Valerianaceae

Valerianaceae Batsch, Tab. Affin. Regni Veg.: 227 (1802), nom. cons.

F. Weberling and V. Bittrich

Annual to perennial, often fetid herbs, subshrubs, sometimes shrubs, rarely ligneous or herbaceous vines; root often a taproot, often slender, sometimes a napiform or fusiform turnip, the stem-borne roots sometimes tuberous; plants often semirosulate, sometimes rosulate; stem often fistulous. Leaves mostly decussate, rarely 3-verticillate, sometimes alternate, rarely distichous or tristichous, entire, pinnatifid or pinnate, exstipulate, rarely ericoid or carnose, glabrous or with simple and glandular hairs. Inflorescence usually bracteate, a dense thyrse or pleiothyrse without terminal flower, basimesotonic or acrotonic and pseudodichotomous, sometimes capitate by condensation of the flower-bearing branches; in some genera supernumerary bracts occur below the flowers. Flowers epigynous, bisexual or unisexual, then plants dioecious, polygamous or often gynodioecious, basically pentamerous, but altered by reduction of organs, usually irregularly zygomorphic; calyx rarely regularly 5-lobed, mostly inconspicuous or strongly reduced, or often divided into up to 30 segments, inrolled during anthesis; corolla sympetalous, funnelform, infundibuliform, salverform, rotate or campanulate, tube often saccate at base and nectariferous inside, sometimes spurred, limb with 3 or 5 more or less unequal lobes, often bilabiate; stamens 1–4(5), usually inserted in the corolla tube, alternating with the corolla lobes, anthers tetrasporangiate or rarely bisporangiate; ovary inferior, 3-locular, one locule with 1 pendent ovule, the other two sterile, often very small; style 1, filiform with a two- or three-lobed stigma. Fruit an achene with a persistent, usually accrescent calyx, sterile locules persistent, sometimes inflated, or apparently absent; the calyx mostly developing into a plumose or awned pappus (segments inrolled in flower) or a solid rim, or consisting of 5 regular teeth or fewer or more irregular lobes, sometimes 1–3 stout horns or a small or larger number of spines, sometimes regularly 6-lobed and coroniform, rarely inflated. Mature seed usually without endosperm, rarely endosperm copious; embryo large, straight.

The family comprises 5 genera (with *Valeriana* s.l. including various Andean segregate genera) and about 400 species, distributed mainly in the northern hemisphere and the mountainous regions of South America, absent from Australia and Polynesia. *Triplostegia* is treated in this volume under Dipsacaceae.

Vegetative Morphology. Mostly annual or perennial herbs are half-rosette plants (sometimes subrosulate) with terminal inflorescences, often with a taproot. The innovation shoots arise from the rosulate zone or the preceding parts, which are more or less lignified. The main stem remains extremely short in several high-elevation Andean species of *Valeriana* s.l. (incl. *Stangea*, *Belonanthus*, *Aretiastrum* and *Phyllactis*), some of which form large and dense globe-shaped cushions by periodical acrotonic ramification of the rosettes (Fig. 74). Some species of *Valeriana* grow as small shrubs, a few species as woody lianas (*V. clematitis*) or herbaceous climbers (*V. scandens*).

Leaves are usually decussate, in some cases, however, starting from a distichous condition (*Valeriana officinalis*). In some species of *Valeriana* s.l. (*Stangea*) a transition from an oblique decussate phyllotaxis in the first nodes into spirodecussate arrangement and higher degrees of dispersion in the inflorescence takes place (Rauh and Weberling 1960). In a similar way phyllotaxis changes in some other high Andean

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Weberling (deceased).

J.W. Kadereit and V. Bittrich (eds.), *Flowering Plants. Eudicots*, The Families and Genera of Vascular Plants 14,
DOI 10.1007/978-3-319-28534-4_35, © Springer International Publishing Switzerland 2016

species of *Valeriana* (*V. pycnantha*, *V. globularis*, a.o.) from orthodistichy in the first nodes to oblique decussation and to a tristichous arrangement. In other species of *Valeriana* s.l. (*Phyllactis*), the position of the first leaves is orthostichous changing to spirodistichous in later leaves and finally to a spiral arrangement. Also in *Valeriana* s.l. (*Belonanthus*), foliage leaves show a divergence of 3/8. In species of *Patrinia* an adnation between the leaf bases and the cortex of the internode below can be observed.

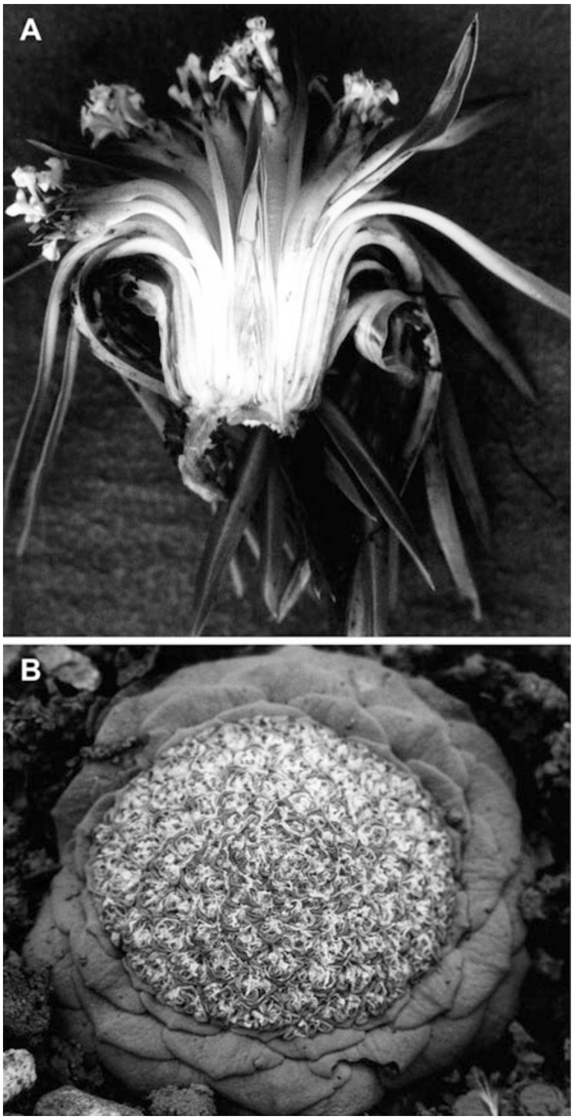

Fig. 74. Valerianaceae. **A** *Valeriana rigida*, rosette in longitudinal section (Cahuish-Tunnel, central Peru, 4178 m elevation). **B** *Valeriana henrici*, fruiting plant (Paso Ticlio, central Peru, 4843 m). **C, D** *Valeriana aschersoniana*. **C** Vegetative shoot. **D** Cushion with patches of snow (Valle Puypuy, central Peru, ca. 4400 m)

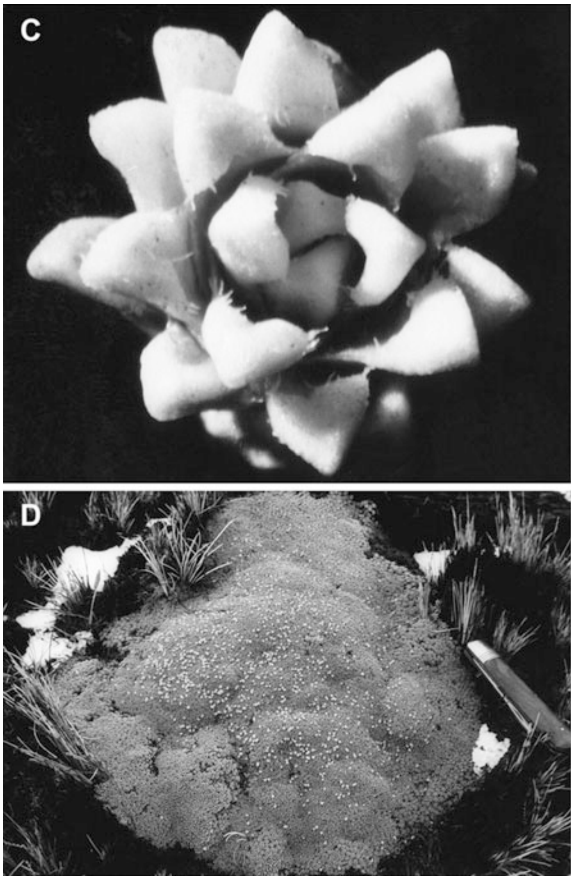

Fig. 74. (continued)

VEGETATIVE ANATOMY. Simple hairs, unicellular or sometimes transversely septate glandular hairs with unicellular or multicellular stalks and small multicellular heads are common. The cortex lacks sclerenchymatic elements. In young shoots a distinct endodermis consisting of large cells is visible (Solereder 1899). Nodal anatomy was studied by Neubauer (1978). The nodes are usually 3-lacunar; *Valeriana aschersoniana* has unilacunar, a few species, like *V. polystachya* and *V. tiliaefolia*, have 5-lacunar nodes, and *V. aliariifolia* has 5-, 6-, or 7-lacunar nodes. As in several genera of Dipsacaceae and *Morina* of Morinaceae, the outer branches of the bifurcating lateral traces of opposite leaves join in the nodal cortex, forming a bridge. From the apex of such a bridge two bundles are leaving, one entering each petiole; thus, in case of a 3-lacunar node, a total of 5 traces enter the base of each petiole. In *Valeriana celtica* and *V. saxatilis* an anomalous vascularization was found. In all species investigated, well-developed transfer cells are present in the primary xylem and the primary phloem of the shoot. They were frequently found in nodes, but also in internodes (Lörcher and Hildenbrand 1987). The derivatives of the procambium and the first cambial derivatives are able to form wall protuberances, persisting especially in the region of the pit membranes (vestured pits). The vessels of the metaxylem and secondary xylem show a continuous transition in their characters (length, pitting, perforation, vestures) and often have scalariform perforation plates. In the secondary xylem of all species investigated except *Patrinia*, tracheids are missing. Fibres and/or fibre tracheids occur. The vessels even of the secondary xylem are mostly short and extremely small (mean tangential diameter <25 μm). They are arranged in long radial multiples, with simple oblique perforations and moderately large alternating intervascular pits. The pitting of a vessel often shows a transition from elongated pits in scalariform arrangement to alternating shorter circular pits. Exclusively alternate pitting in all vessels of the secondary xylem was only observed in a few species of *Valeriana*. Rays usually are 4–6 cells wide and consist almost entirely of square upright cells. In herbaceous species xylem rays usually are absent. The axial xylem parenchyma usually is scanty and paratracheal, in some species vasicentric or confluent. Phloem fibres were found in some woody species. In high Andean species of *Valeriana* s.l. (incl. *Stangea*, *Belonanthus*, *Phyllactis* and *Aretiastrum*), the xylem is interrupted by broad parenchymatic rays. As a consequence, the cross section of vascular bundles of older stems and rhizomes has an almost star-like or deeply lobed shape. Lörcher (1990) interpreted the stem anatomy of these species as showing anomalous secondary growth. However, transversal sections in the branching zone of cushion-like plants or the basal parts of (semi) rosulate plants revealed that the structures described as anomalous secondary growth by Lörcher (1990) represent lateral branches embedded in a common cortex (T. Stützel, pers. comm.). In some species of *Patrinia* and *Valeriana* tannins were found in the parenchyma cells of the cortex. In some high-elevation Andean *Valeriana* species, oil cells are frequently present in the whole shoot. In the above-ground shoot of *Valeriana officinalis* and some other species, numerous lipid droplets occur in the transfer cells.

In allorhizous species of *Valeriana*, especially alpine species with taproots, secondary growth has been observed in the primary root. At the onset of secondary growth, a periderm arises from the outer layers of the cortex. The cortex can persist for a long time. However, in *Centranthus*, *Valerianella*, *Patrinia*, a.o., in which the roots show strong secondary growth, the primary cortex is lost and a periderm develops from the pericycle. Somewhat elongated oil cells with suberized walls occur in the outer part of the cortex and cork of *Centranthus*, *Patrinia*, *Valeriana* and *Valerianella*. The stem-borne roots of *Valeriana officinalis* only have a primary structure, and the exodermis persists after degeneration of the rhizodermis.

The structure of the foliage leaves normally is dorsiventral; in leaves of somewhat xerophytic structure—e.g. the ericoid leaves of *Valeriana* (*Aretiastrum*) *aschersoniana* and the small succulent leaves of *Valeriana* (*Aretiastrum*) *magellanicum*—the lamina can be aequifacial, the stomata being sunken. Stomata are of the ranunculaceous type, sometimes paired (*Valerianella*). In some species they occur on both sides of the leaves, otherwise the leaves are hypostomatic. Hydathodes have been reported for the leaf teeth of *Valeriana sambucifolia*. No crystals have been recorded in leaves except in *Patrinia*. In *Valerianella* (incl. *Fedia*) crystals of calcium oxalate were found in certain layers of the pericarp, called “Cristarque” by Vidal (1903, with reference to Van Tieghem; for further literature, see Ernet 1978).

Inflorescences. Detailed studies were undertaken by Weberling (1961, 1966). Usually the inflorescences are terminal and the mode of ramification is thyrsic. Generally the cymose partial inflorescences of the thyrses are arranged in opposite pairs (Fig. 75B). Exceptions are found in some species of *Valeriana* with alternate leaves. The thyrsic mode of ramification can be repeated by branches preceding the thyrsic region of the main stem, leading to di- or pleiothyrsic ramification. Comparative studies revealed that, despite the lack of a terminal flower, the inflorescences are principally monotelic and can be considered

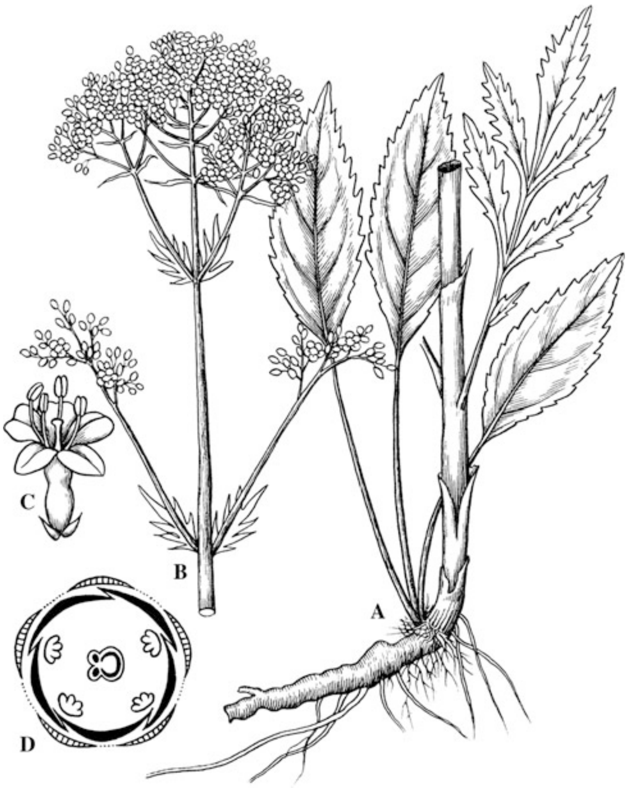

Fig. 75. Valerianaceae. *Patrinia scabiosifolia*. **A** Basal part of plant. **B** Inflorescence. **C** Flower. **D** Floral diagram. (after Steward 1958, courtesy Missouri Bot. Garden)

truncate monotelic synflorescences (Weberling 1961), which can be designated as truncate thyrsoids or pleiothyrsoids. This can be explained by the fact that the uppermost paracladia "arise so early and involve so much of the apical meristem that no residuum of the apex remains between them to continue the main axis" (Philipson 1947). In the extremely acrotonic inflorescences of *Valerianella* (incl. *Fedia*) this happens during the initiation of the only, but strongly developed pair of cymose paracladia. These continue this mode of ramification, and the suppression of the terminal flower continues during their cymose branching until, in the last ramifications, a terminal flower is formed and branching ends in the formation of one or two cincinni. The same acrotonic development occurs in the cymose paracladia of some *Valeriana* species (*V. alliariaefolia*, a.o.). The dichasial ramification in the cymose partial paracladia can continue over a long period, producing extended dichasial flowering systems, which show the regular formation of prophylls. Beyond this, in most species of *Patrinia* and in some of *Valeriana* s.l. (*Stangea*) sterile supernumerary bracts occur above the branches arising from the prophyllar axils (Weberling 1961). In many species of *Patrinia* three supernumerary bracts are united to form a scarious three-lobed or cordate fruit wing (Weberling 1961, 1966; see also Hofmann and Göttmann 1990). Differences in the shape of inflorescences often result from 1) the different number of cymose and thyrsoidal paracladia and the intensity of their ramification, 2) the different growth of the internodes, either intensive elongation of all internodes leading to loosely branched systems (*Valeriana effusa*), or contraction of the entire inflorescence or parts of it (*Valeriana capitata*, *V. nivalis*) or, when restricted to the cymose paracladia, to spike-like forms (*Valeriana celtica*, *V. dinorrhiza*), 3) the mesotonic or acrotonic support of the development of the paracladia, in the latter case often leading to an extremely vigorous development of the only pair of cymose paracladia and dichotomous-like branching being characteristic for *Valerianella* and some species of *Valeriana*.

In some species of *Valeriana* (e.g. *V. macrorhiza*, *V. carnosa*, *V. clarioniaefolia*), the apex of the strong and extremely short primary shoot remains permanently indeterminate and forms foliage leaves. After giving rise to a series of 'sterile' leaves, it produces 'fertile' leaves which have thyrsoidal paracladia in their axils. Then the shoot again returns to vegetative growth. This alternation even takes place in the dense cushions of rosettes by rhythmic production of new, at first vegetative branches which arise from the lower, lignified parts of the rosulate branches (*Valeriana* s.l.: *Phyllactis pulvinata*). In some rosette-forming species of *Valeriana* (e.g. *V. henrici*, cf. Eriksen 1989b, fig. 5), the terminal inflorescence forms a broad head by intensive primary growth of the pith of the short inflorescence axis.

FLOWER MORPHOLOGY. The calyx is variously developed, accrescent or not, rarely absent. Following other authors, Eichler (1875) confirmed that the feathery pappus present in the majority of Valerianaceae is equivalent to a pentamerous calyx. It develops from 5–30 sections inrolled in flower. The gamopetalous, mostly five-lobed, in some species of *Valeriana* s.l. (*Phyllactis*, *Belonanthus*, *Aretiastrum*) three-lobed corolla is subactinomorphic to more or less zygomorphic and often bulged, saccate or spurred at the base (Fig. 75C). Inside the corolla tube, it contains a nectary formed by a cushion of one-celled epidermal hairs. This is situated at the base of the tube or somewhat higher or in the gibba or spur which then serves both as nectary and nectar container (*Patrinia*, *Valeriana*, *Centranthus*). In the upper part of the petal tube, strong, usually single lateral veins occur between adjacent petals ("transpetal veins"), typical also for Dipsacaceae (Gustafsson 1995). In *Valeriana* the nectary is separated from the corolla tube by a septum, in *Centranthus* the septum is separating the nectary-bearing spur (see Weberling 1970). The zygomorphic form of the 5- or rarely 3-lobed corolla and the position of its lobes, the position of the 1–5 stamens, the three-carpellate structure of the gynoecium in combination with the position of the bulge or spur and the separating septum result in an asymmetric structure of the flower. Form and size of the corolla, and the length of the corolla tube can be very different; in some species of *Valeriana* or *Valerianella* (sect. *Siphonella*), a long tube can be formed, whereas in others, especially many species of *Valerianella*, the tube remains very short. The size of the corolla can even vary within a species.

In the Eurasian, African and North and Central American taxa the anthers are tetrasporangiate, whereas all South American taxa of *Valeriana*, except *Valeriana chaerophylloides* and *Valeriana* sect. *Porteria*, have bisporangiate anthers (Eriksen 1989a), possible related to the development of smaller, selfing flowers (Moore and Donoghue 2007). The ovules are anatropous, solitary, unitegmic and tenuinucellate. As reported by Eichler (1875), only the carpel facing the β-prophyll of the inferior three-carpellate ovary is fertile, the other two carpels are sterile and pressed to the side of the α-prophyll. Mostly the sterile locules are more or less degenerated; however, in *Nardostachys*, *Patrinia*, some species of *Valeriana* (e.g. *V. saliunca*, *V. hyalinorhiza*, *V. chaerophylloides*) and *Valerianella*, the empty locules are inflated, appearing externally as bulges. Asplund (1920) found that the sterile locules of *Patrinia*, *Valerianella* and *Valeriana* can contain one or two more or less reduced ovules (see also Wichura 1846; Buchenau 1854/55; Payer 1857; Eckardt 1937).

Embryology. The tapetum of the Valerianaceae is periplasmodial, and its nuclei can be highly polyploid (*Valeriana officinalis*, Skalinska 1958). The pollen grains are 3-nucleate. The raphe of the anatropous pendulous ovules is lateral. The ovules are unitegmic and tenuinucellate. There is a tendency to the formation of several (2–5) archesporial cells, appearing before the initiation of the integument. As in most sympetalous families, the megaspore mother cell develops without separation of parietal cells. The tetrad of megaspores resulting from the meiotic division of the megaspore mother cell is often irregularly T-shaped, the lowest of the cells giving rise to the embryo sac. Megasporogenesis follows the monosporic type (Polygonum type). After its completion the antipodial cells undergo mitotic divisions of their nuclei, thus becoming bi- to polynucleate, and persist during early fertilization stages. The embryo sac is enclosed by an endothelium developing from the inner epidermis of the integument. With the possible exception of species of *Patrinia*, the endosperm, which develops according to the nuclear type, is almost completely used up by the developing embryo (Asplund 1920; Peng et al. 1995). Thus, an endosperm is lacking in the mature fruit.

Pollen Morphology. The family is relatively stenopalynous (Patel and Skvarla 1979). The pollen grains are 3-zonocolpate to 3-colpo-roidate, more or less spheroidal (suboblate to subprolate), the longest axis up to 34–67 μm long, their size often depending on the degree of polyploidy. According to the literature, there is no endexine in Valerianaceae. However, during the development of the pollen wall, lamellated structures can be seen by SEM on the inner side of the exine before the formation of the intine. The "white lines" occurring at this stage were interpreted as an indication for the existence of an endexine (Rowley 1981; Guédès 1982). The colpi are bounded by a margin encircled by a band which appears bright in the light microscope (halo) and is formed by a columella-free area of sexine and a thin discontinuous nexine. While the margin is nearly exclusively formed by the tectum, this is absent on the surface of the colpus, the bacula on the surface of the aperture being homologous to columellae (as assumed already by Wagenitz 1956). Only few differences are found in supratectate structures. The exine surface is usually echinate, in *Stangea* and *Valeriana pygmaea* baculate (*Stangea* type, Blankenhorn 1978), in *Centranthus* spinulose (*Centranthus* type). *Valerianella*, *Plectritis* (*Valerianella* type), *Aretiastrum*, *Belonanthus* and some species of *Centranthus* are exclusively micro-echinate or granulate. In *Patrinia* and *Nardostachys* the individual spines are supported by dome-shaped portions of the exine (*Patrinia* type), "very large verrucae" in the sense of Clarke (1978). All these types are found in *Valeriana*. According to the results of Blankenhorn (1978) and Clarke (1978), pollen morphology suggests the subdivision of the family into the basal Patrinieae (*Nardostachys* and *Patrinia*, a group now known to be paraphyletic) and the other genera. *Nardostachys* and *Patrinia* are characterized by the dome-shaped soccles of the exine bearing the individual spines (*Patrinia* type of Blankenhorn 1978), or by "thick walled grains with verrucae on the sexine and in which the columellae are not differentiated at the poles" (Clarke 1978). Within the rest of the family there "is a tendency for these characters to become progressively reduced". In *Valeriana* s. l., Blankenhorn (1978) found a wide range of forms. *Valerianella* (incl. *Fedia*), *Valeriana* spp. (*Plectritis*) and *Centranthus* have similar pollen with very reduced supratectate structures (*Valerianella* type) and are "characterized by the differentiation of the columellae at the poles, showing an increase of length and being fused in their lower parts and branched above" (Clarke 1978). In a comparative study of pollen wall structure by means of light microscopy, SEM and TEM of longitudinal and cross sections, Reese-Krug et al. (2001) could distinguish four different pollen "types": 1. *Patrinia* type, with a transitional *Valeriana coarctata* subtype, somewhat corresponding to the *Patrinia* type of Blankenhorn (1978), 2. *Valeriana palmeri* type, with a waved or folded and partially extremely thickened tectum forming arched sculptures, 3. *Valerianella* type, corresponding to the *Valerianella* type distinguished by Blankenhorn (1978), and 4. *Stangea* type, characterizing the genus *Stangea* (= *Valeriana* s.l.), from which Blankenhorn (1978) derived the name, but also including the pollen grains of some high Andean species of *Valeriana*. These "types", however, represent slightly distinct reference points within a more or less continuous spectrum of forms. In contrast to the data in the literature, the occurrence of an endexine in pollen of Valerianaceae could be ascertained.

KARYOLOGY. The chromosome numbers often form polyploid series based on $x = 7, 8, 9, 12$, unusual numbers being $x = 11, 2n = 22$ in *Patrinia* (up to $2n = 88$) and $x = 13, 2n = 26$ in *Nardostachys*. In *Valerianella* (incl. *Fedia*), the predominant chromosome numbers are $n = 8$, $2n = 16, 32$ (Xena de Enrech et al. 1991), but also $n = 7, 2n = 14$ or $n = 15, 44, 45$ have been reported (Ernet in Weberling 1970). In *Valeriana* the basic numbers reported are $x = 7, 8, 11, 12$. Besides diploids, there are many tetraploid and octoploid taxa, sometimes as infraspecific polyploid races. In the Eurasian taxa (*Valeriana officinalis* group, a.o.) the series are based on $x = 7$. This also applies to the South African *Valeriana capensis* ($2n = 14$) and to the tropical American *V. scandens* ($2n = 28, 56$). In the Eurasian mountain species as well as all the high-elevation Andean species (incl. the segregate genera *Astrephia*, *Stangea*, *Aretiastrum*, *Phyllactis* and *Belonanthus*) investigated, the chromosome number is $2n = 32$. The same applies to *Centranthus*. For further literature, see Engel (1976). Hidalgo et al. (2010) optimized chromosome numbers on a Valerianaceae phylogeny. According to their results, a clade of *Valerianella* (incl. *Fedia*), *Centranthus* and most *Valeriana* spp. has $x = 8$ with further reduction to $x = 7$ in a subclade of *Valeriana* p.p. The three basal clades of the family have higher base numbers: *Patrinia* $x = 11$, *Nardostachys* $x = 13$, and a small clade of *Valeriana* p.p. (see below under "Subdivision of and relationship within the family") has $x = 11$. The counts (IPCN reports online 2012) for the 3 species in this clade, however, are somewhat ambiguous: *V. celtica* (3 different subspecies) $2n = 24, 48, 96$, *V. hardwickii* $n = 8, 2n = 16, 28$, and *V. saxatilis* $2n = 22, 24$.

FRUIT AND SEEDS. The fruit is an achene, i.e. a dry indehiscent monospermous fruit derived from an inferior ovary (Wagenitz 1976). The evolution of fruit and seed characters based on a phylogeny of the family was recently investigated by Jacobs et al. (2010). The achenes of *Nardostachys* and *Patrinia* have a persistent and regularly five-lobed calyx. In most species of *Valeriana*, all species of *Centranthus* and one species of *Valerianella* (*V. hirsutissimia*; Richardson 1975), a pappus consisting of 5 or up to 30 plumose rays is formed during maturation of the fruit. Achenes with pappus appear in the Valerianaceae in the distal clade of *Valeriana* + *Centranthus* (Jacobs et al. 2010) but also in the more basal clade composed of few *Valeriana* species (see Hidalgo et al. 2010). Thus, either the pappus evolved once at the base of Dipsacaceae and Valerianaceae and was reduced again in *Patrinia*, *Nardostachys* and *Valerianella*, or the pappus evolved independently in Dipsacaceae and once or twice in the Valerianaceae. In several species of *Valeriana* s.l. (incl. *Phyllactis*, *Belonanthus*, *Aretiastrum*, *Plectritis*, *Stangea*), a solid ring-shaped rim is formed instead of a pappus. In some taxa (*Nardostachys*, *Patrinia*, several species of *Valeriana*, e.g. *V. saliunca*, *V. hyalinorrhiza* and *Valerianella* spp.), the two sterile locules are persistent and even inflated. Jacobs et al. (2010), on the other hand, found the sterile locules to be absent in the mature fruits of *Centranthus* and the *Valeriana* (incl. *Plectritis*) species studied by them. In several species of *Valerianella* (*V. patellaria*, *V. amblyotis*, a.o.), the sterile locules form wing-like projections which, however, are not homologous with the wings found in some species of *Valeriana* s.l. (*Plectritis*; Morey 1962). *Plectritis* (*Valeriana* s.l.) has dimorphic fruits, individuals of the same population may have wings as outgrowths of the fruit wall of the fertile locule or not (Dempster 1958). For *P. brachystemon*, Ganders et al. (1977) reported that "the polymorphism is controlled by a single locus with the allele for winged fruits exhibiting complete dominance". Heterocarpy as well as achene polymorphism are found in some species of *Valerianella* (Ernet 1978; Mathez and Xena de Enrech 1985a, 1985b). The different development of fruits in the same individual depends on the position in the inflorescence: in the proximal parts of the inflorescence, the sterile locules of the achenes are poorly developed but they are well developed in the distal parts; intermediate types occur as well. The achenes of the distal parts of the inflorescences are deciduous and can be dimorphic or more rarely trimorphic within the same population regarding development of the calyx and the sterile locules. Genetic models for the observed fruit polymorphism were developed by Eggers Ware (1983) and Xena de Enrech and Mathez (1998). *Valeriana ozarkana* (incl. *V. bushii*) shows simple Mendelian inheritance, with the *ozarkana* (winged) fruit-type allele dominant over the *bushii* (fusiform) allele (Eggers Ware 1983). Fruit polymorphism in *Valeriana* (species of the former genus *Plectritis*) and in *Valerianella* evolved independently according to their morphology and the family phylogeny (Jacobs et al. 2010). See following section for elaiosomes.

The seed is enclosed in the indehiscent fruit. It basically lacks endosperm in the core valerians (probably a synapomorphy for this clade), but the seeds of *Patrinia* (basal branch in the family phylogeny) have copious endosperm and also a smaller embryo than in the other genera. No data about the endosperm are available for *Nardostachys*. In the chalazal region of *Centranthus* an unlignified "hypostasis" occurs, apparently missing in *Valeriana*; the embryo is sometimes green, and contains oil but no starch (Netolitzky 1926).

Pollination and Dispersal. Reproductive biology of *Nardostachys jatamansi* was studied by Chauhan et al. (2008), who observed bees, flies and butterflies as flower visitors. The flowers are protogynous and autogamous, although fruit set is higher under open-pollination conditions. The fragrant and nectariferous flowers of some *Valerianella* species, especially those with large funnel- or salverform corollas, are pollinated by insects. Flies, beetles, Hymenoptera and even Lepidoptera are known as flower visitors. Predominant autogamy is found in numerous other *Valerianella* species with small funnel-shaped flowers (Ernet 1977). The flowers of *Valeriana*, although highly derived in their morphology by being asymmetric, gibbous or even spurred, are regarded to be only slightly specialized. Since the corolla tubes of most flowers are short, the nectar is accessible even for insects with a short proboscis. The scent of the flowers is characterized as paraffinoid. Predominantly Diptera, but also Coleoptera, Hymenoptera (bees), Lepidoptera (in *Valeriana dioica*) and Nematocera (*V. montana*, *V. tripteris*) have been observed as visitors. *Valeriana officinalis* is reported to be strictly allogamous (Skalinska

1947). The long-spurred flowers of most *Centranthus* species are accessible only to insects with a long proboscis (Lepidoptera, mainly Papilionoidea, Hymenoptera with long proboscis). The flowers of all species investigated are distinctly protandrous.

Achenes with a pappus are adapted to wind dispersal, but also can attach to the fur or feathers of passing animals. Many species of *Valerianella* have fruits with clinging devices (uncinate aristae, horns on calyx teeth, uncinate hairs). Furthermore, in this genus larger calyx lobes or wings may serve for anemochory, and inflated sterile locules or calyces (*Valerianella*) and air-filled tissues as floating organs. The supernumerary bracts of many species of *Patrinia* become wing-like in fruit, and the wings of the fruits of some *Valeriana* spp. probably enhance wind dispersal. Tumble weeds are found in some *Valerianella* species. In some species of *Valeriana* (species formerly included in *Astrephia*) and *Valerianella* (species formerly included in *Fedia*), the inflorescence axis and nodes begin to swell after anthesis. When the resulting tension is released by, for example, touch, the fruits are expelled (Eriksen 1989a). Sernander (1906) and Bresinsky (1963) found pericarp swellings below the exocarp between the walls of the sterile locules of *Valerianella* (*Fedia*), consisting of a small-celled tissue containing lipids. Both authors interpreted them as elaiosomes. Sernander (1906) already observed that the lipid containing tissue in the ventral pericarp of the "elaiosomic" fruits (Bresinsky 1963) is macroscopically visible as a white basal swelling, and only this form of fruit is myrmecochorous. Around the zone of abscission of the fruits of several species of *Valerianella*, Ernet (1978) also found swellings of the pericarp formed of cells with an oily liquid, and identified them as elaiosomes. Sernander (1906) observed myrmecochory in the field. In many species the viability of the seed extends over several years. Germination, especially of mountain species, is often somewhat delayed and was found to take place in light and to be enhanced by frost.

PHYTOCHEMISTRY. The principal compounds responsible for the long-known healing properties of Valerianaceae, especially the sedative effects, have been revealed as a specific and otherwise unknown group of iridoid substances named valeriana-epoxy-triesters, for convenience abbreviated valepotriates (Thies 1966, 1968; Thies and Funke 1966). Meanwhile, a large series of valepotriates has been detected which differ by the presence of one or two double bonds in the ring structures of the cyclopenta-[c]-pyran skeleton and diverse residues at five different positions (for further information incl. biosynthesis, methods of extraction and analysis, literature, see Backlund and Moritz 1998). Variation in distribution and concentration of different valepotriates often are characteristic for taxa. In general they indicate a "chemosystematic difference" between South American and Eurasian taxa (Schild and Seitz 1971). In contradiction to older investigations, valepotriates have also been found in *Patrinia* and *Nardostachys* (see Backlund and Moritz 1998). Until now, no traces of valepotriates could be detected in taxa outside the Valerianaceae, suggesting the uniqueness of valepotriates for this family. However, since *Triplostegia* is now considered a basal branch in the Dipsacaceae, it cannot be excluded that in the Dipsacaceae the valepotriates might have been reduced secondarily. The characteristic smell of most plants of the family is due to the degradation product isovaleric acid. For further information and literature, see Backlund and Moritz (1998). During the search for the principal compounds responsible for the pharmacological effects, several iridoid-like alkaloids as well as a number of sesquiterpenes and monoterpenes and derivatives have been identified. In the roots of *Patrinia* glycosidically bound saponines have been found—e.g. patrinin being separated from patrigenin (Matveeva and Abubakirov 1964).

Useful taxonomic data were provided by comparative analyses of flavonoids in foliage leaves, which revealed their distinctive chemistry for *Nardostachys* and *Patrinia* (occurrence of isorhamnetin, luteolin and acacetin), and yielded new perspectives for the classification of *Valerianella* (Greger and Ernet 1971, 1973). The essential oils of the roots and rhizomes of various *Valeriana* species used for the preparation of perfumes were studied in detail. The oil of *V. hardwickii* contains α-patchoulene, patchoulol, viridiflorol and α-cadinol, besides various unknown compounds (Novak et al. 2000), that of *V. hardwickii* var. *arnottiana* had as major compounds valeracetate, bornyl acetate, methyl linoleate, cuparene and α-cedrene (Sati and Mathela 2004); in *V. wallichii* Bos et al. (1997) found an unidentified sesquiterpene hydrocarbon, α-santalene, *ar*-curcumene and xanthorrhizol in European material, while in the material from Nepal patchoulol was the major compound. Similarly, Tanaka and Komatsu (2008) studied the volatile components of rhizomes of *Nardostachys jatamansi* and identified β-maaliene, 9-aristolene, calarene and patchoulol, aromadendrene, cube-11-ene, epi-α-selinene, spirojatamol and valeranone.

Subdivision of and Relationship Within the Family. The Patrinieae, with *Patrinia* and *Nardostachys*, were usually regarded as a natural group because of their regularly 5-lobed calyx, usually 4 stamens and well-developed sterile locules in the gynoecium. However, these characters are probably plesiomorphic. Evidence obtained from the analyses of DNA sequence data appears somewhat contradictory. From combined *rcb*L and *ndh*F sequences, Pyck et al. (2002) concluded "that the traditionally circumscribed Patrinieae can no longer be recognized", whereas "parsimony analysis based on a morphological data set supported a monophyletic Patrinieae". Hidalgo et al. (2004) deduced from a cladistic analysis of DNA sequence data (*mat*K) that tribe Patriniae is monophyletic (with 94 % bootstrap support) and that tribe Valerianeae also forms a clade. Bell and Donoghue (2005), on the other hand, concluded that Patrinieae are paraphyletic, with *Patrinia* being sister to the rest of the family and *Nardostachys* the next basal branch (100 % bootstrap support; see also Jacobs et al. 2011). In consequence, a formal infrafamilial classification was abandoned in this treatment.

Although diverging from earlier results of Backlund and Donoghue (in Backlund 1996), recent data (Hidalgo et al. 2004; Bell and Donoghue 2005; Jacobs et al. 2011) suggest that *Triplostegia* needs to be removed from Valerianaceae as the genus is more closely related to the Dipsacaceae. In this volume it is thus included in a monogeneric subfamily Triplostegioideae of Dipsacaceae. Hofmann and Göttmann (1990) already suggested that, after the exclusion of *Triplostegia* from the Valerianaceae, this family is very homogeneous. Differing from a prior statement (Bell et al. 2001), Bell and Donoghue (2005), based on a much improved data set, stated that their new data clearly indicate that *Plectritis* is nested within South American *Valeriana*. Hidalgo et al.'s (2004) data also support this view, and this genus is therefore merged with *Valeriana*. It has long been discussed whether *Aretiastrum*, *Astrephia*, *Belonanthus*, *Phuodendron*, *Phyllactis* and *Stangea* should also be included into *Valeriana* (Borsini 1944; Eriksen 1989a). Eriksen (1989a) regarded the reduction of the number of anther locules in most South American *Valeriana* species as a strong argument supporting a wider circumscription of the genus. Whereas all Asian, European, African and North American species of the genus *Valeriana* have tetrasporangiate anthers, those of nearly all South American species, except *Astrephia* and the Venezuelan sect. *Porteria* of *Valeriana*, are bisporangiate (cf. Eriksen 1989a). Moreover, in Central America and the West Indies both southern species with bisporangiate and northern species with tetrasporangiate anthers occur. Eriksen (1989a) suggested that the South American species with bisporangiate anthers represent "an independent evolutionary line" derived from North American *Valeriana*. She therefore regarded the South American species group, including the former genera *Phyllactis*, *Aretiastrum*, *Belonanthus*, and *Stangea* with bisporangiate anthers, as a subgenus of *Valeriana* (subgen. *Phyllactis* (Pers.) Borsini emend. Eriksen). Indeed, bisporangiate anthers seem to be a synapomorphy of a large clade of mainly Central and South American species (cf. cladogram in Bell and Donoghue 2005). This clade also includes species with tetrasporangiate anthers, however, and the data suggest three independent reversals to the tetrasporangiate condition (the former genera *Astrephia* and *Plectritis* and the former sect. *Porteria* of *Valeriana*). This clade is deeply nested within *Valeriana* (Bell and Donoghue 2005), and its formal recognition would necessitate a formal subdivision of the remainder of the genus into at least three monophyletic taxa. Furthermore, in the most recent phylogenetic analyses (Hidalgo et al. 2004, 2010; Bell and Donoghue 2005), three Eurasian species of *Valeriana* surprisingly appeared in positions clearly outside of *Valeriana* even in the wider circumscription proposed by Eriksen (1989a, 1989b) and also adopted in the present treatment. Thus, *V. celtica*, *V. hardwickii* and *V.*

saxatilis appeared as basal branches in the Valerianeae clade and *V. longiflora* as sister to *Centranthus*. This would suggest an even wider circumscription of a monophyletic *Valeriana* with the inclusion of *Centranthus* and *Valerianella* (incl. *Fedia*). It seems that species like *V. celtica*, etc. should be included in a new genus (these species also show a different chromosome base number than the Valerianeae clade, Hidalgo et al. 2010). *Valeriana longiflora* could be included in *Centranthus* (already Willkomm 1851, when describing *V. longiflora* as new, mentioned similarities in the corolla morphology with *Centranthus*) but, according to the phylogeny of Hidalgo et al. (2010), *Valeriana* appears still paraphyletic with the exclusion of *Centranthus*. More data are needed, however, and we here abstain from the radical solution to include *Centranthus* and *Valerianella* in *Valeriana*. A new infrageneric classification of *Valeriana* at the current state of knowledge is certainly premature. The DNA sequence data also indicate an inclusion of *Fedia* into *Valerianella*. Already Höck (1882) concluded that morphological characters pointed to a derivation of *Fedia* from *Valerianella* series *Locustae*.

AFFINITIES. It is generally agreed that the family is to be placed in the Dipsacales together with Caprifoliaceae (incl. the now sometimes separated Diervillaceae and Linnaeaceae), Morinaceae and Dipsacaceae. This is based on morphological and anatomical studies (see Weberling 1966) as well as on molecular data (e.g. Backlund 1996; Bell et al. 2001; Winkworth et al. 2008; Jacobs et al. 2011). Molecular data supported the idea that Adoxaceae s.l. also belong into the order as a basal branch. Besides vegetative characters (predominantly decussate and often pinnate leaves with often amplexicaulous bases), the deep-seated cork cambium, perulate buds, a ± inferior ovary, a calyx persistent in fruit, and a vascularized testa might be synapomorphic for the order (e.g. version 2008 of Stevens 2001 onwards). A close relationship of Valerianaceae to Diervillaceae, Caprifoliaceae, Linnaeaceae, Morinaceae and Dipsacaceae is also shown by general trends in flower and inflorescence morphology—e.g. the shift in several lineages from monotelic over truncated monotelic to polytelic inflorescences (Weberling 1961); the supernumerary sterile bracts found in many Caprifoliaceae and some Valerianaceae may be seen as a tendency which has led to the formation of an epicalyx as a constant feature in Dipsacaceae. The reduction of flower parts also is a prominent feature, which is also expressed by a decrease of carpel number, carpel fertility and the number of ovules to finally one fertile carpel with a single pendulous ovule. The nectaries described are a common character of Caprifoliaceae, Diervillaceae, Valerianaceae, Morinaceae and Dipsacaceae (Wagenitz and Laing 1984), as are monosymmetric flowers, larger calyx lobes, tubular corollas, elongate styles and capitate stigmas (e.g. Howarth and Donoghue 2005). A strong similarity between Valerianaceae and Dipsacaceae is reported especially in shoot (Metcalfe and Chalk 1983, II, 197f.) and trichome anatomy (Weberling 1977), and the strong and mostly single transpetal veins (Gustafsson 1995). Recent studies using DNA sequence data also confirm a sister-group relationship of Dipsacaceae (incl. *Triplostegia*) and Valerianaceae (e.g. Hidalgo et al. 2004; Winkworth et al. 2008). APG III (2009) unites Caprifoliaceae s.s., Morinaceae, Dipsacaceae and Valerinaceae into Caprifoliaceae s.l., which is sister to Adoxaceae s.l.

DISTRIBUTION AND HABITATS. The family comprises five genera and about 400 species distributed mainly in the northern hemisphere and the mountainous regions of western South America, but absent from Australia and Polynesia. Important data about the historical biogeography have been contributed by Bell and Donoghue (2005) and Bell et al. (2012), based on phylogenetic studies using sequences of several cpDNA markers and the nuclear ribosomal ITS. The crown Valerianaceae may be about 50–60 million years old. It is now well supported that the family probably originated in the eastern Himalaya and the mountainous regions of SW China, corresponding to the present range of *Nardostachys* and many species of *Patrinia*. Both genera form the first subsequent splits in the family phylogeny (Pyck et al. 2002; Bell and Donoghue 2005; Hidalgo et al. 2010). *Patrinia* is distributed eastwards towards Taiwan and Japan. From the Himalaya region, dispersal to Europe and the New World took place. *Valeriana* in South America is not monophyletic, and probably four colonization events occurred from the north (Bell et al. 2012). Eriksen (1989a) hypothesized that the first colonization event occurred only after the closure of the Isthmus of Panama, but the data of Bell and Donoghue (2005) and Bell et al. (2012) rather support that independent colonization events occurred earlier (about 12–20 Ma) via long-distance dispersal. For some widespread species such as *Valeriana scandens*, however, colonization via the Isthmus of Panamá seems also possible. Within New World *Valeriana* s.l., a monophyletic group of mainly high Andean species is supported by the data, although weakly. This clade contains several small segregate genera such as *Phyllactis* and *Stangea*. For one group of *Valeriana*, including *Plectritis*, dispersal from western South America to western North America may have occurred. It seems that the newly formed habitats in the Andes with many unoccupied niches allowed a very rapid diversification with the formation of an estimated 0.8–1.34 species/million years (Weberling 1968; Bell and Donoghue 2005; Moore and Donoghue 2007). Diversification seems to be more due to the colonization of new habitats, especially in mountainous regions, than to morphological innovations like pappose fruits (Moore and Donoghue 2007; Bell et al. 2012).

Many of the Eurasian *Valeriana* species, which all are perennials and often have vigorous cryptocorms (*V. tuberosa* with bulbs), occur in mountainous regions, often in alpine meadows and rocky heaths, in crevices (*V. saxatilis*, *V. tripteris*) or more or less creeping on gravelly soil (*V. supina*, *V. montana*, *V. montana*); others persist in half-shade in deciduous or coniferous forests. Most occur in moist habitats. In the winter rain zones around the Mediterranean Sea, *Valerianella* and *Centranthus* have many species well adapted to these climatic conditions in life cycle and dispersal strategies. *Valerianella* is distributed around the Mediterranean Sea, but extends into SW Asia towards Afghanistan. In North America *Valerianella* is represented with about ten or more species, a few of them (*V. locusta*, *V. carinata*) naturalized from Europe. Two species (*V. longiflora*, *V. nuttallii*) are endemic to Arkansas. In North America *Valeriana* comprises about 11 species and the tropical American *V. scandens* (sect. *Sorbifoliae*), which is also found in the southern, tropical part of Florida. In Mexico, Central America and the West Indies the genus is represented by 20 more species, most of them perennials, but also several annuals (e.g. *V. apiifolia*, *V. sorbifolia*) with fusiform or subnapiform taproots, which still enable the plants to ripen their fruits at the beginning of a dry period when these plants die. There are also some lianas like *V. clematitis*, while *V. scandens* f. *scandens* and f. *candolleana* are completely herbaceous. Many of the high Andean species of *Valeriana* are growing as semirosulate or pulvinate plants in the Puna at altitudes of up to nearly 5000 m. Here, they have to survive recurrent night frosts of sometimes −1 to −4.5 °C, with the risk of frost drought because the upper layers of soil often remain frozen for many hours. In the páramos of Colombia, Ecuador and northern Peru, associations of ligneous, shrubby or even more or less arborescent species occur. On the other hand, especially in Chile, a considerable number of annual species is found. Some species, e.g. *V. polystachya* and *V. salicifolia*, grow in swampy areas.

PARASITES. Virus diseases (e.g. cucumber mosaic virus) have been reported for diverse species of *Valerianella* (especially *V. locusta*) used as “corn salad”. Parasitic fungi such as downy mildew (*Peronospora valerianellae*) and powdery mildew (*Erysiphe polyphaga*) cause mycoses in *Valerianella*. In *Valerianella* aecidiospores of *Puccinia* species have also been found. *Erysiphe valerianae* often causes considerable damage in cultures of *Valeriana officinalis* and also attacks other species of this genus. The roots of *Valeriana officinalis* are damaged by *Phoma*. Beyond these, many other fungi (Uromyces, *Puccinia valerianae*, *P. commutata*, *Colleotrichum valerianae*, *Ramularia valerianae*) are known as parasites of *Valeriana* species. Among the animal parasites, *Macrophaga albicincta*, the “valerian wasp”, can cause complete defoliation of *Valeriana* cultures. Damages are also caused by aphids, gall midges (*Dasyneura valerianae*) and gall mites (*Eriophyes macrotuberculatus*), and *Contarinia crispans* often causes deformations in leaves, inflorescences and flowers (virescence). Destruction by feeding is caused by caterpillars of several butterfly species, especially *Hepiolus humuli*, and a species of *Tephroclystia* has been named *T.*

valerianata because of its association with *Valeriana*. There are also miners among the Lepidoptera, Diptera and Coleoptera.

Economic Importance. Since ancient times rhizomes of *Valeriana*, especially *V. officinalis* and *V. phu*, have been widely used in Europe for sedative purposes. The same applies to *V. wallichii*, *V. hardwickii*, *V. jatamansi* in southern Asia, and to *V. edulis* and other species as well as *Stangea henrici* in Central and Andean America. Rhizomes of *Nardostachys jatamansi*, the "Spike Nard" or spikenard, have been used as a perfume drug since the time of Hammurabi (1792–1750 B.C.), and were transported as precious ointment from the high Himalaya to Mesopotamia. This is mentioned in the bible (Song of Solomon *1*, 12, *4*, 13–14, in Mark *14*, 3 and John *12*, 3 in the report of the anointment of Christ in Bethania). From India to China the drug still serves as a stimulant in the ayurvedic medicine. It is now included in CITES Appendix II. *Valeriana celtica* was used as a perfume drug under the name spica "nardi" or "nardus celtica" by the Romans and is still in use. In Europe and the Mediterranean, species of *Valerianella* (*V. locusta*, *V. cornucopiae*, a.o.) are widely consumed as "corn salad", "lamb's lettuce", "mâche", "Feldsalat", and the same applies to *Valeriana edulis* in Mexico and the S.E. United States. Some species of *Centranthus* (*C. ruber*, *C. macrosiphon*) and *Patrinia* as well as *Valerianella cornucopiae* serve as ornamental plants.

Key to the Genera of Valerianaceae

1. Stamen 1; achene pappose; corolla red, lilac or white, never yellow **4. *Centranthus***
– Stamens 2–5 (rarely one, then corolla yellow); achenes pappose or not 2
2. Calyx lobes 5, not developing into a pappus (Asia) 3
– Calyx inconspicuous in flower, developing into a pappus or forming 1 or several teeth of various shape at maturity, or forming a solid ring only (Asia, Europe, Africa, Americas) 4
3. Rosette plants, not terminating with an inflorescence, with spathulate-lanceolate leaves with axillary partial inflorescences; the 5 calyx lobes well developed in flower, accrescent in fruit; corolla white or pink, stamens 4 **2. *Nardostachys***
– Semirosulate plants with dentate, pinnatifid or pinnate leaves, terminating with an inflorescence; the 5 calyx lobes smaller than 1 mm, not accrescent in the fruit; corolla yellow (in *P. villosa* white to pink); stamens (1–) 3–4(5) **1. *Patrinia***
4. Annuals, appearing dichotomously branched; stamens 2–3; achenes very rarely with pappus (*V. hirsutissimia*) **3. *Valerianella***
– Annuals or perennials, not appearing dichotomously branched (except for a few species with extremely acrotonic inflorescences, mostly stunted forms), life form various (herbs, cushion and rosette plants, vines, shrubs, small trees); stamens 3; achenes pappose or epappose **5. *Valeriana***

Genera of Valerianaceae

Patrinia-Nardostachys grade

Calyx lobes 5, persistent, but not forming a pappus. Stamens mostly 4 (rarely 1–3 or 5), sterile locules of the fruit well developed. Perennial herbs.

1. ***Patrinia*** Juss. Fig. 75

Patrinia Juss., Ann. Mus. Natl. Hist. Nat. 10: 311 (1807), nom. cons.; Hong Deyuan et al., Flora of China 19 (2010).

Rhizomatous herbs with subentire to pinnatifid leaves and corymbiform pleiothyrsic inflorescences. Flowers in many species preceded by supernumerary bracts which are concrescent and form a scarious three-lobed or cordate fruit wing; calyx lobes small, ovate, not accrescent in fruit; corolla tube short, with subequal lobes, obscurely gibbous near the base, yellow or (*P. villosa* Juss.) white to pink; stamens (1–3)4(5); stigma capitate. Achene ovoid, obovoid or oblongoid, crowned by the persistent calyx. $2n = 22$, 44, 88.

About 25 species from Central Asia and the Himalaya to E Asia. Sect. *Centrotrinia* Maxim., ca. six species, sect. *Patrinia* ("*Palaeopatrinia*" Höck), about 17 species, sect. *Monandropatrinia* Höck, ca. two species.

2. ***Nardostachys*** DC.

Nardostachys DC., Prodr. 4: 624 (1830); Mém. Valér.: 4, t. 2 (1832); Weberling, Bot. Jahrb. Syst. 99: 188–221 (1978), monogr.; Hong Deyuan et al., Flora of China 19 (2010).

Rhizomatous herbs of very different size, subrosulate, with entire, elongate, spathulate-lanceolate leaves, first leaves distichous, later leaves decussate; rhizome covered with the reticulated remains of marcescent leaves. Inflorescences originating from the axils of living or dead basal leaves, pleiothyrsic, flowers condensed in a terminal and one or two pairs of lateral heads, the lateral heads originating in the axils of spathulate or ovate cauline leaves; bracts lanceolate to narrowly lanceolate. Calyx with 5 upright lobes, accrescent in fruit; corolla 3,5–13(−24) mm long, tubular-campanulate, lobes subequal, tube with a slight gibbous protrusion with nectary, white or pink; stamens 4, inserted at the base of the corolla, mostly somewhat exserted, long-haired in the lower half of the filaments; style exserted, stigma capitate; ovary hairy or glabrous. Achene somewhat compressed, elongate-ovate with two longitudinal swellings (the sterile locules), crowned by cartilaginous calyx, the 5 calyx lobes united at the bases by a low fringe. $2n = 26$.

One or two species, from the W Himalaya to SW China.

Valeriana clade

Perennial or annual herbs, subshrubs, shrubs, lianas. Calyx mostly not fully developed before fruit ripens, then regularly or irregularly lobed, inflated, forming 1 to 3 stout horns or several spines, a regularly 6-lobed crown, a spreading star, a cartilaginous cup or a solid rim only, or up to 30 segments often developing into a plumose or awned pappus.

3. ***Valerianella*** Mill.

Valerianella Mill., Gard. Dict. abr. ed. 4 (1754); Krok, Kgl. Svensk. Vet.-Akad. Handl., N.F. 5(1): 1–105 (1864), rev.; Ernet, Plant Syst. Evol. 127: 243–276 (1977a), 128: 1–22 (1977b), 130: 85–126 (1978), morph.; Xena de Enrech & Mathez, Naturalia monspeliensia, sér. Bot., Fasc. 54: 3–77 (1989), rev. of *Fedia*; Devesa & Martínez, Flora Ibérica 15: 233–258 (2007).
Fedia Gaertn. (1791), nom. cons., non Adanson (1763).
Pseudobetckea (Höck) Lincz. (1958).
Siphonella (Torrey & A. Gray) J.K. Small (1903).

Annuals, appearing dichotomously branched, due to the acrotonic development of the inflorescence. Flowers usually small, in dense cymosely branched partial inflorescences; in some species the prophylls within the monochasial (cincinnus-like) parts at maturity form rows of spreading sclerified horns. Calyx limb inconspicuous or not developed in flower; corolla funnelform or in some species salverform with a long tube, subactinomorphic or zygomorphic, bluish, white, red or pink; stamens 2–3, two sometimes united; stigma bifid or trifid. Achenes displaying a large variety of forms, sometimes heterocarpic, sterile locules inflated to inconspicuous, calyx transformed into regular or irregular lobes, sometimes 1–3 stout horns or a small or larger number of spines, a regularly 6-lobed crown, a spreading star, a cartilaginous cup, or a solid rim only, calyx and sterile locules can be inflated in fruit; in some species the distal deciduous achenes are dimorphic (rarely trimorphic) within the same population. $n = 8$, $2n = 16$, 32, but also $n = 7$, $2n = 14$, or $n = 15$, 44, 45.

60–70 species, mainly in SW Asia, the Mediterranean and Europe, but also in North America, rare in South America.

Phylogenetic studies (Hidalgo et al. 2004; Bell and Donoghue 2005) suggest paraphyly for *Valerianella* after exclusion of *Fedia*; thus, the latter genus is here included in *Valerianella* s.l.

4. ***Centranthus*** DC.

Centranthus DC. in Lam. & DC., Fl. franç. (ed. 3) 4: 238 (1805); Richardson, Bot. J. Linn. Soc. 71: 211–234 (1975), rev.; Martinez & Devesa, Flora Ibérica 15: 223–233 (2007).

Annuals or rhizomatous perennials, glabrous, usually glaucous, leaves simple or divided. Inflorescences pleiothyrsic, the thyrsic parts with numerous cymose partial inflorescences which end in many-flowered cincinni. Flowers perfect; calyx divided into up to 25 segments, inrolled in flower, forming a plumose pappus in fruit; corolla with 5 unequal lobes, infundibuliform or with a long cylindrical tube, gibbous near the middle of the tube or spurred near the base and with an internal longitudinal membrane reaching from the insertion of the spur to the mouth of the corolla tube, red, lilac or white; stamen 1; stigma subclavate to trifid. Sterile locules of the achene reduced. $2n = 32$.

Ten species and several subspecies. Southern Europe, Mediterranean and SW Asia. *Centranthus* *ruber* (L.) DC. is planted as an ornamental and today occurs as a garden escape outside the original distribution area.

5. ***Valeriana*** L. Fig. 74

Valeriana L., Sp. Pl. 31 (1753); Weberling, Bot. Jahrb. Syst. 79: 394–404 (1960), tax.; Borsini, Lilloa 32: 369–374 (1966), tax.; Hong Deyuan et al., Flora of China 19 (2010), reg. rev.; Borsini, Lilloa 8: 353–377 (1942), reg. rev.; Larsen, Nord. J. Bot. 6: 427–446 (1986), rev. *Phyllactis*; Lörcher, Flora 184: 231–254 (1990), morph. *Phyllactis*; Meyer, Ann. Miss. Bot. Gard. 38: 377–503 (1951), reg. rev.; Morey, thesis, Stanford Univ. (1962), biosyst. *Plectritis*; Weberling & Uhlarz, Plant Syst. Evol. 127(4): 217–242 (1977), morph. *Aretiastrum*; Weberling & Weberling, Akad. Wiss. Lit. Mainz, Trop. subtrop. Pflanzenwelt 36 (1981), morph. anat. *Belonanthus*; Weberling, Abh. Akad. Wiss. Lit. Mainz, math.-naturw. Kl. 2 (2001), morph. *Stangea*; Weberling & Stützel, Wulfenia 13: 193–205 (2006), morph. anat. *Aretiastrum*; Hidalgo et al., J. Bot. (2010), karyol., phylog.
Aretiastrum (DC.) Spach (1841).
Astrephia Dufr. (1811).
Belonanthus Graebn. (1906).
Phuodendron (Graebn.) Dalla Torre & Harms (1905).
Phyllactis Pers. (1805).
Plectritis (Lindl.) DC. (1831).
Porteria Hook. (1851).
Stangea Graebn. (1906).

Annual or perennial rhizomatous herbs, often semirosulate or rosulate, subshrubs or shrubs, small trees or lianas; innovation shoots of perennial species arising from the axils of basal leaves. Leaves entire, pinnatifid or pinnate, herbaceous, coriaceous or rarely fleshy. Inflorescences pleiothyrsic, of very diverse shape, supernumerary bracts on pedicel sometimes present. Flowers bisexual or unisexual, then plants dioecious, polygamous or often gynodioecious; calyx either forming a solid ring, not accrescent in fruit, or up to 30 segments inrolled in the flower and expanding into a plumose pappus in fruit; corolla with (3–)5 mostly unequal lobes, infundibuliform, salverform or tubular, mostly slightly gibbous near the base, rarely spurred, white, yellow, pink or red; stamens 3(4), anthers tetrasporangiate or bisporangiate; stigma 2(3)-lobed. Achenes of different shape, in some species di- or trimorphic, usually somewhat compressed, elongate-ovate, rarely winged, pappose or epappose, sterile locules usually small, sometimes well developed. $n = 8$, $2n = 14, 16, 18, 22, 24, 28, 32, 48, 54, 64, 96$.

About 270 species in Eurasia, North and South America and the southern part of Africa. High Andean species were included in various segregated genera, but these were shown to be deeply nested with *Valeriana* s.s. and belong to a clade of mainly high Andean species ("páramo clade" of Bell and Donoghue 2005). Even in the wider sense as accepted here, the genus is currently still paraphyletic or polyphyletic with exclusion of *Centranthus* and even *Valerianella* (incl. *Fedia*). Further studies on critical species are needed (see Hidalgo et al. 2010 and sections "Karyology" and "Subdivision of and relationship within the family").

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