

Flowering Plants. Dicotyledons

Celastrales, Oxalidales, Rosales, Cornales, Ericales

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Actinidiaceae

S. DRESSLER and C. BAYER

Actinidiaceae Gilg & Werderm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 21: 36 (1925), nom. cons.
Saurauiaceae J. Agardh (1858).

Trees, shrubs or climbers, with simple or variously branched trichomes. Leaves alternate, simple, usually serr(ul)ate or dentate, pinnatinerved, petiolate; stipules absent or minute. Flowers in axillary cymes or thyrsoid-paniculate inflorescences, sometimes solitary, pedicellate, actinomorphic, hermaphroditic or unisexual; sepals (3–)5(–8), imbricate-quincuncial in bud, usually persistent; petals (3–)5(–9), longer than sepals, distinct or \pm fused at base, imbricate in bud; stamens (10–)20–240, filaments distinct, sometimes adnate to petals and falling with these, anthers dithecal, dorsifixed, versatile, extrorsely dehiscent by longitudinal slits or subapical pores; ovary superior, syncarpous, (3–)5- to many-locular, sometimes incompletely septate, pubescent or glabrous, sometimes with apical depression; placentation axile, placentae sometimes split; ovules numerous, anatropous, unitegmic; stylodia distinct, as many as locules, sometimes persistent, or style simple, stigma sometimes capitate; fruit usually a berry, sometimes dehiscent; seeds numerous, exarillate, enclosed by pulp, albuminous, embryo large, usually straight.

A family of c. 360 spp. in three genera native to tropical Asia and America, a few spp. of *Actinidia* in temperate E Asia.

VEGETATIVE ANATOMY. Young organs are covered with simple or multicellular, sometimes glandular hairs, which can be of diagnostic value (see Hunter 1966). Raphides contained in elongated idioblasts occur in most tissues. Crystal sand is reported for *Clematoclethra* (Lechner 1914).

The leaves are dorsiventral and sometimes have an arm palisade mesophyll. Some species form a multilayered hypodermis. Stomata of the ranunculaceous type are restricted to the abaxial side (Lechner 1914; Metcalfe and Chalk 1950). Venation is pinnate and of the camptodromous type. The ultimate marginal veins are looped, but some branches extend into the teeth (Yu and Chen 1991).

Vessels of the primary xylem are mostly solitary, often large, and often arranged in radial rows. They can have annular, helical, reticulate, or scalariform thickenings. Perforation plates are scalariform, more rarely simple. The pericycle includes a continuous ring of sclerenchyma. Young stems have a solid pith, which may later disintegrate and/or become lamellate in some *Actinidia* species. The lamellae and a cylinder of outer pith cells become sclerenchymatous with age.

The wood of *Actinidia* has dimorphic vessel elements: few very large, moderately long vessel elements with simple perforations, and numerous smaller, usually scattered or solitary, with oblique scalariform perforation plates. *Saurauia* has exclusively solitary vessels with many-barred scalariform perforation plates. Parenchyma is diffuse apotracheal. Non-septate fibre tracheids have numerous bordered pits. Rays are uniseriate and multiseriate, heterogeneous (Lechner 1914; Metcalfe and Chalk 1950).

Wang et al. (1994) studied the root anatomy of five *Actinidia* species; cortex and endodermis persist during secondary thickening.

REPRODUCTIVE STRUCTURES. Cauliflory is reported for some species. *Saurauia callithrix* is special by having leafless inflorescences at the base of the trunk which spread in the soil and leaf litter, elevating the flowers just above the forest floor (Gilg and Werdermann 1925). The flowers are often arranged in cymes, which are subtended by foliage leaves or bracts. Some *Saurauia* have axillary thyrsoid-paniculate inflorescences that include monochasia. Bracteose prophylls are frequently found.

The flowers are mostly pentamerous but a few *Saurauia* and *Actinidia* species have tetramerous flowers, and other exceptions occur also. In pentamerous flowers, quincuncial aestivation of sepals is evident even in open flowers, since the abaxial face is often pubescent in the two outermost sepals, half pubescent in one other, and glabrous in the two innermost sepals. For anatomical features see Dickison (1972) and Schmid (1978a).

Petals and stamens may be fused to various degrees and often fall together. The microsporangia of each theca merge. Pollen is released through longitudinal slits or pores that become extrorse by inversion of the anthers.

Brown (1935) reported nectar-secreting tissue at the base of the petals of *Saurauia subspinosa*. According to his study, the androecium is basically diplostemonous. The outer whorl is formed by single stamens in front of the sepals, whereas the majority of stamens develop in centrifugal succession by splitting of antepetalous primordia. For *Actinidia deliciosa*, Brundell (1975) described two or three whorls of staminal initials, depending on the cultivar. In a more detailed study of *A. melanandra* and *A. deliciosa*, van Heel (1987) found a single whorl of staminal primordia in the former, and centrifugal multiplication of such primary primordia in the latter. The numerous carpel primordia arise in a single whorl.

EMBRYOLOGY. The anther wall consists of epidermis, fibrous endothecium, 2–3 ephemeral middle layers, and a secretory tapetum of multinucleate cells the nuclei of which may fuse and become polyploid. Raphides are present in the anther wall and connective. Meiotic division of microspore mother cells is simultaneous. Pollen is shed at the two-celled stage.

The ovules are anatropous, unitegmic and tenuinucellar. A hypostase is present. The nucellus is thin and ephemeral. A hypodermal archesporial cell forms the chalazal megaspore mother cell which develops into a linear tetrad. Embryo sac development is of the Polygonum type (Vijayaraghavan 1965; An et al. 1983). Inverted embryo sac polarity is reported of *Saurauia nepalensis* (Rao 1953). Endosperm formation is cellular; embryogeny corresponds to the Solanad type (Crété 1944b; Vijayaraghavan 1965). Polyembryony due to the proliferation of suspensor cells was observed in *Actinidia deliciosa* (Crété 1944a).

POLLEN MORPHOLOGY. Pollen of Actinidiaceae is remarkably uniform and rather unspecialised. Pollen is usually shed in monads; *Saurauia elegans* has tetrads. The grains are usually 3(4)-colporate, oblate-spheroidal to prolate, the longest axis 13–26(–33) μm . The colpi are long, crassimarginate and usually exhibit an equatorial bridge of ektexine over the endoaperture. Exine is (1–)1.5–2 μm thick. Sexine is as thick as nexine. The complete tectum is psilate, (micro-)granulate or rugulate; columellae are reduced. Exine stratification and sexine pattern are obscure in light microscopy

(Erdtman 1952; Dickison et al. 1982; Zhang 1987; Li et al. 1989; Kang et al. 1993). Similar pollen occurs in Theaceae, Ochnaceae and Clethraceae (Erdtman 1952; Zhang 1987), but there are some differences to Dilleniaceae (Dickison et al. 1982).

Functionally female flowers of *Actinidia deliciosa* shed nonviable pollen, which is usually enucleate and shrivelled but otherwise similar to viable pollen (Schmid 1978a; White 1990).

KARYOLOGY. Chromosome counts are known for many *Actinidia* species (see Yan et al. 1997). The basic chromosome number is $x = 29$; diploids, tetraploids, hexaploids and octoploids occur. Intraspecific variation appears to be common (mainly diploid and tetraploid cytotypes, $4\times$ and $6\times$ in *A. valvata*, and $4\times$, $6\times$ and $8\times$ in *A. arguta*). For *Saurauia*, counts of $n = 30$ (South American species: Soejarto 1969, 1970) and $n = 20$ (Asian species: Mehra 1976) were reported.

REPRODUCTIVE BIOLOGY. *Actinidia* is usually dioecious, *Clematoclethra* and *Saurauia* have mostly bisexual flowers. American *Saurauia*, however, is described as functionally dioecious with dimorphic flowers: long-styled, functionally female flowers with malformed, sterile pollen, and short-styled ones with fertile pollen (Soejarto 1969). Brown (1935) reported protandry.

In *Actinidia deliciosa*, staminate flowers open about seven days before pistillate ones. Plants of the pistillate cultivar 'Hayward' in New Zealand bloom 10–18 days, staminate clones usually flower 3–5 days longer (Hopping 1990). Because of this limited overlap in flowering and the linear relationship between seed number and fruit weight, fruit set is improved by artificial pollination. Pollen tubes from the distinct stylar branches are evenly distributed to the numerous carpels and ovules by a compitum ("pollen tube distributor cup": Howpage et al. 1998). For pollen–pistil interaction, pollen tube growth and fertilisation of *Actinidia*, see Hopping and Jerram (1979), Harvey et al. (1987) and González et al. (1996).

Actinidia deliciosa is said to be bee- or wind-pollinated. Despite the abundance of literature on the floral biology of cultivated kiwifruit (e.g. Schmid 1978a; Harvey et al. 1987; Harvey and Fraser 1988; Hopping 1990; Howpage et al. 1998), there is only little information on pollination in the wild. Gilg and Werdermann (1925) suspect insect pollination for *Actinidia* and *Clematoclethra*. For *Saurauia*, observations on insect visits (e.g. Hymenoptera) are reported (Soejarto 1969). The flowers are showy, often fragrant and at least

sometimes nectariferous (Brown 1935 for *S. subspinoso*).

FRUIT AND SEED. Fruits are usually berries with massive placentae, and the seeds embedded in a mucilaginous pulp which is mostly greenish, sticky, sweet and edible. Since this pulp originates from the placenta, it does not correspond to an aril (Schmid 1978a). Berries of *Actinidia* may include more than 40 locules and 1500 seeds. In some *Saurauia* species, the pericarp is dehiscent and more or less dry (Soejarto 1969; Dickison 1972). The fruits of *Clematoclethra* have been described as capsular (Gilg and Werdermann 1925), indehiscent (Ying et al. 1993) or drupaceous (Lechner 1914). Generally, endozoochory seems most likely. In *Saurauia*, dispersal is by rain and animals such as birds (Soejarto 1969).

The seed coat is thin and finely reticulate. As in other Ericales, the seeds of Actinidiaceae are exotestal, with thickened inner walls of the outer epidermis (Cr  t   1944b; Corner 1976; Huber 1991; Takhtajan 1991).

PHYTOCHEMISTRY. Iridoid compounds were found in *Actinidia* and *Roridula* (Jensen et al. 1975). Webby et al. (1994) studied leaf flavonoids of several *Actinidia*, which are based on common flavonols including myricetin. Procyandin and prodelphinidin point to the presence of condensed tannins (Hegnauer 1964). Actinidin, a proteinase similar to papain, was detected in kiwifruit (McDowall 1970), which makes it a potential cause of contact dermatitis. The same name was applied to a terpenoid pseudoalkaloid found in *Actinidia polygama* (Hegnauer 1964). The mucilage of *Actinidia* contains acidic polysaccharides (Redgwell 1983).

AFFINITIES. Actinidiaceae have been variously placed; especially Theaceae, Dilleniaceae, Cornales and Ericales were considered as closest relatives (see, for example, Schmid 1978a). Ericalean affinities are now mostly accepted, which is supported by agreement in embryological characters (Cr  t   1944b), floral features (Dickison 1972) and results of molecular analyses (Kron and Chase 1993; Chase et al. 1993 and subsequent studies). According to recent analyses, Actinidiaceae are sister to *Roridula*, both being sister to Sarraceniaceae (Anderberg et al. 2002). In all analyses, nonetheless, statistical support for this topology is not strong, and some studies have found different topologies (e.g. Savolainen, Fay et al. 2000). A potential synapomorphy of a clade comprising

Actinidiaceae, Roridulaceae and Sarraceniaceae is the presence of a hypostase. Other features considered by Anderberg et al. (2002), such as the presence of stilar branches and a fibrous endothe-cium, are not found in all members of this clade.

DISTRIBUTION AND HABITATS. *Actinidia* is centred in hilly S and E China (between 25 and 30   N), but some species occur in the cold-temperate and arctic forests of Siberia, Korea and Japan, and the tropics. They inhabit the lower forest storey. *Clematoclethra* occupies similar habitats up to 3100 m but is confined to China. In contrast, *Saurauia* species are trees and shrubs mainly of humid montane forests of tropical Asia and America, and occur in altitudes up to 3600 m. Some species are rheophytic (van Steenis 1981).

PALAEOBOTANY. Seeds resembling those of extant *Saurauia* were recorded from the Maastri-chtian onwards in Europe (Knobloch and Mai 1986), and *Actinidia*-like seeds are known from the Upper Eocene in Europe, sometimes in abundance (Mai and Gregor 1982; Friis 1985; Mai 2001). Leaves similar to those of *Saurauia* were found in the Middle Eocene of North America (Taylor 1990), and *Actinidiophyllum* was described from the Tertiary of Japan (Nathorst 1888). A Pliocene wood from the German Westerwald was described as *Actinidioxylon* (M  ller-Stoll and M  del-Angeliewa 1969). Flowers from the early Campanian of Georgia, North America, were described as *Parasaurauia*, mainly differing from modern *Saurauia* in having only 10 stamens (Keller et al. 1996).

ECONOMIC IMPORTANCE. Kiwifruit, produced by *Actinidia deliciosa* cultivars, are an economically important crop, especially in New Zealand but also in Italy, Spain, China and other countries. Since this species was formerly treated mostly as a variety of *A. chinensis*, most literature on cultivated *A. chinensis* refers to what is now *A. deliciosa* (Liang and Ferguson 1986; Ferguson 1990). All commercial plantations in New Zealand can be traced back to a single introduction of seed from China in 1904 (Ferguson and Bollard 1990). There are indications that the hexaploid *A. deliciosa* originated from diploid *A. chinensis* (Crowhurst et al. 1990; Atkinson et al. 1997). Breeding of *A. chinensis*, up to 1997 collected only in the wild and industrially processed in China, led to the recent introduction of the Kiwi Gold (cv. 'Hort 16 A') from New Zealand. Relatively hardy species such as *A. arguta* and *A. kolomikta* are cultivated as orna-

mentals in Europe and North America. In the former Soviet Union, attempts were made to use their aromatic fruits, which contain even more vitamin C than do kiwifruit. Berries of some *Saurauia* species are sold at local markets in South America. Wood is occasionally used for construction, fire wood and charcoal, but is of no commercial importance. Some uses in folk medicine are reported (Soejarto 1980).

KEY TO THE GENERA

1. Trees or shrubs; stamens basally connate with petals; Asia and America 3. *Saurauia*
 - Woody climbers; stamens free; Asia 2
2. Flowers usually functionally unisexual; stamens numerous; stylar branches distinct 1. *Actinidia*
 - Flowers usually hermaphroditic; stamens 10(-30); style simple 2. *Clematoclethra*

GENERA OF ACTINIDIACEAE

1. *Actinidia* Lindl.

Fig. 3

Actinidia Lindl., Intr. Nat. Syst., ed. 2: 439 (1836); Li, J. Arnold Arbor. 33: 1-61 (1952), rev.; Liang, Fl. Reip. Pop. Sin. 49(2): 196-268 (1984), reg. rev.; Wei, Higher plants of China 4: 657-672 (2000), reg. rev.

Woody climbers, dioecious or polygamous, \pm pubescent; sepals distinct or somewhat fused at base; petals white or yellow to reddish; stamens numerous, anthers longitudinally dehiscent; ovary pubescent or glabrous, many-locular; stylar branches distinct, persistent; fruit a globose to oblong berry, sometimes pubescent; seeds numerous, embedded in pulp. $n = 29$ or multiples. About 60 spp.; E Asia, mostly W to E China, north to Sakhalin and Kuril Is., south to Taiwan, Himalayas, NE India, Indochina, Malaysia.

2. *Clematoclethra* (Franch.) Maxim.

Fig. 4

Clematoclethra (Franch.) Maxim., Trudy Imp. S.-Peterburgsk. Bot. Sada 11: 36 (1890); Tang & Xiang, Acta Phytotax. Sin. 27: 81-95 (1989), rev.; Wei, Higher plants of China 4: 672-674 (2000), rev.

Woody climbers, deciduous, \pm pubescent; flowers in up to 12-flowered cymes or solitary, hermaphroditic or unisexual; sepals united at base; petals white or reddish; stamens c. 10-30, filaments dilated at base; anthers longitudinally dehiscent; ovary globose, 5-angled, (4)5-locular; style simple, persistent, stigma small, swollen; ovules numerous; fruit berry-like, blackish. One species, *C. scandens* (Franch.) Maxim. (or 5), in montane forests above 1000 m in W and C China.

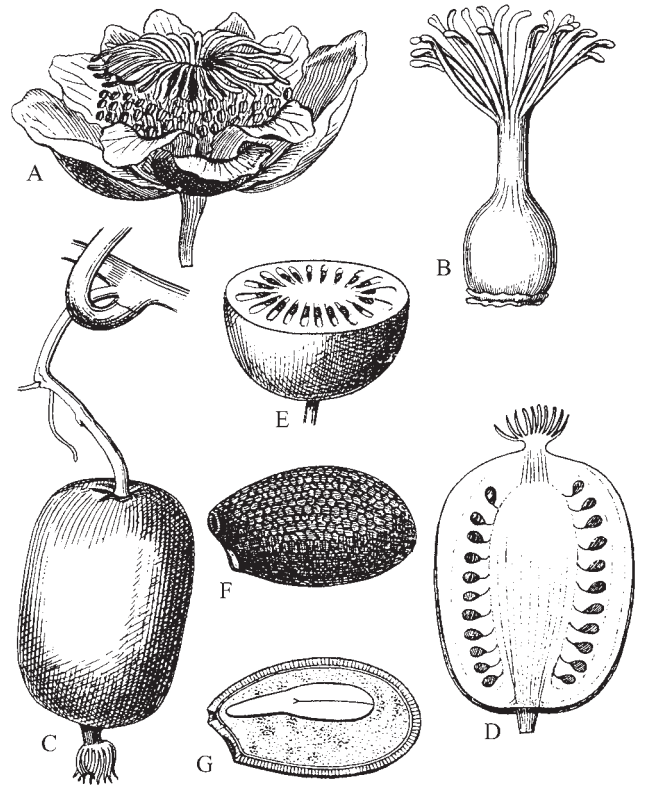


Fig. 3. Actinidiaceae. A, F, G *Actinidia strigosa*. B-E *A. polygama*. A Flower. B Pistil. C Fruit. D, E Same, vertical and transverse section. F Seed. G Same, longitudinal section. (Schneider 1912)



Fig. 4. Actinidiaceae. *Clematoclethra lasioclada*. A Flowering twig. B Flower. C Androecium and gynoecium of young flower, longitudinal section. D Androecium and gynoecium at anthesis, note inversion of anthers. E Young anthers. F Mature anther. G Ovary in cross section. (Gilg and Werdermann 1925)

3. *Saurauia* Willd.

Saurauia Willd., Ges. Naturf. Freunde Berlin Neue Schriften 3: 407 (1801), nom. cons.; Hunter, Ann. Missouri Bot. Gard. 53: 47–89 (1966), reg. rev.; Soejarto, Fieldiana Bot. N.S. 2: 1–141 (1980), reg. rev.; Wei, Higher plants of China 4: 674–677 (2000), reg. rev.

Trees or shrubs, usually pubescent; flowers hermaphroditic or sometimes functionally unisexual; sepals fused at very base, petals white or pink; stamens 15-numerous, filament bases fused with petals, pubescent, anthers dehiscing by pores; ovary (3–)5(–8)-carpellate, usually glabrous, styler branches entirely or distally distinct, stigmas simple to capitate or discoid; fruit a berry, rarely a leathery capsule; seeds numerous, minute, embedded in pulp. $n = 30$ (20 in Asian spp.). About 300 spp., Asia (Himalayas to E and SE Asia) to Fiji and tropical America (C Mexico to Chile but absent from Antilles, Guianas, Brazil); 1 sp. in Queensland.

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