the original source
size_to – upper value of the genome size in the case that interval of values was provided in the original source
size_units – units expressing the values of the genome size (pg/Mbp)
plants_analysed – number of analysed plants from population (locality)
number_analyses – number of flow-cytometric analyses
note – note by the database authors on the ploidy levels and genome size records, based on flow cytometric measurements
ploidy_revised – ploidy level revised by the database authors

Table 5 – Names of taxa for which chromosome number, ploidy level or genome size **records were published, references to publications (name_publ)**

id_name_publ – identification number
name_as_published – name of taxon as published in the original source (including possible errors)
id_list_of_names – standardised version of the name of taxon as published in the original source (spelling and authorship corrected), reference to the Table 1 – List of names of species and infraspecific taxa (list_of_names)
id_publications – reference to the Table 14 – Publications in which chromosome number, ploidy level or genome size record was published (publications)

note – note by the database authors
page – page number/pages numbers on which chromosome number/ploidy level/genome size record was published

Table 6 – Revision of the identification of plant material (rev_history)

id_rev_history – identification number
id_chrom_data – reference to the Table 3 – Chromosome number data (chrom_data)
(since the Table 3 is the main reference table that connect all others, it is sufficient here to have a reference solely to this table).
revised_name – revised name of taxon as given by the author of the revision (including possible errors)
id_list_of_names – reference to the standardised version of the name of taxon as given by the author of the revision (spelling and authorship corrected) in Table 1 – List of names of species and infraspecific taxa (list_of_names)
revised_by – name of the author of the revision of the identification of plant material, reference to the Table 16 – Person names (persons)
h_date – date of the revision of the identification of plant material
note – note by the author of the revision of the identification of plant material

Table 7 – Annotations to the chromosome number/ploidy level records (chrgs_comments)

id_chrgs_comments – identification number
id_chrom_data – reference to the Table 3 – Chromosome number data (chrom_data)
(since the Table 3 is the main reference table that connect all others, it is sufficient here to have a reference solely to this table).
author – author of the annotation (name, city, country, and, optionally, institution)
annotation – text of the annotation to the chromosome number/ploidy level record
date_posted – date of the posting of the annotation
parent_id – identification number of the previous comment to the same chromosome number/ploidy level record
approved – annotation approved by the database management or not (YES/NO)

Table 8 – Origin of plant material from which chromosome number, ploidy level or genome size **record was acquired and corresponding vouchers (material)**

id_ material – identification number
id_name_publ – reference to the Table 5 – Names of taxa for which chromosome number, ploidy level or genome size records were published, references to publications (name_publ)
country – country name
geographical_district – geographic district name (text)

id_phytogeographic_district – reference to the Table 9 – Phytogeographic districts in the Slovak Republic – applicable to the localities in the Slovak Republic only (phytogeographic_district)

central_european_mapping_unit – Central European mapping scheme grid unit (a 10' longitude × 6' latitude area, Niklfeld, 1971)

closest_village_town – closest city / town / village as given in the original source

altitude – altitute above sea level (m) as given in the original source

exposition – exposition of the collecting place as given in the original source

description – description of the locality as given in the original source

collected_by – name of the collector as given in the original source, reference to the Table 16 – Person names (persons)

collected_date – date of the collection of material as given in the original source

id_persons – name of the person who identified material as given in the original source, reference to the Table 16 – Person names (persons)

voucher_specimen_no – voucher specimen number/numbers as given in the original source

deposited_in – place of deposit of the voucher specimen number as given in the original source

coordinates_lat – geographic latitude (degrees, minutes, seconds, N/S) as given in the original source

coordinates_lon – geographic longitude (degrees, minutes, seconds, E/W) as given in the original source

id_world_4 – reference to the Table 14 – Publications in which chromosome number, ploidy level or genome size record was published (publications)

administrative_unit – administrative unit of the country to which locality of collection belongs to as given in the original source

coordinates_georef_lat – geographic latitude (degrees, minutes, seconds, N/S) ascertained by the authors of the database

coordinates_georef_lon – geographic longitude (degrees, minutes, seconds, N/S) ascertained by the authors of the database

coordinates_lat_dec - geographic latitude (floating point number, positive if northern, negative if southern), used for range search, obtained as follows:
if coordinates_lat is not empty, convert coordinates_lat
else if coordinates_georef_lat is not empty, convert coordinates_georef_lat
else leave empty

coordinates_lon_dec - geographic longitude (floating point number, positive if eastern, negative if western), used for range search, obtained as follows:
if coordinates_lon is not empty, convert coordinates_lon
else if coordinates_georef_lon is not empty, convert coordinates_georef_lon
else leave empty

Table 9 – Phytogeographic districts in the Slovak Republic – applicable to the localities in the Slovak Republic only **(phytogeographic_district)**

id_phytogeographic_district – identification number

code – number of the phytogeographic district in the Slovak Republic (Futák 1984)
district_name – name of the phytogeographic district (Futák 1984)

Table 10 – Levels 1 according to the World Geographical Scheme for Recording Plant Distributions (Brummit 2001) (world_l1)

id_world_l1 – identification number
description – name of the unit

Table 11 – Levels 2 according to the World Geographical Scheme for Recording Plant Distributions (Brummit 2001) (world_l2)

id_world_l2 – identification number
description – name of the unit
id_world_l1 – reference to the Table 10 – Levels 1 according to the World Geographical Scheme for Recording Plant Distributions (Brummit 2001) (world_l1)
iso_code – ISO code of the unit

Table 12 – Levels 3 according to the World Geographical Scheme for Recording Plant Distributions (Brummit 2001) (world_l3)

id_world_l3 – identification number
description – name of the unit
id_world_l2 – reference to the Table 11 – Levels 2 according to the World Geographical Scheme for Recording Plant Distributions (Brummit 2001) (world_l2)
iso_code – ISO code of the unit

Table 13 – Levels 4 according to the World Geographical Scheme for Recording Plant Distributions (Brummit 2001) (world_l4)

id_world_l4 – identification number
description – name of the unit
id_world_l3 – reference to the Table 12 – Levels 3 according to the World Geographical Scheme for Recording Plant Distributions (Brummit 2001) (world_l3)
iso_code – ISO code of the unit

Table 14 – Publications in which chromosome number, ploidy level or genome size **record was published (publications)**

id_publications – identification number
paper_author – author/authors of the paper, chapter, abstract or book in which record is published
paper_title – title of the paper, chapter, abstract or book in which record is published
series_source – title of the series in which record is published (e.g., IAPT/IOPB Chromosome Data), or title of the book in which chapter is published, or proceedings in which abstract is published
volume – volume of the journal in which record is published
issue – issue of the journal in which record is published
publisher – publisher of the book or proceedings in which record is published
editor – editor/editors of the book or proceedings in which record is published
year – year of publishing of the contribution in which record is published
pages – pages of the contribution in which record is published
journal_name – journal in which record is published
input_to_db_by – name of the person who put the record into the database, reference to the Table 16 – Person names (persons)
input_date – date of input of the record into the database
note – note by the person who put the record into the database
checked_by – name of the person who checked the record in the database, reference to the Table 16 – Person names (persons)
checked_date – date of checking of the record in the database
corrected_in_db_by – name of the person who corrected the record in the database, reference to the Table 16 – Person names (persons)
correction_date – date of correcting of the record in the database
id_publ_types – reference to the Table 15 – Types of publications in which chromosome number, ploidy level or genome size record was published (publ_types)

Table 15 – Types of publications in which chromosome number, ploidy level or genome size **record was published (publ_types)**

id_publ_types – identification number
name – type of publication (journal / book / manuscript / chapter in the book / series of chromosome number/DNA ploidy level reports in journal)

Table 16 – Person names (persons)

id_persons – identification number
pers_name – full name of the person

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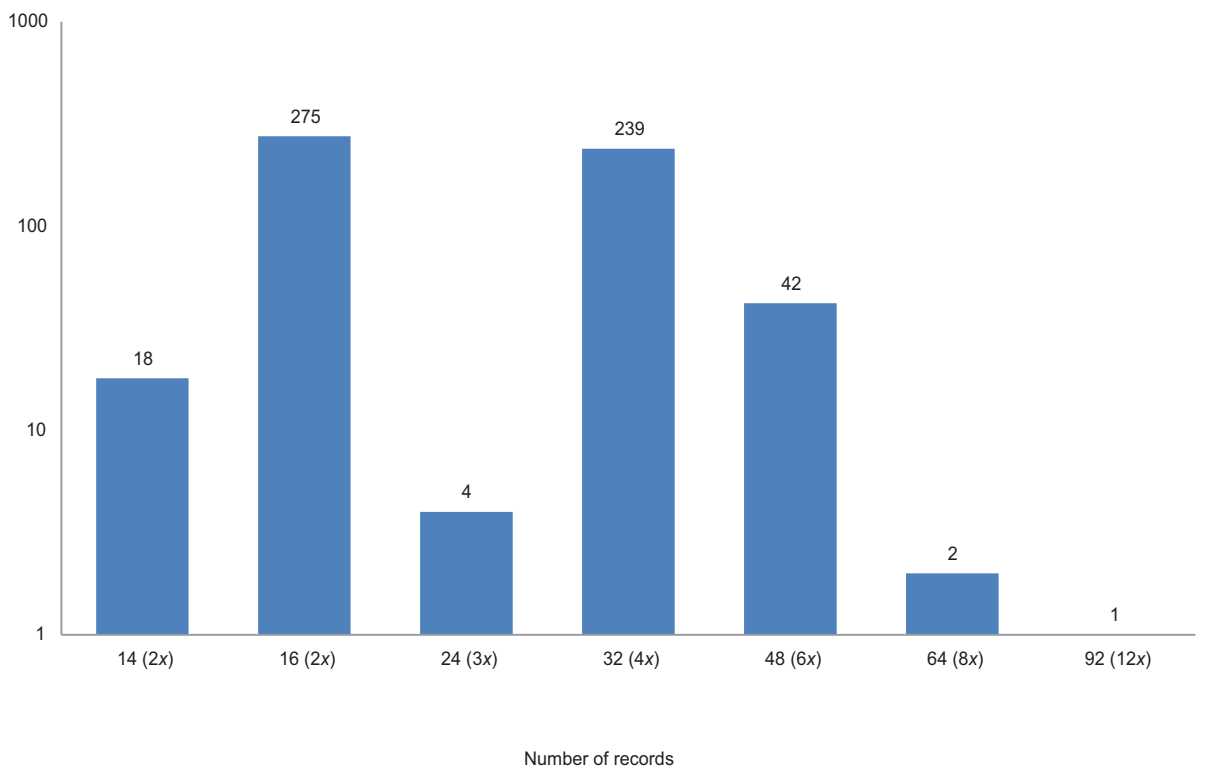
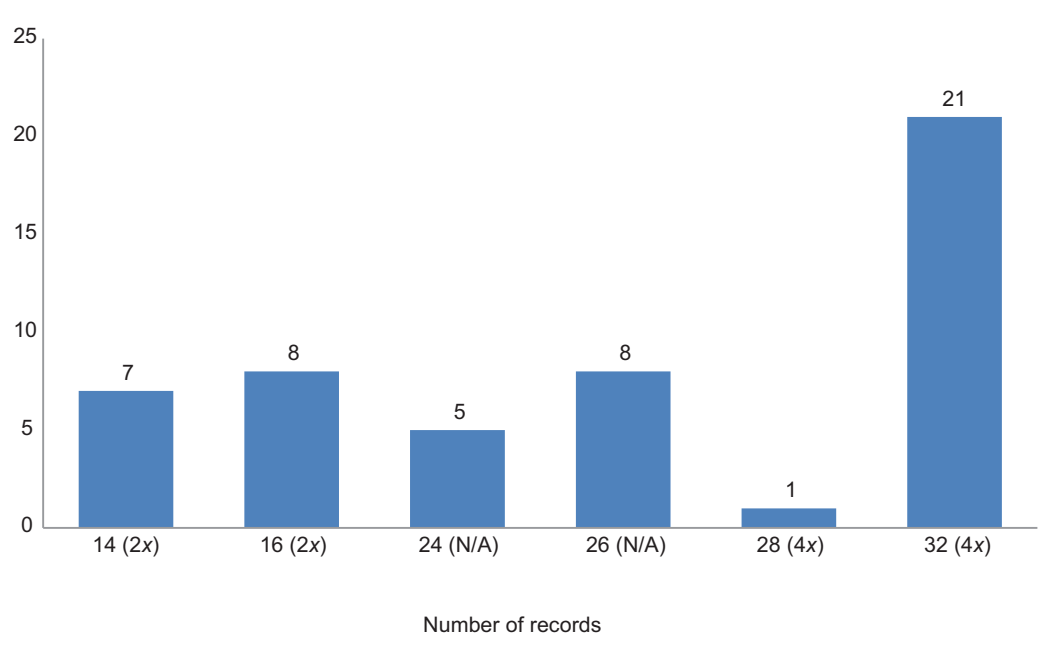
Online Resource 2. Distribution of chromosome numbers and ploidy levels in the genera *Alyssum*, *Clypeola, Hormathophylla* and *Odontarrhena*. For the construction of this histogram, haploid chromosome numbers were multiplied by two and ploidy level estimates were assigned to the relevant chromosome numbers.

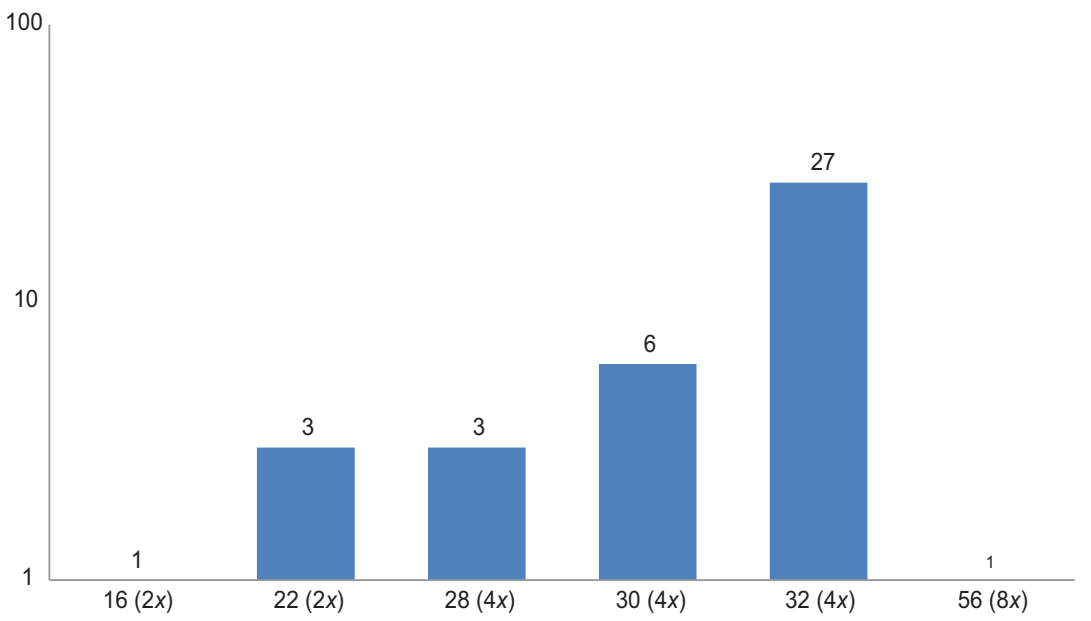
genus *Alyssum*



genus *Clypeola*



genus *Hormathophylla*



genus *Odontarrhena*