

TAXONOMY

A new classification of the polyphyletic genus *Centaurium* Hill (Chironiinae, Gentianaceae): description of the New World endemic *Zeltnera*, and reinstatement of *Gyrandra* Griseb. and *Schenkia* Griseb.

Guilhem Mansion

Laboratoire de Botanique Evolutive, Université de Neuchâtel, Emile Argand 11, 2007 Neuchâtel, Switzerland.
 guilhem.mansion@unine.ch

This paper provides a practical taxonomic treatment of the polyphyletic genus *Centaurium* Hill. This new classification defines monophyletic groups and thus reflects the phylogenetic relationships within the subtribe Chironiinae (Gentianaceae). For this purpose, the establishment of a new genus, *Zeltnera*, along with the reinstatement of *Gyrandra* Griseb. and *Schenkia* Griseb., results in numerous new species combinations, a more restrictive circumscription of *Centaurium* Hill, and novel generic delimitations within Chironiinae. Fifteen genera are recognized, encompassing ca. 108 species. The new genus *Zeltnera* comprises 25 species mainly confined to California, Mexico, and Texas. *Gyrandra* is a small genus with three species restricted to some areas of Mexico (*G. chironioides*, *G. pterocaulis* and *G. tenuifolia*) and two species widespread in Central America (*G. brachycalyx* and *G. pauciflora*). *Schenkia* comprises five species: *S. spicata* is broadly distributed in Eurasia and north Africa, *S. australis*, *S. clementii*, and *S. japonica* are confined to Australia and the Pacific region, while *S. sebaeoides* is a rare and endangered Hawaiian endemic. Finally, the genus *Centaurium* s.s. consists of ca. 20 species of primarily Mediterranean distribution.

KEYWORDS: *Centaurium*, Gentianaceae, *Gyrandra*, nomenclature, *Schenkia*, systematics, taxonomy, *Zeltnera*.

INTRODUCTION

Gentianaceae sensu Struwe & al. (2002) comprise 87 genera and 1615–1688 species grouped in six tribes. This paper focuses on species of the subtribe Chironiinae (tribe Chironieae) that presently are included in the genus *Centaurium* Hill. This group of plants, commonly known as centauries, was generally referred to as *Centaurium* by pre-Linnaean botanists. This name, as a taxonomic entity, appeared for the first time during the 16th century (Dodoens, 1583) and was cited by Bauhin (1623), Tournefort (1700) and Ray (1724).

Nevertheless, in the original edition of the *Species Plantarum*, Linnaeus (1753) placed centauries under *Gentiana* (e.g., *Gentiana centaurium*, *G. spicata*). Hill (1756), in the *British Herbal*, was the first to separate *Centaurium*. De Necker (1790) treated centauries as *Erythraea*, an invalidly published name (Art. 32.7), and these plants have subsequently commonly borne the name *Erythraea* as proposed by Borckhausen (1796). *Erythraea* has been widely used as the generic name until the middle of the 20th century, before it became a synonym of *Centaurium*, following the rule of priority (Robyns, 1954). The name *Centaurium* was finally typified by Gillett (1963), based on *C. littorale* (Melderis, 1972).

The exact number of species in the genus *Centaurium* Hill is difficult to estimate because of the presence of many closely related and morphologically similar species. A high clinal variation in gross morphology, often caused by ecological conditions, is frequently observed. In addition, natural hybridization has sometimes been reported and tends to obscure taxon delimitation (Melderis, 1931; Zeltner, 1970, 1978; Ubsdell, 1979). This has brought about difficulties in the definition of the species, an abundance of synonyms, and nomenclatural divergences between different treatments.

The first taxonomic studies showed the difficulty of species circumscriptions due to a high number of transitional forms between species, for example, in the *C. erythraea* complex (Zeltner, 1970; Melderis, 1972). Schmidt (1828) published the first monograph of the genus, recognizing 15 species in Europe. Grisebach (1839), in the first monograph treating Gentianaceae, recognized 18 species of *Erythraea*. Later, 19 species were described and placed in four sections: *Erythraea* (as “*Euerythraea*”), *Trichostylus*, *Spicaria* and *Xanthaea* (Grisebach, 1845). Moreover, Grisebach (1845) proposed the new genus *Gyrandra* for one Mexican species of *Erythraea* (*G. chironioides*). Gilg (1895), in his synopsis of Gentianaceae, enumerated 29 species of *Erythraea*. In this work, the genus *Gyrandra* was includ-

ed in section *Erythraea* (as “*Euerythraea*”), and had previously been ranked by Gray (1878) to a sectional level in *Erythraea*. Druce (1916) anticipated the replacement of *Erythraea* by *Centaurium* and proposed 47 combinations for the genus.

Nevertheless, most of the systematic treatments undertaken on *Erythraea* or *Centaurium* have failed to cover the whole genus and dealt only with geographical subsets. A list of 14 European species of *Erythraea* was established by Nyman (1881). Later, Ronniger (1916) clustered 22 European centauries in six sections [*Parviflorae*, *Centaurium* (as “*Centauria*”), *Linariifoliae* (as “*Linariaefoliae*”), *Caespitosae*, *Spicaria* and *Xanthaea*]. Melderis (1931) was the first to create subdivisions in section *Erythraea* (as “*Euerythraea*”). A large number of European floristic treatments have since been published (Lemee, 1931; de Litardière, 1948; Robyns, 1954; Hegi, 1966). The most comprehensive contribution of this difficult group was proposed by Zeltner (1970), on the basis of extensive chromosome studies. This treatment involved 22 species of *Centaurium* and eight intraspecific taxa grouped in four sections and three subsections. Melderis’ contribution in *Flora Europaea* (Melderis, 1972) was largely based on Zeltner’s work. Presently (Tutin, 1972), Eurasian species of *Centaurium* are grouped in three sections (*Centaurium*, *Spicaria* and *Xanthaea*).

For the New World centauries, rough estimates of species number have been given in some floras (Standley & Williams, 1969). Broome (1973, 1976 and 1977) provided a valuable contribution in a series of papers mainly dealing with Mexican species. She recommended the resurrection of Gray’s section *Gyrandra* for five Mexican species and clustered the 17 remaining ones in section *Centaurium*. Later, Turner (1993) published a revision of the Texan centauries (11 species). Nevertheless, no comprehensive subdivision has been yet suggested for the North American *Centaurium*.

As a result, no complete study covering the diversity of the whole genus has been recently undertaken. Therefore, the systematics of the genus is presently unresolved or imprecise in many parts and, consequently, the intergeneric relationships remain unclear.

Classifications of Gentianaceae were established by Endlicher (1838), Grisebach (1839), Bentham (1876), Knoblauch (1894) and Gilg (1895). Gilg’s taxonomic treatment, based mainly on pollen characters, was used as a reference for at least a century. In his work, the genus *Erythraea* (including *Gyrandra*) was placed in subtribe Erythraeinae, close to *Sabatia*. Recently, with the development of molecular tools, a new classification combining phylogenetic approaches and traditional data was proposed (Struwe & al., 2002). In that paper, the genus *Centaurium* was included in the subtribe

Chironiinae (12 genera) of Chironieae. Nevertheless, only a few accessions of *Centaurium* were used in the Struwe & al. treatment (2002) and the status of some genera such as *Gyrandra* was not evaluated.

A global phylogenetic study of Chironiinae has recently been performed (Mansion & Struwe, in press; Fig. 1) and includes most of the *Centaurium* species known worldwide. This work, based on the analysis of several DNA sequence regions (ITS region of nrDNA, *trnL* intron and *trnL-F* spacer of cpDNA), reveals for the first time the polyphyly of *Centaurium* and supports the segregation into four well-supported clades: the first contains most of the Eurasian species of *Centaurium* and among them, the type species, *C. littorale*; a second group of Mexican species includes the type of the genus *Gyrandra* Grisebach; a third clade of both Mediterranean and Australian species corresponds to section *Spicaria* Griseb., and is treated here as *Schenkia* Griseb.; lastly, most of the North American species of *Centaurium* form a well-supported clade, described here as a new genus, *Zeltnera*.

In light of molecular and traditional data, a more narrow definition of *Centaurium* is needed. Several possibilities may be proposed to adapt the *Centaurium* diversity in a systematic classification. One way is to consid-

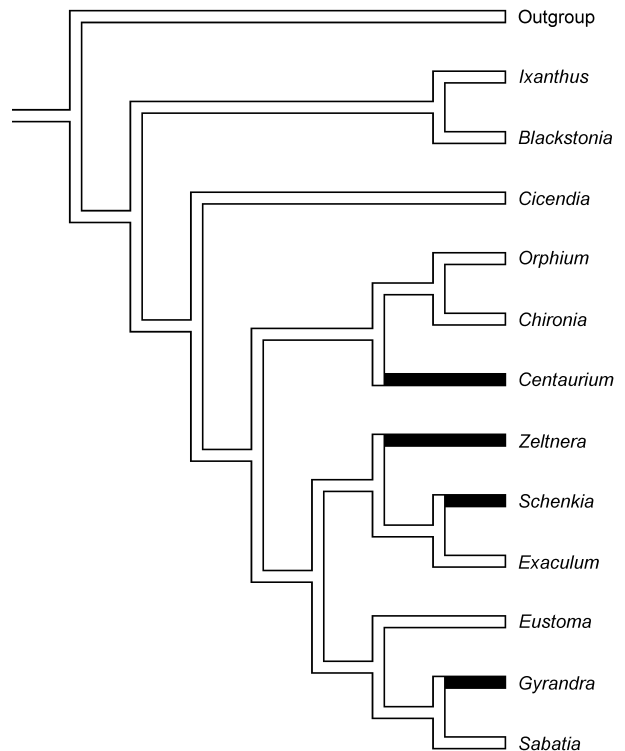


Fig. 1. Simplified phylogenetic relationships within subtribe Chironiinae (from Mansion & Struwe, in press). Black branches represent segregate genera of the *Centaurium* complex.

er a broadly circumscribed genus *Centaurium* in order to maintain monophyly of the genus. In this case, some other members of the subtribe (*Sabatia*, *Eustoma* and *Exaculum*) must be included in *Centaurium*, and probably *Chironia* and *Orphium*, as well. Such recognition of an expanded *Centaurium* poorly reflects diversity in the subtribe and is not practicable from a systematic point of view. If one goal of classifications is to recognize morphologically monophyletic genera, one must then define the most reduced well-supported clade corresponding to such grades. In this perspective, the fusion of morphologically distinct clades into an expanded *Centaurium* is not satisfactory.

Alternatively, a reductionist approach is to attribute a generic status to each well-supported clade of the polyphyletic *Centaurium*. In this case, the last group (namely the North American *Centaurium*) may be seen as a new genus. In this paper, I propose the redefinition and restriction of *Centaurium* Hill to ca. 20 Eurasian species and the reinstatement of the genera *Gyrandra* and *Schenkia*. Furthermore, the North American centauries will now be included in *Zeltnera* gen. nov. (see Appendix).

MATERIALS AND METHODS

For the morphological observations, herbarium material from BM, K, G, LL, MEL, MI, NEU (and personal collections of L. Zeltner) and TEX was used. Flowers and fruits were rehydrated with boiled water and preserved in a 1:1:1 solution of 70% ethanol, glycerol and distilled water. Occasionally, fresh material was collected in the field and preserved in this solution.

TAXONOMY

Key to the genera of the subtribe Chironiinae:

1. Anther never twisted after anthesis 2.
1. Anther slightly to strongly twisted or recurved after anthesis 8.
2. Corolla yellow or yellowish 3.
2. Corolla pink or white 6.
3. Perennial, basally suffrutescent herb *Ixanthus* Griseb.
3. Annual or biennial herb 4.
4. Climbing herb; flower 5-merous *Bisgoeppertia* Kuntze
4. Non-climbing herb; flower 4- or 6-12-merous . . . 5.
5. Flower 4-merous in lax cyme; corolla salverform; stigma subcapitate *Cicendia* Adans.
5. Flower 6–12-merous in dichasia; corolla rotate; stig-

- ma bifid, the lobes apically divided *Blackstonia* Huds.
6. Corolla tube longer than the corolla lobes *Exaculum* Caruel
6. Corolla tube (shorter or) as long as the corolla lobes 7.
7. Flower 5-merous; stamens inserted in the upper part of the corolla tube *Zygostigma* Griseb.
7. Flower 4-merous; stamens inserted between the corolla lobes . . . *Geniostemon* Engelm. & A. Gray
8. Corolla rotate to funnel-shaped, the corolla tube shorter than the corolla lobes in length 9.
8. Corolla salverform, the corolla tube equaling or exceeding the corolla lobes in length 13.
9. Stamen inserted in the corolla tube 10.
9. Stamen inserted between the corolla lobes, near the sinuses 11.
10. Calyx keeled *Chironia* L.
10. Calyx not keeled *Orphium* E. Meyer
11. Stigma deeply bilobed (1/3 the length of the style), the lobes coiling (twisted around one another) at anthesis *Sabatia* Adans.
11. Stigma not deeply bilobed, the lobes not coiling at anthesis 12.
12. Rosette leaves absent; cauline leaves subulate to linear; anthers spirally twisted after anthesis *Gyrandra* Griseb.
12. Rosette leaves present; cauline leaves elliptical; anthers slightly recurved after anthesis *Eustoma* Salisb.
13. Style slightly bifid; stigma lobes reniform to shoe-shaped, fleshy; capsule linear in shape *Centaurium* Hill
13. Style not divided to subcapitate; stigma lobes rhombic to fan-shaped, not fleshy; capsule elliptic to oval in shape 14.
14. Inflorescence a spiciform cyme . . *Schenkia* Griseb.
14. Inflorescence a corymbiform or paniculate cyme *Zeltnera*

TAXONOMIC TREATMENT OF GYRANDRA GRISEB.

Key to the species of *Gyrandra* Griseb.:

1. Stem winged, the wings 1 mm wide and undulate 4. *G. pterocaulis*
1. Stem not winged 2.
2. Leaves narrowly oblanceolate; capsule slightly fusiform. 3. *G. pauciflora*
2. Leaves linear; capsule oblong 3.
3. Corolla less than 15 mm long; style not divided beneath the rounded stigma lobes 1. *G. brachycalyx*

3. Corolla more than 20 mm long; style slightly divided beneath the rounded stigma lobes 4.
4. Plant unbranched; leaves texture membranaceous; apices of leaves and petals acute; corolla pale pink to bluish 5. *G. tenuifolia*
4. Plant branched; leaves texture coriaceous; apices of leaves and petals obtuse; corolla magenta
. 2. *G. chironioides*

***Gyrandra* Griseb.**, in DC. Prod. 9: 44 (1845). ≡ *Erythraea* section *Gyrandra* (Griseb.) A. Gray, Bot. Calif. 1: 479 (1876). Not *Gyrandra* Wall (Euphorbiaceae), Cat. n. 8020 (1847).

Type: *Gyrandra chironioides* Griseb., DC. Prod. IX. 44 (1845). ≡ *Erythraea chironioides* (Griseb.) Torr., Bot. Mex. Bound. 156 (1859). ≡ *Centaurium chironioides* (Griseb.) Druce, Rep. Bot. Exch. Cl. Brit. Isles 4: 613 (1917).

Description. — Herbs annuals, erect or ascending. Roots shallow and fibrous or a thickened taproot. Stems sparingly and strictly branched, sometimes prominently 4-winged (*G. pterocaulis*). Leaves cauline (basal rosette lacking), more abundant below the middle of the stem because of the shortened lower internodes, grass green to bluish, linear to oblanceolate (obovate) becoming longer and narrower upwards. Inflorescence a simple racemose cyme, the lower flowering branches monochasial (the terminal a simple dichasium). Flowers pentamerous, 1–30 per plant, the pedicels longer than the flowers. Calyx 4–6 mm long (calyx tube 1.5–3 mm long), the calyx lobes shorter than the corolla-tube. Corolla pale bluish to pink, nearly rotate, the corolla tube shorter than the lobes (equal in *G. brachycalyx*); corolla-lobes lanceolate to oblong, the tip acute to obtuse. Stamens with oblong anthers (2.2–4.6 mm long), becoming spirally twisted at the anthesis. Ovary longer than the style; stigma subcapitate to slightly bilobed, the lobes hemispheric to reniform. Capsule oval in outline, thick-walled. Seeds 0.3–0.5 mm long. Chromosome number: $n = 36$.

Distribution. — A Central American genus: Costa Rica (San Jose), El Salvador (Chalatenango, San Salvador), Guatemala (Alta Verapaz, Guatemala, Huehuetenango, Quezaltenango, Secatepequez, Sololá, Totonicapán, Zacapa), Honduras (Intibucá), Mexico (Chiapas, Guerrero, Jalisco, Hidalgo, Mexico, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, San Luis Potosí, Tamalipas, Vera Cruz), Nicaragua and Panama (Chiriquí). Species of *Gyrandra* are encountered in mountains, mainly in pine-oak forest associations.

Remarks. — Genus *Gyrandra* is morphologically and phylogenetically close to *Eustoma* and *Sabatia*. These genera share a rotate corolla and a globose to ovoid capsule. They mainly differ by the stigma shape (subcapitate to slightly bilobed [the lobes 0.8–2 mm

wide] in *Gyrandra*; bilobed [the lobes 2.5–8 mm wide] and well separated in *Eustoma*; deeply bilobed [1/3 the length of the style] and twisted about one another at anthesis, in *Sabatia*) and the degree of anther spiralization after pollen release (helically twisted in *Gyrandra*, slightly coiled in *Eustoma* and recurved to circinnately coiled or half-twisted laterally in *Sabatia*).

Taxonomic combinations within *Gyrandra* Griseb.:

1. ***Gyrandra brachycalyx*** (Standley & L. O. Williams) Mansion, **comb. nov.** ≡ *Centaurium brachycalyx* Standley & L. O. Williams, Ceiba 3: 125. 1952. — Type: Honduras, “Dpt. Intibucá, en un robledal, vicinidad de La Esperanza”, Standley 25347 (Holotype: EAP; isotypes: F, US).

Distribution. — A Central American species: Costa Rica, El Salvador, Guatemala, Honduras, central and southern Mexico (Chiapas, Mexico, Oaxaca and Puebla), and Panama. *Gyrandra brachycalyx* occurs in open pine-oak forest communities, between 1500 and 2800 meters.

2. ***Gyrandra chironioides*** Griseb., DC. Prod. 9: 44. 1845. ≡ *Erythraea chironioides* (Griseb.) Torr., Bot. Mex. Bound. 156: 1859. ≡ *Centaurium chironioides* (Griseb.) Druce, Rep. Bot. Exch. Cl. Brit. Isles 4: 613. 1917. — Type: Mexico: “inter Tampico et real del Monte”, Berlandier 295 (Holotype: G; isotype: NY!).

= *Erythraea macrantha* Hook. & Arn. var. *parviflora* Loes., Bull. Herb. Boiss. 2: 55. 1894. — Type: Mexico, Hidalgo, “prope Zacualtipan”, May, Seler 160 (Holotype: B; isotypes: GH, US).

Distribution. — Mountains of the Sierra Madre Oriental of Mexico (Hidalgo, Nuevo León, San Luis Potosí and Tamalipas), in pine forests, between 1800 and 2500 meters.

3. ***Gyrandra pauciflora*** (Martens & Galeotti) Mansion, **comb. nov.** ≡ *Erythraea pauciflora* Martens & Galeotti, Bull. Acad. Roy. Brux. 11: 373. 1844. ≡ *Centauroides pauciflorum* (Martens & Galeotti) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium pauciflorum* (Martens & Galeotti) B. L. Robinson, Proc. Amer. Acad. Arts 45: 397. 1910. — Type: Mexico, Vera Cruz, “croit dans les bois du pic d’Orizaba, à 8 et 9000 pieds, sept.”, Galeotti 1482 (Holotype: BR).

= *Centaurium rosans* Standl. & Steyerl., Publ. Field Mus. Nat. Hist. Bot. Ser. 23: 75. 1944. — Type: Guatemala, Dep. Quazaltenango, moist banks, volcan de Zunil, 2500–3800 m, 22 Jan 1940, Steyerl. 34609 (Holotype: F).

Distribution. — Guatemala (southeastern Cordillera), Honduras, Mexico (from Hidalgo to Vera Cruz, Puebla and Oaxaca) and Nicaragua. *Gyrandra pauciflora* occurs on slopes of mountains, along rivers, between 1500 and 3000 meters (up to 3800 meters for the holotype of *Centaurium rosans*, *Steiermark 34609*, F).

4. *Gyrandra pterocaulis* (Broome) Mansion, **comb. nov.** \equiv *Centaurium pterocaulis* Broome, *Madroño* 24: 237. 1977. — Type: Mexico, Hidalgo, Zimapan, *Coulter 941* (Holotype: K!; isotype: GH).

Distribution. — Mexico (Hidalgo, Morelos and San Luis Potosi), in mountain pine forest (1800–2500 m).

Remarks. — This species is known from only four collections and shows considerable morphological variation (Broome, 1977). The distinctive characters are the broad stem-wings and the keeled calyx lobes. Otherwise, the large flower, along with some vegetative characters (e.g., bluish color on stems and leaves), are similar to that found in *G. chironioides* and *G. pauciflora*. Therefore, I include here this species in the genus *Gyrandra*.

5. *Gyrandra tenuifolia* (Martens & Galeotti) Mansion **comb. nov.** \equiv *Erythraea tenuifolia* Martens & Galeotti, *Bull. Acad. Roy. Sci. Bruxelles* 11: 372. 1844. \equiv *Centauroides tenuifolium* (Martens & Galeotti) Kuntze, *Revis. Gen. Pl.* 2: 426. 1891. \equiv *Centaurium tenuifolium* (Martens & Galeotti) B. L. Robinson, *Proc. Amer. Acad. Arts* 45: 397. 1910. — Type: Mexico, Jalisco, “Cerro del Coll, pres de Guadalajara, 5500 pieds, fl. roses, Dec. Rare”, *Galeotti 1748* (Holotype: BR!; isotype: G!).

= *Erythraea macrantha* var. *major* Hook. & Arn., *Bot. Beech. Voy.*: 438. 1841. \equiv *Gyrandra speciosa* Benth., *Bot. Voy. Sulph.*: 127. 1845. [based on *Erythraea macrantha* var. *major* Hook. & Arn.] \equiv *Erythraea speciosa* (Benth.) A. Gray, *Bot. Calif.* 1: 479. 1876. \equiv *Centaurium speciosum* (Benth.) Druce, *Rep. Bot. Exch. Club. Br. Isles* 4: 614. 1917. — Type: Mexico, Nayarit, between San Blas and Tepic, *Sinclair s.n.* (Holotype: K!; Fig. 2).

Distribution. — Mountains of western Mexico (Nayarit, Jalisco, Michoacán, Guerrero), in pine forest, between 1300 and 2800 meters.

Remarks. — Hooker and Arnott described *Erythraea macrantha* in 1841 based on a plant collected in Jalisco (misspelled “Talisco”), and recognized one variety from Tepic (“ β major”). The holotype of the autonym (“*Erythraea macrantha* α latifolia”) is a short and grazed plant, with relatively small flowers compared to the second taxon (“ β major”). In the same publication (p. 439), the authors recognized confusion between their new species from Jalisco and *E. texensis* Griseb.

Nevertheless, the latter species doesn’t occur in Jalisco and an examination of the holotype specimen (K) indicates close resemblance with *Zeltnera madrensis* (pers. observ.). Thus *Erythraea macrantha* likely referred to damaged specimens of *Z. madrensis*, and Broome (1973) relegated it to the status of “species non satis nota”.

The variety *major* (“ β major”) from Tepic was typified by the Sinclair collection, which was identical to the Galeotti’s type of *E. tenuifolia*. According to Broome (1973), the holotype of *E. macrantha* var. *major* (BR) is mounted on the same sheet with an isotype of *E. tenuifolia* (*Galeotti 1748*). The two plants have a separate label (written by the same person) “*Gyrandra - Erythraea tenuifolia* Mart. et Gal.” and “*Gyrandra speciosa - E. macrantha* β major Hook. et Arn., San Blas, Tepic, Sinclair”. Since the name *Erythraea tenuifolia* (1844) predates Bentham’s publication of *Gyrandra speciosa* (1845), the new combination *Gyrandra tenuifolia* (Martens & Galeotti) Mansion must be proposed.

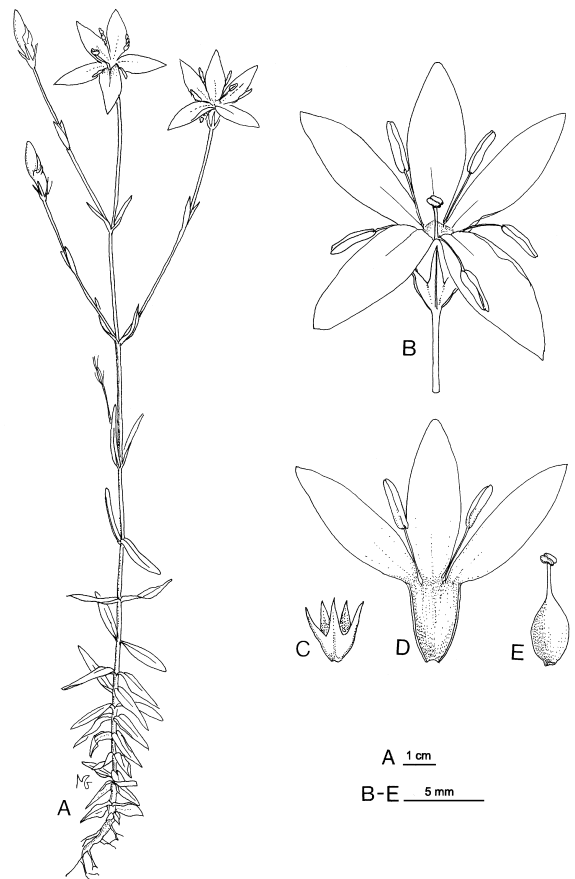


Fig. 2. *Gyrandra tenuifolia* (Martens & Galeotti) Mansion. A, habit; B, flower at anthesis; C, opened calyx; D, opened corolla (longitudinal section); E, gynoecium.

TAXONOMIC TREATMENT OF *SCHENKIA* GRISEB.

Key to the species of *Schenkia* Griseb.:

1. Leaves fleshy 4. *S. sebaeoides*
1. Leaves not fleshy 2.
2. Corolla lobes 6–9 mm long, equaling the corolla tube in length 2. *S. clementii*
2. Corolla lobes 4–5 mm long, shorter than the corolla tube in length 3.
3. Style longer than or equaling the ovary; inflorescence a dense spiciform cyme 5. *S. spicata*
3. Style shorter than the ovary; inflorescence a lax spiciform to racemose cyme 4.
4. Leaves orbicular to elliptic, basal leaves longer than the internodes 3. *S. japonica*
4. Leaves lanceolate, basal leaves absent or shorter than the internodes 1. *S. australis*

Schenkia Griseb., Bonplandia 1: 226 (1853). ≡ *Erythraea* section *Spicaria* Griseb., Genera and species Gentianearum (1839). ≡ *Centaurium* section *Spicaria* (Griseb.) Ronniger, Mitt. Naturw. Ver. Steierm. 52: 312–321 (1916).

Type: *Schenkia sebaeoides* Griseb., Bonplandia 1: 226 (1853). ≡ *Erythraea sebaeoides* (Griseb.) Gray, Proc. Am. Acad. 6: 41 (1859). ≡ *Centaurium sebaeoides* (Griseb.) Druce, Rep. Bot. Exch. Cl. Brit Isles 4: 614 (1917).

Description. — Herbs, annual or biennial. Roots shallow and fibrous or forming a ligneous taproot. Stems branched from the base up to near the middle. Leaves basal (sometimes forming a caduceous rosette) or cauline, generally longer or equal to the internodes; rosette-leaves broadly elliptic to oval; cauline leaves elliptic-oblong to lanceolate, 3-veined. Flowers pinkish-purple, sessile to subsessile, in dense spiciform cymes (*S. sebaeoides*, *S. spicata*) or lax spiciform to racemose cymes (*S. australis*, *S. clementii*, *S. japonica*). Calyx with a short tube (up to 1 mm long); calyx lobes generally exceeding the corolla-tube in length. Corolla salverform, the lobes shorter than the corolla tube (or equal to in *S. clementii*). Stamens inserted at the apex of the corolla-tube (sometimes lower in some populations of *S. spicata*). Ovary bicarpellate, unilocular; style filiform, not divided under the stigma surface, usually shorter than the ovary (longer or equal in *S. spicata*); stigma subcapitate to infundibuliform, the lobes rhombic or fan-shaped. Capsule elliptic to oblong. Seeds numerous, the main axis 0.4–0.5 mm long. Chromosome number: $n = 11$, $n = 22$. A genus of five species, widely distributed in Eurasia, Africa, Australia, and Pacific.

Distribution. — From the Mediterranean Basin to the Black Sea and Caucasus (Albania, Bulgaria, France

[incl. Corsica], Greece [incl. Crete], Italy [incl. Sardinia and Sicily], Portugal, Spain [incl. Azores and Balearic Islands], Romania, Turkey; Afghanistan, Azerbaijan, Georgia, Iran, Jordan, Russia, Syria), East Asia (China and Japan), North Africa (Algeria, Libya, Morocco, Tunisia), Australia, New Caledonia and the Hawaiian Islands; introduced in North America (United States: Delaware, Maryland, Massachusetts, and Virginia).

Remarks. — Grisebach (1853) described *Schenkia* as closely related to *Sebaea* with some affinities with *Erythraea spicata* based on the inflorescence. He clearly separated the monospecific genus from *Erythraea* section *Spicaria*, previously described by him (Grisebach, 1839), on the base of stigma shape (“capitulatum [capitate]” or “crassiusculum [moderately thick]” in *Schenkia* vs. “lobis tamen suturam excedentibus [lobes notwithstanding exceeding the suture]” in section *Spicaria*). According to Gray (1859), who examined the type specimen [*Seeman* 2272 (Holotype: BIS)], there is a mistake in Grisebach’s description of *Schenkia sebaeoides*, mainly concerning the stigma shape (similar to that of *E. spicata*) and other morphological evidence. Thus, Gray included *Schenkia* in *Erythraea* section *Spicaria*. Nevertheless, *Schenkia* is a validly published and legitimate generic name. Furthermore, the paronym *Schenckia* Schumann (1889) has been ruled to be a homonym and is not a legitimate name.

The polymorphic genus *Schenkia* needs a phylogenetic study throughout its entire range. The most common species, *S. spicata*, shows a high degree of variation in size and general habit. Two varieties have been described from Portugal (Fernandes, 1965), of which var. *condensata* possibly deserves to be erected at species-level. In addition, specimens of *S. spicata* collected by Zeltner in Algeria and Jordan present a very particular morphology, with large oval leaves, and much bigger corollas arranged in lax spiciform inflorescence (personal observations). In Australia, Adams (1996) reported several forms of *S. spicata* from coastal areas that may be seen either as separate varieties (e.g., var. *pseudocaspicum* or var. *racemosum* described by Hochreutiner [1928]), genetically stable ecotypes or consequences of environmental influences. Moreover, phylogenetic studies (Mansion and Struwe, in press) suggest that *S. spicata* from Eurasia and Australia are different taxa. Recent karyological investigations on Australian centauries revealed that all specimens investigated were tetraploid as opposed to the diploid Eurasian plants (Zeltner, pers. comm.). As a consequence, I propose the segregation between *S. spicata* and the Australian tetraploid species, treated here as *S. australis*.

TAXONOMIC COMBINATIONS IN *SCHENKIA* GRISEB.

1. *Schenkia australis* (R. Br.) Mansion, **comb. nov.** ≡ *Erythraea australis* R. Br., *Prodromus Florae Novae Hollandiae*: 451. 1810. ≡ *Centaurium australe* (R. Br.) Druce, *Rep. Bot. Exch. Cl. Brit. Isles* 4: 613. 1917. ≡ *Erythraea spicata* var. *australis* (R. Br.) Domin., *Biblioth. Bot.* 89: 1073. 1928. – Lectotype (designated here): Australia, J. M. T. D. [from the SW coast to tropical Queensland], 1802–1805, *R. Brown s.n.* (BM!; isolectotypes: K!, NY!).
- = *Centaurium spicatum* var. *pseudocaspicum* Hochr., *Candollea* 3: 470. 1928. – Type: Australia, N. S. Wales, Richmond, 1896, *Fawcett 8* (Holotype: MEL).
- = *Centaurium spicatum* var. *racemosum* Hochr., *Candollea* 3: 471. 1928. – Type: Australia, west Australia, 1875, *F. V. Muller 5* (Holotype: MEL).

Lectotypification. — This species was first recognized by Brown (1810) in his *Prodromus Florae Novae Hollandiae*, but the description was rather brief and the location imprecise (“J. M. T. D.”, i.e., most of the Australian coastal fringe [excluding Western Tasmania], and the western mainland Darwin - Albany portion). According to D. Mabberley (pers. comm.), the type must be in Brown’s own herbarium, incorporated with that at BM in the 1870s. The way Brown wrote suggested several collections, and a lectotype from his herbarium needs to be selected. Brown’s herbarium sheets can be recognized by Brown’s manuscript label usually citing *Prodromus* reference and generally a printed label with a “Bennett” number on it. The examination of BM material revealed two sheets. The first sheet represents Brown’s collection of three plants from Port Jackson, but without other indications. The second sheet contains four specimens, and an additional separate inflorescence. Three of these specimens (BM000803702–704) are Brown’s collections, and the fourth (BM000803705) is probably also Brown’s collection, but it is labeled “New South Wales” without further information. This fourth specimen, morphologically the most characteristic, was the original specimen to be mounted on the sheet as part of the Banks herbarium. At some point someone placed a Type Specimen label on the sheet, indicating that this is probably the type species, retained here as the lectotype.

Distribution. — Australia. This species is most frequent in western Australia, in damp and sandy places.

Remarks. — Herbarium sheets examined reveal the absence of basal ovate leaves (forming a pseudo-rossette) generally observed in *S. spicata*. The inflorescence is a lax spicate cyme sometimes turning into a racemose cyme (with short-pedicelled flowers). Sessile flowers are much shorter than the subsequent internode.

The general branching is thus less compact than observed in *S. spicata* or *S. sebaeoides*. Finally, the chromosome number ($2n = 44$) and other genetic features (DNA sequences) clearly distinguish *S. australis* and *S. spicata* ($2n = 22$).

2. *Schenkia clementii* (Domin.) Mansion, **comb. nov.** ≡ *Erythraea clementii* Domin., *Biblioth. Bot.* 89: 1073. 1928. ≡ *Centaurium clementii* (Domin.) L. G. Adams, *Fl. Australia* 25: 315. 1996. – Type: Northern Australia, between the Ashburton and De Gray Rivers, *W. A. E. Clement s.n.* (Holotype: K).

Distribution. — Endemic to Australia, mainly from the Pilbara region of Western Australia to the South Australia / Northern Territory border.

Remarks. — Except from the corolla size, *S. clementii* (corolla lobes 6–9 mm long) is similar to *S. australis* (corolla lobes 4–5 mm long), and the distinction between them is not always obvious. As stated by Adams (1996), some specimens show a steady decrease in the size of the floral parts, suggesting a clinal gradation toward *S. australis*. Both species share the same chromosome number ($2n = 4x = 44$; Zeltner, pers. comm.).

3. *Schenkia japonica* (Maxim.) Mansion, **comb. nov.** ≡ *Erythraea japonica* Maxim. *Bull. Acad. Imp. Sci. Saint Pétersbourg* 3: 67. 1886. ≡ *Centaurium japonicum* (Maxim.) Druce, *Bot. Soc. Exch. Club Brit. Isles* 4: 613. 1917. ≡ *Centaurium spicatum* (L.) Fritsch var. *japonicum* (Maxim.) Toyokuni, *Conspectus Gentianacearum Japonicarum* 7:153. 1963. ≡ *Centaurium spicatum* subsp. *japonicum* (Maxim.) H. Toyokuni, *Fl. Japan*, 3: 139. 1993. – Type: Japan, Liukiu, insulis Oshima et Okinawa, in maritimis, *A. Tashiro s.n.* (Holotype: LE).

Distribution. — Taiwan and Japan. *Schenkia japonica* is generally a weed in cultivated areas.

Remarks. — This species appears morphologically intermediate between *S. spicata* (stems generally branched from the basis, basal leaves large, elliptic to oval) and *S. australis* (inflorescence a lax spicate cyme with the flowers shorter than or equaling the internodes). The chromosome number is unknown.

4. *Schenkia sebaeoides* Griseb. ≡ *Schenkia sebaeoides* Griseb., *Bonplandia* 1: 226. 1853. ≡ *Erythraea sebaeoides* (Griseb.) Gray, *Proc. Am. Acad.* VI: 41. 1859. ≡ *Centaurium sebaeoides* (Griseb.) Druce, *Rep. Bot. Exch. Cl. Brit. Isles* 4: 614. 1917. – Type: In pratis ins. sandwichense “Oahu”, *Seeman 2272* (Holotype: BISH).

Distribution. — Endemic to the Hawaiian Islands (Kaua’i, O’ahu, Moloka’i, Maui). The plant typically grows in volcanic or clay soils or on cliffs in arid coastal

areas.

Remarks. — This annual herb, with fleshy leaves and stalkless flowers, appears morphologically close to *S. spicata* but share a tetraploid chromosome number with *S. australis* ($2n = 4x = 44$).

On October 29, 1991, this species (local name “awiwi”) was designated as endangered in its entire range by the U. S. Fish & Wildlife Service. The major threats to this species include habitat degradation by feral goats and cattle, competition from the non-native plant species (such as *Casuarina equisetifolia* or *Schinus terebinthifolius*), or trampling by humans on or near trails and fire (Medeiros & al., 2000).

5. *Schenkia spicata* (L.) Mansion, **comb. nov.** ≡ *Gentiana spicata* L., Sp. Pl.: 230. 1753. ≡ *Hippion spicatum* (L.) F. W. Schmidt, Roem. Arch. 1: 11. 1796. ≡ *Chironia spicata* (L.) Willd., Sp. Pl. 1. 1: 1069. 1797. ≡ *Erythraea spicata* (L.) Pers., Synopsis Plantarum 1: 283. 1805. ≡ *Centauroides spicatum* (L.) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium spicatum* (L.) Fritsch ex Janch., Mitt. Naturwiss. Vereins Univ. Wien 5: 97. 1907. — Lectotype (designated here): “Habitat in montibus Euganensis Monspelii”, Bauhin s.n. (UPS!). — Fig. 3. = *Centaurium spicatum* (L.) Fritsch var. *condensata* R. Fernandes, Bol. Soc. Brot. 31: 25. 1965. — Type: Portugal, “in solo arenoso humidoque stratorum rupium altorum orae maritimae, loco dicto Praia das Maças”, 2 Sep 1961, J. Matos, A. Marques & M. Alves 8284 (Holotype: COI!). = *Centaurium spicatum* (L.) Fritsch var. *brachyantha* R. Fernandes, Bol. Soc. Brot. 31: 25. 1965. — Type: Portugal, “in solo argilloso-calcareo, supra rupes calcareas promontorii dicti Cabo Carvoeiro”, 6 Sep 1964, A. Fernandes, R. Fernandes & J. Matos s.n. (Holotype: COI!).

Lectotypification. — According of S. Cafferty (pers. com.), the name *Gentiana spicata* L. has not been formally typified. In *Flora of Pakistan* (1995), Omer wrongly gives 328.29 LINN [a 1762 Alstroemer sheet] as type. This is a post-1753 addition to the Linnaean herbarium that cannot be considered as the basis for the name, and consequently is disallowed as lectotype. Finally, there are four original elements from which any lectotype must be chosen: a specimen in the Burser herbarium in Uppsala (Herb. Burser XVI: 14), two illustrations from works by Bauhin (Prodr. t. 130, 1620; Hist. Pl. 3: 353, 1651), and one illustration from Tabernaemontanus’ *Eicones* (780, 1590). The latter two represent *C. erythraea* and are therefore ineligible as lectotype. The line drawing from Bauhin’s *Prodromus Theatri Botanici* is *Gentiana spicata* L., but the representation is rather extravagant. Finally, the Burser herbarium specimen is

relatively damaged (with only the typical spicate inflorescence present), but perfectly recognizable. Consequently, this specimen is selected here as the lectotype of *Gentiana spicata* L.

Distribution. — Western Europe to eastern Asia (Albania, Bulgaria, France [incl. Corsica], Greece [incl. Crete], Italy [incl. Sardinia and Sicily], Portugal, Spain [incl. Azores, Balearic Islands], Romania, Turkey; Afghanistan, Azerbaijan, Georgia, Iran, Jordan, Russia, Syria) and North Africa (Algeria, Libya, Morocco, Tunisia); introduced in North America (United States: Delaware, Maryland, Massachusetts, and Virginia). This largely Mediterranean species occurs in damp sandy or grassy places near the sea.

Remarks. — The variable *Schenkia spicata* is easily recognizable by the basal largely elliptic to oval leaves, sometimes forming a crowded pseudo-rosette. Besides, the numerous sessile flowers are equal in length to the associated internode, giving the impression of a densely spiked inflorescence.

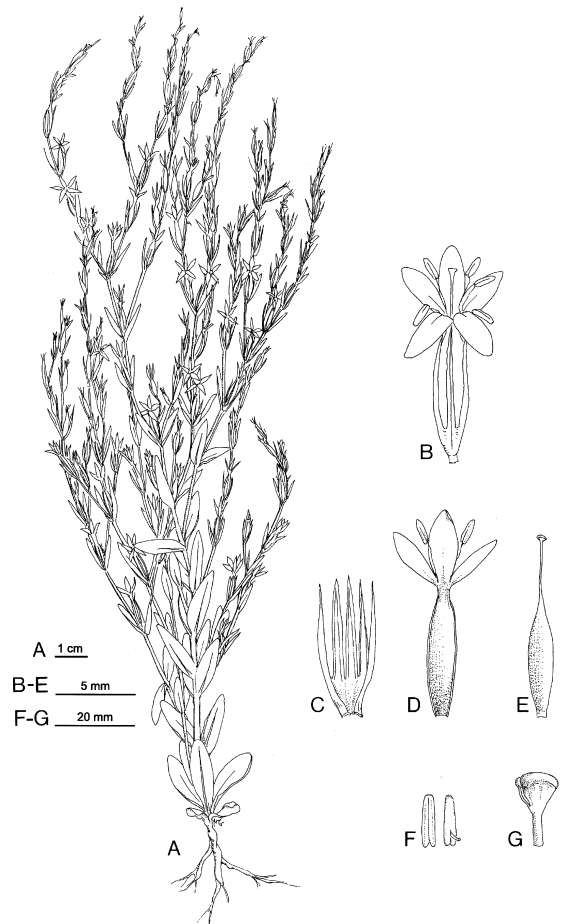


Fig. 3. *Schenkia spicata* (L.) Mansion. A, habit; B, flower at anthesis; C, opened calyx; D, opened corolla (longitudinal section); E, gynoecium; F, erect anther (pre-anthesis); and G, rhombic stigma lobes.

TAXONOMIC TREATMENT OF ZELTNERA MANSION, GEN. NOV.

Zeltnera Mansion, gen. nov. — Type: *Zeltnera trichantha* (Griseb.) Mansion \equiv *Centaurium trichanthum* (Griseb.) B. L. Robinson. \equiv *Erythraea trichantha* Griseb. (Fig. 4).

Diagnosis. — Genus novum Centauriae Hill affine, a quo herbae annuis vel perennis, flores 4-5-meri plerumque pedicellatis cymosis vel paniculatis dispositi, stylus filiformis indivisus sub stigmatate, stigmatate plerumque bilobus flabelliformis vel subcapitatus, capsula ellipticus vel ovalis differt.

Synonymy. — The new genus *Zeltnera* has previously always been treated as part of *Centaurium*. Grisebach (1845) placed some species in a separate section, namely *Trichostylus*. This section included four species based on the capitate shape of the stigma and the undivided style. This artificial group comprised members of three genera, *Zeltnera* (*E. trichantha* = *Z. trichantha*), *Centaurium* (*E. roxburghii* = *C. centaurioides*) or *Schenkia* (*E. caspica* = *S. spicata* auct.). In addition, the sectional description was based on *E. roxburghii*, which belongs to the genus *Centaurium*. Consequently, the name *Trichostylus* is not correct to describe the new genus.

Nomenclature. — The genus *Zeltnera* is dedicated to both Dr. Louis Zeltner (born 1938) and his wife Nicole (born 1934), from Le Locle, Switzerland. These two botanists have greatly contributed to the systematics of the genus *Centaurium* and related genera. It was a pleasure for me to join them in their field work in many countries and particularly in the western part of the United States.

Description. — Herbs, annuals or biennials (*Z. beyrichii* a short-lived perennial), glabrous (*Z. glandulifera* is sometimes papillose on leaves, calyx margins and stem wings). Roots fibrous and shallow or becoming a ligneous taproot. Stems single or several from the base, 4-ridged or 4-winged, branched along the main stem (sparingly to profusely). Leaves in a basal rosette or pseudo-rosette and/or cauline; leaves sessile, cuneate at the base, often decurrent with the stem wings, changing shape along the stem; blades linear, lanceolate to elliptic, grass-green to yellow-green, 1–3 nerved from the base. Inflorescence a simple or compound cyme with a dichasial or monochasial, strict or divaricate branching pattern; cymes corymbiform, paniculate, racemose or capituliform, lax or compact, few- to multi-flowered. Flowers erect, subsessile to pedicellate, tetra- or pentamerous. Calyx (4–15 mm long) with a short tube (up to 1 mm long); calyx lobes lanceolate, triangular, subulate or filiform, sometimes carinate, with broad or scarious margins. Corolla salverform (dextrorsely contorted in

bud); corolla tube cylindrical (sometimes broadly widened in *Z. setacea*), whitish to yellowish (greenish in *Z. maryanna*), equaling or exceeding the ovary in length; corolla lobes magenta to rose-pink or white, sometimes forming a central white eye (with additional greenish spots in *Z. venusta*), lanceolate or ovate; apex acute or obtuse; lobes shorter or equaling the tube (sometimes longer). Stamens inserted in the upper part of the corolla tube; filaments filiform, usually longer than the anthers, not expanding at the base (except in *Z. maryanna*); anthers linear to oblong or sagittate, sub-basifixed, introrse, helically coiled at anthesis; pollen grains in monads, tricolporate, striato-reticulate. Ovary bicarpellate, unilocular, with intrusive placenta, each carpel margin bearing 2–10 longitudinal rows of ovules; style longer or shorter than the ovary (at anthesis), most often exerted, undivided or shallowly bifid (< 1 mm long) below the stigmatic area; stigma lobes usually rhomboid

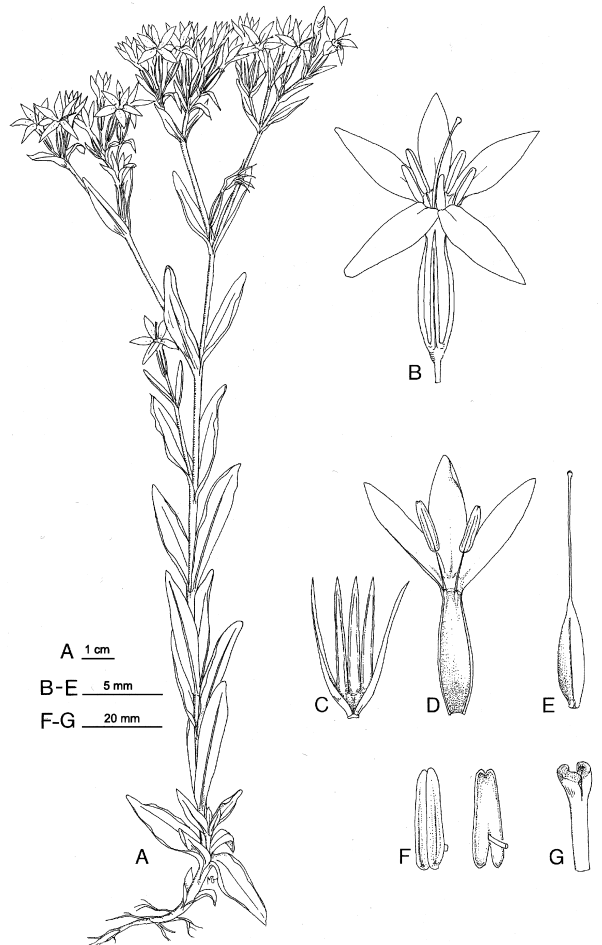


Fig. 4. *Zeltnera trichantha* (Griseb.) Mansion. A, habit; B, flower at anthesis; C, opened calyx; D, opened corolla (longitudinal section); E, gynoecium; F, erect anther (pre-anthesis); and G, subcapitate stigma.

or flabelliform, sometimes subcapitate. Capsule septicial, elliptic to oblong or oval, pericarp papery to thick and woody. Seeds numerous, 200–700 per capsule, the main axis 0.15–0.70 mm long; seed shape pyramidal to nearly oblate; seed coat reddish to yellowish-brown or blackish, reticulate, with papillae in lacunae. Chromosome number: $n = 17, 20, 21, 22, 37$. An American genus of 25 species.

Distribution. — United States (Arkansas, Arizona, California, Colorado, Idaho, Kansas, Louisiana, Mississippi, Montana, Nebraska, Nevada, New Mexico, Oklahoma, Oregon, Texas, Utah, Washington and Wyoming), Canada (British Columbia), Central America (Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, Panama and West Indies) and South America (Colombia, Ecuador and Peru).

Discussion. — The genus *Zeltnera* mainly differs from *Centaurium* and allied genera by its floral characters (Table 1). First, the style division under the stigma surface is distinct in *Centaurium* (2–5 mm), whereas it is absent or very inconspicuous in *Zeltnera* (it occurs sometimes in *Z. madrensis*). Second, in most of the allogamous species of *Zeltnera* (with relatively conspicuous corollas), the slender and filiform style mostly exceeds the corolla tube in length and is much longer than the stamens; in *Centaurium*, the style does not exceed the stamens in length. Third, the reniform or shoe-shaped stigma is an immediately recognizable trait in *Centaurium*, and additionally, the stigmatic surface is distinctly thickened to fleshy, and is becoming dark brown or green, when dry. In contrast, in *Zeltnera* the stigma lobes are more variable in shape (frequently flabelliform, rhombic or subcapitate) with no (or very weak) fleshy surface.

Finally, the capsule shape (elliptic to oblong or oval in *Zeltnera* vs. cylindrical in *Centaurium*) is a good discriminating character.

Species from similar ecological conditions (e.g., on gypseous soils) of *Centaurium* (e.g., *C. gypsicola* from Spain) and *Zeltnera* (e.g., *Z. glandulifera* from Texas) show striking morphological convergence, but are easily recognizable using the previously mentioned characters.

Remarks. — On the basis of DNA sequence analyses, the genus *Zeltnera* may be divided in three groups (Mansion & Zeltner, in press). The basal set is not fully resolved and comprises primarily Californian species (*Z. abramsii*, *Z. exaltata*, *Z. namophila*, *Z. nevadensis*, *Z. trichantha*, and *Z. venusta*). The two last groups are well supported clades of either predominantly Texan species (*Z. arizonica*, *Z. beyrichii*, *Z. breviflora*, *Z. calycosa*, *Z. glandulifera*, *Z. maryanna*, *Z. multicaulis*, and *Z. texensis*) or Mexican ones (*Z. madrensis*, *Z. martinii*, *Z. nudicaulis*, *Z. pusilla*, *Z. quitensis*, *Z. stricta*, and *Z. wiggin-sii*).

The first group, called here “Californian group”, comprises plants generally single-stemmed from the base, the stems branching usually near or above middle of main axis. The flowers are small (10–15 mm in diameter) to large (more than 20 mm in diameter), the capsule is elliptic in shape, and the seed length ranges from 0.35 to 0.75 mm. *Zeltnera davyi*, present in the geographic range, but not included in the molecular analyses, may belong to this group.

The second group (“Texan group”) comprises plants with generally several more or less equal stems from the basis, the stems branching from near basis as well as distally. The flowers are large (15–20 mm in diameter),

Table 1. Morphological comparison of *Zeltnera* with allied genera.

	<i>Centaurium</i>	<i>Gyandra</i>	<i>Schenkia</i>	<i>Zeltnera</i>
Leaves shape	lanceolate to oval (linear)	linear to elliptic	elliptic to oval	linear to elliptic (oval)
Stem branching	predominantly dichasial (distal divisions monochasial)	predominantly dichasial	predominantly monochasial (main branching dichasial)	predominantly dichasial (distal divisions monochasial)
Inflorescence	simple or compound, dense or lax cyme	simple or compound, lax cyme; sometimes panicle or raceme	compound, dense or lax cyme	simple or compound, dense or lax cyme; sometimes panicle or raceme
Type of cyme	corymbiform or capitate (sometimes paniculate or racemose)	paniculate or racemose	spiciform (to racemose)	paniculate or racemose (sometimes capitate or corymbiform)
Corolla shape	salverform	funnelform to rotate	salverform	salverform to funnelform
Anther	oblong to linear	linear	oblong	linear or oblong
Style	filiform to linear, shorter than the ovary	linear, shorter than the ovary	filiform, shorter than or equaling the ovary	filiform, shorter to longer than the ovary
Style division	divided beneath stigmata surface	not divided beneath stigmata surface	not divided beneath stigmata surface	not divided beneath stigmata surface
Stigma lobes	reniform, shoe-shaped; fleshy	capitate or subcapitate; not fleshy	rhomboid, reniform or subcapitate; slightly fleshy	rhomboid to flabelliform (sometimes subcapitate); slightly fleshy
Capsule	linear	oval	elliptic	elliptic to oblong or oval

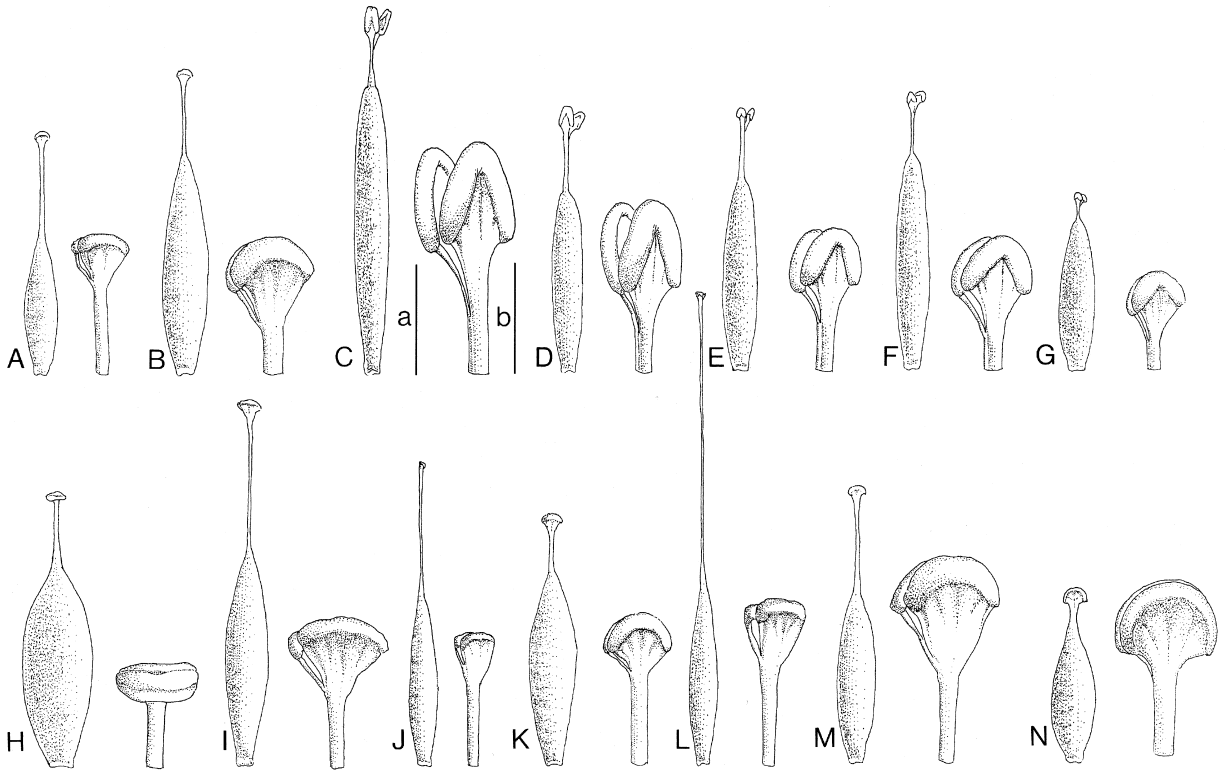


Fig. 5. Gynoecium types found in *Schenkia* (A, *S. spicata*; B, *S. australis*), *Centaurium* (C, *C. maritimum*; D, *C. majus*; E, *C. erythraea*; F, *C. littorale*; G, *C. favargerii*), *Gyandra* (H, *G. brachycalyx*) and *Zeltnera* (I, *Z. venusta*; J, *Z. namophila*; K, *Z. exaltata*; L, *Z. beyrichii*; M, *Z. madrensis*; N, *Z. martinii*), respectively. Left: gynoecium (scale: a = 5 mm); right: detail of style and stigma (scale: b = 20 mm).

sometimes small (10 mm in diameter), the capsule is elliptic in shape, and the seed length ranges from 0.25 to 0.45 mm.

In the last group (“Mexican group”), the capsule is either oblong, oval or elliptic. The flowers are generally small (i.e., less than 10 mm in diameter, except for *Z. madrensis*), and the corolla lobes are shorter than the corolla tube (or equal in *Z. madrensis*). The seed length ranges from 0.20 to 0.40 mm. *Zeltnera gentryi*, a very rare Mexican species, absent from our molecular studies, may be included in this group.

Key to the species of *Zeltnera* Mansion. —

The gynoecium characteristics, such as ovary shape, style length and division, and stigma shape, are shown in Fig. 5. Chromosome number counts are from Mansion & Zeltner (in press).

- 1. Cauline leaves subulate to linear 2.
- 1. Cauline leaves lanceolate to oblong 10.
- 2. Capsule ovate to oblong 3.
- 2. Capsule elliptic to fusiform 7.
- 3. Corolla 11–20 mm in diameter 4.
- 3. Corolla 5–10 mm in diameter 5.

- 4. Basal leaves shorter than cauline leaves 18. *Z. madrensis*
- 4. Basal leaves longer than cauline leaves 17. *Z. gentryi*
- 5. Pedicel longer than the corolla in length; basal rosette present 20. *Z. nudicaulis*
- 5. Pedicel shorter than or equaling the corolla in length; basal rosette absent 6.
- 6. Inflorescence a compound monochasial cyme, the branching highly divaricate; cauline leaves divergent from the stem 23. *Z. setacea*
- 6. Inflorescence a simple paniculate cyme, the branching acute; cauline leaves appressed to stem 19. *Z. martinii*
- 7. Leaves, stems, and calyces papillate-puberulent 13. *Z. glandulifera*
- 7. Leaves, stems, and calyces glabrous 8.
- 8. Basal rosette with numerous leaves present; perennial plant 10. *Z. beyrichii*
- 8. Basal rosette absent; annual plant 9
- 9. Corolla 15–20 mm in diameter; stigma subcapitate 5. *Z. namophila*
- 9. Corolla 7–14 mm in diameter; stigma slightly bilobed 16. *Z. texensis*

10. Corolla 5–10 mm in diameter; anthers 0.5–2.4 mm long before anthesis 11.
10. Corolla 11–35 mm in diameter; anthers 2.5–4.5 mm long before anthesis 18.
11. Anthers 0.5–1.5 mm long before anthesis 12.
11. Anthers 1.6–2.4 mm long before anthesis 16.
12. Plants up to 10 cm high; basal rosette present; several equal stems from the basis 21. *Z. pusilla*
12. Plants 10–40 cm high; basal rosette absent; generally a single main stem branched in the middle part 13.
13. Inflorescence a compound monochasial and paniculate cyme, the branching divaricate 22. *Z. quitensis*
13. Inflorescence a panicle or a racemose cyme, the branching nearly parallel to diverging 14.
14. Pedicel of the central flower 10–50 mm long; leaves elliptic 3. *Z. exaltata*
14. Pedicel of the central flower up to 10 mm long; leaves oblong to obovate 15.
15. Leaves oblong, the basal ones equaling the cauline ones in length 25. *Z. wigginsii*
15. Leaves obovate, the basal ones much longer than the cauline ones in length 24. *Z. stricta*
16. Flowers sessile, the pedicels 1–9 mm long 4. *Z. muhlenbergii*
16. Flowers distinctly pedicellate, the pedicels 10–60 mm long 17.
17. Pedicels thick (0.6–0.8 mm in diameter), 10–30 mm long 2. *Z. davyi*
17. Pedicels slender (0.4–0.5 mm in diameter), 30–60 mm long 6. *Z. nevadensis*
18. Plants usually branched above the middle of the stem 19.
18. Plants usually branched from the base of the stem 21.
19. Corolla 21–35 mm in diameter 8. *Z. venusta*
19. Corolla 15–20 mm in diameter 20.
20. Corolla lobes acuminate; stigma subcapitate 7. *Z. trichantha*
20. Corolla lobes obtuse to acute; stigma slightly bilobed 1. *Z. abramsii*
21. Basal leaves numerous at flowering time; stigma subcapitate. 14. *Z. maryanna*
21. Basal leaves generally absent or withered at flowering time; stigma slightly bilobed 22.
22. Plants with several equally long stems from the base; flowering laterals branched 1–2 times 15. *Z. multicaulis*
22. Plants uniaxial or with several stems branching from near base as well as distally; flowering laterals branched 3–6 times 23.
23. Corolla 10–15 mm in diameter 11. *Z. breviflora*
23. Corolla 16–30 mm in diameter 24.
24. Inflorescence a dense corymbose to helicoidal cyme; corolla 15–20 mm in diameter. 12. *Z. calycosa*
24. Inflorescence a lax racemose cyme; corolla 21–30 mm in diameter 9. *Z. arizonica*

TAXONOMIC COMBINATIONS IN ZELTNERA MANSION.

“**Californian group**”. — Chromosome number: $n = 17, 20, 37$. Distribution: United States (California, Oregon and Washington), Canada (British Columbia) and north of Mexico (Baja California).

1. *Zeltnera abramsii* (Munz) Mansion, **stat. et comb. nov.** \equiv *Centaurium venustum* subsp. *abramsii* Munz, *Aliso* 4: 96. 1958. — Type: United States, California, Shasta Co., 6 miles N of Redding, head of Sacramento Valley, 800 feet, 8 Aug 1937, *C. B. Wolf 9072* (Holotype: RSA; isotype: CAS).

Distribution. — United States, California (Sierra Nevada mountains), from Kern County to Butte and Shasta Counties. This is a montane species growing in subalpine meadows, grasslands or yellow pine forests.

Remarks. — *Zeltnera abramsii* and *Z. venusta* occur in different ecological zones. The former is encountered in open meadows and yellow pine communities of the Sierra Nevada Mountains, often at high elevations (up to 2200 m), and blooms between July and September; the latter is present in chaparral and coastal communities, at low elevations (blooming between May and July). Both species can be distinguished by their differences in leaf shape (linear to ensiform with an acute apex in *Z. abramsii* vs. lanceolate and an obtuse apex in *Z. venusta*) and the corolla size (up to 20 mm in diameter in *Z. abramsii* vs. 30–35 mm in *Z. venusta*). Experimental crosses have failed between the two species, suggesting reproductive isolation (Broome, 1973). Moreover, phylogenetic analyses support the separation between *Z. abramsii* and *Z. venusta*, the later forming a clade with *Z. exaltata* (Mansion and Zeltner, in press). Thus, I have adopted here a specific rank for *Z. abramsii*, instead of a subspecific or varietal one.

2. *Zeltnera davyi* (Jepson) Mansion, **comb. nov.** \equiv *Centaurium exaltatum* var. *davyi* Jepson, *Man. Fl. Pl. Calif.*: 762. 1925. \equiv *Centaurium davyi* (Jepson) Abrams., *Fl. Pacific States* 3: 352. 1951. — Type: United States, California, West Berkeley, *Davy 596* (Holotype JEPS).

Distribution. — United States, California, from Mendocino County to San Luis Obispo County and Santa Cruz Islands. This rare plant may be encountered in regular or serpentine chaparrals, sometimes in vol-

canic areas, in moist, sunny, rocky, brushy or grassy riparian places like seeps or springs.

Remarks. — *Zeltnera davyi* is immediately recognizable by the presence of keeled calyx lobes (making the calyx wider than those of related species of *Zeltnera*) and a deeply pink pigmented corolla. It differs from *Z. muhlenbergii* (which has ridged calyx lobes) by its long-pedicelled flowers (the pedicel up to 30 mm) and the less-marked dichasial branching.

3. *Zeltnera exaltata* (Griseb.) Mansion, **comb. nov.** ≡ *Cicendia exaltata* Griseb., Gen. Sp. Gent.: 159. 1838. ≡ *Erythraea douglasii* A. Gray, Bot. Calif. 1: 480. 1876 [based on *Cicendia exaltata* Griseb. and *Erythraea nuttallii* Watson in part]. ≡ *Centauroides douglasii* (A. Gray) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Erythraea exaltata* (Griseb.) Coville, Contr. U. S. Natl. Herb. 4: 150. 1893. ≡ *Centaurium exaltatum* (Griseb.) W. F. Wight ex Piper, Contr. U. S. Natl. Herb. 11: 449. 1906. ≡ *Centaurium douglasii* (A. Gray) Druce, Rep. Bot. Exch. Club Brit. Isles 4: 613. 1917. – Type: United States, Washington, between the Kettle Falls and Narrows of the Columbia River, *N. W. C. Douglas s.n.* (Holotype: K!).
= *Erythraea nuttallii* S. Watson, Botany King Surv. 276. 1871. ≡ *Centauroides nuttallii* (S. Watson) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium nuttallii* (S. Watson) A. Heller, Muhlenbergia 4: 86. 1908. – Lectotype (designated by Broome, 1981): *C. L. Anderson 29* (GH).

Distribution. — United States (California, Idaho, Montana, Nevada, Oregon, Utah and eastern Washington), Canada (British Columbia) and Mexico (Baja California). *Zeltnera exaltata* occurs in coastal sage scrub, chaparral and creosote bush scrub in alkaline soil under moist conditions.

Remark. — This variable and widespread species has often been confused with *Z. nevadensis* and sometimes intergrades with it (Broome, 1981; G. Mansion, pers. observ.). As a result, the synonymy is abundant and confusing.

Watson (1871) referred Nuttall's manuscript names, “*E. elata*”, “*E. longiflora*” and “*E. tenella*” to *E. nuttallii*. The protologue was established on Watson's personal collection (*Watson 945*, GH), and was accompanied by a plate based on an Anderson collection (*Anderson 29*, GH) from Carson City, Nevada. According to Broome (1981), “*E. elata*” was typical *Centaurium exaltatum* (similar to *Anderson 29*), “*E. longiflora*” was *C. namophilum* var. *nevadense* and “*E. tenella*” represented *C. floribundum* (a heterotypic name for *C. muhlenbergii*). She lectotypified *E. nuttallii* on the base of *Anderson 29* because it served as the model for the plate of Watson's protologue, and concluded *E. nuttallii* to be

a taxonomic synonym of *C. exaltatum*. The observation of Watson's plate shows that the right line drawing is clearly *Z. exaltata*; nevertheless, the left line drawing may represent *Z. nevadensis* (calyx lobes 4–5 mm long, half as short as the corolla tube; corolla lobes 5 mm long; style 3 mm long, shorter than the ovary; seeds 0.8 mm long). As a result, the specific delimitation of *E. nuttallii* remained unclear for Watson, and his description was made based on two distinct species.

Gray (1876) was the first to accurately distinguish Watson's *Erythraea nuttallii* from his *E. douglasii*. He excluded “*E. elata*” and “*E. tenella*” (treated by him as *E. nuttallii* var. *tenella*, an heterotypic name for *Zeltnera muhlenbergii*) from the concept of *E. nuttallii*, keeping only “*E. longiflora*” from the Watson collection (*Watson 945*, GH). Thus, Gray's concept of *E. nuttallii* was clearly *Z. nevadensis* and consequently, his *E. douglasii* was similar to “*E. elata*” (i.e., *Z. exaltata*). Coville (1893) and Howell (1901) followed Gray and separated *E. nuttallii* from *E. exaltata* or *E. douglasii*, respectively. The two latter species are nomenclatural synonyms, based on *Cicendia exaltata* Griseb., and thus the epithet “*douglasii*” is superfluous.

To conclude, Watson's protologue of *E. nuttallii* was unclear and later lectotypified as a taxonomic synonym of *E. exaltata* (≡ *E. douglasii*), whereas subsequent authors clearly discriminate between *E. nuttallii* (= *Z. nevadensis*) and *E. exaltata*. Thus the combination *E. nuttallii* became invalid to describe what Broome (1981) treated as *C. namophilum* var. *nevadense* (≡ *Z. nevadensis*).

The main morphological characters to discriminate between *Z. exaltata* ($n = 20$) and *Z. nevadensis* ($n = 17$), are the broad and elliptic leaves (vs. oblong or lanceolate ones in *Z. nevadensis*), the dichotomous peduncles (vs. trichotomous ones in *Z. nevadensis*) and the seed size (0.4–0.5 mm in *Z. exaltata* vs. 0.7–0.8 mm in *Z. nevadensis*).

4. *Zeltnera muhlenbergii* (Griseb.) Mansion, **comb. nov.** ≡ *Erythraea muhlenbergii* Griseb., Gen. Sp. Gent.: 146. 1838. ≡ *Centauroides muhlenbergii* (Griseb.) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium muhlenbergii* (Griseb.) W.F. Wight ex Piper, Contrib. U.S. Natl. Herb. 11: 449. 1906. – Type: United States, California, without locality, 1831, *Douglas s.n.* (Lectotype: K; isolectotype: BM, lectotype designated by Piper, 1906).
= *Centaurium muhlenbergii* var. *albiflorum* W. N. Suksdorf, Werdenda 1: 30. 1927. ≡ *Centaurium curvistamineum* forma *albiflorum* W. N. Suksdorf, Fl. S. E. Washington 314. 1937. – Type: United States, Washington, Spokane Co., Near Latah Creek SE of Spangle, 20 Jul 1916, *W. N. Suksdorf 8903*

(Holotype: WS; isotypes: BM, CAS, GH, K!, MO, NY!, PH, US!, WS).

- = *Erythraea floribunda* Benth., Pl. Hartw.: 322. 1849. ≡ *Centaurodes floribundum* (Benth.) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium floribundum* (Benth.) B. L. Robinson, Proc. Amer. Acad. Arts 45: 396. 1910. – Type: United States, California, in valle Sacramento, 1847, *K. T. Hartweg 405* [also numbered 1832 by Bentham] (Holotype: K!; isotypes: GH, NY!).
- = *Erythraea nuttallii* var. *tenella* A. Gray, Proc. Amer. Acad. Arts 8: 398. 1872. – Type: United States, Oregon, 1871, *E. Hall 425* (Holotype: GH; isotype: NY!).
- = *Erythraea curvistaminea* Wittr., Bot. Centr. 26: 317. 1886. ≡ *Centaurium curvistamineum* (Wittr.) Druce, Rep. Bot. Exch. Club Brit. Isles 4: 613. 1917. – Type: United States, Washington, Spokane Co., Falcon Valley, 30 Jul 1885, *W. N. Suksdorf 8903* (Holotype: S; isotypes: BM, GB, GH, K!, LD, MANCH, MPU, NY!, US!, WRSL).
- = *Erythraea minima* Howell, Fl. N. W. Amer. 443. 1901. ≡ *Centaurium minimum* (Howell) Piper, in Piper & Beattie, Fl. N. W. Coast: 288. 1915. – Type: United States, Oregon, Near Hillsboro, *Howell s.n.*, June 1883 (Holotype: ORE).

Distribution. — United States, California, along the coast from Mendocino County to Santa Barbara County. The plant occurs on serpentine formations, in moist, sunny, rocky or clayey grassy flats or meadows.

Remarks. — The taxonomic history of *Zeltnera muhlenbergii* is complex and much of the confusion has arisen both with the typification of the species and with the recent report of *Centaurium tenuiflorum*, a Mediterranean native, in North America (Pringle, pers. comm.). In his original description of *Erythraea muhlenbergii*, Grisebach (1839) cited several specimens collected by Muhlenberg throughout the United States, including some specimens of the European *C. pulchellum*. Later, some authors (Hooker & Arnott, 1830–1841; Gray, 1878) reduced *Z. muhlenbergii* to contain only the western populations where the type was originally collected, whereas others treated these populations as a new species, namely *Centaurium floribundum* (Benth.) B. L. Robinson (Dunn, 1967). This name has further been applied to several misidentified Californian species. The lectotypification of *Z. muhlenbergii* was finally completed by Piper (1906). On the other hand, annotations on herbarium sheets mention *C. tenuiflorum* as a synonym of *Z. muhlenbergii* or *C. floribundum* (Broome, unpubl.). *Centaurium tenuiflorum* is of Mediterranean origin, but has also been reported as an abundant naturalized species in Australia (Adams, 1996), and recently in North America (by the 1890s: Pringle, pers. comm.). Some

authors may have possibly confused *Z. muhlenbergii* with *C. tenuiflorum*, treating the alternate form (i.e., the typified *C. muhlenbergii*) under *C. curvistamineum* (Abrams, 1951; Munz & Keck, 1959). Lastly, some confusion with *C. erythraea*, another European species naturalized in the United States, has made delimitation of *Z. muhlenbergii* unclear.

- 5. *Zeltnera namophila* (Reveal, Broome & Beatley) Mansion, **comb. nov.** ≡ *Centaurium namophilum* Reveal, Broome & Beatley, Bull. Torrey Bot. Club 100: 353. 1973. – Type: United States, Nevada, Nye Co., Colline Ranch, 6 miles S of Devil's Hole, Ash Meadows Road, moist soil near spring, sm 1/4 Sec. 1, R 50E, T18S, 2300 feet, 25 Jul 1972, *J. Beatley & J. L. Reveal 13447* (Holotype: GH!; isotypes: ARIZ, CAS, COLO, GH, NY!, US!).

Distribution. — United States, Nevada. This species, endemic to Nye Co., occurs in mesic to wet alkaline clay soils of seeps, springs, outflow drainages and meadows.

Remarks. — On the basis of molecular markers (DNA sequences) and chromosome number ($n=17$), this species is close to *Z. trichantha* and *Z. nevadensis*. Morphologically, *Z. namophila* resembles *Z. trichantha*. Both species have short pedicellate flowers (pedicels 1–9 mm long on the ultimate branch), relatively large corolla (12–16 mm in diameter), and subcapitate stigma lobes and occur in marshy places or alkaline soil. In contrast, *Z. nevadensis* approaches *Z. exaltata*, both having long pedicelled flowers (the pedicels 10–70 mm long on the ultimate branch) with small corollas (8–12 mm in diameter).

This endangered plant is protected by the U. S. Fish & Wildlife Service (listed as “Threatened”) and the state of Nevada (“Fully Protected”) (USDA, NRCS, 2002). The major threats are regional groundwater pumping, competition with invasive weeds and water diversion.

- 6. *Zeltnera nevadensis* (Broome) Mansion, **stat. et comb. nov.** ≡ *Centaurium namophilum* var. *nevadense* Broome, Great Basin Naturalist 41: 192. 1981. – Type: United States, Nevada, Esmeralda Co., Gap Springs, 2.8 mi southeast of intersection of Nevada Highway 3A and US highway 6, T1N, R36E, sec. 6, ca 4600 ft, 22 Aug 1978, *C. R. Broome 2388* (Holotype: CAS; isotype: NY).

Distribution. — United States, Nevada, on the margins of alkaline springs (often sulfur springs), seeps and grassy meadows.

Remarks. — According to Broome (1981), *Z. nevadensis* may be found in California, Idaho, Nevada, Oregon and Utah. However, I have encountered this species in only two populations in Nevada.

7. *Zeltnera trichantha* (Griseb.) Mansion, **comb. nov.** ≡ *Erythraea trichantha* Griseb., Gen. Sp. Gent.: 146. 1838. ≡ *Centauroides trichanthum* (Griseb.) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium trichanthum* (Griseb.) B. L. Robinson, Proc. Amer. Acad. 45: 397. 1910. — Type: United States, In California nova, 1833, *Douglas s.n.* (Holotype K!; isotypes: GH, K!, NY!). — Fig. 4.

Distribution. — United States, in northern California (San Mateo Co. to Siskiyou Co.). This species can be encountered in mixed evergreen forest, chaparral, coastal prairies or moist places along streams, on alkaline soils, serpentine or volcanic formations.

8. *Zeltnera venusta* (A. Gray) Mansion, **comb. nov.** ≡ *Centauroides venustum* (A. Gray) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium venustum* (A. Gray) B. L. Robinson, Proc. Amer. Acad. 45: 397. 1910. — Type: United States, California, *T. Coulter 561* (Holotype: GH). ≡ *Erythraea venusta* A. Gray, Bot. Calif. 1: 479 (1876).

= *Erythraea venusta* var. *micrantha* Witt., Bot. Not. 1899: 281. 1899. — Type: Mexico, Baja California, Todos Santos Bay, 19 May 1886, *Orcutt s.n.* (Holotype: UC; isotype: NY!).

= *Centaurium venustum* forma *tupae* Creutz, Wild Fl. 38: 19. 1962. — Type: California, San Diego Co., Torrey Pine State Park, *Creutz 5* (Holotype: CM).

Distribution. — United States and Mexico, from south California to Baja California, in chaparral and coastal sage scrub communities.

“Texan group”. — Chromosome number: $n = 20, 21$. Distribution: United States (Arizona, New Mexico, Oklahoma and Texas); northern Mexico (Chihuahua, Coahuila, Durango, Nuevo León, Puebla, San Luis Potosí, Sonora and Tamaulipas).

9. *Zeltnera arizonica* (A. Gray) Mansion, **comb. nov.** ≡ *Erythraea calycosa* var. *arizonica* A. Gray, Syn. Fl. N. Amer. 2: 113. 1878. ≡ *Erythraea arizonica* (A. Gray) Rydb., Bull. Torrey Bot. Club 33: 148. 1906. ≡ *Centaurium arizonicum* (A. Gray) Heller, Muhlenbergia 4: 86. 1908. ≡ *Centaurium calycosum* var. *arizonicum* (A. Gray) Tidestrom, Proc. Biol. Soc. Wash. 48: 42. 1935. — Type: United States, Utah, Washington Co., St. George, 1875, *E. Palmer s.n.* (Lectotype: GH; isolectotype: NY!; lectotype designated by B. L. Turner, 1993).

Distribution. — Southwestern part of the United States (Arizona, New Mexico and Texas) and Mexico (Chihuahua, Coahuila, Durango and Sonora). *Zeltnera arizonica* grows on alluvial soils of stream banks, pond

margins or wet seeps.

Remarks. — This species has often been treated as a variety of *Z. calycosa* (Broome, 1973). Morphologically *Z. arizonica* approaches *Z. multicaulis*, both the species having a poorly branched pattern with weakly spreading stems, and pedicelled flowers (pedicels 2–3 cm long).

10. *Zeltnera beyrichii* (Torr. & A. Gray) Mansion, **comb. nov.** ≡ *Erythraea beyrichii* Torr. & A. Gray in Marcy, Explor. Red River Louisiana 13: 291. 1853. ≡ *Centauroides beyrichii* (Torr. & A. Gray) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium beyrichii* (Torr. & A. Gray) B. L. Robinson, Proc. Amer. Acad. Arts 65: 396. 1910. — Type: United States, Arkansas, *C. Beyrich s.n.* (Holotype: GH; isotype: NY!).

= *Centaurium beyrichii* forma *albiflorum* U. T. Waterfall, Rhodora 50: 98. 1948. — Type: United States, Oklahoma, Murray Co., limestone hillside, 2 miles east and 2 miles north of Sulphur, 21 Jul 1946, *U. T. Waterfall 6529* (Holotype: UC; isotype: GH, US).

Distribution. — United States, from central Texas to Oklahoma. This species occurs on wet calcareous soils, frequently in gravelly or rocky places. The specimens from New Mexico have been reidentified as *Z. maryanna* (Turner, 1993).

Remarks. — Unlike the other large-flowered *Zeltnera* species, the stamens are radially divergent at the anthesis, and thus form a wide circle rather than a lateral cluster (Broome, 1973).

11. *Zeltnera breviflora* (Shinners) Mansion, **comb. nov.** ≡ *Centaurium calycosum* var. *breviflorum* Shinners, Field & Lab. 18: 130. 1950. ≡ *Centaurium breviflorum* (Shinners) B. L. Turner, Phytologia 75: 263. 1993. — Type: United States, Texas, Cameron Co., NW of Brownsville, 6 Apr 1941, *C. L. Lundell 10022* (Holotype: SMU).

Distribution. — United States. This species, endemic to the southern part of Texas, occurs along roadside or in open meadows, mainly on sandy or alluvial soils.

Remarks. — The clade consisting of *Z. breviflora*, *Z. calycosa* and *Z. texensis* is not fully resolved in the molecular analysis and these species share the same chromosome number ($2n = 40$) (Mansion & Zeltner, in press). Nevertheless, these species are distinguishable using field characters such as flower or inflorescence features and leaf shape. Clinal variation is sometimes observed in large sympatric populations, but these three species are found in allopatric situations. In addition, each one occurs in a distinctive ecogeographic setting (Turner, 1993). *Zeltnera breviflora* is found in southern

Texas, on sandy soils; *Z. calycosa* is more frequent rocky soils, in the more western portion of the Edwards Plateau. This plateau is an uplifted and elevated region originally formed from marine deposits of sandstone, limestone, shale, and dolomites, which extends in the southwestern regions of northcentral Texas. *Zeltnera texensis* is encountered in the eastern part of this plateau on calcareous seeps.

12. *Zeltnera calycosa* (Buckl.) Mansion, **comb. nov.** ≡ *Erythraea calycosa* Buckl., Proc. Acad. Sc. Philad. 2: 7. 1862. ≡ *Centaurodes calycosum* (Buckl.) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium calycosum* (Buckl.) Fernald, Rhodora 10: 54. 1908. – Type: United States, Texas, North of Fort Mason, *Buckley s.n.* (Holotype: PH; isotype: GH).
= *Erythraea calycosa* var. *nana* A. Gray, Syn. Flo. 2: 113. 1878. ≡ *Centaurium calycosum* var. *nanum* (A. Gray) B. L. Robinson, Proc. Amer. Acad. 45: 396. 1910. – Type: United States, Texas, Stony Hills, *Wright 1662* (Lectotype: GH; isolectotype: GH [2 sheets]; lectotype designated by B. L. Turner, 1993).

Distribution. — United States, from the Edwards Plateau region of Texas to Mexico (Coahuila, Nuevo Leon and Tamaulipas). This locally abundant species occurs on dry, calcareous or shallow rocky soils, often along roadsides.

Remarks. — Broome (1973) recognized three varieties within *Centaurium calycosum*: var. *arizonicum*, var. *calycosum* and var. *nanum*. The former is treated here as a good species (*Z. arizonica*) whereas the distinction between the two latter taxa is problematic. Dunn (1967) considered var. *nanum* to be a hybrid between *C. calycosum* and *C. texense* whereas Broome (1973) noted that this variety is “greatly suspect”. Because of the difficulty to discriminate between these putative varieties, I follow Turner (1993) in considering *Z. calycosa* as a heterogeneous assemblage of variable populations, without defining varieties.

13. *Zeltnera glandulifera* (Correll) Mansion, **comb. nov.** ≡ *Centaurium beyrichii* var. *glanduliferum* Correll, Wrightia 4: 76. 1968. ≡ *Centaurium glanduliferum* (Correll) B. L. Turner, Phytologia 75: 265. 1993. – Type: United States, Texas, *D. S. Correll & M. C. Johnston 24580* (Holotype: LL).

Distribution. — United States, Texas. A rare species, endemic to Terrell county, and occurring on rocky soils along roadsides.

Remark. — The papillose glands present on the stems, leaves and calyces are not always easy to observe, even at magnification of 20–40×. Nevertheless, this species is relatively easy to recognize in the field by a particular character combination. The basal linear leaves

form a dense rosette (as in *Z. beyrichii*), the equally developed stems are divaricately branched from the base of the plant (as in *Z. maryanna*), and the corolla lobes are similar in length and shape with those of *Z. calycosa* (Turner, 1993).

14. *Zeltnera maryanna* (B. L. Turner) Mansion, **comb. nov.** ≡ *Centaurium maryannum* B. L. Turner, Phytologia, 75: 269. 1993. – Type: United States, Texas, Culberson Co., ca 2 mi E of intersection of states highways 1108 and 652, ca. 15 airline mi S of White City, New Mexico, 22 May 1967, *B. L. Turner 5660* (Holotype: LL!).

Distribution. — United States, from western Texas (Culberson Co.) to southern New Mexico (Chaves Co., De Baca Co., Eddy Co. and Otero Co.). This rare species occurs mainly on gypseous soils.

Remarks. — This species resembles *Z. glandulifera* by the divaricate branching of the stems and the corolla size but the chromosome number ($n = 21$) suggests a closer relationship with *Z. multicaulis*.

15. *Zeltnera multicaulis* (B.L. Robinson) Mansion, **comb. nov.** ≡ *Centaurium multicaule* B. L. Robinson, Proc. Amer. Acad. 45: 396. 1910. – Type: Mexico, Chihuahua, moist meadow, Hacienda of San Diego, 2 Jun 1891, *Hartman 717* (Holotype: GH; isotype: US!, NY!).

Distribution. — Northern Mexico (Chihuahua, Durango, Puebla, San Luis Potosi and Sonora) and southwestern part of the United States (New Mexico and Texas). This species occurs mainly in moist meadows.

16. *Zeltnera texensis* (Griseb. ex Hook.) Mansion, **comb. nov.** ≡ *Erythraea texensis* Griseb. ex Hook., Fl. Bor. Am. 2: 58. 1838. ≡ *Centaurodes texense* (Griseb. ex Hook.) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium texense* (Griseb. ex Hook.) Fern., Rhodora 10: 54. 1908. – Type: United States, Texas, Austin Co., San Felipe, 1834, *Drummond 231* (Holotype: K!; isotypes: GE!, GH [2 sheets], NY!).

Distribution. — United States, mainly in the eastern part of the Edwards Plateau of Texas and northwards, in Arkansas, Kansas, Missouri and Oklahoma. *Zeltnera texensis* occurs on calcareous soil, in open and rocky sites, barrens or prairies.

Remarks. — This species, closely related to *Z. breviflora* and *Z. calycosa*, is mainly recognizable in the field by the monochasial inflorescence branching (helicoidal cymes), the linear leaves and the small size of its corollas (7–10 mm in diameter).

“Mexican group”. — Chromosome number: $n = 21, 22$. Distribution: Mexico and Central America (Costa

Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama and West Indies); South America (Colombia, Ecuador and Peru); United States (Arizona).

17. *Zeltnera gentryi* (Broome) Mansion, **comb. nov.** ≡ *Centaurium gentryi* Broome, Madroño 24: 236. 1977. – Type: Mexico, Rancho Byerly, Sierra Charuco (ca. 27°30'N, 108°40'W), on rocky igneous slopes in pine-oak forest, 1525–1770 m, 17–25 Apr 1948, *Howard S. Gentry 8035* (Holotype UC; isotypes: ARIZ!, CAS, DS, MEXU, MICH, US).

Distribution. — Mexico (Chihuahua). This species occurs in the Rio Mayo region of western Mexico, in pine-oak forest.

Remarks. — *Zeltnera gentryi* is a very rare species, known only from a single population. According to Broome's description and line drawing of herbarium sheets (*Gentry 8035, Smith M81*), this species in its habit, leaf shape, inflorescence and size of corolla lobes resembles *Z. madrensis*.

18. *Zeltnera madrensis* (Hemsl.) Mansion, **comb. nov.** ≡ *Erythraea madrensis* Hemsl., Biol. Centr. Am. Bot. 2: 346. 1882. ≡ *Centaurium madrense* (Hemsl.) B. L. Robinson, Proc. Amer. Acad. 45: 396. 1910. – Type: Mexico, Sierra Madre, *Seeman 2067* (Holotype: K!; isotype: GH).

= *Erythraea pringleana* Wittr., Bot. Gaz. 16: 85. 1891. ≡ *Centaurium pringleanum* (Wittr.) B. L. Robinson, Proc. Amer. Acad. 45: 397. 1910. – Type: Mexico, Jalisco, “in collibus prope Guadalajara”, 5 Dec 1888, *Pringle s.n.* (Holotype: S; isotypes: BR, F, GH, K, MICH, UC, US).

Distribution. — Western Mexico (Durango, Jalisco and Sinaloa), in margin of pine-oak forests or dry and open meadows.

19. *Zeltnera martinii* (Broome) Mansion, **comb. nov.** ≡ *Centaurium martinii* Broome, Brittonia 28: 423. 1976. – Type: Mexico, Jalisco, plains of Guadalajara, Nov 1889, *C. G. Pringle 2595* (Holotype: US!; isotypes: K!, GE!, NY! [2 sheets], US!).

Distribution. — Transverse volcanic belt of Mexico (Guerrero, Jalisco, Michoacan and Morelos) and mountains of Honduras, in pine-oak forest.

Remarks. — *Zeltnera martinii* has very narrow leaves appressed to the stem, giving the plant a leafless and achlorophyllous aspect. This species shows an unusual disjunction in its distribution, for populations can be found in Mexico and in Honduras, but not in the intervening area despite the presence of suitable habitats.

Broome (1973) used the name “*Centaurium phenax* Martin”. She referred to it as “*C. phenax* Martin ex

Broome”. However, her thesis was never effectively published. When Broome published a paper on *Centaurium* taxonomy (Broome, 1976), she published the name *C. martinii*, for the species she had originally referred to as “*C. phenax*”, retaining the same type specimen, *Pringle 2595*.

20. *Zeltnera nudicaulis* (Engelm.) Mansion, **comb. nov.** ≡ *Erythraea nudicaulis* Engelm., Proc. Am. Acad. 17: 222. 1882. ≡ *Centaurium nudicaule* (Engelm.) B. L. Robinson, Proc. Amer. Acad. 45: 397. 1910. – Type: United States, Arizona, by streams of the Santa Catalina Mountains, Apr 1881, *Pringle s.n.* (Holotype: GH!; isotypes: GE!, K!, MO, NY! [2 sheets]).

= *Centaurium peninsulare* Brandegees, Univ. Calif. Publ. Bot. 6: 502. 1919. – Type: Mexico, Baja California, “Sierra de San Francisquito, a high mountain of the Cape Region”, *Brandegee s.n.* (Holotype: UC; isotype: GH).

Distribution. — Mainly a Mexican species (Sierra Madre occidental of Chihuahua, Southern Baja California, Durango, Nayarit, Jalisco, Sinaloa, Sonora), also present in the United States (southern Arizona), along stream banks of open pine-oak forests.

Remarks. — On the basis of molecular analyses, this taxon may refer to two distinct entities (Mansion & Zeltner, in press). Further studies are necessary to determine if they correspond to *C. peninsulare* (slender form) and *C. nudicaule* (shorter, stout and single-stemmed form), respectively.

21. *Zeltnera pusilla* (Eastwood) Mansion, **comb. nov.** ≡ *Centaurium pusillum* Eastwood, Proc. Amer. Acad. 44: 605. 1909. – Type: Mexico, Michoacan, Morelia, on a damp bare mesa, 29 November 1907, *Pringle 10408* (Holotype: GH; isotypes: ARIZ, ASU, CAS, COLO, F, LL, MI, UC, US).

Distribution. — Mexico (Jalisco, Michoacán), in pine-oak forests.

Remarks. — This species superficially resembles small forms of *Zeltnera quitensis*. They mainly differ by the branching (basal in *Z. pusilla*) and the stigma shape (reniform in *Z. pusilla* vs. flabelliform in *Z. quitensis*).

22. *Zeltnera quitensis* (Kunth) Mansion, **comb. nov.** ≡ *Erythraea quitensis* Kunth, Nov. Gen. Sp. 3: 178. 1819. ≡ *Exacum quitense* (Kunth) Spreng., Syst. Veg. 1: 425. 1824. ≡ *Cicendia quitensis* (Kunth) Griseb., Linnaea 22: 33. 1849. ≡ *Centaurium quitense* (Kunth.) B. L. Robinson, Proc. Amer. Acad. 45: 397. 1910. – Type: Ecuador, “In planitie alta Chilloensi pr. Quito”, 8000 ft., *Bonpland & Humboldt* (Holotype: P).

- = *Erythraea divaricata* W. Schaffn. ex Schltdl., Bot. Zeit. 13: 920. 1855. ≡ *Centauroides divaricatum* (W. Schaffn. ex Schltdl.) Kuntze, Rev. Gen. 2: 426. 1891. ≡ *Centaurium divaricatum* (W. Schaffn. ex Schltdl.) Millsp. & Greenm., Field Col. Mus. Bot. Ser. 2: 309. 1909. – Type: Mexico, Veracruz, “Ad Huatusco”, *Schaffner 81* (Holotype: HAL).
- = *Centaurium brittonii* Millsp. & Greenm., Publ. Field Columbian Mus., Bot. Ser. 2: 308. 1909. – Type: Bahamas Islands, Watling’s Island, NW of Cockburntown, 15 Mar 1907, *Britton & Millspaugh 6224* (Holotype: F; isotype: NY!).

Distribution. — From Central America (Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama and West Indies) to South America (Colombia, Ecuador and Peru) and in Mexico (Chiapas, Guerrero, Jalisco, Oaxaca, San Luis Potosí, Sinaloa and Veracruz). This species is tolerant of both very wet and dry conditions.

Remarks. — Two chromosome numbers occur in *Zeltnera quitensis* (Broome, 1973; Mansion and Zeltner, in press). Populations with $n = 21$ have been mainly collected in the northern part of Mexico (except one), whereas populations with $n = 22$ were encountered in a more southern range (Mansion & Zeltner, in press). These preliminary data might support further segregation in the *Z. quitensis* complex.

23. *Zeltnera setacea* (Benth.) Mansion, **comb. nov.** ≡ *Erythraea setacea* Benth., Bot. Voy. Sulph.: 128. 1845. ≡ *Centauroides setaceum* (Benth.) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium setaceum* (Benth.) B. L. Robinson, Proc. Amer. Acad. Arts 45: 397. 1910. – Type: Mexico, Guerrero, Acapulco, 1842, *Hinds s.n.* (Holotype: K).

Distribution. — From western Mexico (Durango, Guerrero, Jalisco, Mexico, Michoacán and Sinaloa) to mountains of Guatemala, often in open pine forests.

Remarks. — The distinct character combination of the basal rosette, the setaceous cauline leaves, the divaricately branched inflorescence and the slightly funnelform corolla set this species apart from all others.

24. *Zeltnera stricta* (Schiede) Mansion, **comb. nov.** ≡ *Erythraea stricta* Schiede, Pers. Acad. Med. Mej. 1: 14. 1836. ≡ *Centauroides strictum* (Schiede) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium strictum* (Schiede) Druce, Rep. Bot. Exch. Club Br. Isles 4: 614. 1917. – Type: Mexico, Vera Cruz, “propre Huatusco”, *Schaffner 80* (Holotype: HAL).

- = *Erythraea tetramera* Schiede, Pers. Acad. Med. Mej. 1: 15. 1836. ≡ *Centauroides tetramerum* (Schiede) Kuntze, Revis. Gen. Pl. 2: 426. 1891. ≡ *Centaurium tetramerum* (Schiede) Eastw., Proc. Amer. Acad.

Arts 44: 606. 1909. – Type: Mexico, Morelos, Cuernavaca, Herba Centaurea minor der Amerikanischen Pharmazeuten, Jul 1853, *W. Schaffner s.n.* (Holotype: HAL!).

- = *Erythraea retusa* B. L. Robinson & Greenm., Proc. Amer. Acad. Arts 32: 38. 1896. ≡ *Centaurium retusum* (B. L. Robinson & Greenm.) B. L. Robinson, Proc. Amer. Acad. Arts 45: 396. 1910. ≡ *Centaurium retusum* (B.L. Robinson & Greenm.) Druce, in Rep. Bot. Exch. Cl. Brit Isles 4: 614. 1917. – Type: Mexico, Oaxaca, Springy meadows, Sierra de San Felipe, 7500 ft, 11 Dec 1895, *Pringle 6300* (Holotype: GH; isotypes: COLO, F, GH, NY!, UC, US).
- = *Erythraea micrantha* Greenm., Proc. Amer. Acad. Arts 39: 83. 1903. ≡ *Centaurium micranthum* (Greenm.) B. L. Robinson, Proc. Amer. Acad. Arts 45: 396. 1910. – Type: Mexico, Jalisco, wet soil near Guadalajara, alt. 1540 m, 12 May 1901, *Pringle 8482* (Holotype: GH; isotypes: F, K!, NY!, UC, US).

Distribution. — Endemic to south and central Mexico (Guerrero, Jalisco, Mexico, Michoacán, Oaxaca and Veracruz), in wet, generally shady places, ditches or on stream-banks.

25. *Zeltnera wigginsii* (Broome) Mansion, **comb. nov.** ≡ *Centaurium wigginsii* Broome, Madroño 24: 239. 1977. – Type: Mexico, Sinaloa, Hwy 40, 47.25 mi E of intersection with Hwy 15, and 34.35 mi E of Concordia on curve with pull off, house a few yards on up road, pines with some oaks, 5800 ft, 17 Feb 1971, *C. R. Broome 763* (Holotype: DUKE!; isotypes: NY!, US!).

Distribution. — Sierra Madre Occidental of Mexico (Durango, Nayarit and Sinaloa), in moist and partly shaded clay banks of pine-oak forests, between 1600 and 2200 m.

Remarks. — *Zeltnera wigginsii* is phylogenetically related to *Z. stricta*. Morphologically, these species are very similar and only distinguishable by the inflorescence (flowering branches divaricate and with few bracts in *Z. wigginsii* vs. flowering branches nearly parallel and densely leafy in *Z. stricta*) and the corolla size (8–10 mm diameter for *Z. wigginsii* vs. 4–6 mm for *Z. stricta*).

SPECIES INCERTAE SEDIS

- Centaurium ameghinoi* (Speg.) Druce, Rep. Bot. Exch. Club Brit. Isles 4: 613. 1917. ≡ *Erythraea ameghinoi* Speg., Anales Soc. Ci. Argent. 53: 73. 1902. – Type: Argentina, in pratis saxosis prope Lago Colu-Huapi, s.d., *Ameghinoi s.n.* (Holotype: LPS).

Distribution. — Endemic to Argentina.

Remarks. — According to Fabris (1953), this long-pedicelled plant is morphologically close to *C. cachanlahuen*. The main differences are the corolla size (1 cm in diameter for *C. ameghinoi* vs. 1.5 cm in diameter for *C. cachanlahuen*) and the capsule shape (oval in *C. ameghinoi* vs. linear in *C. cachanlahuen*).

Centaurium cachanlahuen (Molina) B. L. Robinson, Proc. Amer. Acad. Arts 45: 396. 1910. ≡ *Gentiana cachanlahuen* Molina, Sagg. Chil. 147. 1782. ≡ *G. peruviana* Lam., Encycl. 2: 642. 1786. ≡ *Chironia chilensis* Willd., Sp. Pl. 1. 1: 1067. 1797, nom. illeg. [Art 52.1]. ≡ *Erythraea chilensis* (Willd.) Pers., Syn. Pl. 1. 283. 1805, nom. illeg. [Art 52.1]. ≡ *Erythraea cachanlahuen* (Molina) Roem. & Schult., Syst. 4: 167. 1819. ≡ *Centaurium chilense* (Willd.) Druce, Rep. Bot. Exch. Club Brit. Isles 4: 613. 1917, nom. illeg. [Art 52.1]. — Type: *Centaurium minus*, purpureum, patulum, vulgo Cachen., Feuillée, J. Obs. 2, vol. 2: 747–748, plate 35 (1714).

Remarks. — Molina (1782) based *Gentiana cachanlahuen* on an illustration in Feuillée (1714). Later, Willdenow (1797) described *Chironia chilensis*, yet placed *Gentiana cachanlahuen* in synonymy under it, relegating his name superfluous and illegitimate (Art 52.1, Greuter & al., 2000). Lamarck (1786) described *Gentiana peruviana*, also partially based on the Feuillée illustration. Therefore, the oldest validly published name for this taxon is *Gentiana cachanlahuen*.

Distribution. — Endemic to Chile. This species can be encountered from the Pacific littoral to the Andean precordillera and from the Atacama Province to the Chiloé Province.

Remarks. — Most of the specimens seen of this species were misidentified collections of *C. erythraea*, a species introduced in South America. *Centaurium cachanlahuen* is an important medicinal herb in Chile, also exported in Peru and Argentina, and used to fight “loss of appetite”, stomach pain and fever (Feuillée, 1714; Molina, 1782).

Centaurium lomae (Gilg) Druce, Rep. Bot. Exch. Cl. Brit. Isles 4: 613. 1917. ≡ *Erythraea lomae* Gilg, Repert. Spec. Nov. Regni Veg. 2: 34. 1906. — Type: Peru, in montibus Barranco prope Lima, solo calcaria in formatione “Loma” dicta, 300–600 m, Oct, s.d., *Weberbauer 1647* (Holotype: B).

Distribution. — Endemic to Peru. This rare species can be found in “loma” (“small hill”) vegetation, existing from sea level to approximately 1000 meters along the arid Pacific coast. Some terrestrial plants have adapted themselves to the desert-climate and live from the humidity of the fog (called “garúa”) that condenses on the surface of stones.

Remarks. — According to Zarucchi (1993: 534), this species is a “local variant” of the introduced European *Centaurium erythraea*. Because I have not examined the type specimen, I prefer to consider this species as *incertae sedis* before further conclusions.

ACKNOWLEDGEMENTS

I would like to express thanks to Jason Grant, for his kind support in earlier versions of this paper, help in typification and nomenclature, and for the Latin diagnoses, Lena Struwe for her pertinent comments and helpful suggestions, and James Reveal for expert advice. I am grateful to Louis and Nicole Zeltner for their constant help and for access to their important collection of *Centaurium* and relatives. I thank the curators of the following herbaria for allowing access or loans of specimens: BM, G, K, LL, MEL, MI, NEU, and TEX. I particularly want to express gratitude to Charlie Jarvis and Steve Cafferty of the Linnaean Plant Name Typification Project (Natural History Museum of London) and to Roy Vickery (Curator of Vascular Plants, BM) for their help with lectotypification. I finally wish to thank the University of Neuchâtel and the Fond National Suisse de Recherche Scientifique (Grant 31-52885.97) for funding this research.

LITERATURE CITED

- Abrams, L. R. 1951. *An Illustrated Flora of the Pacific States, Washington, Oregon and California*. Stanford Univ. Press, Stanford.
- Adams, L. G. 1996. Gentianaceae. Pp. 72–104 in: Wilson, A. (ed.), *Flora of Australia*, vol. 15. CSIRO, Melbourne.
- Bauhin, G. 1623. *Pinax Theatri Botanici, sive Index in Theophrasti, Dioscoridis, Plinii et Botanicorum qui a saeculo scripserunt*. L. Regis, Basiliae.
- Bentham, G. 1845. Gentianaceae. Pp. 127–128 in: Hinds, R. (ed.), *The Botanical Descriptions*, vol. 1. Smith, Elder & Co., London.
- Bentham, G. 1876. Gentianeae. Pp. 799–820 in: Bentham, G. & Hooker, J. (eds.), *Genera Plantarum*, vol. 2. L. Reeve & Co., London.
- Borckhausen, M. B. 1796. Über Linne’s Gattung *Gentiana*. Pp. 29–30 in: Roemer, D. J. J. (ed.), *Archiv für die Botanik*, vol. 1. Schäfer’sche Buchhandlung, Leipzig.
- Broome, C. R. 1973. *Systematics of Centaurium (Gentianaceae) of Mexico and Central America*. Ph.D. Thesis, Duke University, Durham, North Carolina.
- Broome, C. R. 1976. The Central American species of *Centaurium* (Gentianaceae). *Brittonia* 28: 413–426.
- Broome, C. R. 1977. Four new species of *Centaurium* from Mexico. *Madroño* 24: 237–244.
- Broome, C. R. 1981. A new variety of *Centaurium namophilum* (Gentianaceae) from the Great Basin. *Great Basin Nat.* 41: 192–197.
- Brown, R. 1810. *Prodromus Florae Novae Hollandiae et Insulae Van-Diemen*. L. Schrag, Nürnberg.

- Coville, F. V. 1893. Botany of the Death Valley expedition. *Contr. U. S. Natl. Herb.* 4: 1–363.
- Dodoens, R. 1583. *Stirpium Historiae Pemptades Sex*, vol. 30. Plantin, Antwerpen.
- Druce, G. C. 1916. *The Botanical Exchange Club of the British Isles*. T. Buncle, Arbroath.
- Dunn, R. A. 1967. *A Revision of the Genus Centaurium of Continental United States*. Ph.D. thesis, Catholic Univ. America, Washington, D.C.
- Endlicher, S. L. 1838. *Genera Plantarum Secundum Ordines Naturales Disposita*. S. Beck, Vienna.
- Fabris, H. A. 1953. Sinopsis preliminar de las Gencianaceas Argentinas. *Bol. Soc. Argent. Bot.* 4: 233–259.
- Fernandes, R. 1965. Duas variedades novas de *Centaurium spicatum* (L.) Fritsch. *Bol. Soc. Brot.* 31: 15–29.
- Feuillée, L. 1714. Journal des observations physiques, mathématiques et botaniques, faites par l'ordre du Roy sur côtes orientales de l'Amérique Méridionale, & dans les Indes Occidentales, depuis l'année 1707, jusques en 1712. L. P. Giffart, Paris.
- Gilg, E. 1895. Gentianaceae. Pp. 50–108 in: Engler, A. & Prantl, K. (eds.), *Die Natürlichen Pflanzenfamilien*, vol. 4. Verlag von Wilhelm Engelmann, Leipzig.
- Gillett, J. M. 1963. *The Gentians of Canada, Alaska and Greenland*. Research Branch, Canada Department of Agriculture, Ottawa.
- Gray, A. 1859. “*Erythraea*”. *Proc. Amer. Acad. Sci.* 6: 41.
- Gray, A. 1876. “*Erythraea*”. Pp. 477–480 in: Brewer, W. H. & Watson, S. (eds.), *Polypetalae. California Geological Survey. Botany of California*, vol. 1. J. Wilson, Cambridge.
- Gray, A. 1878. Gamopetalae after Compositae. Pp. 110–128 in: Ivison, Blakeman, Taylor, & Co., (eds.), *Synoptical Flora of North America*, vol. 2. American Book Co., New York.
- Greuter, W., McNeill, J., Barrie, F. R., Burdet, H. M., Demoulin, V., Filgueiras, T. S., Nicolson, D. H., Silva, P. C., Skog, J. E., Trehane, P., Turland, N. J. & Hawksworth, D. L. (eds.). 2000. *International Code of Botanical Nomenclature (Saint Louis Code) adopted by the Sixteenth International Botanical Congress St. Louis, Missouri, July–August 1999*. Koeltz Scientific Books, Königstein. [Regnum Veg. 138.]
- Grisebach, A. H. R. 1839. *Genera et Species Gentianacearum Adjectis Observationibus Quibusdam Phytogeographicis*. J. G. Cotta, Stuttgart and Tübingen.
- Grisebach, A. H. R. 1845. Gentianaceae. Pp. 39–141 in: Candolle, A. de (ed.), *Prodromus Systematis Naturalis Regni Vegetabilis*, vol. 9. Masson, Paris.
- Grisebach, A. H. R. 1853. *Schenkia*, novum genus Gentianacearum. *Bonplandia* 1: 226.
- Hegi, G. 1966. Gentianaceae. Pp. 1953–2047 in: *Illustrierte Flora von Mittel-Europa*, vol. 5. C. H. C. Hanser, München.
- Hill, J. 1756. *The British Herbal*. Osborne & Shipton, London.
- Hochreutiner, B. P. G. 1928. Note sur les *Centaurium* d'Australie. *Candollea* 3: 467–471.
- Hooker, W. J. & Arnott, G. A. W. 1830–1841. *Erythraea*. Pp. 302 and 438–439 in: Cramer, J. (eds.), *The Botany of Captain Beechey's Voyage*, vol. 8. The Secretary of State for Colonial Affairs, London.
- Howell, T. 1901. *A Flora of Northwest America*. T. Howell, Portland.
- Knoblauch, E. 1894. Beiträge zur Kenntniss der Gentianaceae. *Bot. Centralbl.* 60: 321–401.
- Lamarck, J. B. A. P. M. de. 1786. *Encyclopedie Méthodique. Botanique*, vol. 2. Panckoucke, Paris.
- Lemee, A. 1931. *Dictionnaire Descriptif et Synonymique des Genres de Plantes Phanérogames*, vol. 3. Le Chevalier, Paris.
- Linnaeus, C. 1753. *Species Plantarum*. Salvii, Stockholm.
- Litardière, R. de 1948. Nouvelles contributions à l'étude de la flore de Corse. *Candollea* 11: 213.
- Mansion, G. & Struwe, L. In press. Generic delimitation and phylogenetic relationships within the subtribe Chironiinae (Chironieae: Gentianaceae), with special reference to *Centaurium*: evidence from nrDNA and cpDNA sequences. *Molec. Phylog. Evol.* 32.
- Mansion, G. & Zeltner, L. In press. Phylogenetic relationships within the New World endemic *Zeltnera* (Gentianaceae-Chironiinae) inferred from molecular and karyological data. *Amer. J. Bot.* 91.
- Medeiros, A. C., Chimera, C. G., Loope, L. L., Joe, S. M. & Krushelnycky, P. D. 2000. Notes on status and ecology of the endangered Hawaiian annual “Awiwi”, *Centaurium sebaeoides* (Gentianaceae). *Pac. Sci.* 54: 417.
- Melderis, A. 1931. Genetical and taxonomical studies in the genus *Erythraea* Rich. *Acta Horti. Bot. Univ. Latv.* 6: 123–256.
- Melderis, A. 1972. Taxonomic studies on the European species of the genus *Centaurium* Hill. *Bot. J. Linn. Soc.* 65: 224–250.
- Molina, J. I. 1782. *Saggio Sulla Storia Civile del Chili*. Bologna, Nella Stamperia de S. Tommaso d'Aquino.
- Munz, P. A. & Keck, D. D. 1959. *A California Flora*. Univ. California Press, Berkeley.
- Necker, J. de. 1790. *Elementa Botanica*. Neowedeae ad Rhenum Societatem Typographicam, Neuwied.
- Nyman, C. F. 1881. *Conspectus Florae Europaeae*. Örebro, Sueciae.
- Omer, S. 1995. Gentianaceae. Pp. 1–172 in: Ali, S. I. & Qaiser, M. (eds.), *Flora of Pakistan*, vol. 197. Department of Botany, Univ. Karachi, Karachi.
- Piper, C. V. 1906. *Flora of the State of Washington*. Contributions from the U.S. National Herbarium, vol. 11. Smithsonian Institution, Washington, D.C.
- Ray, J. 1724. *Synopsis Methodica Stirpium Britannicarum, in qua tum Notae Generum Characteristicae Traduntur, tum Species Singulae Breviter Describuntur*, vol. 3. London.
- Robyns, A. 1954. Essai d'étude systématique et écologique des *Centaurium* de Belgique. *Bull. J. Bot. Bruxelles* 24: 349–398.
- Ronniger, K. 1916. *Centaurium (Erythraea)*. *Mitt. Naturw. Ver. Steierm.* 52: 312–321.
- Schmidt, W. L. E. 1828. *De Erythraea*. Dissertatio inauguralis botanico-medica. Typis Krausianis, Berolini.
- Schumann, K. 1889. Rubiaceae. Pp. 279–318 in: Martius, C. P. F., Eichler, A. G. & Urban, I. (eds.), *Flora Brasiliensis*, vol. 6. F. Fleischer, Lipsiae.
- Standley, P. C. & Williams, L. O. 1969. *Flora of Guatemala*. *Fieldiana Bot.* 8: 263–474.
- Struwe, L., Kadereit, J. W., Klackenberg, J., Nilsson, S., Thiv, M., von Hagen, K. B. & Albert, V. A. 2002. Systematics, character evolution, and biogeography of

- Gentianaceae, including a new tribal and subtribal classification. Pp: 21–309 in: Struwe, L. & Albert, V. A. (eds.), *Gentianaceae—Systematics and Natural History*. Cambridge Univ. Press, Cambridge.
- Tournefort, J. P.** 1700. *Institutiones Rei Herbariae*. Typographia Regia, Paris.
- Tutin, T. G.** 1972. Gentianaceae. Pp. 56–67 in: Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. & Webb, D. A. (eds), *Flora Europaea*, vol. 3. Cambridge Univ. Press, Cambridge.
- Turner, B. L.** 1993. The Texas species of *Centaurium* (Gentianaceae). *Phytologia* 75: 259–275.
- Ubsdell, R. A. E.** 1979. Studies and evolution in *Centaurium Erythraea* Rafn and *Centaurium littorale* (D. Turner) Gilmour in the British Isles; breeding systems, floral biology and general discussion. *Watsonia* 12: 225–232.
- USDA, NRCS.** 2002. *The PLANTS Database*, Version 3.5 (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA.
- Watson, S.** 1871. *Report of the Geological Exploration of the Fortieth Parallel*. vol. 5. The Botany. U. S. Government Printing Office, Washington, D.C.
- Willdenow, C. L.** 1797. *Caroli a Linné Species Plantarum*, vol. 1, part. 1. G. C. Nauk, Berlin.
- Zarucchi, J. L.** 1993. Gentianaceae. Pp. 534–545 in: Brako, L. & Zarucchi, J. L. (eds.), *Catalogue of the Flowering Plants and Gymnosperms of Peru*. Missouri Botanical Garden Press, St. Louis.
- Zeltner, L.** 1970. Recherches de biosystématique sur les genres *Blackstonia* Huds. et *Centaurium* Hill (Gentianaceae). *Bull. Soc. Neuchâtel Sci. Nat.* 93: 1–164.
- Zeltner, L.** 1978. Recherches sur le *Centaurium bianoris* (Sennen) Sennen. *Rev. Biol. et Ecol. Médit.* 5: 51–58.

Appendix. Segregate genera of the *Centaurium* complex reflecting the clades supported by morphological and molecular data (Mansion & Struwe, in press). New combinations are indicated in bold face (left column). The synonyms employed in previous and contemporary floras are listed in the right column.

New classification	Previous classification
1. <i>Centaurium</i> Hill [20 species*]	
<i>Centaurium barrelieri</i> (Duf.) F. Q. & Rothm.	
<i>C. bianoris</i> (Sennen) Sennen	
<i>C. capense</i> Broome	
<i>C. centaurioides</i> (Roxb.) Rolla Rao & Hemadri	
<i>C. chloodes</i> (Brot.) Samp.	
<i>C. erythraea</i> Rafn	
<i>C. favargerii</i> Zeltner	
<i>C. gypsicola</i> (Boiss. & Reut.) Ronniger	
<i>C. littorale</i> (D. Turner) Gilmour	
<i>C. mairei</i> Zeltner	
<i>C. majus</i> (Hoffingg. & Link) Ronniger	
<i>C. malzacianum</i> Maire	
<i>C. maritimum</i> (L.) Fritch	
<i>C. pulchellum</i> (Sw.) Druce	
<i>C. scilloides</i> (L. fil.) Samp.	
<i>C. serpentinicola</i> A. Carlström	
<i>C. somedanum</i> Lainz	
<i>C. suffruticosum</i> (Griseb.) Ronniger	
<i>C. tenuiflorum</i> (Hoffingg. & Link) Fritsch	
<i>C. turcicum</i> (Velen.) Ronniger	
2. <i>Gyandra</i> Griseb. [5 species]	
<i>G. brachycalyx</i> (Standley & L. O. Williams) Mansion	<i>Centaurium</i> section <i>Gyandra</i> (Griseb.) A. Gray
<i>G. chironioides</i> Griseb.	<i>C. brachycalyx</i> Standley & L. O. Williams
<i>G. pauciflora</i> (Martens & Galeotti) Mansion	<i>C. chironioides</i> (Griseb.) Druce
<i>G. pterocaulis</i> (Broome) Mansion	<i>C. pauciflorum</i> (Martens & Galeotti) B.L. Robinson
<i>G. tenuifolia</i> (Martens & Galeotti) Mansion	<i>C. pterocaulis</i> Broome
	<i>C. tenuifolium</i> (Martens & Galeotti) B.L. Robinson
3. <i>Schenkia</i> Griseb. [5 species]	
<i>S. australis</i> (R. Br.) Mansion	<i>Centaurium</i> section <i>Spicaria</i> Griseb.
<i>S. clementii</i> (Domin.) Mansion	<i>C. australe</i> (R. Br.) Druce
<i>S. spicata</i> (L.) Mansion	<i>C. clementii</i> (Domin.) L.G. Adams
<i>S. japonica</i> (Maxim.) Mansion	<i>C. spicatum</i> (L.) Fritsch
<i>S. sebaeoides</i> Griseb.	<i>C. spicatum</i> subsp. <i>japonicum</i> (Maxim.) H. Toyokuni
	<i>C. sebaeoides</i> (Griseb.) Druce
4. <i>Zeltnera</i> Mansion [25 species]	
<i>Z. abramsii</i> (Munz) Mansion	<i>Centaurium venustum</i> subsp. <i>abramsii</i> Munz
<i>Z. arizonica</i> (A. Gray) Mansion	<i>C. arizonicum</i> (A. Gray) Tidestrom
<i>Z. beyrichii</i> (Torr. & A. Gray) Mansion	<i>C. beyrichii</i> (Torr. & A. Gray) B.L. Robinson
<i>Z. breviflora</i> (Shinners) Mansion	<i>C. breviflorum</i> (Shinners) B.L. Turner
<i>Z. calycosa</i> (Buckl.) Mansion	<i>C. calycosum</i> (Buckl.) Fernald
<i>Z. davyi</i> (Jeps.) Mansion	<i>C. davyi</i> (Jeps.) Abrams.
<i>Z. exaltata</i> (Griseb.) Mansion	<i>C. exaltatum</i> (Griseb.) W. F. Wight ex Piper
<i>Z. gentryi</i> (Broome) Mansion	<i>C. gentryi</i> Broome
<i>Z. glandulifera</i> (Correll) Mansion	<i>C. glanduliferum</i> (Correll) B.L. Turner
<i>Z. madrensis</i> (Hemsl.) Mansion	<i>C. madrense</i> (Hemsl.) B.L. Robinson
<i>Z. martinii</i> (Broome) Mansion	<i>C. martinii</i> Broome
<i>Z. maryanna</i> (B. L. Turner) Mansion	<i>C. maryannum</i> B.L. Turner
<i>Z. muhlenbergii</i> (Griseb.) Mansion	<i>C. muhlenbergii</i> (Griseb.) W.F. Wight ex Piper
<i>Z. multicaulis</i> (B. L. Robinson) Mansion	<i>C. multicaule</i> B.L. Robinson
<i>Z. namophila</i> (Reveal, Broome & Beatley) Mansion	<i>C. namophilum</i> var. <i>namophilum</i> Reveal, Broome & Beatley
<i>Z. nevadensis</i> (Broome) Mansion	<i>C. namophilum</i> var. <i>nevadense</i> Broome
<i>Z. nudicaulis</i> (Engelm.) Mansion	<i>C. nudicaule</i> (Engelm.) B.L. Robinson
<i>Z. pusilla</i> (Eastwood) Mansion	<i>C. pusillum</i> Eastwood
<i>Z. quitensis</i> (Kunth.) Mansion	<i>C. quitense</i> (Kunth.) B.L. Robinson
<i>Z. setacea</i> (Benth.) Mansion	<i>C. setaceum</i> (Benth.) B.L. Robinson
<i>Z. stricta</i> (Schiede) Mansion	<i>C. strictum</i> (Schiede) Druce
<i>Z. texensis</i> (Griseb. ex Hook) Mansion	<i>C. texense</i> (Griseb. ex Hook.) Fern.
<i>Z. trichantha</i> (Griseb.) Mansion	<i>C. trichanthum</i> (Griseb.) B.L. Robinson
<i>Z. venusta</i> (Gray) Mansion	<i>C. venustum</i> (Gray) B.L. Robinson
<i>Z. wigginsii</i> (Broome) Mansion	<i>C. wigginsii</i> Broome

* The number of species in *Centaurium* Hill depends on the interpretation of the rank of numerous subspecies and varieties described under *C. erythraea* Rafn. [including subsp. *bernardii* (Maire et Sauvage) Zeltner, subsp. *rumelicum* (Velen.) Melderis, subsp. *subcapitatum* (Corb.) Zeltner], *C. majus* (Hoffingg. & Link) Ronniger [including subsp. *rhodense* (Boiss. & Reut.) Zeltner] or *C. tenuiflorum* (Hoffingg. & Link) Fritsch [including subsp. *acutiflorum* (Schott) Zeltner].