Phytochemistry

Chemical constituents of N. purpurea Schltr. have been investigated in detail because of the use of this plant in the Taiwanese folk medicine 'I-tiam-hong'. Compounds identified to date include the amino acid L-norleucine, 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 (24\xi-ethyl-29norcycloart-22E-en-3β-ol) (Kikuchi et al. 1981b, 1985a), 22, 23-dihydrocyclonervilol (Kikuchi et al. 1985a), nervisterol (24ξ-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 (24ξ-isopropenyl-29norcycloartan-3β-ol) (Kikuchi et al. 1981b, 1985a; Kadota et al. 1987), 24(R)- and 24(S)-methyl-29-norcycloartan-3 β -ol (the C-24 epimers of dihydrocycloeucalenol) (Kikuchi et al. 1985a, 1986a), cyclohomonervilasterol (14-methyl-5,19-cyclostigmasta-9(11),22-dien-3-ol), and neocyclonervilasterol (14,28-dimethyl-5, 19-cyclostigmasta-9(11),25-dien-3-ol) (Kadota et al. 1986). Previously identified compounds cyclofuntemiol (24Z-ethylidene-29-norcycloartan-3β-ol) and cycloeucalenol (24-methylene-29-norcycloartan-3β-ol) (Kikuchi et al. 1985a), ergosterol, stigmasterol, 24-epi-brassicasterol, and 24ξ-methylcholesterol (Kikuchi et al. 1985b) were also reported.

A survey of alkaloid content of more than 200 orchids from New South Wales and Queensland gave positive results for *N. discolor* Schltr. and *N. holochila* Schltr. (Lawler and Slaytor 1969). Other species investigated for alkaloids include *N. aragoana* (negative result) and *N. gammieana* Schltr., *N. macroglossa* Schltr., *N. plicata* Schltr., and *N. scottii* Schltr. (positive results) (Lüning 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. Kyimbilaea nested within N. sect. Linervia and could not be maintained. Schlechter's sections Nervilia, Linervia (including Kyimbilae), and Vinerlia 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. pectinata* P. J. Cribb, *N. subintegra* Summerh., *N. fuerstenbergiana* Schltr., and *N. bicarinata* Schltr. also occur in moister forest types such as riverine and coastal rain forests (Pettersson 1990*a*). **(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. gassneri* B.Pett. and *N. pectinata*.

Flowers of *N*. sect. *Nervilia* lack nectar and are probably deceit flowers attracting solitary true wasps. Wasps (Eumenidae) pollinate *N. shirensis* Schltr. and *N. bicarinata* Schltr. *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* Schltr. and/or *N. pectinata*. Halictid bees are known to be pollinators of *N. petraea* and *N. crociformis* in Malawi and Madagascar. Anthophorid bees also pollinate both of these species. **(AP)**

Uses

The tubers of *N. flabelliformis* (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

Pettersson, B. (1990*a*). *Nervilia* (Orchidaceae) in Africa. *Acta Universitatis Upsaliensis*, **281**, 1–26.

Pettersson, B. (1990*b*). Studies in the genus *Nervilia* (Orchidaceae) in Africa. *Nordic Journal of Botany*, **9**, 487–97.

Schlechter, R. (1911). Nervilia. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie, 45, 399–405.

Schlechter, R. (1915). Nervilia. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie, 53, 550–5.

SUBTRIBE EPIPOGIINAE

Epipogiinae Schltr., *Notizbl.*, **9**, 571. Type: *Epipogium* S.G.Gmel. ex Ehrh.

Description

Terrestrial, leafless, holomycotrophic berbs 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 subsimilar, 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 Epipogiinae 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 Arethuseae and Epipogium in his Diurideae. Pfitzer (1887) reevaluated 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 Pogoniinae.

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 Epipogiinae, 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 Epipogiinae 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 Epipogiinae 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 Gastrodieae are distinct and do not appear to be homologous with those of Orchideae, 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 Gastrodieae 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 Epipogiinae in Nervilieae. (MM, PK)

Artificial key to the genera of Epipogiinae

- 1. Labellum with a basal spur and a callus of several papillose ridges**393. Epipogium**
- 2. Inflorescence two-flowered, flowers opening widely; labellum trilobed, the midlobe smaller than the oblong-
 - Inflorescence many-flowered, flowers not opening widely; labellum entire, concave, with two sessile glands at the

393. EPIPOGIUM

Epipogium S. G. Gmel. ex Ehrh., Beitr., 4, 149 (1789). Type species: Epipogium aphyllum Sw. (basionym: Satyrium epipogium L.).

Epipogum S. G. Gmel., Fl. Sibirica, 1, 11, t. 2, f. 2 (1747). Galera Blume, Bijdr., 415, t. 3 (1825). Type species: Galera nutans

Blume (= *Epipogium roseum* (D. Don) Lindl.).

Ceratopsis Lindl., Gen. Spec. Orch. Pl., 383 (1840). Type species: Ceratopsis rosea Lindl.

Podanthera Wight, Icones, 5, 22, t. 1759 (1851). Type species: Podanthera pallida Wight.

Derivation of name

From the Greek epi, upon, and pogon, beard, in reference to the bearded or papillose 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. Inflorescence racemose, ephemeral, lasting about 10 days before withering, rachis terete. Flowers pendent, non-resupinate or resupinate, often self-pollinating. Sepals and petals subsimilar, connivent or spreading, free, lanceolate. Labellum sessile, entire, with a 2-6-rowed lamellate, papillose, 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)

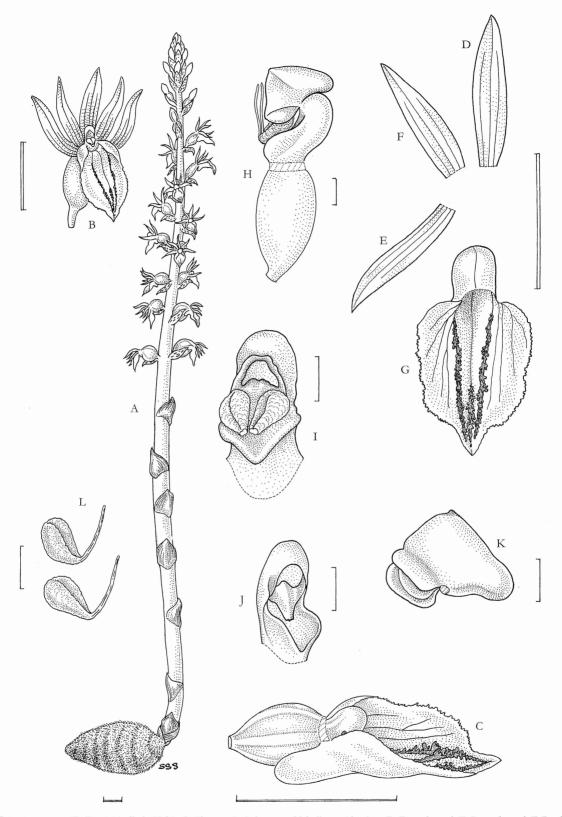


Fig. 393.1. Epipogium roseum (D. Don) Lindl. A. Habit; B. Flower; C. Column and labellum, side view; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Column and ovary, side view; I. Column apex; J. Column apex, anther and pollinia removed; K. Anther cap; L. Pollinaria. Single bar = 1 mm, double bar = 1 cm. Drawn by Susanna Stuart-Smith from Garsgead 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.

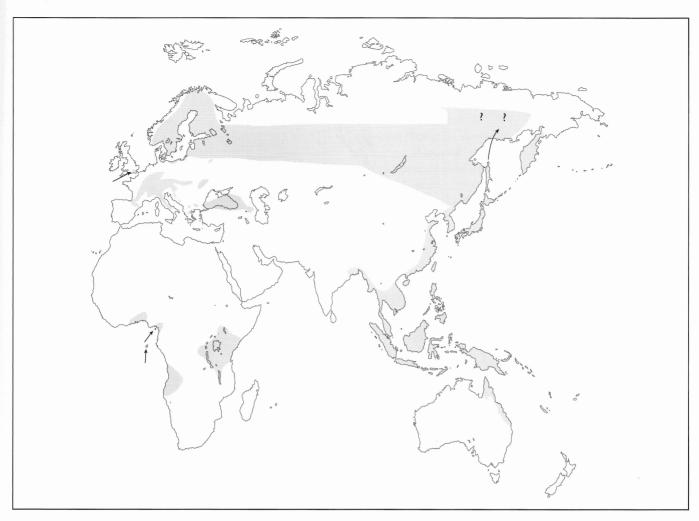


Fig. 393.2. Distribution map of Epipogium.

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. Møller 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 detailed 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

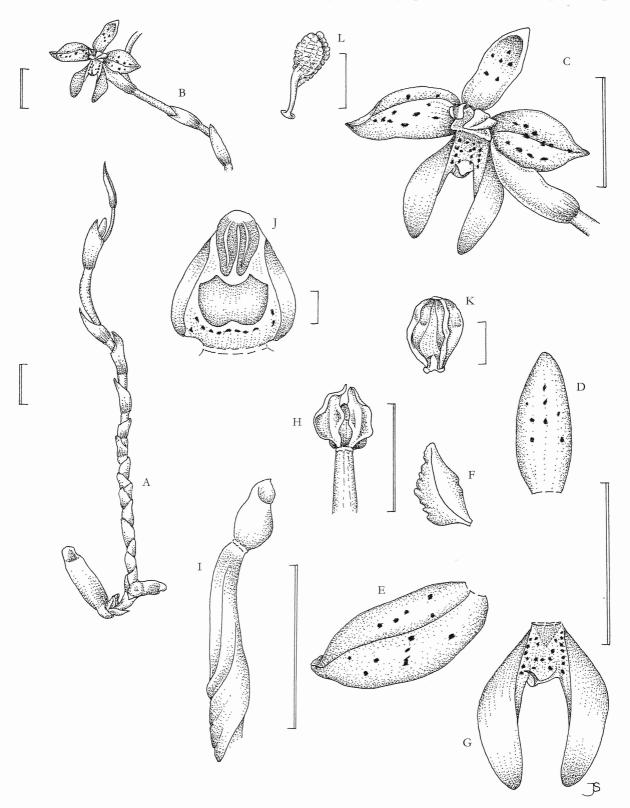


Fig. 394.1. Silvorchis colorata J. J. Sm. A. Habit; B. Inflorescence; C. Flower and bract; D. Dorsal sepal; E. Lateral sepal; F. Petal; G. Labellum; H. Petals and dorsal surface of column; I. Column and ovary, side view; J. Column, ventral view; K. Anther cap; L. Pollinarium. Single bar = 1 mm, double bar = 1 cm. Redrawn by Judi Stone from J. J. Smith, Bull. Dep. Agric. Lnd. Neerl, 13, t.1 (p. 3).

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

Rao, A. N. (1987). A note of the sectional delimitation in the genus *Epipogium* R.Br. (Orchidaceae). *Indian Orchid Journal*, 2, 13–18.

Seidenfaden, G. (1978). Orchids of Thailand 6. Neottioideae. *Dansk Botanisk Arkiv*, **32**, Part II, 171.

Tuyama, T. (1967). On *Epipogium roseum* (D. Don) Lindl. in Japan and its adjacent regions, with remarks on other species of the genus. *Journal of Japanese Botany*, **42**, 295–316.

Vermeulen, P. (1965). The place of *Epipogium* in the system of Orchidales. *Acta Botanica Neerlandica*, **14**, 230–41.

394. SILVORCHIS

Silvorchis J. J. Sm., *Bull. Dép. Agric. Indes Néerl.*, **13**, 2 (1907). 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-porrect, 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)**

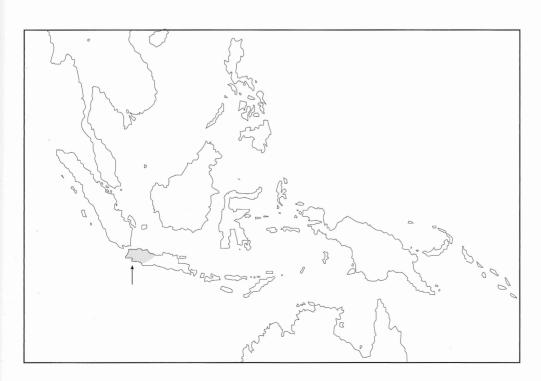


Fig. 394.2. Distribution map of *Silvorchis*.

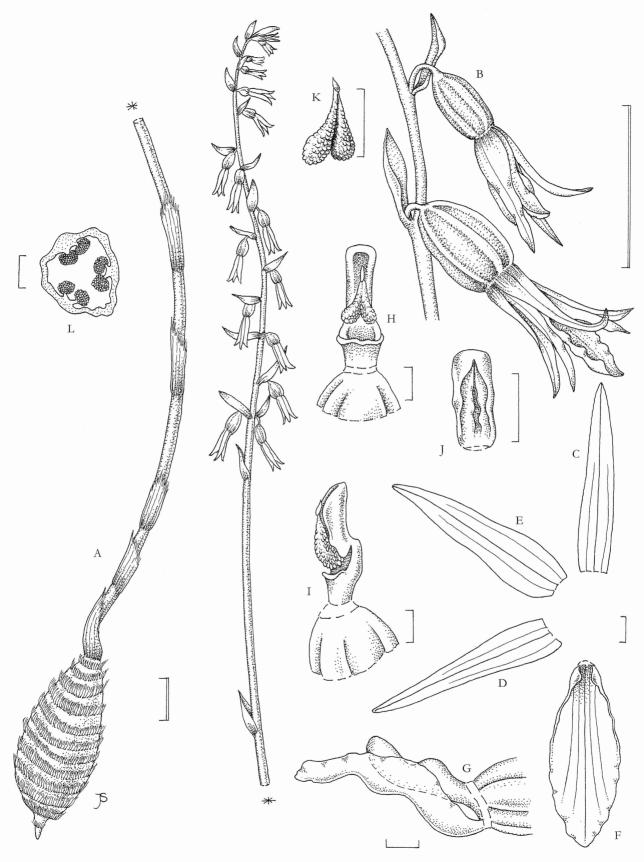


Fig. 395.1. *Stereosandra javanica* Blume. A. Habit; B. Portion of inflorescence; C. Dorsal sepal; D. Lateral sepal; E. Petal; F. Labellum; G. Column and labellum, side view; H. Column, ventral view; I. Column, side view; J. Anther cap; K. Pollinarium; L. Ovary, transverse section. Single bar = 1 mm, 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 Epipogiinae, and Dressler (1993) kept it there. **(PC)**

Taxonomic literature

Comber, J. (1990). Orchids of Java. Bentham–Moxon Trust, Royal Botanic Gardens, Kew.

Garay, L. A. (1986). Olim Vanillaceae. *Botanical Musuem Leaflets*, *Harvard University*, **30**, 223–37.

395. STEREOSANDRA

Stereosandra Blume, *Mus. Bot. Lugd. Bat.*, **2**, 176 (1856). Type species: *Stereosandra javanica* Blume.

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 subpendent, 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

Backer, C. A. and Bakhuizen van den Brink, R. C. (1968). *Flora of Java*, Vol. 3. Walters-Nordhoff, Groningen.

Comber, J. B. (1990). *Orchids of Java*. Bentham-Moxon Trust, Royal Botanic Gardens, Kew.

Seidenfaden, G. and Wood, J. J. (1992). *The orchids of peninsular Malaysia and Singapore*. Olsen & Olsen, Fredensborg.