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STUDIES IN THE THYMELAEACEAE III:* the status of Diarthron, Dendrostellera, Stelleropsis and Stellera

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ABSTRACT. Following morphological and anatomical studies, the genera *Dendrostellera* and *Stelleropsis* are reduced to subgenera of *Diarthron* and as a result of this 20 new combinations are made. *Stellera*, however, is maintained as a separate genus.

During a comprehensive study of the Thymelaeaceae, morphological and anatomical work was carried out on four genera, *Diarthron*, *Dendrostellera*, *Stelleropsis* and *Stellera*, all of Thymelaeaceae subfamily Thymelaeoideae and occurring in the SW and C Asiatic region. The important characters of the genera are summarized in Table 1.

As a result of the study it was decided that *Diarthron*, *Dendrostellera* and *Stelleropsis* could not be maintained as separate genera. The morphological characters used to differentiate *Dendrostellera* from *Stelleropsis* are the densely sericeous-villous lower half of the perianth, acrodromous as opposed to eucamptodromous venation, the conical, rarely ovoid, stigma, and a generally more woody habit. Of these characters only the first two are constant diagnostics and they are not of sufficient magnitude to warrant generic separation. *Diarthron* differs from these genera mainly in its annual habit (see Table 1) and again does not merit generic rank; in this account I have therefore reduced all three previously recognized genera to subgenera of *Diarthron*, the name which has priority. As a result of the widened circumscription *Diarthron* now includes annual herbs (subgen. *Diarthron*), suffrutices (subgen. *Stelleropsis* and *Dendrostellera*) and shrubs (subgen. *Dendrostellera*) and in this respect parallels the habit differences occurring in *Thymelaea* (Kit Tan, 1978, 1980).

Subgeneric rather than sectional rank has been adopted for the three subgroups of the recircumscribed *Diarthron* because the morphological discontinuities between them are of a different order to those I have used in distinguishing sections of the genus *Thymelaea*. The level of infrageneric grouping adopted in some instances seems to be a matter of chance, but consistency of treatment must be the chief consideration, the 'gaps' between the groups being, as far as possible, of similar magnitude in different genera.

Diarthron, with its three subgenera *Diarthron*, *Dendrostellera* and *Stelleropsis*, is thought to be more closely related to *Stellera* than to any other genus in the northern hemisphere. *Thymelaea* shares the annual (sect. *Ligia*) and suffrutescent habit (sect. *Thymelaea*) with *Diarthron* but this certainly does not imply a common ancestry as habit is an adaptation to evade or withstand extreme effects of summer drought and winter cold in steppe regions. Although one might expect a suffrutescent habit also to result from the adverse effect of heavy grazing, it should be noted that field notes accompanying herbarium material often state that 'plants are so toxic and unpalatable that not even goats will touch it . . .'.

* Studies in the Thymelaeaceae I & II. *Notes RBG Edinb.* 38:149–164 & 189–246 (1980).

TABLE 1

Characters in *Stellera*, *Stelleropsis*, *Dendrostellera* and *Diarthron*

Stellera	**Stelleropsis**	**Dendrostellera**	**Diarthron**
Suffrutescent; stems unbranched, woody at base	Suffrutescent; stems unbranched or sparingly branched, woody at base or up to middle	Shrubby or suffrutescent; stems branched, woody up to middle	Annual herbs
Leaves alternate	Alternate	Alternate	Alternate
Inflorescence axis not elongating in fruit	Elongating	Elongating	Elongating
Bracts forming involucre	Bracts absent	Bracts absent	Bracts absent
Flowers hermaphrodite	Hermaphrodite	Hermaphrodite	Hermaphrodite
Perianth persistent in lower part, deciduous above ovary	As in *Stellera*	As in *Stellera*	As in *Stellera*
Perianth lobes 5–6; stamens 10–12	Lobes 4; stamens 8	Lobes 4; stamens 8	Lobes 4; stamens 4 or 8
Hypogynous disc unilateral, ligulate, margin entire	Disc oblique, margins entire or shallowly lobed	Disc cup-shaped, margins entire or obliquely lobed	Disc absent
Style terminal	Terminal	Terminal	Terminal or sub-terminal

Stigma globose, centrally depressed	Rarely ovoid, usually globose and centrally depressed	Conical, rarely ovoid	Clavate
Pericarp membranous at maturity	Membranous	Membranous	Membranous
Fruit enclosed in glabrous lower part of perianth	Enclosed in glabrous or pubescent lower part of perianth	Enclosed in densely sericeous-villous lower part of perianth	Enclosed in slightly inflated lower part of perianth
Internal phloem fibres in stem absent	Absent	Absent	Absent
Leaves amphi- or hypostomatic	Amphistomatic	Amphistomatic	Amphistomatic
Stomata anomocytic to complex modified tetracytic	Modified tetracytic or indistinct anomocytic	Anisocytic or modified tetracytic	Modified tetracytic
Anticlinal walls of leaf epidermis straight	Weakly undulated, straight in costal region	Straight or weakly undulated	Undulated
Sclereids absent in leaf	Absent	Present	Present
Venation acrodromous, suprabasal	Eucamptodromous	Acrodromous, basal	Eucamptodromous
Leaves isobilateral or weakly dorsiventral	Isobilateral	Isobilateral or weakly dorsiventral	Isobilateral or dorsiventral
Vascular system of one main bundle in leaf with sclerenchyma not extending to epidermis	As in *Stellera*	As in *Stellera*	As in *Stellera*
Internal phloem absent in leaves	Absent	Absent	Absent

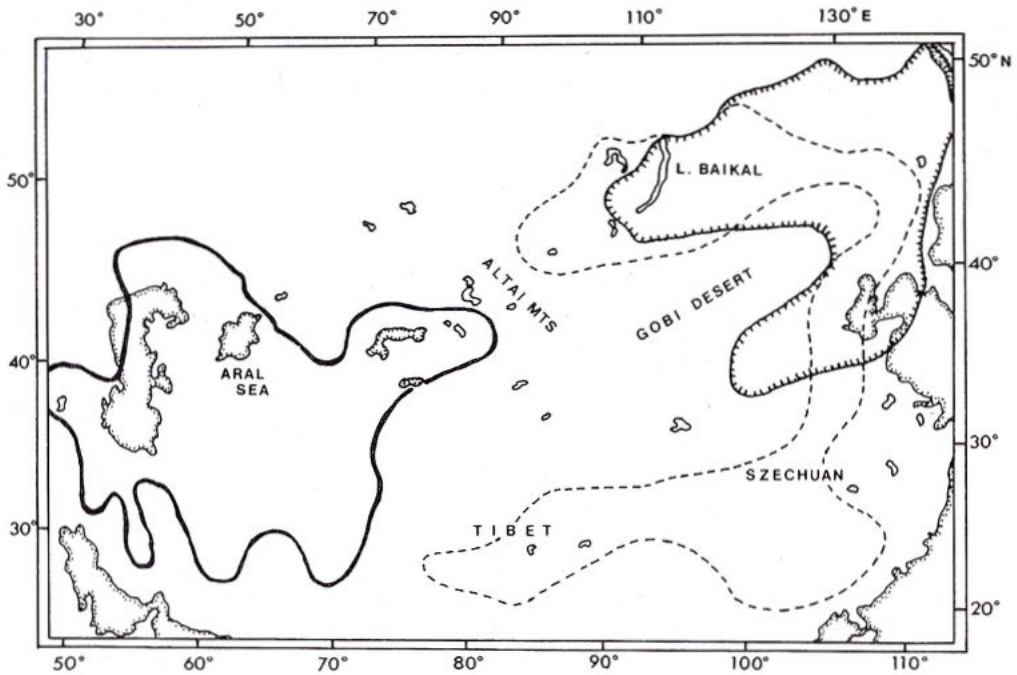

FIG. 1. Distribution of *Stellera* and *Diarthron* subgen. *Diarthron*: *S. chamaejasme*, broken line; *D. vesiculosum*, continuous line; *D. linifolium*, hatched line.

Stellera can be easily distinguished from the *'Diarthron-Dendrostellera-Stelleropsis'* complex by its inflorescence axis which never elongates during or after anthesis (the inflorescence thus remaining capitate), and the upper leaves which simulate involucral bracts. The flowers are 5–6-merous, not 4-merous, and the hypogynous disc unilateral and ligulate.

Only the type of the genus, *S. chamaejasme* L. which has two subspecies, has been studied. I have not found any other C Asiatic species, and as the characters appear to be distinct and uniformly constant, *Stellera* should be maintained as a separate and probably monotypic genus.

Stellera L., Sp. Pl. 559 (1753); diss. Dassow, Nov. Pl. Gen. no. 1053 (1747), *p.p.* non *Stellera* Turcz. (1840).
Type species. *Stellera chamaejasme* L., *loc. cit.* (1753).
Type. Described from Siberia.
Monotypic. Wholly Asiatic and widespread, ranging from the W Himalayas, through Tibet, to Yunnan and Szechuan, Hupeh, Manchuria, Mongolia and Lake Baikal.

SYSTEMATIC TREATMENT OF DIARTHRON

Diarthron Turcz. in Bull. Soc. Nat. Mosc. 5:204 (1832).
Incl.: *Dendrostellera* van Tieghem, *Stelleropsis* Pobed.

Annuals, suffrutescent or suffruticose perennials. Stems virgate, simple or branched at base. Leaves simple, entire, exstipulate, alternate, petiolate or subsessile, herbaceous or subcoriaceous. Inflorescence terminal, subcapitate, becoming spicate or racemose; axis elongating in fruit. Bracts absent. Flowers

hermaphrodite, shortly pedicellate. Perianth actinomorphic, tubular, petaloid, 4-lobed, upper part deciduous. Stamens 4 or 8, adnate to perianth, included or upper whorl semi-exserted. Ovary 1-locular, pericarp membranous at maturity. Fruit indehiscent, 1-seeded, dry.

KEY TO SUBGENERA

1a. Herbaceous annuals; flowers 1.5–5 mm .....I. Subgen. *Diarthron*
1b. Suffrutescent or shrubby perennials; flowers 6–15 mm.....2
2a. Lower half of perianth sericeous-villous .....II. Subgen. *Dendrostellera*
2b. Lower half of perianth glabrous or sparsely pubescent
III. Subgen. *Stelleropsis*

SYNOPTIC DESCRIPTIONS OF SUBGENERA

I. Subgen. **Diarthron**

Annuals with slender, ± dichotomously branched stems. Inflorescence becoming laxly racemose. Lower half of perianth slightly inflated-membranous in fruit. Stamens 4 or 8, included. Hypogynous disc absent. Ovary subsessile, glabrous; style terminal or becoming subterminal, short; stigma clavate. Ditypic. Type species. *Diarthron linifolium* Turcz., *loc. cit.* (1832).

1a. Stamens 4 .....Sect. *Diarthron*
1b. Stamens 8.....Sect. *Arthrochlamys*

Sect. **Diarthron**

Syn.: *Eu-diarthron* C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:359 (1843), *pro ser.*
Distribution: E Asia–E Siberia, NE China and Mongolia (Fig. 1).
Type species. *Diarthron linifolium* Turcz., *loc. cit.* (1832).
Type. [N Mongolia] in lapidosis ad flum. Tschikoi Sibiriae Transbaicalensis, *Turczaninow* Enum. Pl. Chin. no. 28 (holo. LE, iso. G).
Monotypic.

Sect. **Arthrochlamys** C. A. Meyer, *loc. cit.* (1843).
Distribution: Disjunct in European Russia, SW and C Asia; geographically separated from the area of *D. vesiculosum* by Altai Mts and Gobi Desert (Fig. 1).
Type species. *Diarthron vesiculosum* (Fisch. & Mey. ex Kar. & Kir.) C. A. Meyer, *loc. cit.* (1843).
Type. [USSR] in Turcomania boreali, *Karelin* Enum. Pl. Turcom. no. 790 (holo. LE, iso. G).
Monotypic.

II. Subgen. **Dendrostellera** (C. A. Meyer) Kit Tan, **comb. et stat. nov.**

Syn.: *Stellera* sect. *Dendrostellera* C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:359 (1843).
Dendrostellera (C. A. Meyer) van Tieghem in Ann. Sci. Nat. Bot. 7(17):199 (1893); Bull. Soc. Bot. France 40:74 (1893), *pro. gen.*

Suffrutescent or suffruticose plants, stems branched at or near base. Leaves

herbaceous or subcoriaceous. Inflorescence axis and lower half of perianth densely sericeous-villous. Stamens 8, included, or upper whorl semi-exserted. Hypogynous disc cup-shaped, margins entire or obliquely lobed. Ovary subsessile, villous or hirsute at apex; style terminal, short; stigma conical, rarely ovoid.

Distribution: Only one species, *D. lessertii*, is widespread in SW Asia. The others are endemic to certain localized areas in Soviet Central Asia (Fig. 2).

Type species. **Diarthron lessertii** (Wikstr.) Kit Tan, **comb. nov.**

Syn.: *Passerina lessertii* Wikstr. in Kungl. Svenska Vet.-Akad. Handl., 341 (1818)—Basionym. Type. Described from Persia, *de Lessert* (holo. C).

Passerina persica Boiss., Diagn. ser. 1(7):85 (1846). type. [Iran] in collibus apricis prope urbem Schiraz [3 v 1842], *Kotschy* 321 (holo. G).

Dendrostellera persica (Boiss.) Pobed. in Not. Syst. (Leningrad) 16:252 (1954).

Dendrostellera glaucescens Pobed. in Not. Syst. (Leningrad) 16:254 (1954). Type. Iran. Ghilan, in aridis inter Kilischun et Pul-i-Ombu, 24 vii 1902, *Alexeenko* 419 (holo. LE).

Other species:

Diarthron ramosissima (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Dendrostellera ramosissima* Pobed. in Not. Syst. (Leningrad) 16:252 (1954).
Type. [Iran] Irania austro-orientalis, Birdshan [Birjand] in arenis prope Bagran-Kucha, 10 [30] ix 1925, *Czerniakowska* 287 (holo. LE).

Diarthron stachyoides (Schrenk) Kit Tan, **comb. nov.**
Basionym: *Stellera stachyoides* Schrenk in Bull. Phys.-Math. Acad. (Pétersb.) 10:253 (1842); Enum. Pl. Nov. 2:16 (1842).
Type. [USSR] flum. Emel et Lepsa, *Karelin & Kirilow* 1934 (holo. LE, iso. G).

Diarthron arenaria (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Dendrostellera arenaria* Pobed. in Fl. URSS 15:689 (1949).
Type. [USSR] arenae Kzyl-Kum austro-orientalis; puteum Abischkuduk, 27–28 vii 1931, *E. A. Dubjans* (holo. LE).

Diarthron linearifolia (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Dendrostellera linearifolia* Pobed., *loc. cit.* (1949).
Type. [USSR] Asia media Kzyl-Kum prope puteum Egali, 27 [14] vi 1914, *A. I. Michelson* (holo. LE).

Diarthron macrorhachis (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Dendrostellera macrorhachis* Pobed., *op. cit.*, 690 (1949).
Type. [USSR] in decursu inferiore fluminis Amu-darja, in declivibus montium Sultan-uiz-dagh, prope mt. Scheph-dsheli, 10 v 1915, *H. M. Krascheninnikov* 155 (holo. & iso. LE).

Diarthron olgae (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Dendrostellera olgae* Pobed., *op. cit.*, 691 (1949).
Type. [USSR] Prov. Krasnovodsk, prope stationem ferroviae Dzhelila, 6 v 1912, *Lipsky* 2661 (holo. & iso. LE).

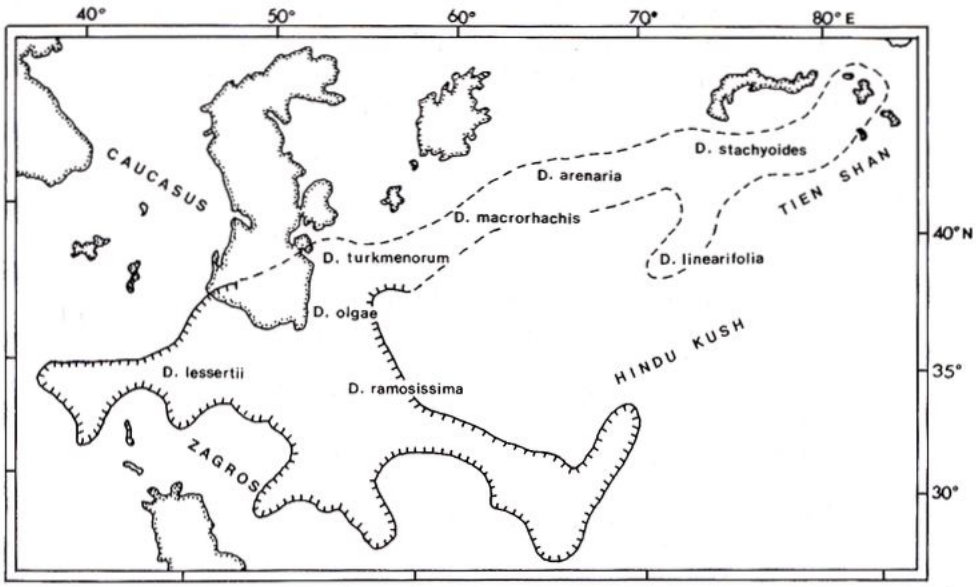

FIG. 2. Distribution of *Diarthron* subgen. *Dendrostellera*: as far as is known, the species occur only where marked apart from *D. lessertii* the distribution of which is indicated by the hatched line.

Diarthron turkmenorum (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Dendrostellera turkmenorum* Pobed., *op. cit.*, 691 (1949).
Type. [USSR] Krasnovodsk, in arenis prope stationem Achcza-Kuima, 4 v 1911, *A. Seidmuratov* (holo. & iso. LE).

III. Subgen. **Stelleropsis** (Pobed.) Kit Tan, **comb. et stat. nov.**
Syn.: *Stellera* sect. *Chamaestellera* C. A. Meyer in Bull. Phys.-Math. Acad. (Pétersb.) 1:359 (1843), *p.p. excl. typ.*
Stelleropsis Pobed. in Not. Syst. (Leningrad) 12:148 (1949), *pro. gen.*
Suffrutescent perennials, stems simple or sparingly branched at base. Leaves herbaceous. Inflorescence-axis and lower half of perianth not sericeous-villous. Stamens 8, included. Hypogynous disc oblique, margins entire, shallowly crenate or 3-lobed. Ovary stipitate or subsessile, villous-pilose at apex; style terminal, short; stigma ovoid or globose.
Type species. **Diarthron altaica** (Thieb.) Kit Tan, **comb. nov.**
Basionym: *Stellera altaica* Thieb. in Pers. Syn. 1:436 (1805).

1a. Stems herbaceous, slightly woody at base; flowers pink, white within
Sect. *Stelleropsis*
1b. Stems thick-woody at base or up to middle; flowers yellowish
Sect. *Turcomanica*

Sect. **Stelleropsis**
Syn.: *Altaicae* Pobed. in Not. Syst. (Leningrad) 12:149 (1949), *pro ser.*
Distribution: restricted to C Asia (Fig. 3). The species are assumed to have a narrow distribution, this is partly due to the narrower species concept held by Pobedimova and also to under-collecting.
Type species. *Diarthron altaica* (Thieb.) Kit Tan
Syn.: *Stelleropsis altaica* (Thieb.) Pobed., *loc. cit.* (1949).
Type. [USSR] in montibus altaicis, *Thiebaud* (holo. MPU — *n.v.*).

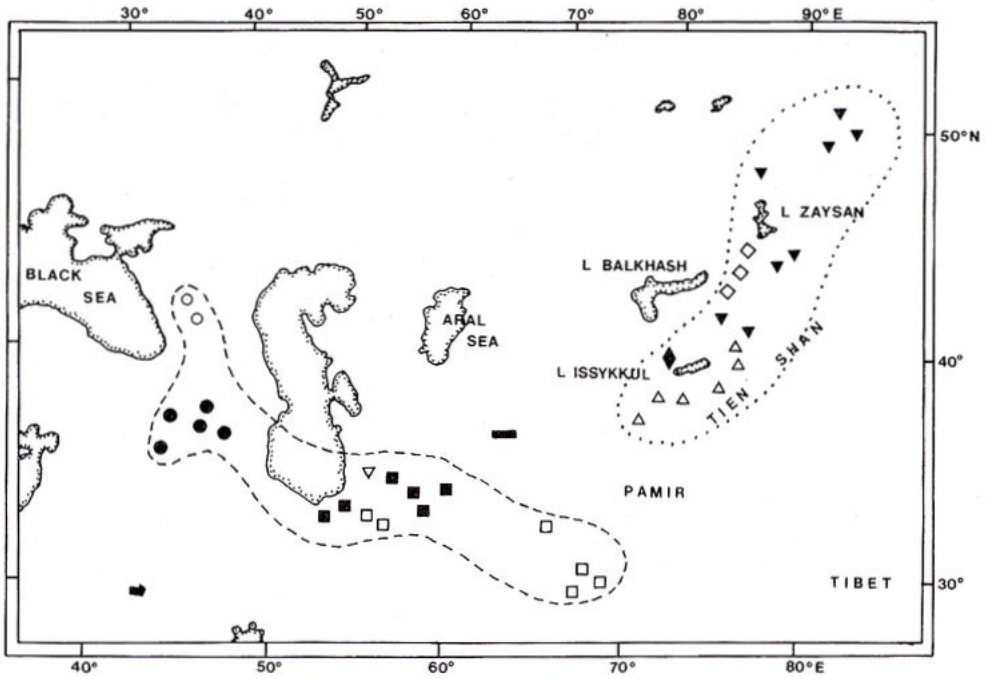

FIG. 3. Distribution of *Diarthron* subgen. *Stelleropsis*. Sect. *Stelleropsis* (dotted line): ▼ *D. altaica*; ◇ *D. tarbagataica*; ◆ *D. issykkulensis*; △ *D. tianschanica*. Sect. *Turcomanica* (broken line): ▽ *D. turcomanica*; ■ *D. antoninae*; □ *D. iranica*; ○ *D. caucasica*; ● *D. magakjanii*.

Other species:

Diarthron tarbagataica (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Stelleropsis tarbagataica* Pobed., *op. cit.*, 151 (1949).
Type. [USSR] Tarbagatai occidentalis, Tanatsch, vi 1841, *Schrenk* 162 (holo. & iso. LE).

Diarthron issykkulensis (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Stelleropsis issykkulensis* Pobed., *op. cit.*, 152 (1949).
Type. [USSR] litus septentrionale lacus Issykkul, Ovgirte, sovchos Tamtschi, 10 [20] v 1930, *Nikitina & Tarnowski* (holo. LE).

Diarthron tianschanica (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Stelleropsis tianschanica* Pobed., *op. cit.*, 153 (1949).
Type. [USSR] Kirghisia in valle Arpa, Teren-Komandy, tundra alpina, 1 vii 1913, *B. Saposhnikov* (holo. LE).

Sect. **Turcomanica** (Pobed.) Kit Tan, **stat. nov.**
Syn.: *Turcomanicae* Pobed., *op. cit.*, 155 (1949), *pro ser.*
Distribution: Caucasus, Turkmenia, N & NW Iran, E Afghanistan (Fig. 3).
Type species. **Diarthron turcomanica** (Czern.) Kit Tan, **comb. nov.**
Basionym: *Stellera turcomanica* Czern. in Feddes Rep. 27:273 (1930), *p.p.*
Type. [USSR] Turcomania, in montes Palysak, ad fines Persiae in Zona Juniperi . . . *Czerniakowska* [Iter Karakalense 1916] 764 (lecto. LE).

Other species:

Diarthron antoninae (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Stelleropsis antoninae* Pobed., *op. cit.*, 157 (1949).
Type. [USSR] Turcomania. Kopet-dagh, distr. Geoktepe prope puteum Prochladnoe, in declivibus lapidosis prope mont. Kisilchasar, 27 vi 1934, *A. G. Borissova* 317 (holo. LE).
Syn.: *Stellera turcomanica* Czern. in Feddes Rep. 27:273 (1930), *p.p. excl. lecto.*
Type. [USSR, Transcaspia] ad fines Persiae Sulukü [Saratowka] in glareosis montium, *Sintenis* 1900:833 (holo. LE, iso. E), as *Aethionema* sp.

Diarthron iranica (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Stelleropsis iranica* Pobed., *op. cit.*, 158 (1949).

subsp. **iranica**
Syn.: *Stellera altaica* Thieb. var. *minor* Boiss., Fl. Or. 4:1051 (1879), *p.p.*
Type. Iran, prope Schahrud et Tasch, *Bunge* (holo. LE).

subsp. **pilosa** (B. Peterson) Kit Tan, **comb. nov.**
Basionym: *Stelleropsis iranica* Pobed. subsp. *pilosa* B. Peterson in Rech., Fl. Iranica 95:15 (1972).
Type. [E Afghanistan, Ghazni, 2300 m] *Koeie* 3846 (holo. C, iso. W).

Diarthron caucasica (Pobed.) Kit Tan, **comb. nov.**
Basionym: *Stelleropsis caucasica* Pobed., *op. cit.*, 161 (1949).
Type. [USSR] Caucasus occidentalis. In rupestribus subalpinis versus rivulum Kassaut . . . 5800–6000 ft, 16[3] vii 1829, *C. A. Meyer* (holo. LE—*n.v.*).

Diarthron magakjanii (Sosn.) Kit Tan, **comb. nov.**
Basionym: *Stellera magakjanii* Sosn. in Dokl. Akad. Nauk Arm. SSSR 7(3):138 (1947).
Type. [USSR, Nakhichevan] distr. Mikoyan in loco Kajadere in pascuis prope Gnishik, 15 vi 1940, *A. Magakjan* (holo. TBI).

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