

Generic division of *Sedoideae* in Europe and the adjacent regions

Rodové členění podčeledi *Sedoideae* v Evropě a přilehlých oblastech

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Europe and the adjacent parts of North Africa and West Asia contain ca. 120 species of subf. *Sedoideae*. The genus *Sedum* L. is especially heterogeneous and is composed of several natural groups whose evaluation until now has been unsatisfactory. Some groups are closely allied to other recently distinguished genera, and it is necessary to treat them as separate genera. Therefore genera *Aizopsis* GRULICH, *Asterosedum* GRULICH, *Petrosedum* GRULICH and *Oreosedum* GRULICH are described.

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The taxonomic classification of succulents is difficult, because the variability of most species is fairly large and the phenomenon of succulence often conditions convergencies. Several species (including many cultivars) are used in horticulture, which tends to complicate their taxonomy.

All species of the family *Crassulaceae* are of succulent habit. The generic division of this family is most unclear, since extreme types have been classed as monotypic genera, e.g. *Pagella* SCHÖNL. Further taxa are natural, e.g. subf. *Sempervivoideae*, *Hylotelephium* OHBA, *Umbilicus* DC. Many species, however, remain in two polymorphic genera *Crassula* L. and *Sedum* L., each with numerous species, and whose differentiation from the other genera is not clear. Most of the “intermediate” types create difficulties, especially when using classic morphological methods based on their succulent parts.

The present division of the family *Crassulaceae* to subfamilies (BERGER 1930) is rather unnatural: the subf. *Cotyledonoideae* and *Sedoideae* are not homogeneous. For example, it is known that hybrids exist between some American taxa of *Sedum* and *Echeveria*, though the hybridization of the same taxa with other *Sedum* is not possible (MORAN et UHL 1975). The subf. *Cotyledonoideae* contains three separate groups: the shrubby South African genera *Cotyledon* L. and *Adromischus* LEM., the peculiar Mediterranean hemi-cryptophytes *Umbilicus* DC. and *Chiastophyllum* (LEDEB.) STAPF and small therophytes of western parts of the Mediterranean region *Pistornia* DC. and *Mucizonia* (DC.) BERGER, also differing in fundamental features (the arrangement of corolla and stamens).

The delimitation of the genus *Sedum* L. is one of the greatest problems. The existing monographs (SCHÖNLAND 1890, PRAEGER 1921, BERGER 1930, FRÖDERSTRÖM 1930—35, OHBA 1978) delimit this genus more or less with success, but none provide a clear indication of the position of some of its species. The greatest complications were caused by the unfortunate de-

scription of the sect. *Epeteium* BOISS. (BOISSIER 1872), which united the evolutionary convergents ranging from polycarpic to monocarpic species. This fact has influenced the taxonomy of *Sedum* until the present day. WEBB (1964) did not express his view on the infrageneric classification, and neither HUBER (1961) nor OHBA (1978) accepted the sect. *Epeteium*. OHBA (1977, 1978) showed that the only way out of this situation was a division of the genus *Sedum* into separate genera. His delimiting of the genera *Rhodiola* L., *Hylotelephium* OHBA, *Prometheum* (BERGER) OHBA and others was thereby justified.

The subf. *Sedoideae* contains more than 600 species occurring predominantly in the northern hemisphere. Only a few species have spread to the southern hemisphere, through the Cordillera Mts. to Bolivia and in mountain ranges of equatorial Africa and Madagascar. It is possible to distinguish three separate areas characterized by the greatest diversity of species and features. These areas lie in East Asia, the Mediterranean region and North America. The speciation processes occurred more or less independently in each of these regions. Only some groups of allied species are distributed in all three regions — *Rhodiola* L. and *Hylotelephium* OHBA (fig. 1) — but the greatest diversity occurs in East Asia. Their ways of migration are distinct; therefore, the geographical view of the taxonomy of *Sedum* used by FRÖDERSTRÖM (1930 to 35) was, to some extent, substantiated. More contacts probably appear between European and Asiatic centres, where for example *Sedum* s. str. occurs.

Europe and adjacent parts of North Africa and West Asia are inhabited by ca. 120 species of subf. *Sedoideae*. According to OHBA (1978), in the region

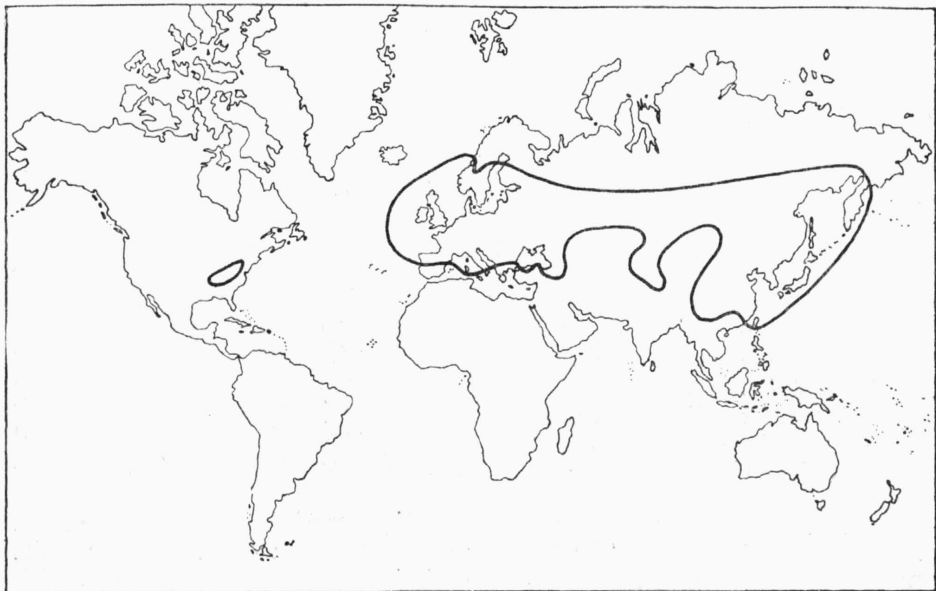


Fig. 1. — Distribution of *Hylotelephium* (Orig.).

Tab. 1. — Growth-form convergencies between *Hylotelephium* and *Aizopsis*

Growth-form	<i>Hylotelephium</i> (examples)	<i>Aizopsis</i> (examples)
Hemicyptophyts stems unbranched erect leaves deciduous	<i>H. maximum</i>	<i>A. aizoon</i>
Hemicyptophyts stems unbranched ascending leaves deciduous	<i>H. sieboldii</i>	<i>A. kamczatica</i>
Chamaephyts stems unbranched leaves wintered	<i>H. anacampseros</i>	—
Chamaephyts stems branched leaves deciduous	<i>H. ewersii</i>	—
Chamaephyts stems branched leaves wintered	<i>H. cyaneum</i>	<i>A. hybrida</i>

between the European and Asiatic areas (Pakistan, Afghanistan, Soviet Middle Asia, Siberia) only *Rhodiola* L., *Hylotelephium* OHBA, *Orostachys* (DC.) FISCH., *Rosularia* (DC.) STAPF (many species) and *Pseudosedum* BERGER (all species) grow. OHBA's restricted genus *Sedum* L. is represented there by only four species: *S. (Aizoon) hybridum* L. and *S. (Aizoon) aizoon* L., spreading from eastern Asia to the Ural, and *S. (s. str.) tetramerum* TRAUTV. and *S. (s. str.) bucharicum* BORISS., spreading from the Caucasian region to the Tchien-shan.

OHBA divided the reduced genus *Sedum* L. (only the old world species) into five subgenera: subg. *Aizoon* (KOCH) OHBA, subg. *Balfouria* OHBA, subg. *Spathulata* (BORISS.) OHBA, subg. *Sedum* and subg. *Telmissa* (FENZL) OHBA. He did not classify subg. *Sedum* at all though he noted that this taxon is unnatural and heterogeneous and many of its species create natural groups. HUBER (1961) commented on the infrageneric classification of *Sedum* and delimited the acceptable groups but he did not classify them nomenclaturally.

Because *Sedum* is very heterogeneous, such a broad view of it is untenable and nothing remains other than to develop HUBER's and OHBA's opinions. The only way out of the present situation is to break down this genus into smaller independent natural genera.

NOTES ON SOME CHARACTERISTICS

Growth form

The majority of species of the subf. *Sedoideae* is chamaephytic. The hemicyptophytic character is typical for primitive groups with flat leaves: *Rhodiola*, *Hylotelephium*, *Aizopsis*, though within these groups the independent tendencies to chamaephytic species appears in *Hylotelephium* sect. *Populisedum* and *Aizopsis hybrida* (tab. 1).

Two species produce the subterraneous bulbillike buds: *Asterosedum obtusifolium* and *Sedum tuberiferum*.

Both phenomena represent good examples of evolutionary convergency.

Pubescence

The yellow flowering species of *Sedum* s. str. and *Aizopsis* are not hairy, only *Aizopsis selskiana* is densely puberulent. Most species of *Petrosedum* bear glandular hairs or papillae on bracts, pedicels, sepals, filaments and carpels. All species of *Asterosedum* are glabrous, only leaves and flowers can be minutely papillose. Glandular hairs or papillae appear on some white or reddish flowering (mostly annual) species of *Sedum* s. str. and generally on white or rose flowering genera *Rosularia*, *Oreosedum* and *Mucizonia*. Papillae are present on carpels of some glabrous species, e.g. *Oreosedum album*.

Leaves and their arrangement

Leaf shape is a very important feature for classification. The hemicryptophytic types (excl. *Pseudosedum*) have primarily flat broad leaves. Flat, spathulate leaves are characteristic for the genus *Asterosedum*, flattened leaves appear also in some (more primitive?) species of *Oreosedum* (e.g. *O. alsinefolium*); this genus, however, includes the types with semiterete (*O. magellense*, *O. monregalense*) and terete (e.g. *O. album*) leaves.

Leaf apex of the species with terete or semiterete leaves is more or less obtuse; only *Petrosedum* is characterized by a rigid, acute leaf apex.

Rosettes can be formed by "radical" leaves (e.g. *Rhodiola* p. p.) (cf. OHBA 1978) or by a crowding of leaves on the upper part of the stem (*Orostachys*, *Oreosedum* p. p., e.g. *O. alsinefolium*). Flat leaves of *Hylotelephium*, *Aizopsis* and *Asterosedum* are rigid and coriaceous, and during drying they do not become transparent; flat leaves of most species of *Oreosedum* are soft and during drying the veins stand out and leaves become transparent.

Inflorescence

The species of subf. *Sedoideae* have flowers arranged in three basic types of inflorescence:

1. Inflorescence corymbothyrsoidal, bracts usually absent. This type is known in *Hylotelephium* and *Rhodiola* (some species).
2. Inflorescence is a dichasium compounded from several (2—10) scorpioid branches, bracts mostly present, flowers are sessile or subsessile. We meet this type in *Sedum* s. str., *Aizopsis*, *Asterosedum* and *Petrosedum*.
3. Inflorescence is based on a (apparent?) raceme, derived forms from this are the panicle or corymbothyrsus, bracts are often absent, flowers are thinly to filiform pedicellate, pedicells are mostly longer than the calyx. In Europe and the adjacent regions, this type is present in genera *Oreosedum*, *Mucizonia*, *Orostachys* and *Rosularia*.

Colour of flowers

The characteristic yellow colour of flowers (such as in *Sedum acre*) is present in *Sedum* s. str., *Aizopsis* and *Petrosedum*, but some species of

Sedum (e.g. *S. atratum*, *S. confertiflorum*, *S. anglicum* and *S. hispanicum* group) and *Petrosedum* (*P. sediforme* and *P. anopetalum*) lack this deep colour. Further genera do not contain this pigment; flowers are white, rose, purple, red, seldom blue (*Oreosedum caeruleum*) or yellowish (*O. versicolor*, *O. nanum*).

Some African species (*Sedum ruwenzoriense* BAKER etc.) with pedicellate flowers have deep yellow flowers. The systematic position of this group is uncertain but it may be allied to *Oreosedum*.

Gynoeceum

The arrangement of the gynoeceum is a very important characteristic for the classification of *Crassulaceae* (cf. OHBA 1977, 1978). Peculiarly, basally attenuate carpels occur on *Hylotelephium* and *Orostachys*. The rest of the genera have two basic types of carpels:

1. Carpels orthocarpic¹⁾: carpels are always (even at maturity) straight, free or basally minutely connate (fig. 7, 8).
2. Carpels kyphocarpic¹⁾: carpels are at maturity stellate patent (exceptionally so on some species of *Asterosedum*), basally distinctly connate. They have, as a rule, lips detached by a distinct ventral groove (fig. 2, 5).

Aizopsis is characterized by kyphocarpic carpels similar to *Sedum* s. str. (fig. 2). Some species of *Asterosedum* (e.g. *A. spurium*) have straight but basally strikingly connate mature carpels with distinct lips; other species (e.g. *A. stellatum*, *A. obtusifolium*) have "normal" kyphocarpic gynoeceum (fig. 5). Carpels of *Petrosedum* are free, narrow, and orthocarpic, with a long style; their upper part is slightly submerged in a "receptaculum" formed by connate parts of sepals and enlarged pedicels and are strongly reminiscent of carpels of subf. *Sempervivoideae*, especially *Jovibarba* (fig. 7). *Oreosedum*, *Rosularia*, *Mucizonia* have short orthocarpic carpels with a short style, their basal parts being slightly connate (fig. 8).

Mature kyphocarpic fruits are mostly strongly lignified and become dark brown, and only the fruits of *Sedum acre* do not quite lignify. Orthocarpic fruits (excl. *Rhodiola*) do not constantly lignify and always remain membranaceous, paperlike and white.

Chromosome number

¶ The basic chromosome number is also an important feature of the genera analysed, even if there is the typical derivation of dysploid numbers. Until now the chromosome counts of many species were not known (cf. FEDOROV 1969), but some principles are shown (tab. 2).

According to t'HART (1978), *Petrosedum* contains an intricate complex of hybridogenous origin, its genome has little function and produces aneuploids easily. It is also interesting that there are no known hybrids between the numerous species of the genus *Oreosedum*, where also polyploidy seldom appears.

¹⁾ These terms are commonly used in the taxonomic literature of *Crassulaceae*.

Tab. 2. — Basic chromosome numbers of European genera of subf. *Sedoideae*

Genus	basic chromosome number															
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Hylotelephium</i>	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.
<i>Petrosedum</i>	.	.	.	(+)	.	.	.	+	+	.	.	+	+	.	.	.
<i>Aizopsis</i>	.	.	.	(+)	.	.	.	.	.	.	.	+	.	.	.	.
<i>Sedum</i>	.	+	+	+	+	+	+	+	+	.	.	(+)	.	.	.	(+)
<i>Asterosedum</i>	+	.	(+)	.	.	.	.	.	.	+	.	.	.	.	.	.
<i>Oreosedum</i>	.	.	.	+	.	.	+	.	.	.	.	.	.	.	.	.
<i>Mucizonia</i>	.	.	.	(+)	.	.	.	+	.	.	.	.	.	.	.	.

Tab. 2. — Continued

Genus	polyploidy			
	3 ×	4 ×	higher	dysploidy
<i>Hylotelephium</i>	+	+	.	+
<i>Petrosedum</i>	+	+	+	+
<i>Aizopsis</i>	+	+	+	.
<i>Sedum</i>	+	+	+	+
<i>Asterosedum</i>	.	(+)	.	.
<i>Oreosedum</i>	+	+	(+)	.
<i>Mucizonia</i>	.	.	.	.

Geographic distribution

Most species of subf. *Sedoideae* of Europe and adjacent countries are concentrated in the Mediterranean region. Only individual species of *Orostachys* and *Aizopsis*, which spread to Europe from the Far East, occur solely in East Europe in the South Urals (fig. 3).

Only the eastern part of the region investigated (from the Aegean to South Persia and North Caucasus) is inhabited by *Rosularia*, *Prometheum*, most species of *Asterosedum* (fig. 4) and many, especially small annual species of *Oreosedum*. Most species of *Sedum* s. str. are also distributed in this region: some stenochorous and diploid yellow flowering taxa (especially in the Balkan Peninsula) and a greater part of the species of *S. hispanicum* group. *Telmissa* is also endemic in this region.

Another region with great specific diversity is the Western part of the Mediterranean (from Morocco to SW. Alps). This district contains the endemic genus *Mucizonia* and some species of *Oreosedum*. The southwestern Alps and Southern France are centers of distribution of *Petrosedum*, where most of its species occur (fig. 6). A few species of the genus *Sedum* s. str. occur there (some endemics in NW. Africa) and some have also spread to the Macaronesia.

Central Europe contains a few species of *Sedum* s. str., *Oreosedum* and *Petrosedum*. Species of *Hylotelephium* are also concentrated there. The Central European species of *Oreosedum* and *Petrosedum* have the distinct oceanic character of their distribution and are completely missing from continental East Europe.

North Europe is inhabited only by the Arctic-alpine *Rhodiola rosea* and European species *Sedum acre*, *S. annuum* and *Oreosedum villosum*. They spread to Iceland; additionally, *S. annuum* to Greenland and *Rhodiola rosea* and *Oreosedum villosum* to North America. Other species extend north to the Åland islands (*Petrosedum reflexum*, *Sedum boloniense* and *Oreosedum album*).

SYSTEMATIC PART

Aizopsis GRULICH, gen. novum

Syn.: *Sedum* L. sect. *Aizoon* KOCH, Syn. Fl. Germ., ed. 1, 259 (1835). — *Sedum* L. subg. *Aizoon* (KOCH) OHBA, Journ. Fac. Sci. Univ. Tokyo, sect. III, 12 : 179 (1978).

Plantae perennes, glabrae vel raro totae glandulosae. Rhizoma incrassatum, lignescens. Caules foliiferi erecti, ascendentes vel repentes, decidui, raro aestate creati et sempervirentes, e gemmis

apicem rhizomatis vel ad basim caulium orti. Caules floriferi erecti vel ascendentes. Folia alternata, plana, linearilanceolata, lanceolata vel usque obovata, dentata vel crenata, basi cuneata. Inflorescentia densa, cymosa, e ramis scorpioides composita, bracteata. Flores 5-6-meri, paene sessiles, hermaphroditi, sepala basi connata, petala lutea, basi connata, patentia. Androeceum obdiplostemonum. Gynoeceum kyphocarpicum, basi connatum, styli breviores, folliculi stellate patentes. —

Typus generis: *Aizopsis aizoon* (L.) GRULICH

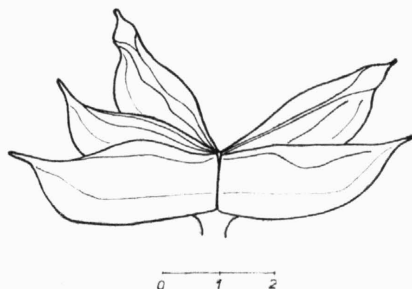


Fig. 2. — Fruits of *Aizopsis hybrida* (Orig.).

Aizopsis is a well-delimited natural group of predominantly hemicryptophytic species (only *A. hybrida* is chamaephytic) with flat and more or less broad, toothed leaves, yellow flowers, kyphocarpic stellate patent fruits (fig. 2), and a basic chromosome number of $x = 16$ (8). *Aizopsis* originated

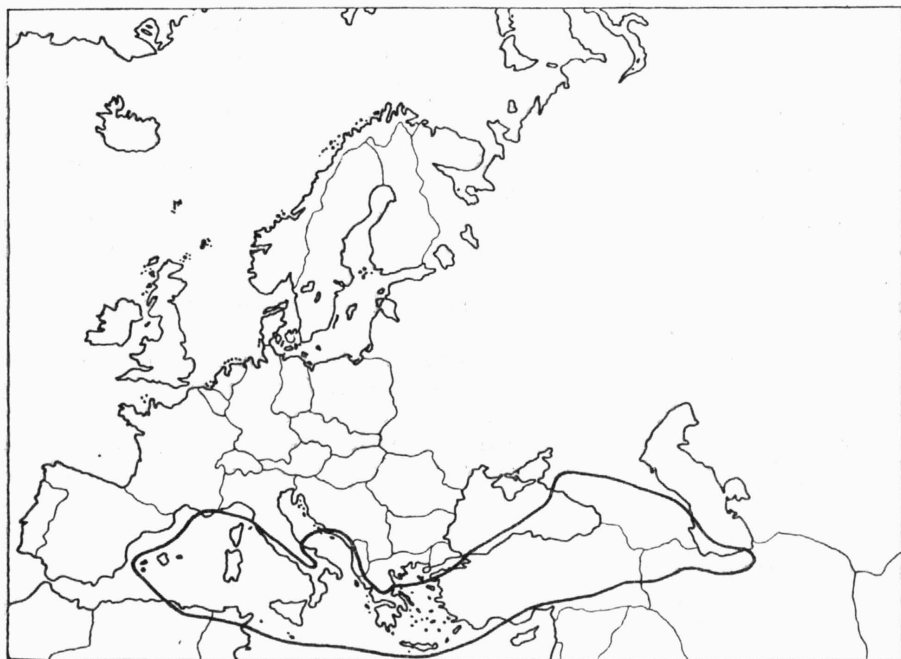


Fig. 3. — Distribution of *Aizopsis* (Orig.).

in East Asia, where the majority of its species occur. Only *A. hybrida* spread to South Ural (fig. 3). *Aizopsis* is morphologically primitive and is derived from the predecessors of *Sedum* s. str. This is visible in the similar form of carpels and fruits and in the chemical and genotype relationships.



ig. 4. — Distribution of *Asterosedum* (Orig.).

- Aizopsis aizoon* (L.) GRULICH, comb. nova. — Bas.: *Sedum aizoon* L., Sp. Pl. 430 (1753).
Aizopsis hybrida (L.) GRULICH, comb. nova. — Bas.: *Sedum hybridum* L., Sp. Pl. 431 (1753).
Aizopsis kamezatica (FISCH.) GRULICH, comb. nova. — Bas.: *Sedum kamezaticum* FISCH., Index Sem. Horti Petrop. 7 : 54 (1840).
Aizopsis middendorffiana (MAXIM.) GRULICH, comb. nova. — Bas.: *Sedum middendorffianum* MAXIM., Prim. Fl. Amur. 116 (1859).
Aizopsis odontophylla (FRÖD.) GRULICH, comb. nova. — Bas.: *Sedum odontophyllum* FRÖD., Acta Horti Gothob., 7 [App.] : 117 (1931).
Aizopsis selskiana (REGEL et MAACK in REGEL) GRULICH, comb. nova. — Bas.: *Sedum selskianum* REGEL et MAACK in REGEL, Tent. Fl. Ussur. 66 (1861).
Aizopsis sikokiana (MAXIM.) GRULICH, comb. nova. — Bas.: *Sedum sikokianum* MAXIM., Diagn. Pl. Nov. Asiat. 8 : 1 (1893).

Sedum L.

Sedum L. s. str. includes small, perennial or annual species with terete or semiterete leaves, inflorescence developed from scorpioids with almost bracteate, sessile or subsessile flowers scorpioids with almost bracteate, sessile or subsessile flowers, and kyphocarpic fruits, which are stellate patent and usually lignified at maturity. Within this taxon there are two basic groups:

The first is characterized by glabrous, mostly yellowish flowering species with obdiplostemonous androeceum (only *S. litoreum* has been treated as haplostemonous), but some species probably belonging to it have (secondary?)

rose or whitish flowers (e.g. *S. anglicum*, *S. atratum*). The second group contains taxa without yellow flowers, that are sometimes covered by glandular hairs and sometimes haplostemonous (*S. hispanicum*, *S. rubens*, *S. aetnense* etc.).

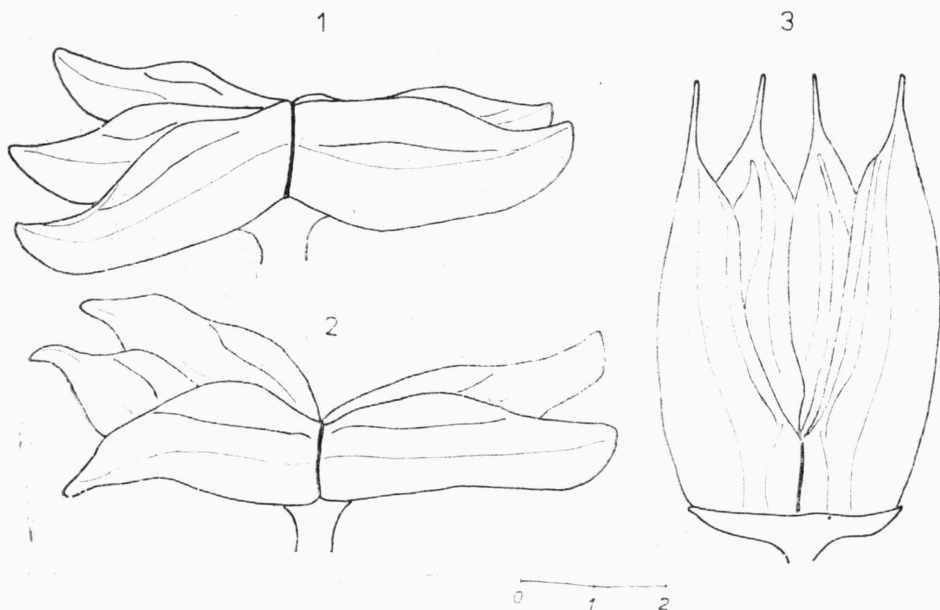


Fig. 5. — Fruits of *Asterosedum*: 1 — *A. stellatum*, 2 — *A. obtusifolium*, 3 — *A. spurium* (Orig.).

Telmissa is derived from the second group and represents an extremely reduced monotypic taxon with only terminal haplostemonous flowers and carpels with only 1–2 ovules.

The species of *Sedum* s. str. are distributed from the Canary Islands to the Tchien-Shan and extend to North Europe and Greenland. Several species of this genus also appear in East Asia (e.g. *S. japonicum*, *S. multi-caule*). Relationships within this genus need further investigation.

Sedum s. str. differs in its small terete or semiterete leaves from the kyphocarpic genera *Aizopsis*, which contains mostly hemicyryptophytic species, and from *Asterosedum*, the flowers of which are never yellow and the fruits are strikingly large. *Oreosedum* differs in racemose inflorescence and orthocarpic gynoeceum. *Petrosedum* is distinguished by the arrangement of flowers with semi-inferior ovary and orthocarpic fruits, and by apiculate leaves.

***Asterosedum* GRULICH, gen. novum**

Syn.: *Sedum* L. sect. *Epeteium* BOISS. ser. *Planifolia* PRAEGER, Journ. Roy. Hortic. Soc., 46 : 293 (1921), p. p. — *Sedum* L. sect. *Sedum* ser. *Involucrata* MAXIM. ex BERGER in ENGLER et PRANTL, Natur. Pfl.-Fam., ed. 2, 18 a : 449 (1930). — *Sedum* L. sect. *Sedum* ser. *Propontica*

BERGER, l.c. 450 (1930). — *Sedum* L. sect. *Sedum* ser. *Spurium* FRÖD., Acta Horti Gothob., 7 (App.): 9 (1931). — *Sedum* L. sect. *Sedum* ser. *Stoloniferum* FRÖD., l.c. 49 (1931), p. p. — *Sedum* L. sect. *Sedum* subsect. *Spathulata* BORISS., Nov. Sist. Vyss. Rast. 6 : 117 (1969). — *Sedum* L. subg. *Spathulata* (BORISS.) OHBA, Journ. Fac. Sci. Univ. Tokyo, sect. III, 12 : 178 (1978).

Plantae perennes vel annuae, glabrae vel minutissime papillosae. Surculi steriles herbacei-ramosi, procumbentes vel repentes, raro tuberosos subterraneos ferrentes, caules floriferi ascendentes vel arcuato-erecti. Folia opposita vel raro alternata, plana, spathulata, pseudopetiolata, non calcarata, crenata vel integra. Inflorescentia densiuscula vel laxa et dichotome divaricata, e ramis scorpioideis composita. Flores bracteati, subsessiles vel sessiles. Sepala oblonga, basi connata, subacuta, apice saepe mamillata. Petala lanceolata, 6–10 mm longa, erecta vel late patentia, alba vel rosea. Stamina obdiplostemonia. Carpella per 0,5–1,0 mm connata, kyphocarpica, 5–9 mm longa, lignescens, erecta vel stellata sub fructu. —

Typus generis: *Asterosedum stellatum* (L.) GRULICH.

Members of the Caucasian perennial *spurium* — *obtusifolium* aggregate are closely allied morphologically and characterized by herbaceous branching stems, spathulate leaves and inflorescence containing scorpioid branches and bracteate flowers. Spathulate leaves are remarkable also on the annual Mediterranean *Sedum stellatum*, which resembles the Caucasian species (especially *S. stoloniferum*) in the shape of inflorescence, the size of flowers and the size and shape of fruits (fig. 4). Stellate patent or straight fruits of the Caucasian species belong to the infrageneric speciation trends (cf. OHBA 1978), and both types of fruits in this case are certainly of common origin (fig. 2).

Asterosedum obtusifolium (C. A. MEYER) GRULICH, comb. nova. — Bas.: *Sedum obtusifolium* C. A. MEYER, Enum. Pl. Cauc., 150 (1831).

Asterosedum spurium (M. BIEB.) GRULICH, comb. nova. — Bas.: *Sedum spurium* M. BIEB., Fl. Taur.-Cauc. 1 : 352 (1808).

Asterosedum stellatum (L.) GRULICH, comb. nova. — Bas.: *Sedum stellatum* L., Sp. Pl. 431 (1753).

Asterosedum stevenianum (ROUY et CAMUS) GRULICH, comb. nova. — Bas.: *Sedum stevenianum* ROUY et CAMUS, Fl. Fr. 7 : 94 (1901).

Asterosedum stoloniferum (S. G. GMEL.) GRULICH, comb. nova. — Bas.: *Sedum stoloniferum* S. G. GMEL., Reise 3 : 311 (1774).

***Petrosedum* GRULICH, gen. novum**

Syn.: *Sedum* L. sect. *Acutifolia* HAWORTH, Phil. Mag. 173 (1825). — *Sedum* L. sect. *Sedum* ser. *Rupestris* BERGER in ENGLER et PRANTL, Natur. Pfl.-Fam., ed. 2, 18a : 456 (1930).

Plantae perennes glabrae vel in inflorescentia glandulosae, surculi steriles ramosi et radican-tes, ascendentes, repentes vel dehiscens. Caules floriferi erecti, 15–60 cm longi, basi saepe lignescens. Folia alternata, linearia usque oblonga, teretia vel semiteretia, acuminata, calcarata. Inflorescentia e multis (4–10), raro tantum (2–3) ramis scorpioidei composita, sub anthesis erecta vel nutans. Flores breve pedicellati, saepe bracteati, lutei vel albi, plerumque 6–7-meri, hermaphroditi, obdiplostemoni. Gynoecium cum calyce et pedicellis basi connatum, receptaculum formans, semi-inferior, orthocarpicum. Styli longiores, folliculi erecti, angustati. —

Typus generis: *Petrosedum reflexum* (L.) GRULICH

Petrosedum is a natural group, without any close relationship to other groups, which is distributed in the Mediterranean region and in West and Central Europe (fig. 6). The north American *Sedum stenopetalum* PURSH and *S. lanceolatum* TORREY are sometimes also placed under *Sedum* L. ser. *Rupestris* (BERGER 1930). These species have obtuse leaf apices and are not related to *Petrosedum* (cf. t'HART 1978).

The production of flavonoids by some species of *Petrosedum* resembles this process in *Sedum* s. str., although both genera differ in the arrangement of the gynoeceum.

Petrosedum contains a complex of auto- and allopolyploids. t'HART (1978) ascertained that all species readily tend towards hybridization. Some cyto-

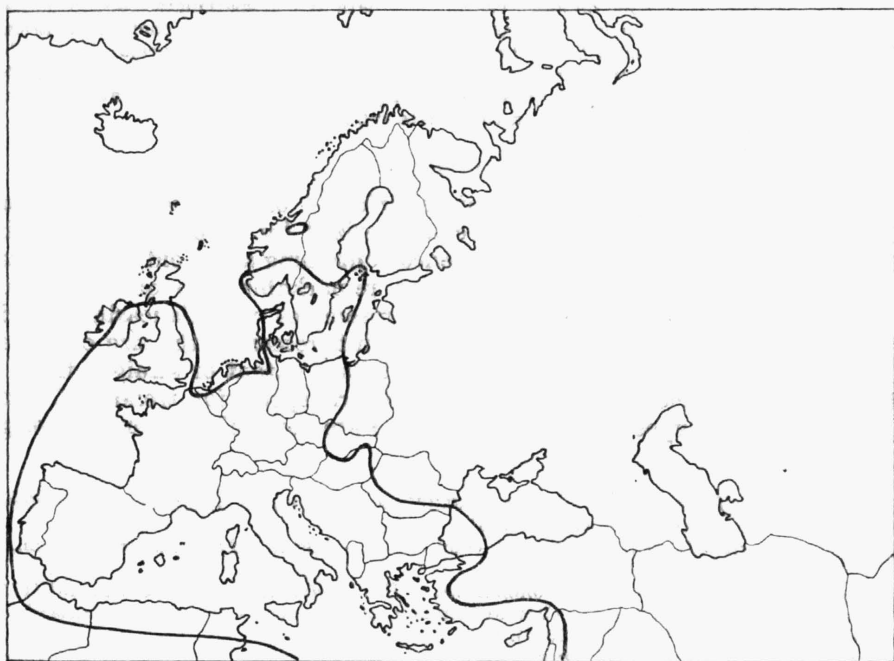


Fig. 6. — Distribution of *Petrosedum* (Orig.).

types of *P. orientale* and *P. reflexum* have aneuploid chromosome numbers and have evidently a hybridogenuous origin.

The arrangement of usually 6–7(–12)-merous flowers with free carpels basally connate with the upper part of the calyx and pedicels reminiscent of semi-inferior receptaculum and leaves with apiculate apices does not exclude a relationship with subf. *Sempervivoideae*, especially with genus *Jovibarba* (DC.) OPIZ (fig. 7).

Petrosedum anopetalum (DC.) GRULICH, comb. nova. — Bas.: *Sedum anopetalum* DC., Rapp. Voy. Bot. Agr. 2 : 80 (1808).

Petrosedum erectum (t'HART) GRULICH, comb. et stat. nov. — Bas.: *Sedum rupestre* L. subsp. *erectum* t'HART, Biosyst. Stud. 101 (1978).

Petrosedum forsterianum (SM. in SOWERBY) GRULICH, comb. nova. — Bas.: *Sedum forsterianum* SM. in SOWERBY, Engl. Bot. 26 : t. 1802 (1808).

Petrosedum x luteolum (CHAB.) GRULICH, comb. nova. — Bas.: *Sedum x luteolum* CHAB., Bull. Soc. Bot. France 10 : 296 (1863). — *Sedum reflexum* x *sediforme*.

Petrosedum montanum (SONG. et PERR.) GRULICH, comb. nova. — Bas.: *Sedum montanum* SONG. et PERR., Billotia 1 : 77 (1864).

Petrosedum orientale (t'HART) GRULICH, comb. et stat. nov. — Bas.: *Sedum montanum* SONG. et PERR. subsp. *orientale* t'HART, Biosyst. Stud. 106 (1978).
Petrosedum pruinatum (BROT.) GRULICH, comb. nova. — Bas.: *Sedum pruinatum* BROT., Fl. Lusit. 2 : 209 (1804).
Petrosedum reflexum (L.) GRULICH, comb. nova. — Bas.: *Sedum reflexum* L., Fl. Suec., ed 2, 463 (1755).

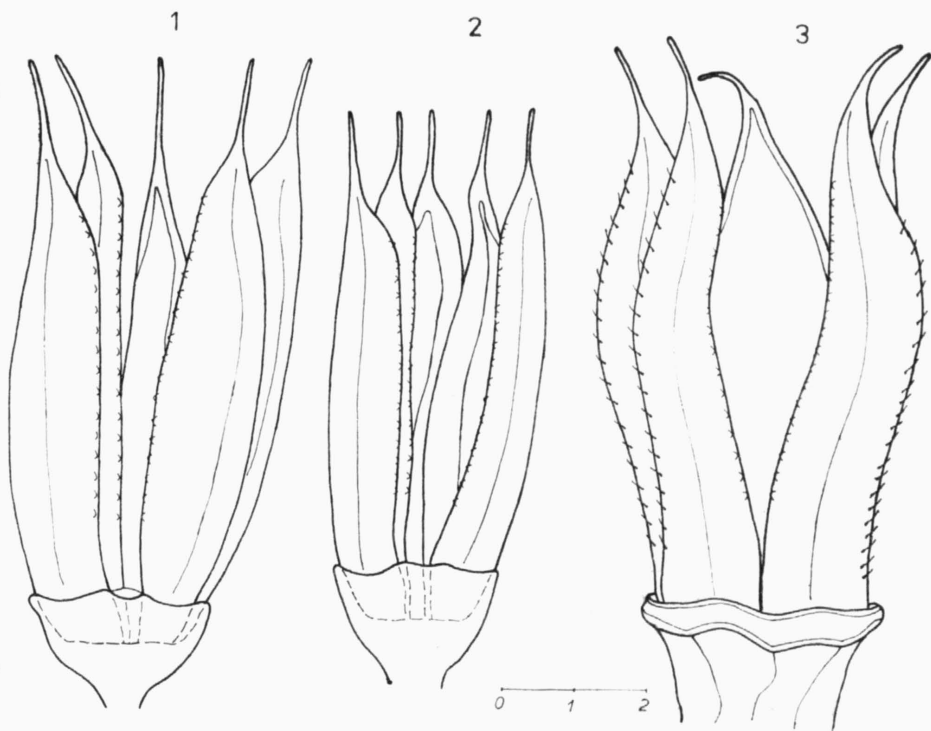


Fig. 7. — Fruits of *Petrosedum* and *Jovibarba*: 1 — *Petrosedum reflexum*, 2 — *P. anopetalum*, 3 — *Jovibarba sobolifera* (Orig.).

Petrosedum sediforme (JACQ.) GRULICH, comb. nova. — Bas.: *Sempervivum sediforme* JACQ. Hort. Bot. Vindob. 1 : 35 (1770). — Syn.: *Sedum sediforme* (JACQ.) PAU, Act. Mem. Prim. Congr. Nat. Esp. Zaragoza 246 (1909).
Petrosedum tenuifolium (SIBTH. et SM.) GRULICH, comb. nova. — Bas.: *Sempervivum tenuifolium* SIBTH. et SM., Fl. Graec. 1 : 335 (1806). — Syn.: *Sedum tenuifolium* (SIBTH. et SM.) STROBL, Österr. Bot. Zeitschr. 34 : 295 (1884).
Petrosedum tenuifolium (SIBTH. et SM.) GRULICH subsp. *ibericum* (t'HART) GRULICH, comb. nova. — Bas.: *Sedum tenuifolium* (SIBTH. et SM.) STROBL. subsp. *ibericum* t'HART, Acta Bot. Neerl. 23 : 553 (1974).

Oreosedum GRULICH, gen. novum

Syn.: *Leucosedum* FOURR., Ann. Soc. Linn. Lyon, n. ser., 16 : 384 (1868), nom. nudum. — *Sedum* L. sect. *Sedum* ser. *Alba* BERGER in ENGLER et PRANTL, Natur. Pfl.-Fam., ed. 2, 18a : 452 (1930) p. p. — *Sedum* L. sect. *Epeteium* BOISS., Fl. Orient., 2 : 772 (1872) p. min. p. — *Sedum* L. sect. *Villosa* R. T. CLAUSEN, Sedum N. Amer. 92 (1975).

Plantae perennes, biennes vel annuae, glabrae vel pubescentes. Surculi steriles specierum perennium caespitosi, ramosi, repentes vel ascendentes, radicanes, species biennes et annuae ascendentes vel erectae, paulo ramosae vel simplices. Caules floriferi 2—30 cm longi. Folia alternata, opposita vel rarissime verticillata, raro rosulata, parva, teretia, semiteretia vel planiuscula, globosa, ovoida, lineari-lanceolata vel linearia, integra, obtusa, ecalcarata, mollia. Inflorescentia racemosa, paniculata vel corymbothyrsioidea, terminalia. Pedicelli calycem longiores, filiformes.

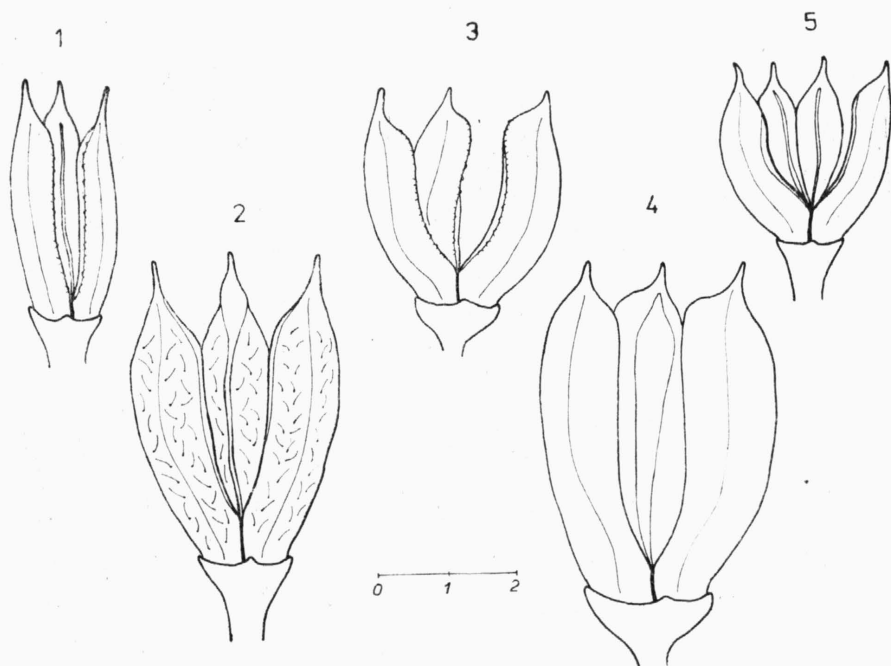


Fig. 8. — Fruits of *Oreosedum* and *Sedum* s.l.: 1 — *Oreosedum album*, 2 — *O. villosum*, 3 — *Sedum cepaea*, 4 — *Oreosedum magellense*, 5 — *Sedum microstachyum* (Orig.).

Flores multi, raro flos unus, saepe ebracteati, hermaphroditi, obdiplostemoni vel haplostemoni, (4—) 5 (—9)-meri. Calyces basi connati, saepe glandulosi, virides, Corolla saepe basi connata, raro campanulata, alba, luteola, rosea vel caerulea. Gynoeceum orthocarpicum, carpella basi paulo connata, papillosa vel glabra. Styli breviores, folliculi erecti, 3—5 mm longi, albidii, membranacei, non lignescentes. —

Typus generis: *Oreosedum album* (L.) GRULICH.

The genus *Oreosedum* is characterized by a (apparently?) racemose, never distinctly scorpioid, inflorescence. Simple racemes appear, especially in the annual species, but of the perennials only *O. magellense* has a racemose inflorescence. Richly branched (paniculate) inflorescences appear in most species, some derived species have a thyrsoidal inflorescence (e.g. *O. album*). Pedicels are thin or filiform, and, in most species, longer than their sepals. Bracts are often absent (e.g. *O. album*).

Sedum s. str. differs in the production of characteristic flavonoids, scorpioid inflorescences with bracteate, sessile or subsessile flowers, and kyphocarpic, mostly lignified carpels, which are stellate patent at maturity. *Petrosedum* differs in having apiculate leaves, scorpioid inflorescence, the presence of

a semi-inferior gynoeceum and longer style. The nearest genus is probably *Rosularia*, which also has a racemose inflorescence and differs in its rosulate leaves and tubular-campanulate corolla (*O. winkleri* has petals united for 1/4 of their length). *Rosularia adenotricha* (EDGEW.) JANSSEN is strongly reminiscent of some *Oreosedum*. The delimitation of both genera needs further investigation. *Mucizonia* also resembles *Oreosedum* and is characterized by campanulate flowers. The evolution of the genus *Oreosedum* progressed independently from complex *Asterosedum* — *Aizopsis* — *Sedum* — *Telmissa*.



Fig. 9. — Distribution of *Oreosedum* (Orig.).

Sedum cepaea L., which seems to be related with *Oreosedum* occurs in South Europe, and occasionally also in southern parts of Central Europe. This hapaxanth species that creates basal rosettes, is characterized by a gynoeceum analogous with *Oreosedum* (fig. 8), but differs in its diffuse paniculate inflorescence, which is why the whole flowering plant seems to have a pyramidal shape. Another related group is *Sedum lampusae* aggregate from Kriti, Karpathos and Cyprus, containing 3—4 monocarpic species with basal rosettes and extremely dense paniculate inflorescence. According to KRÁL (1968) both *Sedum cepaea* and *S. lampusae* agg. are allied, but their taxonomic status is uncertain.

The trends within this genus are visible in many features. *Oreosedum alsinefolium* has flat rosulate leaves, also *O. winkleri* has rosulate upper leaves. *Oreosedum winkleri* has quarter-connate petals, lightly connate ones are present on other species.

The distribution of the genus *Oreosedum* includes Europe, NW. Africa and West Asia (fig. 9). The greatest diversity appears in the Western part of this area (from NW. Africa to South France) and in the Turkey — Caucasian

region where we find some stenochorous (often annual) species. Only a few species are distributed in Central Europe. They are *Oreosedum dasyphyllum* (occurs only in southern parts), *O. album* and *O. villosum*. The latter also occurs in North Europe, Iceland, Greenland, and on several small island in the St. Lawrence river estuary.

Some additional species, probably related to *Oreosedum* also occur in East Asia (*Sedum filipes* agg.) and Central Africa (*S. ruwenzoriense* agg.).

- Oreosedum album* (L.) GRULICH, comb. nova. — Bas.: *Sedum album* L., Sp. Pl. 432 (1753).
Oreosedum alsinefolium (ALL.) GRULICH, comb. nova. — Bas.: *Sedum alsinefolium* ALL., Fl. Pedem. 2 : 119 (1785).
Oreosedum brevifolium (DC.) GRULICH, comb. nova. — Bas.: *Sedum brevifolium* DC., Rapp. Voy. Bot. 2 : 79 (1808).
Oreosedum caeruleum (L.) GRULICH, comb. nova. — Bas.: *Sedum caeruleum* L., Mantissa Alt. 241 (1771).
Oreosedum callichroum (BOISS.) GRULICH, comb. nova. — Bas.: *Sedum callichroum* BOISS., Diagn. Pl. Orient. Nov. 1 (6) : 56 (1848).
Oreosedum dasyphyllum (L.) GRULICH, comb. nova. — Bas.: *Sedum dasyphyllum* L., Sp. Pl. 431 (1753).
Oreosedum farinosum (LOWE) GRULICH, comb. nova. — Bas.: *Sedum farinosum* LOWE, Trans. Camb. Phil. Soc. 4 : 31 (1831).
Oreosedum gattefossei (BATT. et JAHAND.) GRULICH, comb. nova. — Bas.: *Sedum gattefossei* BATT. et JAHAND., Bull. Soc. Hist. Natur. Afr. Nord 12 : 26 (1921).
Oreosedum gypsicola (BOISS. et REUT.) GRULICH, comb. nova. — Bas.: *Sedum gypsicola* BOISS. et REUT., Diagn. Pl. Nov. Hisp. 13 (1842).
Oreosedum hewittii (CHAMBERLAIN) GRULICH, comb. nova. — Bas.: *Sedum hewittii* CHAMBERLAIN Not. Roy. Bot. Gard. Edinburgh 31 : 325 (1972).
Oreosedum hierapatrae (RECH. fil.) GRULICH, comb. nova. — Bas.: *Sedum hierapatrae* RECH. FIL., Denkschr. Akad. Wiss. Math.-Nat. Kl. (Wien), 105 (2) : 86 (1943).
Oreosedum hirsutum (ALL.) GRULICH, comb. nova. — Bas.: *Sedum hirsutum* ALL., Fl. Pedem. 2 : 122 (1785).
Oreosedum hispidum (DESF.) GRULICH, comb. nova. — Bas.: *Sedum hispidum* DESF., Fl. Atl. 1 : 361 (1798).
Oreosedum inconspicuum (HAND.-MAZZ.) GRULICH, comb. nova. — Bas.: *Sedum inconspicuum* HAND.-MAZZ., Ann. Naturhist. Hofmus. 27 : 66 (1913).
Oreosedum kotschyianum (BOISS.) GRULICH, comb. nova. — Bas.: *Sedum kotschyianum* BOISS., Diagn. Pl. Orient. Nov. 1 (6) : 56 (1848).
Oreosedum lagascae (PAU) GRULICH, comb. nova. — Bas.: *Sedum lagascae* PAU, Not. Bot. Fl. Esp. 6 : 53 (1895).
Oreosedum magellense (TEN.) GRULICH, comb. nova. — Bas.: *Sedum magellense* TEN., Prodr. Fl. Nap. 26 (1811).
Oreosedum modestum (BALL) GRULICH, comb. nova. — Bas.: *Sedum modestum* BALL, Journ. Bot. 11 : 333 (1873).
Oreosedum monregalense (BALBIS) GRULICH, comb. nova. — Bas.: *Sedum monregalense* BALBIS, Mém. Acad. Sci. Turin 7 : 339 (1804).
Oreosedum nanum (BOISS.) GRULICH, comb. nova. — Bas.: *Sedum nanum* BOISS., Diagn. Pl. Orient. Nov. 1 (6) : 57 (1848).
Oreosedum nevadense (COSSON) GRULICH, comb. nova. — Bas.: *Sedum nevadense* COSSON, Not. Pl. Crit. 2 : 163 (1849).
Oreosedum pedicellatum (BOISS. et REUT.) GRULICH, comb. nova. — Bas.: *Sedum pedicellatum* BOISS. et REUT., Diagn. Pl. Nov. Hisp. 13 (1842).
Oreosedum serpentinii (JANCHEN) GRULICH, comb. nova. — Bas.: *Sedum serpentinii* JANCHEN, Österr. Bot. Zeitschr. 69 : 173 (1920).
Oreosedum stefco (STEFANOV) GRULICH, comb. nova. — Bas.: *Sedum stefco* STEFANOV, God. Sof. Univ. (Agro.-Les. Fak.) 24 (2) : 105 (1946).
Oreosedum subulatum (C. A. MEYER) GRULICH, comb. nova. — Bas.: *Cotyledon subulata* C. A. MEYER, Verz. Pfl. Cauc. 150 (1831). — Syn.: *Sedum subulatum* (C. A. MEYER) BOISS., Fl. Orient. 2 : 783 (1872).
Oreosedum tenellum (M.-BIEB.) GRULICH, comb. nova. — Bas.: *Sedum tenellum* M.-BIEB., Fl. Taur. — Cauc. 3 : 315 (1819).

- Oreosedum tristriatum* (BOISS.) GRULICH, comb. nova. — Bas.: *Sedum tristriatum* BOISS., Diagn. Pl. Orient. Nov. 2 (10): 16 (1849).
- Oreosedum versicolor* (HAMET) GRULICH, comb. nova. — Bas.: *Sedum caeruleum* L. var. *versicolor* HAMET, Feddes Rept. 13: 22 (1913). — Syn.: *Sedum versicolor* (HAMET) MAIRE, Bull. Soc. Hist. Natur. Afr. Nord 14: 144 (1923).
- Oreosedum villosum* (L.) GRULICH, comb. nova. — Bas.: *Sedum villosum* L., Sp. Pl. 432 (1753).
- Oreosedum winkleri* (WILLK.) GRULICH, comb. nova. — Bas.: *Umbilicus winkleri* WILLK., Ber. Deutsch. Bot. Gess. 5: 269 (1883).

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SOUHRN

Rod *Sedum* L. (ca. 600 druhů) je vůči příbuzným rodům vymezen velmi neostře a skládá se z celé řady příbuzenských skupin, jejichž hodnocení ztěžuje velký počet „přechodných“ typů, které ve skutečnosti představují evoluční konvergence. Použití běžných morfologických metod je ve značné míře omezeno rozsáhlou variabilitou sukulentních orgánů.

Rod *Sedum* L. je rozšířen především na severní polokouli a jeho areál je tvořen třemi arealami s velkou druhovou i znakovou diversitou (východní Asie, Středomoří, severní Amerika), ve kterých proběhl speciální procesy více méně oddělené.

Analýza nejvyhraněnějších typů, provedená Ohbou (OHBA 1978) prokázala, že stávající široké pojetí rodu *Sedum* není možno udržet. Přestože OHBA řadu těchto typů vyčlenil nebo prokázal oprávněnost jejich rodového pojetí, rod *Sedum* zůstal i nadále velmi heterogenní.

Na základě odlišné životní formy, tvaru listů, květenství, barvy květů a stavby semeníků a plodů je možno oddělit rody *Aizopsis* GRULICH, *Asterosedum* GRULICH, *Petrosedum* GRULICH a *Oreosedum* GRULICH. Rod *Petrosedum* stavbou gynoecea silně připomíná rod *Jovibarba* z podčeledi *Sempervivoideae*, rod *Oreosedum* je blíže příbuzný rodům *Rosularia* a *Mucizonia*, z nichž druhá jistě nepatří do heterogenní podčeledi *Cotyledonoideae*. Vyčleněním těchto rodů bylo dosaženo relativní homogenity taxonů podčeledi *Sedoideae* na úrovni rodu v evropské arele.

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