

A taxonomic note on *Sterigmostemum* and related genera (*Anchonieae*, *Cruciferae*)

Заметка о *Sterigmostemum* и близких родах (*Anchonieae*, *Cruciferae*)

D. A. German¹, I. A. Al-Shehbaz²

¹Heidelberg University, Centre for Organismal Studies,
Department of Biodiversity and Plant Systematics
Im Neuenheimer Feld, 345, D-69120, Heidelberg, Germany;
South-Siberian Botanical Garden, Altai State University
Lenina Ave., 61, Barnaul, 656049, Russia
oreoloma@rambler.ru

²Missouri Botanical Garden
P. O. Box 299, St. Louis, Missouri, 63166-0299, USA
ihсан.al-shehbaz@mobot.org

Д. А. Герман¹, И. А. Аль-Шебаз²

¹Гейдельбергский университет, Центр исследований
организмов, кафедра биоразнообразия и систематики
растений
Им Нойенхаймер Фельд, 345, D-69120, Гейдельберг, Германия;
Южно-Сибирский ботанический сад, Алтайский
государственный университет
пр. Ленина, 61, Барнаул, 656049, Россия
oreoloma@rambler.ru

²Миссурийский ботанический сад
а/я 299, Сент-Луис, Миссури, 63166-0299, США
ihсан.al-shehbaz@mobot.org

Abstract. Our critical re-evaluation of diagnostic characters of *Anchonium* DC., *Oreoloma* Botsch., *Sterigmostemum* M. Bieb., and *Zerdana* Boiss. on the basis of phylogenetic evidence resulted in merging these genera. *Anchonium* and *Zerdana* are synonymized with *Sterigmostemum*, and relevant combinations are validated. A checklist and a key for the expanded *Sterigmostemum* are presented. *Synstemon* Botsch. is found unrelated to this genus and should be transferred from the tribe *Anchonieae* DC. to *Euclidieae* DC.

Keywords: *Anchonium*, *Brassicaceae*, Middle East, *Oreoloma*, SW and Central Asia, taxonomy, *Zerdana*.

Аннотация. На основании критической ревизии диагностических признаков родов *Anchonium* DC., *Oreoloma* Botsch., *Sterigmostemum* M. Bieb. и *Zerdana* Boiss. в свете имеющихся молекулярно-филогенетических данных сделан вывод о целесообразности признания единственного таксона родового ранга вместо четырех. *Anchonium* и *Zerdana* впервые отнесены к синонимам *Sterigmostemum*, обнародованы соответствующие комбинации. Приведен конспект и ключ для определения видов *Sterigmostemum* s. l. Род *Synstemon* Botsch. предложено исключить из трибы *Anchonieae* DC. и перевести в *Euclidieae* DC.

Ключевые слова: Ближний Восток, систематика, Юго-Западная и Центральная Азия, *Anchonium*, *Brassicaceae*, *Oreoloma*, *Zerdana*.

Sterigmostemum M. Bieb. was established to accommodate two species originally described under *Cheiranthus* L. (= *Erysimum* L.) that have connate pairs of median (long) stamens and presumably indehiscent (in fact partly dehiscent in *S. caspicum* (Lam.) Rupr.) fruits (Marschall von Bieberstein, 1819). Unlike the majority of genera of the mustard family (*Brassicaceae* Burnett or *Cruciferae* Juss.), both morphological limits and affinities of *Sterigmostemum* did not undergo drastic changes during the history of its systematics. The main update of the generic characteristics was adding the species with completely dehiscent fruit (Jacquemoud, 1988; Appel, Al-Shehbaz, 2003). It is also a relatively rare case within *Cruciferae* that the very first tribal affiliation proposed for the genus (*Anchonieae* DC.; Candolle, 1821a, b) is being accepted nowadays (Al-Shehbaz, 2012). Three genera, *Anchonium* DC. (Candolle, 1821a, b),

Zerdana Boiss. (Boissier, 1842), and *Oreoloma* Botsch. (Botschantzev, 1980) were described and traditionally considered as closely related to *Sterigmostemum*, and this morphology-based affinity was subsequently confirmed by molecular phylogenetic studies (Warwick et al., 2007; German et al., 2009; Couvreur et al., 2010) proving the monophyly of the group in question.

Morphology and taxonomy of *Sterigmostemum* and related genera were the focus of a number of studies during past four decades (Dvořák, 1972; Botschantzev, 1980; Léonard, 1980, 1988; Kamelin, German, 2001; Sonboli et al., 2001, 2006; Appel, Al-Shehbaz, 2003) among which the most extensive and detailed are the monographic treatments of Jacquemoud (1984b, 1985, 1988). As evidenced by thorough analyses of the last author, accompanied by the data of Dvořák (1972), Zhou et al. (2001), Appel, Al-Shehbaz (2003) and own obser-

vations, *Sterigmostemum* (with exclusion of more distant *Petiniotia* J. Léonard) shares with *Anchonium*, *Oreoloma*, and *Zerdana* nearly all features, both common to the tribe (uniform dense indumentum of many-branched dendritic trichomes usually throughout the plant, often presence of multicellular glands, non-auriculate cauline leaves poorly differentiated into petiole and blade, distinctly lobed stigmas, base chromosome number of $n = 7$, etc.) and specific of all the four genera (filaments of median stamens united into pairs, terete to rarely subquadrangular, somewhat torulose fruits often gradually tapering towards apex, diverged stigma lobes, oblong and wingless seeds, and incumbent cotyledons). The latter character combination is not found elsewhere in the tribe *Anchonieae*, and the connation of median staminal filaments does not occur in any other genus of the tribe (except for problematic *Synstemon* Botsch.; see below). Most of the characters used in differentiating these genera are mosaically distributed among them, and very few unique characters are minor and lacking a strong taxonomic value. In particular, slightly apiculate anthers, leafless stems, zygomorphic flowers, and (sub)scapose habit are diagnostic of *Zerdana*, though specimens of the highly polymorphic *Anchonium elichrysofolium* (DC.) Boiss. may share such a habit as well. Furthermore, the reduction of the ovule number to 4–6 per ovary in *Anchonium* is found in *Sterigmostemum ramosissimum* (O. E. Schulz) Rech. f., a species typically with 4–8 ovules per ovary. Finally, the sepals are erect and saccate in *Oreoloma*, erect and subsaccate in *Anchonium*, erect and non-saccate in *Zerdana*, and ascending to erect-ascending and non-saccate (but rarely erect and subsaccate) in *Sterigmostemum*. The differentiation of petals into a claw and a limb is strong in *Oreoloma*, weak in *Zerdana*, weak to strong in *Anchonium*, and weak (but rarely strong) in *Sterigmostemum*. In a similar way, fruits are completely dehiscent in monospecific *Zerdana*, tardily dehiscent distally in three species of *Oreoloma*, and completely indehiscent in both members of *Anchonium*, whereas all these fruit types can be found in *Sterigmostemum* s. str. (seven species). Many other characters, e. g., leaf dissection (entire to pinnatisect), style form (cylindric or conical) and length (obsolete or to 5 mm long), stigma lobes (elongate up to linear to shortened), etc., reveal the same picture.

In the absence of strong morphological differences among these closely related genera, it would be far more practical and scientifically sound that species of *Sterigmostemum*, *Anchonium*, *Oreoloma*, and *Zerdana* are treated as members of one instead of four genera. However, by now a merge with *Sterigmostemum* has only been proposed for *Oreoloma* (Yang, 1987; Kamelin, German, 2001), a viewpoint followed by some (Al-

Shehbaz, 2012; present study) but not others (Zhou et al., 2001; Appel, Al-Shehbaz, 2003; Warwick et al., 2006, 2007; Yang, 2009). Surprisingly, the status of *Anchonium* and *Zerdana* has never been questioned.

The above-mentioned molecular phylogenetic studies, which included collectively 11 out of the 13 species currently accepted in *Sterigmostemum* and its relatives, clearly highlight the concerns of recognizing four, poorly defined genera. The overall similarities among these genera in intermingling habit, floral and fruit morphology are perfectly matched by the evident paraphyly of *Sterigmostemum* in which *Anchonium*, *Oreoloma*, and *Zerdana* are partly or completely embedded (Warwick et al., 2007; German et al., 2009). Possible taxonomic solutions were briefly mentioned in these works and are further discussed and summarized here. One option could be the further splitting and recognition of all terminal monophyletic clades as separate genera. This would, in particular, mean the transfer of *S. longistylum* (Boiss.) Kuntze to *Zerdana* and establishing a new genus for *S. ramosissimum*, a species morphologically intermediate between *Sterigmostemum* and *Anchonium* (Jacquemoud, 1988). On the other hand, *A. elichrysofolium* would be either placed back in *Sterigmostemum* (German et al., 2009) in agreement with initial concept of Candolle (1821b, as *Sterigma* DC., nom. illeg.), or also recognized as a genus by its own. Such a reshuffling would result in some morphological grouping (e. g., assembling all species combining completely dehiscent fruits, erect sepals, narrow and elongated stigma lobes, and long, narrowly cylindrical styles under the generic name *Zerdana*). However, such changes would barely outweigh the shortcomings of this decision because in general delimitation between the newly defined genera will be even more blurred than before. For instance, among the above features characterizing the potentially dispecific *Zerdana*, only relatively readily dehiscent fruit is unique for both species while other characters occur, individually or in various combinations, in some representatives of *Sterigmostemum* s. l. However, even fruit dehiscence is not fully diagnostic in this case because very tardily dehiscent fruits may be observed in *S. acanthocarpum* (Fisch. et C. A. Mey.) Kuntze (Jacquemoud, 1988; Sonboli et al., 2006), another species with long cylindrical styles and elongated stigma lobes which revealed closest phylogenetic affinity with *S. sulphureum* (Banks et Soland.) Bornm., a species with indehiscent fruit and short style. Meanwhile, states of a number of characters (such as base of sepals, petal differentiation into a claw and a blade, flower symmetry, etc.), separate *Z. anchonioides* Boiss. from *S. longistylum* and either make each of them morphologically closer to other species of *Sterigmostemum* s. l. or (e. g., flower

zygomorphy) emphasize exclusive nature of *Z. anchonioides*. As a result, expanded *Zerdana* will be more heterogeneous rather than separated from the related genera. With the recognition of *S. ramosissimum* and *A. elichrysifolium* as two new monospecific genera to maintain *Sterigmostemum* s. str. (including *Oreoloma*) as monophyletic, the situation will get even worse. In particular, completely indehiscent fruits will be found in *Anchonium*, *Sterigmostemum*, and in both newly established genera, and the rest of characters will be distributed similarly. In our opinion, splitting is not a good taxonomic decision in *Sterigmostemum* s. l.

Hence, the alternative approach of lumping the four genera under the earliest-published *Sterigmostemum* seems far more justified because it requires only minor changes in the morphological characteristics of the expanded genus, and the support of the common clade is rather high (Warwick et al., 2007; German et al., 2009). The only concern regarding this taxonomic decision is the phylogenetic position of *Synstemon* as a sister taxon to the type species of *Anchonium*, *A. billardierei*, which was found by Warwick et al. (2007). This finding was extremely unexpected because *Synstemon* differs from the *Anchonieae* by the lack (vs. usually presence) of multicellular glands and by having strongly crisped simple and forked trichomes (vs. exclusively or predominantly dendritic with usually straight branches) and pilose (vs. glabrous) petal claws and sometimes filaments (Al-Shehbaz et al., 2000). The only feature which could be considered as a hint of the possible relationship of *Synstemon* with the rest of the respective clade is its basally united median filaments pairs (vs. connate above the middle in *Anchonium*, *Oreoloma*, *Sterigmostemum*, and *Zerdana*). Possible explanations of the strange position of *Synstemon* are either a laboratory mistake or, in view of several cases of successful ancient inter-tribal hybridization within the family (e. g., Joly et al., 2009; Mandáková et al., 2010, 2017; German, Friesen, 2014), a hybrid origin of *Synstemon*. Additional sequencing of nuclear (ITS) and chloroplast (*trnL-F*) fragments of both species of *Synstemon* (German & Koch, unpubl. data) revealed its unambiguous relationship with *Euclidieae* DC. and no sign of inter-tribal hybridization. This agrees well with the data of Chen et al. (2016) who, based on the analysis of several chloroplast markers, found *Synstemon petrovii* Botsch. within the clade formed also by *Pycnoplathus uniflora* (Hook. f. et Thoms.) O. E. Schulz and *Cryptospora falcata* Kar. et Kir., both of which are members of the *Euclidieae*. Apparently, *Synstemon* is much at home in *Euclidieae* rather than in *Anchonieae*, and the sequence DQ357599 of *S. petrovii*, the generic type, in Warwick et al. (2007), which was the basis for assigning the genus to the *An-*

chonieae, is nearly identical to DQ357512 of *A. billardierei* and to which it should be attributed.

The removal of this *Synstemon* obstacle proves the congruence of morphological and phylogenetic data and supports a broader concept of *Sterigmostemum*. The last item to be mentioned is the sister position of *A. billardierei* to the rest of the discussed group (Warwick et al., 2007). One might argue for keeping *Anchonium* as a monospecific genus separate from *Sterigmostemum* because it has bracteate (vs. ebracteate) racemes, but this character is usually trivial taxonomically at the generic level because both raceme types are found within numerous genera of the family. Therefore, an expanded concept of *Sterigmostemum* is proposed here with a formal synonymization of *Anchonium* and *Zerdana* and necessary combinations for their three species and three subspecies when transferred to *Sterigmostemum*. The united genus encompasses 13 species of predominantly SW and Central Asian distributions, of which a complete checklist is provided below.

Sterigmostemum M. Bieb. 1819, Fl. Taur.-Cauc. 3: 444.

≡ *Sterigma* DC. IV 1821, Mém. Mus. Hist. Nat. 7: 242; id. V 1821, Reg. Veg. Syst. Nat. 2: 579, nom. illeg. superfl.

Lectotypus (Jacquemoud, 1984a: 303): *S. incanum* M. Bieb.

= *Anchonium* DC. IV 1821, Mém. Mus. Hist. Nat. 7: 242; id. V 1821, Reg. Veg. Syst. Nat. 2: 578, syn. nov. — Typus: *A. billardierei* DC.

= *Zerdana* Boiss. 1842, Ann. Sci. Nat. Bot., sér. 2, 17: 84, syn. nov. — Typus: *Z. anchonioides* Boiss.

= *Oreoloma* Botsch. 1980, Bot. Zhurn. 65, 3: 425. — Typus: *O. matthioides* (Franch.) Botsch.

1. ***Sterigmostemum acanthocarpum*** (Fisch. et C. A. Mey.) Kuntze, 1891, Revis. Gen. Pl. 1: 36. ≡ *Sterigma acanthocarpum* Fisch. et C. A. Mey. 1835, Index Sem. Hort. Petropol. 1: 38.

2. ***Sterigmostemum anchonioides*** (Boiss.) D. A. German et Al-Shehbaz, comb. nova. ≡ *Zerdana anchonioides* Boiss. 1842, Ann. Sci. Nat. Bot., sér. 2, 17: 84.

2a. ***Sterigmostemum anchonioides* subsp. stenocarpum** (Jacquemoud) D. A. German et Al-Shehbaz, comb. nova. ≡ *Zerdana anchonioides* subsp. *stenocarpa* Jacquemoud, 1985, Candollea, 40, 2: 369.

2b. ***Sterigmostemum anchonioides* subsp. stenophyllum** (Boiss. et Hausskn.) D. A. German et Al-Shehbaz, comb. nova. ≡ *Zerdana anchonioides* [var.] β. *stenophylla* Boiss. et Hausskn. 1888, Fl. Orient. Suppl.: 46. ≡ *Z. anchonioides* subsp. *stenophylla*

(Boiss. et Hausskn.) Jacquemoud, 1985, *Candollea*, 40, 2: 368.

3. ***Sterigmostemum billardierei*** (DC.) D. A. German, comb. nova. ≡ *Anchonium billardierei* DC. IV 1821, *Mém. Mus. Hist. Nat.* 7: 242; id. V 1821, *Reg. Veg. Syst. Nat.* 2: 578.

4. ***Sterigmostemum caspicum*** (Lam.) Rupr. 1869, *Mém. Acad. Sci. Pétersb.*, sér. 7, 15: 95. ≡ *Cheiranthus caspicus* Lam. 1794, in Pall., *Voy. Plus. Prov. Russ.*, App. 8: 348.

= *Cheiranthus nitrarius* Pall. 1799, *Reise Südl. Russ. Reichs*, 1: 105, 124, 141.

= *Cheiranthus tomentosus* Willd. 1800, *Sp. Pl.* 3: 523. ≡ *Sterigmostemum tomentosum* (Willd.) M. Bieb. 1819, *Fl. Taur.-Cauc.* 3: 444. ≡ *Sterigma tomentosum* (Willd.) DC. 1821, *Reg. Veg. Syst. Nat.* 2: 579.

5. ***Sterigmostemum eglandulosum*** (Botsch.) H. L. Yang, 1987, *Fl. Desert. Reipubl. Popul. Sin.* 2: 66. ≡ *Oreoloma eglandulosum* Botsch. 1980, *Bot. Zhurn.* 65, 3: 427.

= *Sterigmostemum grandiflorum* K. C. Kuan, 1980, *Bull. Bot. Lab. N. E. Forest. Inst., Harbin*, 8: 43. ≡ *Oreoloma grandiflorum* (K. C. Kuan) H. L. Yang, 2009, *J. Desert Res.* 29, 3: 433.

6. ***Sterigmostemum elichrysofolium*** (DC.) D. A. German et Al-Shehbaz, comb. nova. ≡ *Sterigma elichrysofolium* DC. 1821, *Reg. Veg. Syst. Nat.* 2: 581. ≡ *Anchonium elichrysofolium* (DC.) Boiss. 1867, *Fl. Orient.* 1: 240. ≡ *A. tournefortii* Boiss. 1842, *Ann. Sci. Nat. Bot.*, sér. 2, 17: 386, nom. illeg. superfl.

= *Matthiola persica* DC. 1821, *Reg. Veg. Syst. Nat.* 2: 168. ≡ *Anchonium persicum* (DC.) Bornm. 1904, *Bull. Herb. Boissier*, sér. 2, 4: 1265. ≡ *A. elichrysofolium* subsp. *persicum* (DC.) Coode et Cullen, 1965, *Notes Roy. Bot. Gard. Edinburgh*, 26, 2: 193.

= *Anchonium elichrysofolium* var. *brachycarpum* Trautv. 1873, *Acta Horti Petrop.* 2: 503. ≡ *A. brachycarpum* (Trautv.) Vass. 1939, *Fl. URSS*, 8: 321.

= *Anchonium tournefortii* var. *canescens* Hausskn. ex Bornm. 1904, *Bull. Herb. Boissier*, sér. 2, 4: 1265. ≡ *A. elichrysofolium* subsp. *canescens* (Hausskn. ex Bornm.) Coode et Cullen, 1965, *Notes Roy. Bot. Gard. Edinburgh*, 26, 2: 194.

= *Anchonium elichrysofolium* [var.] β. *tournefortii* (Boiss.) Bornm. subvar. *cilicicum* Hausskn. ex Bornm. 1936, *Feddes Repert.*, Beih. 89, 1: 39. ≡ *A. elichrysofolium* subsp. *cilicicum* (Hausskn. ex Bornm.) Coode et Cullen, 1965, *Notes Roy. Bot. Gard. Edinburgh*, 26, 2: 193.

= *Anchonium elichrysofolium* subsp. *glandulosum* Coode et Cullen, 1965, *Notes Roy. Bot. Gard. Edinburgh*, 26, 2: 193.

6a. ***Sterigmostemum elichrysofolium*** subsp. ***villosum*** (Coode et Cullen) D. A. German et Al-Shehbaz, comb. nova. ≡ *Anchonium elichrysofolium* subsp. *villosum* Coode et Cullen, 1965, *Notes Roy. Bot. Gard. Edinburgh*, 26, 2: 194.

7. ***Sterigmostemum fuhaiense*** H. L. Yang, 1987, *Fl. Desert. Reipubl. Popul. Sin.* 2: 445. ≡ *Oreoloma fuhaiense* (H. L. Yang) H. L. Yang, 2009, *J. Desert Res.* 29, 3: 433.

= *Sterigmostemum schmakovii* Kamelin et D. A. German, 2001, *Turczaninowia*, 4, 3: 5.

8. ***Sterigmostemum incanum*** M. Bieb. 1819, *Fl. Taur.-Cauc.* 3: 444. ≡ *Cheiranthus torulosus* M. Bieb. 1808, *Fl. Taur.-Cauc.* 2: 121, non Thunb. 1800. ≡ *Sterigma torulosum* (M. Bieb.) DC. 1821, *Reg. Veg. Syst. Nat.* 2: 580, comb. illeg. ≡ *Sterigmostemum torulosum* (M. Bieb.) Stapf, 1886, *Denkschr. Kaiserl. Akad. Wiss. Wien, Math.-Naturwiss. Kl.* 51: 301, comb. illeg.

= *Sterigma contortuplicatum* Boiss., 1842, *Ann. Sci. Nat. Bot.*, sér. 2, 17: 387. ≡ *Sterigmostemum contortuplicatum* (Boiss.) Kuntze, 1891, *Revis. Gen. Pl.* 1: 36.

9. ***Sterigmostemum longistylum*** (Boiss.) Kuntze, 1891, *Revis. Gen. Pl.* 1: 36. ≡ *Sterigma longistylum* Boiss. 1842, *Ann. Sci. Nat. Bot.*, sér. 2, 17: 387.

10. ***Sterigmostemum matthioides*** (Franch.) Botsch. 1959, *Bot. Zhurn.* 44, 10: 1487. ≡ *Dontostemon matthioides* Franch. 1883, *Pl. David.* 1: 35. ≡ *Oreoloma matthioides* (Franch.) Botsch. 1980, *Bot. Zhurn.* 65, 3: 426.

11. ***Sterigmostemum ramosissimum*** (O. E. Schulz) Rech. f. 1968, *Fl. Iranica*, 57: 280. ≡ *Anchonium ramosissimum* O. E. Schulz, 1933, *Bot. Jahrb. Syst.* 66, 1: 97.

– *Anchonium sterigmoides* Lipsky ex Vass. 1939, *Fl. URSS*, 8: 322, nom. inval.

12. ***Sterigmostemum sulphureum*** (Banks et Soland.) Bornm. 1911, *Beih. Bot. Centralbl.* 28, 2: 110. ≡ *Cheiranthus sulphureus* Banks et Soland. 1794, in Russell, *Nat. Hist. Aleppo*, ed. 2, 2: 257. ≡ *Sterigma sulphureum* (Banks et Soland.) DC. 1821, *Reg. Veg. Syst. Nat.* 2: 580.

= *Sterigma brachypetalum* Boiss. 1842, *Ann. Sci. Nat. Bot.*, sér. 2, 17: 386.

13. ***Sterigmostemum violaceum*** (Botsch.) H. L. Yang, 1987, *Fl. Desert. Reipubl. Popul. Sin.* 2: 65.

≡ *Oreoloma violaceum* Botsch. 1980, Bot. Zhurn. 65, 3: 426.

= *Oreoloma sulphureum* Botsch. 1980, Bot. Zhurn. 65, 3: 427. ≡ *Sterigmostemum regeliorum* Kamelin et D. A. German, 2001, Turczaninowia, 4, 3: 8, non *S. sulphureum* (Banks et Soland.) Bornm. 1911.

Key for species of *Sterigmostemum*

1. Ovules 4–8 per ovary; fruit indehiscent, 3–4 times wider than pedicels 2.
- + Ovules (8)10–50 per ovary; fruit partially to completely dehiscent, or indehiscent, as wide as or up to 2(2.5) times wider than pedicels 4.
2. Fruit oblong to linear, terete-quadrangular in cross section, usually pendulous or patent-pendulous on reflexed or recurved pedicels 6. *S. elichrysofolium*.
- + Fruit oblong-conical, suberect, divaricate-ascending or spreading, sometimes recurved, terete, on erect-ascending to spreading fruiting pedicels 3.
3. Fruit straight, smoothly torulose; raceme bracteate; petals purplish to pale yellow with dark veins, slightly exceeding erect purple sepals 3. *S. billardierei*.
- + Fruit curved, ribbed-moniliform; raceme ebracteate; petals uniformly bright yellow, distinctly exceeding ascending pale green sepals 11. *S. ramosissimum*.
4. Styles in fruit (2.5)3–8 mm long, stigma lobes oblong to linear 5.
- + Styles in fruit to 2.5(3) mm long, stigma lobes semicircular to oblong 10.
5. Plants scapose; leaves exclusively basal; flowers zygomorphic 2. *S. anchonioides*.
- + Plants with well-developed, branched, and usually leafy stems; flowers actinomorphic 6.
6. Annuals; flowers yellow; styles narrowly cylindrical; fruit not or rarely slightly widened at base, completely dehiscent or irregularly transversely breaking into fragments 7.
- + Perennials, occasionally biennials; flowers yellow, violet, or white; styles narrowly conical; fruit widest at base, dehiscent only in the upper part 8.
7. Sepals erect-ascending; fruiting pedicels (2)3–8(10) mm long; fruit usually covered throughout with long glandular setae, very late dehiscent or transversely breaking into fragments 1. *S. acanthocarpum*.
- + Sepals erect; fruiting pedicels to 3 mm long; fruit not setose, dehiscent 9. *S. longistylum*.
8. Plants sparsely glandular on sepals and pedicels, rarely throughout; petals 15–22 mm long; stigma lobes 2.5–4.5 mm long; ovules 40–50 per ovary ... 5. *S. eglandulosum*.
- + Plants densely glandular throughout; petals 8–18 mm long; stigma lobes 1–3 mm long; ovules 20–30 per ovary ... 9.
9. Petals 14–18 × 5–7 mm; sepals 8–10 mm long, lateral pair distinctly saccate at base; stigma lobes 2–3 mm long; leaves mostly deeply sinuate-dentate to pinnatisect 13. *S. violaceum*.
- + Petals 8–12 × 3–4 mm; sepals 5–7 mm long, lateral pair not or slightly saccate; stigma lobes to 1.5 mm long; leaves mostly shallowly sinuate-dentate to entire 7. *S. fuhaiense*.
10. Stigma not wider than style; lateral sepals saccate at base; petals pink, creamy white or yellow, 14–18 mm long 10. *S. matthioides*.
- + Stigma wider than style; lateral sepals not saccate; petals bright to dull yellow, (5)7–11(12.5) mm long 11.
11. Plants perennial, completely eglandular; fruit not widened at base, terete, straight or slightly curved, late dehiscent at least in the upper part 4. *S. caspicum*.
- + Plants annual or biennial, occasionally perennial, glandular throughout or in the lower part, rarely eglandular; fruits not or widened at base, usually slightly tetragonal, straight or often contorted or circinnate, normally indehiscent 12.
12. Petals 6–8(9) mm long; fruiting pedicels erect-ascending to subappressed; fruit glandular 8. *S. incanum*.
- + Petals 9–11(12.5) mm long; fruiting pedicels divaricate-ascending to divaricate; fruit eglandular 12. *S. sulphureum*.

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