Phytochemistry

Chemical constituents of *N. purpurea* Schlr. have been investigated in detail because of the use of this plant in the Taiwanese folk medicine 'I-tiam-bong'. Compounds identified to date include the amino acid l-rotaneucine, fatty acids, glycerides, and phytosterols (Kikuchi et al. 1981a). A similar chemical profile was recorded for *N. aragoana* (Kikuchi et al. 1981a). Structures of several new phytosterols isolated from *N. purpurea* were described in a series of articles as cyclonervilol (24E-ethyl-29-norcycloart-22E-en-3β-ol) (Kikuchi et al. 1981b, 1985a), 22, 23-dihydrocyclonervilol (Kikuchi et al. 1985a), nervisterol (24E-isopropenylcholesta-5,22E-dien-3β-ol) (Kikuchi et al. 1982, 1985b), cyclonervilasterol (14-methyl-5,19-cycloergosta-9(11), 22-dien-3-ol), 24-epi-cyclonervilasterol, 22, 23-dihydronervilasterol and 24-epi-22, 23-dihydronervilasterol (Kadota et al. 1984; Kikuchi et al. 1986b), cyclohomonervilol (24E-isopropenyl-29-norcycloartan-3β-ol) (Kikuchi et al. 1981b, 1985a; Kadota et al. 1987), 24(R)- and 24(S)-methyl-29-norcycloartan-3β-ol (the C-24 epimers of dihydrocycloerucalanol) (Kikuchi et al. 1985a, 1986a), cyclohomonervilasterol (14-methyl-5, 19-cycloergosta-9(11), 22-dien-3-ol), and neocyclonervilasterol (14-methyl-5, 19-cycloergosta-9(11), 25-dien-3-ol) (Kadota et al. 1986). Previously identified compounds cyclofunctenol (24-Z-ethylidene-29-norcycloartan-3β-ol) and cyclohomonervilol (24-methylene-29-norcycloartan-3β-ol) (Kikuchi et al. 1985a) (Kikuchi et al. 1986b), ergosterol, stigmasterol, 24-epi-brassicasterol, and 24E-methylcholesterol (Kikuchi et al. 1985b) were also reported.

A survey of an alkaloid content of more than 200 orchids from New South Wales and Queensland gave positive results for *N. discolor* Schltr. and *N. bolobila* Schlr. (Lawler and Slaytor 1969). Other species investigated for alkaloids include *N. aragoana* (negative result) and *N. gammieana* Schlr., *N. macroglossa* Schlr., *N. plicata* Schlr., and *N. scottii* Schlr. (positive results) (Luning 1967). (NV, RG)

Phylogenetics

Pettersson (1990a) used morphological characters in an analysis of the African species, representing three of the sections, and concluded that *N. sect. Kjimihlæa* nested within *N. sect. Linervia* and could not be maintained. Schlechter's sections *Nervilia*, *Linervia* (including *Kjimihlæa*), and *Vineria* were monophyletic. (PC)

Ecology

Plants of *Nervilia* are terrestrial in deciduous and semi-deciduous forests and wooded savanna in dappled light or shade from sea level to 2500 m. A few species such as *N. petraca* Schltr., and *N. bicarinata* Schlr. also occur in moister forest types such as riverine and coastal rain forests (Pettersson 1990a). (PC)

Pollination

Pettersson (1990) studied the pollination biology of several species of *Nervilia* in Africa. Autogamy and/or apogamy and cleistogamy are known for *N. gosneri* B.Pett. and *N. petraca*.

Flowers of *N. sect. Nervilia* lack nectar and are probably deceit flowers attracting solitary true wasps. Wasps (Eumenidae) pollinate *N. bicarinata* Schlr. and *N. bicarinata* Schlr. *Nervilia sect. Linervia* is characterized by gregarious flowering triggered by the first rains of the season with anthesis lasting a day at most. A subsequent mass flowering may occur a fortnight later. Wasps (Vespidae, Eumenidae, Ichneumonidae) pollinate *N. stolziana* Schlr. and/or *N. petraca*. Halicitid bees are known to be pollinators of *N. petraca* and *N. crociformis* in Malawi and Madagascar. Anthophorid bees also pollinate both of these species. (AP)

Uses

The tubers of *N. flavelliformis* (Lindl.) T. Tang & F. T. Wang are chewed in Guam to quench thirst, and the leaves of the same species are boiled and used as a post-parturition prophylactic. In addition, leaves of *N. discolor* are variously used as an analgesic and in childbirth (Lawler 1984). No species is commonly cultivated. (AP)

Taxonomic literature


SUBTRIBE EPIPOGIINAE

Epiogiiinae Schlr., *Notizbl.*, 9, 571. Type: *Epiogium*

SG.Gmel. ex Ehrh.

Description

Terrestrial, leafless, holomycotrophic *herbs* growing from a tuberous rhizome or coralloid underground stem, lacking chlorophyll. *Roots* absent or reduced and hairy, without velamen. *Stem* erect, fleshy, white to buff-coloured, bearing white to buff-coloured, sheathing scales. *Inflorescence* ephemeral, terminal, unbranched, racemose, rachis terete; floral bracts persistent, white to buff-coloured. *Flowers* fleshy, resupinate or not. *Sepals* subparallel, free to base. *Petals* free, smaller than sepals. *Labellum* simple to trilobed, spurred or not, callose or not, callus (if present) with papillate ridges. *Column* fleshy, terete; anther incumbent or suberect, pollinia two, sectile, attached by one or two caudicles to one or two small elliptical viscidia; stigma ventral, entire, concave; rostellum transverse. *Ovary* ellipsoidal. (PC)

Distribution

A subtribe of three genera distributed in the temperate and tropical regions of the Old World from Europe and Africa across to Asia, the southwest Pacific islands, and Australia. (PC)
Phylogenetics
The rank and placement of Epipoginae within the monandrous orchids has been one of the most controversial questions in orchid systematics. The type genus *Epipogium* was originally assigned to the subtribe Gastrodiinae by Lindley in *Genera and Species of Orchidaceous Plants* on the basis of its sectile pollinia and the position of the stigma. A second genus, *Stereosandra*, thought to be closely related to *Epipogium*, was established by Blume in 1858. However, Bentham (1881) considered the two genera sufficiently different to warrant the placement of *Stereosandra* in Arthureae and *Epipogium* in his Diurideae. Pfitzer (1887) re-evaluated the floral morphology of the two genera and concurred with Blume’s assessment that they were closely related. Initially he placed both genera in his Caladeniinae but later changed his mind (Pfitzer 1888), assigning *Epipogium* to his Cephalantherinae and *Stereosandra* to his Pogoninae.

Schlechter (1911) took a different approach, focusing primarily on vegetative characters when he initially treated the two genera. He noted the present of corm-like rhizomes in both genera and on this basis returned *Epipogium* and *Stereosandra* to Gastrodiinae. Later, Schlechter (1926) observed that the perianth parts in *Epipogium* and *Stereosandra* were free, whereas the other representatives of Gastrodiinae had more or less fused perianth parts. Utilizing this difference, he established the subtribe Epipoginae, which he considered closely related to Gastrodiinae. Schlechter’s subtribe was actually based on the older tribal name Epipogieae and eventually reinstated by Dressler (1974). Since Dressler’s treatment many other accounts of the family have continued to maintain Epipogieae as a tribe (Dressler 1981; Rasmussen 1982, 1985; Burns-Balogh and Funk 1986; Szlachetko 1995) or subtribe (Dressler and Dodson 1960; Dressler, 1993), but the placement of the taxon within the monandrous orchids was still disputed. Thus Epipoginae have been included at various times within Orchidoideae (Dressler and Dodson 1960), Epidendroideae (Vermeulen 1965; Dressler 1981, 1993; Rasmussen 1982, 1985; Burns-Balogh and Funk 1986) or Vanilloideae *sensu* Szlachetko (1995).

A number of anatomical, developmental, and phylogenetic studies have clarified the placement of Epipoginae within the monandrous orchids. Vermeulen (1965) and Rasmussen (1982) both noted that the structure of the column and position of the anther in Epipoginae are clearly different from those of the basitonic orchids. Further evidence of an epidendroid affinity is provided in a detailed study by Freudenstein and Rasmussen (1997) of orchids with sectile pollinia. Their work indicated that sectile pollinia have probably arisen repeatedly within the family, and their presence is not necessarily indicative of a close evolutionary relationship. The two authors noted that sectile pollinia in most Epipoginae and all Gastrodiaceae are distinct and do not appear to be homologous with those of Orchidaceae, Diurideae, or Cranichideae. Freudenstein and Rasmussen’s conclusions regarding the placement of *Epipogium* are also supported by embryological studies (Clements 1995, 1999) and phylogenetic work on saprophytic orchids utilizing DNA sequences (Molvray *et al.* 2000). The results of this last study indicated that saprophytism has arisen repeatedly within the monandrous orchids and that the vegetative similarity between the different groups of achlorophyllous orchids is most likely due to convergence. Based on molecular data, *Epipogium* is not closely related to the other representatives of Gastrodiaceae but is allied to Nervilieae (Dressler 1990b). Similarities between the two include the absence of velamen on the roots, sectile pollinia, and ultrastructural pollen characters and support the inclusion of Epipoginae in Nervilieae. (MM, PK)

### Artificial key to the genera of Epipoginae

1. Labellum with a basal spur and a callus of several papillosse ridges ............................................ 393. *Epipogium*
   - Labellum lacking a spur and callus .................. 2

2. Inflorescence two-flowered, flowers opening widely; labellum trilobed, the middle lobe smaller than the oblong-falcate side lobes ........................................... 394. *Silevorchis*
   - Inflorescence many-flowered, flowers not opening widely; labellum entire, concave, with two sessile glands at the base .................................................. 395. *Stereosandra*

### 393. *EPIPOGIUM*


*Galera* Blume, *Bjdr.*, 415, t. 3 (1825). Type species: *Galera nutans* Blume (= *Epipogium rosseum* (D. Don) Lindl.).


### Derivation of name

From the Greek *epi*, upon, and *pogon*, beard, in reference to the bearded or papillosse labellum of the type species. (PC)

### Description

(Plate 168; Fig. 393.1)

Holomycotrophic, terrestrial *herbs*. *Rhizome* tuberous or obscure but with coralloid roots, covered in root hairs. *Stem* erect, lacking chlorophyll. *Leaves* reduced to buff or whitish scales. *Inflowernce* racemose, ephemeral, lasting about 10 days before withering, rachis terete. *Flowers* pendent, non-resupinate or resupinate, often self-pollinating. *Sepal* and *petals* subsimilar, connivent or spreading, free, lanceolate. *Labellum* sessile, entire, with a 2–6-rowed lamellate, papillosse, or bearded longitudinal callus, spur basal, shorter than labellum. *Column* fleshy, clinandrium membranous; anther incumbent, pollinia two, granulose, clavate, deeply dissected, with slender caudicles and small viscidia; rostellum broad. *Ovary* ellipsoidal, ribbed. (PC)
Fig. 393.1. *Epipogium roseum* (D. Don) Lindl. A. Habit; B. Flower; C. Column and labellum, side view; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Column and ovary, side view; I. Column apex; J. Column apex, anther and pollinia removed; K. Anther cap; L. Pollinaria. Single bar = 1 mm, double bar = 1 cm. Drawn by Susanna Stuart-Smith from *Garagead 2142* (K). Reproduced with permission from N. R. Pearce and P. J. Cribb (2002), *The Orchids of Bhutan*. The Royal Botanic Garden Edinburgh and Royal Government of Bhutan.
**Distribution** (Fig. 393.2)  
*Epipogium* is a small genus of two, or possibly three widespread species in temperate Europe and temperate and tropical Asia, south to the Malay Archipelago, the Philippines, and northeast Australia. (PC)

**Anatomy**  
Solereder and Meyer (1930) listed the works of others, who reported that the vascular cylinder of the rhizome consists of cambiform cells without vessels. Möller and Rasmussen (1984) observed no stegmata in the stem and rhizome of *E. aphyllum*. (AP)

**Cytogenetics**  
Brandham (1999) reported a chromosome count of $2n = 68$ for *Epipogium*. (AP)

**Ecology**  
*Epipogium* grows in a wide range of habitats that have sufficient rainfall and accumulations of organic material in the soil to sustain the mycorrhizal fungus associated with the subterranean rhizomes. Species of the genus are most frequently found in dense to open forest but sometimes also occur in grassland. Inflorescences emerge after a period of heavy rain and mature within a matter of days (Docters van Leeuwen 1937; Jones 1988). Individual colonies tend to persist at the same location for only a few years, and their rapid flowering and seed set means they are often overlooked by collectors. (MM, PK)

**Pollination**  
The life history and reproductive biology of *E. roseum* were studied in detail by Docters van Leeuwen (1937). In this study he noted that every flower formed a capsule, and he speculated that the species was autogamous. According to Rasmussen (1982), the clinandrium in *E. roseum* is not as well developed as in *E. aphyllum*, and the rostellum is reduced. Flowers are resupinate, and the mature anther, located above the stigma, projects beyond the rostellum. Apparently, self-pollination occurs in *E. roseum* when portions of the pollinia crumble away and come in contact with the stigma. Once pollination occurs, maturation of the capsules proceeds at a rapid rate, with seed dispersal...
occurring in as little as four days. This is possibly the fastest rate of seed production known for any orchid.

In *Epipogium aphyllum* flowers are non-resupinate, placing the anther below the stigma during anthesis. The clinandrium and rostellum are better developed, and the mature anther hardly projects beyond the rostellum, rendering self-pollination less likely. Flowers of *E. aphyllum* are often tinged or marked with pink or faint purple, and the flowers are reported to produce a
musk-like odour that may play a role in attracting insect pollinators. Although the species is reported to set fruit rarely in the wild, its flowers are occasionally visited by a native species of bumble-bee, Bombus lucorum (Kirchner 1928). (MM, PK)

**Uses**
There are no known uses for *Epipogium*. (AP)

**Taxonomic notes**
Rao (1987) reviewed the genus and proposed dividing it into two sections (*E. sect. Epipogium* and *E. sect. Roseum*), based on gynostemium structure. Bearing in mind the few species in the genus, this seems to be an unnecessary case of taxonomic inflation. (PC)

**Taxonomic literature**

**394. SILVORCHIS**
Type species: *Silvorchis colorata* J. J. Sm.

Derivation of name
From the Latin *silva*, forest or woodland, and the Greek *orchis*, orchid, in reference to the woodland habitat of the type species. (PC)

**Description** (Fig. 394.1)
Holomycotrophic terrestrial herbs arising from underground tuberous rhizomes. Roots fleshy, pubescent. Stem erect, lacking green leaves, covered with sterile off-white bracts. Inflorescence 1–2-flowered, erect. Flowers resupinate, white marked with purple spots and streaks and with yellow on the column and the labellum. Sepals spreading, subsimilar, free to base. Petals porrect over column, free, oblique, erose on margins. Labellum trilobed, ecallose, ecalcarate, lateral lobes suberect-por rect, falcate, oblong, rounded at apex, midlobe shorter than the lateral lobes, triangular, with two erect apical lobules. Column lacking a foot; anther basifixed, opening by longitudinal slits, pollinia two, clavate, sectile, each attached by a caudicle to an elliptical viscidium; rostellum cap-shaped. Ovary fusiform, spirally twisted. (PC)

**Distribution** (Fig. 394.2)
There is a single species in western Java, known only from the type. (PC)

**Cytogenetics**
There are no chromosome counts reported for *Silvorchis*. (AP)

**Ecology**
*Silvorchis colorata* is a forest-floor terrestrial found in montane forest in deep shade at approximately 1600 m. (PC)

![Fig. 394.2. Distribution map of *Silvorchis*.](image)
Fig. 395.1. *Stereostrobus javanicus* Blume. A. Habit; B. Portion of inflorescence; C. Dorsal sepal; D. Lateral sepal; E. Petal; F. Labellum; G. Column and labellum, side view; H. Column, ventral view; I. Column, side view; J. Anther cap; K. Pollinarium; L. Ovary, transverse section. Single bar = 1 mm, double bar = 1 cm. Drawn by Judi Stone from *Garrett 785* (K) and Kew Spirit Collection no. 50790.
Pollination
Nothing is known about pollination in Silvorchis. (AP)

Uses
There are no known uses for Silvorchis. (AP)

Taxonomic notes
Known only from the type collection, the taxonomic affinities of Silvorchis are poorly understood. It has been considered to belong to Orchidoideae, possibly close to Platanthera because of its apparently basifixed anther, but other morphological considerations indicate that this is unlikely (Comber 1990). Garay (1986) placed it in Epipoginae, and Dressler (1993) kept it there. (PC)

Taxonomic literature

395. STEREOSANDRA

Derivation of name
From the Greek stereos, firm or rigid, and andros, man, in reference to the rigid anther. (PC)

Description (Plate 169; Fig. 395.1)
Terrestrial, holomycotrophic herbs. Rhizome tuberous, oblong, lacking roots. Fertile stem erect, white with some violet streaks, bearing scale-like, sterile bracts. Inflorescence racemose, rachis terete; floral bracts persistent, lanceolate. Flowers resupinate, pendent or subependent, not opening widely, off-white or white with violet markings on the perianth. Sepals and petals free, connivent, lanceolate, the petals smaller than the sepals. Labellum broader than sepals, oblong, deeply concave, entire, bearing two sessile glands in basal part, ecalcarate, ecallose. Column fleshy; anther erect, pollinia two, with a long common caudicle, clavate, granular;

Fig. 395.2. Distribution map of Stereosandra.
stigma exserted, forming with the rostellum a bilabiate organ. 

Ovary ellipsoid with six prominent ribs. (PC)

**Distribution** (Fig. 395.2)
The single species is widespread in tropical and subtropical southeast Asia and the adjacent islands south to Java and east to New Guinea, the Philippines, and Taiwan. (PC)

**Cytogenetics**
There are no chromosome counts reported for Stereosandra. (AP)

**Ecology**
*Stereosandra javanica* is a humus-terrestrial on the shady floor of primary forests at elevations of 250–1000 m. (PC)

**Pollination**
Several authors have noted that the ovary in *S. javanica* is already conspicuously enlarged at anthesis (Holttum 1953; Comber 1990; Seidenfaden and Wood 1992), indicating that the species is probably autogamous. Pollination may occur when the ventral portion of the pollinia breaks down prior to or during anthesis (Rasmussen 1982). (MM, PK)

**Uses**
There are no known uses for *Stereosandra*. (AP)

**Taxonomic notes**
Although superficially similar to *Epipogium roseum*, *S. javanica* is readily distinguished by its ecalcarate and ecallose lip and by the pollinia being attached to a single caudicle. (PC)

**Taxonomic literature**
