GENERIC AND SECTIONAL DELIMITATION IN ONAGRACEAE, TRIBE EPILOBIEAE[1]

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Abstract

The available evidence is used to produce a revised taxonomy for Onagraceae tribe Epilobieae, with two genera, *Epilobium* and *Boisduvalia*. *Zauschneria* is a specialized, bird-pollinated taxon closely related to one group of *Epilobium*, and it is consequently reduced to the status of a section of that genus. It is treated as comprising a single species with three tetraploid ($n = 15$) and three octoploid ($n = 30$) subspecies, between which extensive intergradation occurs. *Chamerion* (*Chamaenerion*), a Eurasian group of seven species, two reaching North America, is closely related to and doubtless shares a common ancestor with *Epilobium* sect. *Epilobium*; the other four sections are more distantly related. They include a total of seven species, all xerophytes confined to western North America, the probable place of origin of the tribe. *Boisduvalia* is treated as comprising two sections in place of the three recognized earlier, based upon further morphological studies and evidence obtained from artificial hybridization. The taxonomy proposed for the tribe Epilobieae appears to provide a balanced classification for the group that brings it into line with the other five tribes and 15 genera of the family.

The tribe Epilobieae, with some 210 species, differs from the other five tribes in the family Onagraceae (Raven, 1964b) in its dotlike, almost entirely heteropycnotic chromosomes that persist as chromatic dots through interphase (Kurabayashi et al., 1962); basic chromosome numbers $x = 9$, 10, 12, 13, 15, 16, and 18; occurrence of many species in moist places; and, in all but a few species, the habit of shedding the mature pollen as tetrads. It may be related to the less specialized group Jussiaeeae, consisting of the genus *Ludwigia* (including *Jussiaea* and *Isnardia*), which resembles it in having dotlike, heteropycnotic chromosomes; in growing in moist places; and, in many species, in shedding its mature pollen in tetrads. The basic chromosome number of *Ludwigia*, however, is $x = 8$; its tetrads are made up of pollen grains that differ greatly from those of Epilobieae and have probably evolved independently (Skvarla et al., 1975); and it lacks interxylary phloem, present in Epilobieae (Carlquist, 1975). *Ludwigia* seems to be a relatively generalized genus within the family, resembling *Fuchsia* in its retention of primitive characteristics, as inferred by Eyde & Morgan (1973), and it probably is not directly related to Epilobieae, which then appear as a rather isolated group within the family. Although the fossil record is badly in need of reevaluation, Epilobieae probably extend back to Paleogene time (see discussion in Eyde & Morgan, 1973: 785).

Within this tribe, the genera are closely related to one another. This paper is directed to the following question: how many genera and sections, in the sense of Lewis & Lewis (1955) and Raven (e.g., 1963, 1969), is it useful to recognize?

Boisduvalia (Raven & Moore, 1965) includes six species of annual plants of western North and South America. Collectively, they are distinguished from

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Epilobium by their annual habit and lack of a coma, the tuft of long trichomes at the chalazal end of the seed that aids in dispersal. No species of *Epilobium* is both annual and lacks a coma, and no species is transitional between these two genera. In aspect, *Boisduvalia* is sharply distinct from *Epilobium*. Plants of *Boisduvalia* germinate in moist conditions, often actually submerged, and initially produce large, glabrous, opposite leaves similar to those of *Epilobium*. Later, they begin to produce alternate, sometimes densely pubescent, hard leaves, and when they produce flowers and fruits, they are often growing under decidedly xeric conditions. *Boisduvalia* includes two species with a gametic chromosome number of $n = 10$, one with $n = 9$, one with $n = 19$, and two with $n = 15$. The last is the only one of these chromosome numbers that also occurs in *Epilobium*; but, as we shall see, the species of these two genera with $n = 15$ seem to be unrelated.

As to the remainder of the tribe, the bird-pollinated, orange-red-flowered *Zauschneria*, comprising a single polytypic species of western North America, has been recognized as distinct since it was described by Presl in 1831. As early as 1806, Salisbury (1806: pl. 58), in describing *Chamaenerium halimifolium*, used the existence of *Zauschneria*, known to him from plants gathered by Archibald Menzies along the coast of northern California, as an argument for recognizing *Chamaenerion* as a genus distinct from *Epilobium*. *Zauschneria* was obviously generically distinct, yet had the coma of *Epilobium*: why not *Chamaenerion* also?

In fact, *Zauschneria* is more closely related to *Epilobium* sect. *Cordylophorum*, which I shall discuss below, than to *Epilobium* s. str. All species of both groups have a gametic chromosome number of $x = 15$, unique in *Epilobium* (Lewis & Raven, 1961); most have a relatively long floral tube; and all grow in xeric sites and are somewhat woody at the base. Their wood anatomy (Carlquist, 1975) is virtually identical. The single species of *Zauschneria* (see p. 335) shares with *Epilobium nevadense* and *E. nivium* a characteristic unusual for the tribe: a prominent apiculus of brown oil cells at the tip of each leaf (Brandegee, 1892; Stein, 1915; Munz, 1929; Raven, 1962a). Their seeds, like those of *Epilobium* sect. *Xerolobium* (comprising one highly polymorphic xerophytic annual species), are large, obovoid to clavate, and prominently constricted at the micropylar end (Seavey, Magill & Raven, 1977). Furthermore, *Zauschneria*, like *Boisduvalia* and the two sections of *Epilobium* just mentioned, as well as a third, *Epilobium* sect. *Crossostigma*, has large endexine channels in the distal pollen walls, which are therefore different from all other pollen walls in the family Onagraceae and a clear indication of relationship (Skvarla et al., 1976). The viscin threads in their pollen are thick and fluted (incised compound), unlike the less sharply ridged, tightly compound ones of sects. *Chamaenerion* and *Epilobium* (Skvarla et al., 1977). *Zauschneria* differs from the three species of *Epilobium* sect. *Cordylophorum* only in its longer floral tubes, orange-red flowers, and possession of a scale at the base of each stamen within the narrow part of the floral tube. These scales are highly variable and sometimes reduced to an irregular line (Curran, 1888). They appear to be homologous with the ring inside the floral tube in *Boisduvalia* (Curran, 1888: 255; Raven & Moore, 1965: 239, figs.

2–4) and in many species of *Epilobium*, such as *E. obcordatum* A. Gray. In the hummingbird-pollinated flowers of *Zauschneria*, this ring has apparently been somewhat elaborated during the course of evolution in relation to the protection of the abundant nectar from potential nectar thieves of low energetic requirements (Heinrich & Raven, 1972). *Zauschneria* is pollinated by hummingbirds and separated by the syndrome of characteristics typical of bird pollination from its bee-pollinated relatives, but overwhelmingly similar to them in all other respects.

The six species of *Boisduvalia* differ from all species of *Epilobium* in their distinctive seeds, which are irregularly angular-fusiform (Seavey, Magill & Raven, 1977). Furthermore, there is no indication that the ancestor of *Boisduvalia* possessed a coma. The development of a coma in the common ancestor of *Epilobium* and *Zauschneria* was an advance that delimits a demonstrably interrelated group of plants no more diverse than *Camissonia* (Raven, 1964b, 1969), *Fuchsia*, *Lopezia* (Eyde & Morgan, 1973; Plitmann et al., 1973) or *Ludwigia* (Raven, 1963). As early as 1888, Curran (1888: 255) suggested that *Zauschneria* probably should not be kept distinct from *Epilobium* at the generic level. Later Brandegee (1892), in his protologue for *Epilobium nivium*, indicated that this pattern of relationships clearly makes *Zauschneria* untenable as a taxon at the generic level, and I now propose to include it in *Epilobium* as a section.

Aside from *Zauschneria*, the only group within *Epilobium* as defined in this paper which has often been accorded generic status is *Chamerion* (*Chamaenerion*; Holub, 1972), comprising seven species of Eurasia, two of which (*E. angustifolium* L. and *E. latifolium* L.) extend into North America. In sect. *Chamaenerion*, the leaves are all spirally arranged—although cataphylls near the base of the shoots may be opposite in *E. latifolium*—and the flowers, being lateral instead of erect and terminal, are zygomorphic to varying degrees. The floral tube is obsolete, and the pollen is shed singly, not in tetrads.

It is mainly the large flowers and relatively large, hard leaves of sect. *Chamaenerion* which make it appear to be a distinctive group; yet *Epilobium rigidum* Hausskn. and, to a lesser extent, *E. obcordatum* A. Gray, two species of the western United States, undoubtedly belonging to sect. *Epilobium*, combine the large flowers and hard leaves of sect. *Chamaenerion* with actinomorphic flowers and a leaf arrangement that is initially opposite. It has not been doubted that these are "genuine" species of *Epilobium*; yet they suggest the sort of species of sect. *Epilobium* from which sect. *Chamaenerion* might have been derived. In both vegetative and floral characteristics, sect. *Chamaenerion* is specialized within the tribe Epilobieae, and in seeds (Seavey, Magill & Raven, 1977), pollen characteristics (Skvarla et al., 1976, 1977, unpublished), and chromosome number it resembles *Epilobium* s. str. (= sect. *Epilobium*) more closely than it does any other group. Furthermore, hybrids have been made between *E. glaberrimum* Barbey (sect. *Epilobium*; $n = 18$) and *E. angustifolium* (with $n = 36$; Mosquin, 1967), and other hybrids involving these two sections have likewise been made but not yet reported (G. Perraudin, personal communication). In view of all these facts, it seems certain that the obsolete floral tube, floral zygomorphy, unnotched petals, alternate leaves, and single pollen grains in *Chamaenerion* are derived from a common ancestor with sect. *Epilobium*, its closest relative. As pointed out earlier, the recognition of *Chamerion* as a genus distinct from *Epilobium* would necessitate the separation of 4 other genera but still remove only 14 species from a genus with over 200 in all, and add several unfamiliar names in the process, while concealing the close relationship between all of these elements (Raven, 1962b). Recently, Holub (1972), without considering the generic balance in the family or any new facts, has reaffirmed the validity of this group at the generic level. His article is, in my opinion, nomenclaturally excellent but taxonomically not at all helpful.

Turning now to the more generalized and divergent species of *Epilobium*, there are three species, other than *Zauschneria*, with a gametic chromosome number of $n = 15$. Most similar to sect. *Zauschneria*, as pointed out by Brandegee (1892), is *E. nivium* T. S. Brandegee, a very local species of the north Coast Ranges of California, which has but two seeds in each locule of the capsule. This species, which can be regarded as a low, somewhat woody shrub, is interfertile with *E. nevadense* Munz (Seavey & Raven, 1977a) from the Charleston Mountains of southwestern Utah (Higgins, 1972), a spreading plant of loose scree in which there is only one seed in each locule of the capsule. Hybrids with the third species of *Epilobium* (other than *Zauschneria*) with $n = 15$, *E. suffruticosum* Nutt., have likewise been made experimentally (Seavey & Raven, 1977a), but have sharply reduced fertility despite their complete chromosome pairing. *Epilobium suffruticosum* grows along gravelly streams in the interior northwestern United States, and differs from the other two species to which it is related in having cream-colored, not rose-purple, petals, zygomorphic flowers, and many-seeded capsules.

The relationship between the annual *Epilobium paniculatum* Nutt. ex Torr. & A. Gray and the group consisting of *E. nivium* and *E. nevadense* was pointed out by Munz (1929) in his protologue for *E. nevadense*. *Epilobium paniculatum*, with *E. canum*, *E. nevadense*, and *E. nivium*, has a prominent apiculus consisting of brown oil cells (Stein, 1915) at each leaf apex. Oil cells are found in clusters on the leaves of many species of the family, but the apiculus in each of these four species is very similar and characteristic, strongly supporting the notion of a close relationship between them (Brandegee, 1892; Munz, 1929). In addition, *E. nevadense*, *E. nivium*, *E. suffruticosum*, and *E. paniculatum* resemble one another in that the petiole of the reduced leaf subtending each flower is fused with the pedicel so that the leaf appears to arise from the pedicel itself. This characteristic is known elsewhere in the genus only in *E. rigidum*, probably the least specialized species of sect. *Epilobium*, and a xerophyte like the other three. Whether the four species are directly related is uncertain but possible on the basis of other similarities. In *E. canum*, the subtending leaves are free of the pedicels, as in all other species of the genus. Since all three species of sect. *Cordylophorum* have the bract fused to the pedicel and *E. canum* does not, it may have been derived from their common ancestor and not from any existing species.

All strains of the very polymorphic *E. paniculatum* that we have examined have had a gametic chromosome number of $n = 12$; attempts to hybridize this species with *E. nevadense* have produced no results (Seavey & Raven, 1977b).

Nearly all populations of *E. paniculatum* consist of individuals that shed their mature pollen singly, a derived characteristic which they share with the species of sect. *Chamaenerion*; but we have recently discovered a few large-flowered populations in Siskiyou County, California, in which the mature pollen is shed in tetrads, and we intend to study these in more detail. Summing up, *Epilobium paniculatum* ($n = 12$) is a very distinct species, clearly related to sect. *Cordylophorum* ($n = 15$) and especially to *E. nevadense* and *E. nivium*; it seems to share at least one common ancestor with these other tetraploid species.

Remaining to be discussed are the other two annual species of *Epilobium* in addition to *E. paniculatum*: *E. minutum* Lindl. ex Lehm. ($n = 13$) and *E. foliosum* (Nutt. ex Torr. & A. Gray) Suksd. ($n = 16$). These two xerophytic annual species shed their pollen in tetrads and, despite their divergent chromosome numbers, are closely similar to one another and sometimes separable only with difficulty (Seavey, Wright & Raven, 1977). Their relationships within the genus are obscure, but they do have the large endexine channels in the distal walls of their pollen and incised-compound viscin threads (Skvarla et al., 1976, 1977) which negate a direct relationship with sects. *Epilobium* or *Chamaenerion*. In view of the absence of intermediate chromosome numbers, we have hypothesized that *E. minutum* and *E. foliosum* are probably derived independently from extinct diploid species with $n = 8$, 7, and 6; but the hypothesis cannot be verified until and unless such plants are discovered (Seavey, Wright & Raven, 1977).

Aside from the 14 species just discussed, which fall into five distinct groups, there are approximately 185 other species of *Epilobium* among which taxonomic subdivision is difficult if not impossible. Although there are some recognizable series among them, none is clearly defined. For example, the "creeping" species of New Zealand and adjacent islands, in which the flowers are borne laterally in the axils of leaves, all of which are opposite, whereas the terminal inflorescence is suppressed, appear distinctive. On closer examination, however, it can easily be seen (Raven & Raven, 1976), that these "creeping" species constitute a series of different lines that have acquired this habit independently; all hybridize readily with noncreeping species in the experimental garden, and some form natural hybrids also. Consequently, no clearly defined taxonomic group or groups can be separated among them, even though their presence is one of the things that imparts a distinctive aspect to the assemblage of *Epilobium* species found in New Zealand. It might be desirable to separate the species of *Epilobium* into series of the informal sort utilized by Haussknecht (1884), but intergrades between these series would then be so numerous that I consider their recognition, at least for the present, to be more confusing than helpful.

As to phylogenetic relationships within the tribe, I have already suggested that *Boisduvalia* separated before the evolution of a coma in the common ancestor of *Epilobium*. The common ancestor of the Epilobieae clearly had relatively large seeds (Seavey, Magill & Raven, 1977), large endexine channels in the distal walls of the pollen (Skvarla et al., 1976), incised-compound viscin threads (Skvarla et al., 1977), pollen in tetrads, a floral tube, actinomorphic flowers with a notch at the apex of each petal, lower leaves opposite, a perennial habit, anthers differentiated into two sets, a four-lobed stigma, and probably grew in dry places.

From this hypothetical common ancestor *Boisduvalia* was derived as an annual line, almost certainly in western North America, and in moist habitats. The original basic chromosome number in *Boisduvalia* seems to have been $n = 10$, judged both from the relationships within the group (Raven & Moore, 1965) and the fact that the original basic chromosome number for the family is clearly $n = 11$. From $n = 10$ was derived $n = 9$ [in *B. stricta* (A. Gray) Greene] and, indirectly, $n = 19$. Two closely related species of *Boisduvalia*, comprising sect. *Currania*, have $n = 15$, and are inferred to have been derived, probably from a common ancestor, following further aneuploid reduction below $n = 9$ and polyploidy; no species of Epilobieae with a gametic chromosome number less than $n = 9$ has survived to the present, however.

In *Epilobium* s. lat., the original basic chromosome number may have been $n = 9$. Kisch (1941) has shown that up to 9 bivalents, but also some multivalents, are formed in polyhaploids of *E. hirsutum* L. ($2n = 18$). From the basic number $n = 9$, sect. *Epilobium* and sect. *Chamaenerion* were derived by polyploidy, and may have been differentiated from a common ancestor with $n = 18$. Following Stebbins (1971: 193), I consider it likely that descending aneuploidy to $n = 6$ preceded the origin of the species with $n = 15$ ($9 + 6$?), $n = 16$ ($8 + 8$), $n = 13$ ($7 + 6$), and $n = 12$ ($6 + 6$). Our original hypothesis that $x = 6$ might be basic for *Epilobium* and the species with $n = 18$ hexaploid (Lewis et al., 1958) was formulated before the existence of species with $n = 16$, 15, and 13 was known. All four species of *Epilobium* with $n = 15$ ($n = 30$ also present in one) seem to have been derived from a common ancestor and, despite the present-day occurrence of *E. suffruticosum* in permanently moist places, this common ancestor seems to have been a xerophyte. Most of the extinct hypothetical diploids were also probably xerophytes, as implied by the xeric habitats of the three annuals with $n = 16$, 13, and 12. At any event, the common ancestor of *Epilobium* s. lat. clearly had a coma, as well as the other characteristics of the common ancestor of the tribe, and this innovation, which probably occurred in western North America, judged from present patterns of distribution, seems to have been the key to a worldwide distribution and proliferation into about 200 species. There seem to have been at least three independent evolutionary radiations into moist habitats: *Boisduvalia*, *Epilobium suffruticosum* (sect. *Cordylophorum*), and in *Epilobium* sect. *Epilobium*.

SYNOPSIS OF ONAGRACEAE, TRIBE EPILOBIEAE

BOISDUVALIA

Boisduvalia Spach, Hist. Vég. Phan. 4: 383. 1835.

Oenothera sect. *Boisduvalia* (Spach) Torr. & A. Gray, Fl. N. Amer. 1: 505, 1840.
    Onothera group *Boisduvalia* (Spach) H. Lév., Monogr. Onoth. 296. 1908.
Cratericarpium Spach, Nouv. Ann. Mus. Hist. Nat. 4: 397. 1835. TYPE: *C. argyrophyllum* Spach = *Boisduvalia subulata* (Ruiz & Pav.) Raimann.

Annual herbs. Leaves subsessile, the lowest opposite. Flowers actinomorphic. Floral tube evident. Pollen shed in tetrads, the distal walls with large endexine channels. Viscin threads thick and incised-compound or smooth. Stigma 4-lobed, clavate, or capitate. Seeds irregularly angular-fusiform, lacking a coma. Gametic chromosome numbers, $n = 10, 9, 19$, and 15.

Lectotype species: *B. concinna* (D. Don) Spach = *B. subulata* (Ruiz & Pav.) Raimann; Munz, Darwiniana 5: 126. 1941.

A recent monograph is that of Raven & Moore (1965).

1. **Boisduvalia** sect. **Boisduvalia.**

Oenothera sect. *Dictyopetalum* Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 45. 1835. TYPE: *B. concinna* (D. Don) Spach = *B. subulata* (Ruiz & Pav.) Raimann. *Boisduvalia* sect. *Dictyopetalum* (Fisch. & Mey.) Endl., Gen. Pl. 1191. 1840. *Boisduvalia* sect. *Euboisduvalia* Munz, Darwiniana 5: 127. 1941.

Oenothera sect. *Pachydium* Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 45. 1835. TYPE: *B. densiflora* (Lindl.) S. Wats. *Boisduvalia* sect. *Pachydium* (Fisch. & Mey.) Endl., Gen. Pl. 1191. 1840.

Mature leaves and stems villous or strigulose. Flowers usually chasmogamous. Stigma evidently to obscurely 4-lobed. Capsule terete, splitting to the base, the central column readily disintegrating or persistent. Seeds in one row in each locule or pushed together into a single row in the capsule by distortion of the median partition, nearly vertical. Gametic chromosome numbers, $n = 10, 9, 19$.

1. *Boisduvalia macrantha* Heller, Muhlenbergia 2: 101. 1905.
2. *Boisduvalia stricta* (A. Gray) Greene, Fl. Francisc. 225. 1891.
3. *Boisduvalia densiflora* (Lindl.) S. Wats., Bot. Calif. 1: 233. 1876.
4. *Boisduvalia subulata* (Ruiz & Pav.) Raimann, in Engl. & Prantl, Natürl. Pflanzenfam. III. 7: 212. 1893.

The fact that the partitions between the locules in at least some strains of the South American *B. subulata* may be more persistent than those in the three North American species, used as a basis for sectional distinction earlier (Raven & Moore, 1965), no longer seems sufficient for separation. Seavey (unpublished) has obtained hybrids between *B. subulata* and the three other species of this section, and these show good association of chromosomes.

2. **Boisduvalia** sect. **Currania** Munz, Darwiniana 5: 127. 1941.

Mature leaves and stems sparsely pubescent or glabrous. Flowers usually cleistogamous. Stigma clavate, shallowly and irregularly 4-lobed. Capsule terete or sharply quadrangular, usually splitting only in the upper third, the central column readily disintegrating. Seeds in two rows in each locule, inclined about 20–60° from vertical. Gametic chromosome number, $n = 15$.

Lectotype species: *B. cleistogama* Curran; Raven & Moore, Brittonia 17: 251. 1965.

5. *Boisduvalia glabella* (Nutt.) Walp., Repert. Bot. Syst. 2: 89. 1843.
6. *Boisduvalia cleistogama* Curran, Bull. Calif. Acad. Sci. 1: 12. 1884.

EPILOBIUM

Epilobium L., Sp. Pl. 347. 1753; Gen. Pl., ed. 5. 164. 1754.

Chamaenerion Séguier, Pl. Veron. 3: 168. 1754; nom. illeg. LECTOTYPE: *Epilobium hirsutum* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerion S. F. Gray, Natur. Arrang. Brit. Pl. 559. 1821; nom. illeg. TYPE: *C. spicatum* (Lam.) S. F. Gray = *Epilobium angustifolium* L.

Zauschneria Presl, Rel. Haenk. 2: 28, *pl.* 52. 1831. TYPE: *Z. californica* Presl = *E. canum* (Greene) Raven.

Chamerion (Raf.) Raf., Herb. Raf. 51. 1833. Based on *Epilobium* subg. *Chamerion* Raf., Amer. Monthly Mag. & Crit. Rev. 2: 266. 1818. TYPE: *E. amenum* Raf. = *E. angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerion Spach, Hist. Nat. Veg. 4: 346. 1835; nom. illeg. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Crossostigma Spach, Ann. Sci. Nat. Bot., sér. 2, 4: 174. 1835. TYPE: *C. lindleyi* Spach, nom. illeg. = *E. minutum* Lindl. ex Lehm.

Chamaenerion Kostel, Ind. Pl. Hort. Bot. Prag. 34. 1844; nom. illeg. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerium (Tausch) Schur, Sertum Fl. Transsilv. 25. 1853; nom. illeg. Based on *Epilobium* sect. *Chamaenerion* Tausch, Hort. Canal. fasc. 1. 1823. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Pyrogennema Lunell, Amer. Midl. Naturalist 4: 482. 1916; nom. illeg. TYPE: *P. angustifolium* (L.) Lunell = *E. angustifolium* L.

Cordylophorum (Nutt. ex Torr. & A. Gray) Rydb., Fl. Rocky Mts. 590, 1064. 1917. Based on *Epilobium* sect. *Cordylophorum* Nutt. ex Torr. & A. Gray, Fl. N. Amer. 1: 488. 1840. TYPE: *C. suffruticosum* (Nutt.) Rydb. = *E. suffruticosum* Nutt.

Perennial herbs, often flowering the first year, with three species annual. Leaves petioled or sessile, the lowest opposite, or all alternate in sect. *Chamaenerion*. Flowers actinomorphic, zygomorphic in a few species. Floral tube evident, lacking in sect. *Chamaenerion*. Pollen shed in tetrads in all but a few species, the distal walls solid or with large endexine channels. Viscin threads thick, incised-compound; smooth; or tightly compound. Stigma 4-lobed, clavate, or capitate. Seeds variable, not angular, with a coma that has been lost in one species (*E. curtisiae* Raven) and a few strains of another (*E. ciliatum* Raf.). Gametic chromosome numbers, $n = 18$, 16, 15, 13, 12, and multiples of 18 and 15.

Lectotype species: *E. hirsutum* L.; Britton & Brown, Ill. Fl. No. U.S., ed. 2. 2: 590.

The only comprehensive monograph is that of Haussknecht (1884), but there have been recent accounts of the species of Europe (Raven, 1968), Turkey (Chamberlain & Raven, 1972), the *Flora Iranica* area (Raven, 1964a), the Himalayas (Raven, 1962b), Malesia (Raven, 1967a), Japan (Hara, 1942, 1965), Africa (Raven, 1967b), Australasia (Raven & Raven, 1976), North America (Munz, 1965), and South America (Samuelsson, 1923, 1930). A revised treatment of the species of North America is in progress.

1. **Epilobium** sect. **Cordylophorum** (Rydb.) Raven, stat. nov. Based on *Cordylophorum* Rydb., Fl. Rocky Mts. 590, 1064. 1917.

Clumped or rhizomatous perennial herbs. Basal, and in one species most, leaves opposite. Flowers actinomorphic or zygomorphic. Floral tube present, lacking scales within. Petals cream or rose purple, deeply notched. Pollen shed in tetrads, the distal walls of pollen with large endexine channels. Viscin threads thick, more or less incised-compound. Stigma deeply 4-lobed. Seeds large, obovoid to clavate, prominently constricted at the micropylar end. Gametic chromosome number $n = 15$.

Type species: *E. suffruticosum* Nutt.

1a. **Epilobium** sect. **Cordylophorum** subsect. **Nuttalia** Raven, subsect. nov.

Herbae perennes rhizomatosae. Folia plerumque opposita. Flores zygomorphi. Petala eburnea. Capsula seminibus multibus quoque locula. Semina clavata. Numerus chromosomaticus gameticus, $n = 15$.

Rhizomatous. Most leaves opposite. Flowers zygomorphic. Petals cream. Capsule with many seeds in each locule. Seeds clavate.

Type species: *E. suffruticosum* Nutt.

1. *Epilobium suffruticosum* Nutt., in Torr. & A. Gray, Fl. N. Amer. 1: 488. 1840.

Although morphologically distinctive, this species can be hybridized with *E. nevadense* and the chromosomes form 15 bivalents at meiotic metaphase I (Seavey & Raven, 1977a). It seems best to emphasize the similarities by retaining all three species within a single section.

1b. **Epilobium** sect. **Cordylophorum** subsect. **Petrolobium** Raven, subsect. nov.

Herbae perennes confertae ad basin sublingnosae. Folia basalia opposita. Flores actinomorphi. Petala roseo-purpurea, emarginata. Stigma profunde 4-lobatum. Pollen in tetradis effundatum. Capsula semina una vel dua quoque loculo. Semina obovoidea vel anguste obovoidea. Numerus chromosomaticus gameticus, $n = 15$.

Clumped. Basal leaves opposite. Flowers actinomorphic. Petals rose purple. Seeds one or two in each locule, obovoid or narrowly obovoid.

Type species: *E. nivium* T. S. Brandegee.

2. *Epilobium nivium* T. S. Brandegee, Zoe 3: 242, *pl. 24.* 1892.
3. *Epilobium nevadense* Munz, Bull. Torrey Bot. Club 56: 166. 1929.

2. **Epilobium** sect. **Xerolobium** Raven, sect. nov.

Herba annua erecta, saepe ad basin sublignosae; folia ad basin opposita, plerumque alternantia. Flores actinomorphi. Petala roseo-purpurea ad alba, emarginata. Stigma 4-lobatum ad integrum. Pollen plerumque singulariter effundata. Numerus chromosomaticus gameticus, $n = 12$.

Annual, xerophytic herb. Basal leaves opposite. Flowers actinomorphic. Floral tube present, lacking scales within. Petals rose purple or white, deeply notched. Stigma deeply 4-lobed to entire. Pollen shed singly in all but a few strains, the distal walls with large endexine channels. Viscin threads thick, incised-compound. Seeds obovoid, prominently constricted at the micropylar end. Gametic chromosome number, $n = 12$.

Type species: *E. paniculatum* Nutt. ex Torr. & A. Gray.

4. *Epilobium paniculatum* Nutt. ex Torr. & A. Gray, Fl. N. Amer. 1: 490. 1840.

This distinctive xerophytic annual seems to be closely related to the preceding species, but we have not yet succeeded in hybridizing it with them, and prefer to keep it distinct taxonomically. It is highly polymorphic but in a detailed study we have not found it useful to accord formal taxonomic recognition to any infraspecific units (Seavey & Raven, 1977b).

3. **Epilobium** sect. **Zauschneria** (Presl) Raven, stat. nov. Based on *Zauschneria* Presl, Rel. Haenk. 2: 28, *pl.* 52. 1831.

Clumped perennial, often woody at the base. Basal leaves opposite. Flowers zygomorphic, orange red. Floral tube elongate, with a scale at the base of each stamen, within the narrow part of the tube. Petals orange red, notched. Pollen shed in tetrads, the distal walls of pollen with large endexine channels. Viscin threads thick, incised-compound. Stigma deeply 4-lobed. Seeds obovoid, prominently constricted at the micropylar end. Gametic chromosome numbers, $n =$ 15, 30.

Type species: *Zauschneria californica* Presl = *Epilobium canum* subsp. *angustifolium* (Keck) Raven.

5. **Epilobium canum** (Greene) Raven, comb. nov. Based on *Zauschneria cana* Greene, Pittonia 1: 28. 1887.

5a. **Epilobium canum** subsp. **septentrionale** (Keck) Raven, comb. nov. ($n = 15$). Based on *Zauschneria septentrionalis* Keck, Carnegie Inst. Wash. Publ. 520: 219. 1940.

5b. **Epilobium canum** subsp. **garrettii** (A. Nels.) Raven, comb. nov. ($n =$ 15). Based on *Zauschneria garrettii* A. Nels., Proc. Biol. Soc. Wash. 20: 36. 1907.

5c. **Epilobium canum** subsp. **canum** ($n = 15$).

Zauschneria tomentella Greene, Pittonia 1: 25. 1887.

5d. **Epilobium canum** subsp. **angustifolium** (Keck) Raven, comb. nov. ($n = 30$). Based on *Zauschneria californica* subsp. *angustifolia* Keck, Carnegie Inst. Wash. Publ. 520: 221. 1940.

Zauschneria californica Presl, Rel. Haenk. 2: 28. 1831; Raven, Aliso 5: 215–216. 1962; non *Epilobium californicum* Hausskn., Monogr. Epil. 260. 1884.

5e. **Epilobium canum** subsp. **mexicanum** (Presl) Raven, comb. nov. ($n =$ 30). Based on *Zauschneria mexicana* Presl, Rel. Haenk. 2: 29. 1831; non *Epilobium mexicanum* Moc. & Sessé ex DC., Prodr. 3: 41–1828.

Zauschneria villosa Greene, Pittonia 1: 27. 1887; non *Epilobium villosum* Thunb., Prodr. Fl. Cap. 75. 1794.

Zauschneria californica Presl subsp. *mexicana* (Presl) Raven, Aliso 5: 215. 1962.

Zauschneria californica Presl subsp. *typica* Keck, sensu Keck, Carnegie Inst. Wash. Publ. 520: 220. 1940. The type of *Z. californica* is, however, referable to the geographical race here called *Epilobium canum* subsp. *angustifolium* (Raven, Aliso 5: 215–216. 1962).

5f. **Epilobium canum** subsp. **latifolium** (Hook.) Raven, comb. nov. ($n =$ 30). Based on *Zauschneria californica* var. *latifolia* Hook., Bot. Mag. *pl.* 4493. 1840.

Zauschneria latifolia (Hook.) Greene, Pittonia 1: 25. 1887.

Zauschneria californica subsp. *latifolia* (Hook.) Keck, Carnegie Inst. Wash. Publ. 520: 220. 1940.

Since the biosystematic revision of Keck (Clausen et al., 1940), it has been customary to regard this group as consisting of three species with a gametic chromosome number of $n = 15$ and one with $n = 30$. Each of the entities with $n = 15$ intergrades with one of the entities with $n = 30$ to such an extent that separating them is often difficult or impossible, and autoploidy seems clearly to have been the mode in this complex (Clausen et al., 1940, 1945; Clausen, 1951). It has been suggested that the race here called *Epilobium canum* subsp. *mexicanum* has had, in effect, an alloploid origin following hybridization between the two other subspecies with $n = 30$, this again reemphasizing the close and dynamic relationship throughout the section. The complex seems fully comparable to *Eriophyllum lanatum* (Pursh) Forbes (Mooring, 1975), *Eriogonum fasciculatum* Benth. (Stebbins, 1971), *E. latifolium* Sm. (Stokes & Stebbins, 1955), *Haplopappus acradenius* (Greene) Blake (Stebbins, 1971), and *Artemisia tridentata* Nutt. (Ward, 1953), in which diploids or lower polyploids intergrade with their polyploid derivatives to such an extent that it is impossible to make a useful taxonomic separation. It is especially similar to the situation in *Dactylis glomerata* L., for which Stebbins & Zohary (1959) have suggested that a series of diploid, more or less interfertile, subspecies can best be accommodated in the same taxonomic species with their polyploid derivatives. Exchange of genetic material between diploids and polyploids must likewise be considered a serious possibility in a complex of this sort (cf. Müntzing, 1937, for *Dactylis*). In the light of these taxonomic considerations, it seems preferable to regard all entities recognized in *Epilobium* sect. *Zauschneria* as subspecies of a single polytypic species (Seavey & Raven, 1977a).

Only a partial synonymy is given here for this section; for further details consult Clausen et al. (1940), Tralau (1958), and Munz (1965).

4. **Epilobium** sect. **Crossostigma** (Spach) Raven, stat. nov. Based on *Crossostigma* Spach, Ann. Sci. Nat. Bot., sér. 2, 4: 174. 1835.

Annual, xerophytic herbs. Basal leaves opposite. Flowers actinomorphic. Floral tube present. Petals pale rose purple or white, deeply notched. Pollen shed in tetrads, the distal walls of pollen with large endexine channels. Viscin threads thick, incised-compound or smooth. Stigma 4-lobed to subentire. Seeds obovoid. Gametic chromosome numbers, $n = 16, 13$.

Type species: *Crossostigma lindleyi* Spach = *Epilobium minutum* Lindl. ex Lehm.

6. *Epilobium foliosum* (Nutt. ex Torr. & A. Gray) Suksd., Deutsche Bot. Monatsschr. 18: 87. 1900.
7. *Epilobium minutum* Lindl. ex Lehm., in Hook., Fl. Bor-Amer. 1: 207. 1833.

The large endexine channels in the distal walls of the pollen and the incised-compound (or smooth) viscin threads (Skvarla et al., 1976, 1977) negate a possible relationship between these two reduced annual species and sect. *Epilobium*. *Epilobium foliosum* has been placed before *E. minutum* because it has evidently been derived from diploid ancestors with chromosome numbers closer to $n = 9$, the original basic chromosome number for the genus.

5. **Epilobium** sect. **Epilobium.**

Epilobium sect. *Lysimachion* Tausch, Hort. Canal. fasc. 1. 1823. LECTOTYPE: *E. hirsutum* L.

Perennial herbs, mostly of moist places, often flowering the first year. Leaves opposite below, alternate above. Flowers actinomorphic. Floral tube present, lacking scales within. Petals rose purple or white, creamy in *E. luteum* Pursh, deeply notched. Pollen shed in tetrads, the distal walls with solid endexine. Viscin threads tightly compound. Stigma 4-lobed or entire. Seeds variable. Gametic chromosome number, $n = 18$.

This is a complex of approximately 185 species, found at high altitudes and high latitudes worldwide. Apparently all species can be hybridized. Judged by its seed morphology (Seavey, Magill & Raven, 1977), xeric habitat, large flowers, and 4-lobed stigma, *Epilobium rigidum* Haussk. of the Siskiyou Mountains of northwestern California and southwestern Oregon may be the most generalized species, with *E. obcordatum* A. Gray, more widespread in the mountains of the western United States, related but more specialized. Curran (1888: 255) pointed out the similarity between the flowers of the latter and those of *Zauschneria* and *Boisduvalia.* Relationships within this section are highly reticulate, and it is not possible to suggest an overall arrangement with any confidence at this time, as discussed above.

6. **Epilobium** sect. **Chamaenerion** Tausch, Hort. Canal. fasc. 1. 1823.

Perennial herbs, occasionally somewhat woody near the base, of mesic habitats but usually not near water. Leaves alternate, the lowermost cataphylls often opposite in *E. latifolium* L. Flowers zygomorphic. Floral tube obsolete. Petals rose purple, entire. Stigma 4-lobed. Pollen shed singly, the distal walls with solid endexine. Viscin threads tightly compound. Seeds narrowly obovoid, smooth or papillose. Gametic chromosome numbers, $n = 18, 36, 54$.

Lectotype species: *E. angustifolium* L.

This distinctive assemblage is more closely related to sect. *Epilobium* than to any other group on the basis of hybridization experiments (Mosquin, 1967; G. Perraudin, personal communication), seed morphology (Seavey, Magill & Raven, 1977), pollen wall ultrastructure (Skvarla et al., 1976), viscin thread morphology (Skvarla et al., 1977), and chromosome number. It consists of two distinctive groups, for which subsectional rank seems appropriate.

6a. **Epilobium** sect. **Chamaenerion** subsect. **Rosmarinifolium** (T. Tacik) Raven, stat. nov. Based on *Chamaenerion* sect. *Rosmarinifolium* T. Tacik, in W. Szafer, Fl. Polska 8: 254. 1959.

Chamerion sect. *Rosmarinifolia* (T. Tacik) Holub, Folia Geobot. Phytotax. 7: 86. 1972.

Style pubescent in lower part. Seeds papillose. Gametic chromosome number, $n = 18$.

Type species: *Chamaenerion angustissimum* (Weber) Sosn. = *Epilobium dodonaei* Vill.

This subsection consists of four allopatric species of western Eurasia: *Epilobium colchicum* Alboff [including *E. caucasicum* (Hausskn.) Sosnowsky ex Grossheim], *E. dodonaei* Vill., *E. fleischeri* Hochst., and *E. stevenii* Boiss. All of these might conceivably be regarded as subspecies of a single polymorphic species, but that decision must wait further detailed study. Without such study, casual changes in taxonomic status such as those of Holub (1972) are without value: no reasons whatever were given. Natural hybrids between *E. dodonaei* and *E. fleischeri*, which replace one another altitudinally in the Alps, have been reported from time to time.

6b. **Epilobium** sect. **Chamaenerion** subsect. **Leiostylae** (Steinb.) Raven, stat. nov. Based on *Chamaenerium* sect. *Leiostylae* Steinb., Fl. U.S.S.R. 15: 626. 1949.

Chamaenerion Séguier, Pl. Veron. 3: 168. 1754; nom. illeg. LECTOTYPE: *Epilobium hirsutum* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Epilobium subg. *Chamerion* Raf., Amer. Monthly Mag. Crit. & Rev. 2: 266: 1818. TYPE: *E. amenum* Raf. = *E. angustifolium* L.

Chamerion S. F. Gray, Natur. Arrang. Brit. Pl. 559. 1821; nom. illeg. TYPE: *C. spicatum* (Lam.) S. F. Gray = *Epilobium angustifolium* L.

Epilobium sect. *Chamaenerion* Tausch, Hort. Canal. fasc. 1. 1823. LECTOTYPE: *E. angustifolium* L.

Chamerion (Raf.) Raf., Herb. Raf. 51. 1833. Based on *Epilobium* subg. *Chamerion* Raf., Amer. Monthly Mag. Crit. & Rev. 2: 266. 1818. TYPE: *E. amenum* Raf. = *E. angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerion Spach, Hist. Nat. Veg. 4: 346. 1835; nom. illeg. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerion Kostel, Ind. Pl. Hort. Bot. Prag. 34. 1844; nom. illeg. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerium (Tausch) Schur, Sertum Fl. Transsilv. 25. 1853; nom. illeg. Based on *Epilobium* sect. *Chamaenerion* Tausch, Hort. Canal. fasc. 1. 1823. LECTOTYPE: *C. angustifolium* (L.) Scop. = *Epilobium angustifolium* L.; Holub, Folia Geobot. Phytotax. 7: 84. 1972.

Chamaenerium sect. *Hebestylae* Steinb., Fl. U.S.S.R. 15: 622. 1949. LECTOTYPE: *Chamaenerium angustifolium* (L.) Scop. = *Epilobium angustifolium* L.

Chamaenerion sect. *Salicifolium* T. Tacik, in W. Szafer, Fl. Polska 8: 254. 1959. TYPE: *Chamaenerion angustifolium* (L.) Scop. = *Epilobium angustifolium* L.

Style pubescent in lower part or glabrous. Seeds smooth. Gametic chromosome numbers, $n = 18, 36, 54$.

Lectotype species: *Chamaenerium latifolium* (L.) Th. Fr. & Lange = *Epilobium latifolium* L.

This subsection includes three clearly delimited species: *Epilobium angustifolium* L. ($n = 18, 36, 54$; Mosquin, 1966), *E. latifolium* L. ($n = 18, 36$; Small, 1968), and *E. conspersum* Hausskn. The first-mentioned species is circumboreal (Mosquin, 1966), reaching northern Mexico (Munz, 1960) and Morocco (Dahlgren & Lassen, 1972); the second is circumpolar (Small, 1968); and the third is Himalayan (Raven, 1962b). The extent of natural hybridization between *E. angustifolium* and *E. latifolium* has been reviewed by Mosquin (1966: 184), and hybrids between these two species and *E. conspersum* have been mentioned by Raven (1962b). As pointed out by Dandy (1969), even if this group is treated as generically distinct from *Epilobium*, it cannot take the name *Chamaenerion* which is an illegitimate substitute for *Epilobium*.

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