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BREEDING SYSTEM, POST-POLLINATION GROWTH, AND SEED DISPERSAL IN *GASTRODIA EXILIS* (ORCHIDACEAE)

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ABSTRACT

A Thai population of *Gastrodia exilis* was studied in the period 27 October–6 December 2002. Flowering and fruit set, phenology, morphological size relations, and post-pollination growth were examined in the field, and pedicels and seeds were characterized by SEM. The relative fruit set was found to be 25% on average, both under natural conditions and in bagged specimens. No visiting insects were observed, but the shape of the Lorenz curve and other features argue against autogamy. The breeding system probably involves pollination by minute insects, possibly thrips. Contrary to the peduncle and rachis, the pedicels of pollinated flowers underwent pronounced elongation during fruit ripening. This post-pollination growth takes place mainly by cell elongation and describes a more or less sigmoidal curve. Growth ceases just before dehiscence of the capsule. We propose that pedicel elongation during fruit ripening should be seen as a way of maximizing the exposure of the distal part of the plant to the wind, thus facilitating seed dispersal by "miniature, low-power jactitation".

Key words: orchids, Gastrodiinae, phenology, pollination, fruit set, wind dispersal

INTRODUCTION

THE genus *Gastrodia* R.Br. encompasses 16–17 species distributed from India and Madagascar in the west to eastern Siberia, Japan, the Pacific islands, and Australia in the east. A single species, *G. sesamoides* R.Br., is naturalized in South Africa (LINDER & KURZWEIL, 1999: 354).

Gastrodia belongs to the small subtribe Gastrodiinae, a pantropical alliance of presumably primitive epidendroid orchids (DRESSLER, 1993; FREUDENSTEIN & RASMUSSEN, 1999; MOLVRAY *ET AL.*, 2000; FREUDENSTEIN & CHASE, 2001). The seven genera assigned to this subtribe (*Auxopus, Didymoplexiella, Didymoplexiopsis, Didymoplexis, Gastrodia, Neoclemensia, Uleiorchis*) all consist of achlorophyllous species. In MONTFORT & KÜSTERS' (1940: 621) classification of the Orchidaceae into five types, arranged in ascending order of dependence upon their mycosymbionts, the genera under Gastrodiinae fit type V (the *Corallorhiza* type) – except for the circumstance that they are not universally devoid of roots. Thus, these genera belong to the class of ecophysiologically most reduced orchids and can be considered holomycotrophic (sensu H. N. RASMUSSEN, 1995). For details on

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the ecophysiology of *Gastrodia* and *Didymoplexis*, see KUSANO (1911), BURGEFF (1932), MCLENNAN (1959), and CAMPBELL (1962, 1963, 1964).

KURZ (1866) found the pedicels of *Didymoplexis pallens* Griff. to be highly interesting: "Originally they are only 2–6 lin. long, but when the fruit becomes fully ripe, they elongate and are often twice as long as the whole plant". Subsequently, pronounced elongation of the pedicels during fruit ripening turned out to be widely distributed within the subtribe Gastrodiinae. Up to now, this phenomenon has been reported from taxa currently assigned to *Auxopus* (RIDLEY, 1930; SUMMERHAYES, 1953; HUNT, 1984), *Didymoplexiella* (SMITH, 1920; WOOD *ET AL.*, 1993), *Didymoplexis* (e.g., HEMSLEY, 1883; SMITH, 1905; RIDLEY, 1930; BURGEFF, 1932; SUMMERHAYES, 1953, 1956; HALLÉ, 1977; STEWART & HENNESSY, 1980; LEWIS & CRIBB, 1991; PEARCE & CRIBB, 2002), *Gastrodia* (e.g., SMITH, 1905; CARR, 1929, 1935; BURGEFF, 1932; GARAY & SWEET, 1974; JOSEPH *ET AL.*, 1980), and *Uleiorchis* (COGNIAUX, 1893–1896; HOEHNE, 1945).

Pedicel elongation during fruit development in representatives of the Gastrodiinae has never been described in detail, and its adaptive significance (if any) remains poorly understood. Our general knowledge of the reproductive biology of these plants is very limited. To help remedy these deficiencies, we examined a population of *Gastrodia exilis* Hook.f. (syn. *G. siamensis* Rolfe ex Downie, *G. hayatae* Tuyama) in 2002.

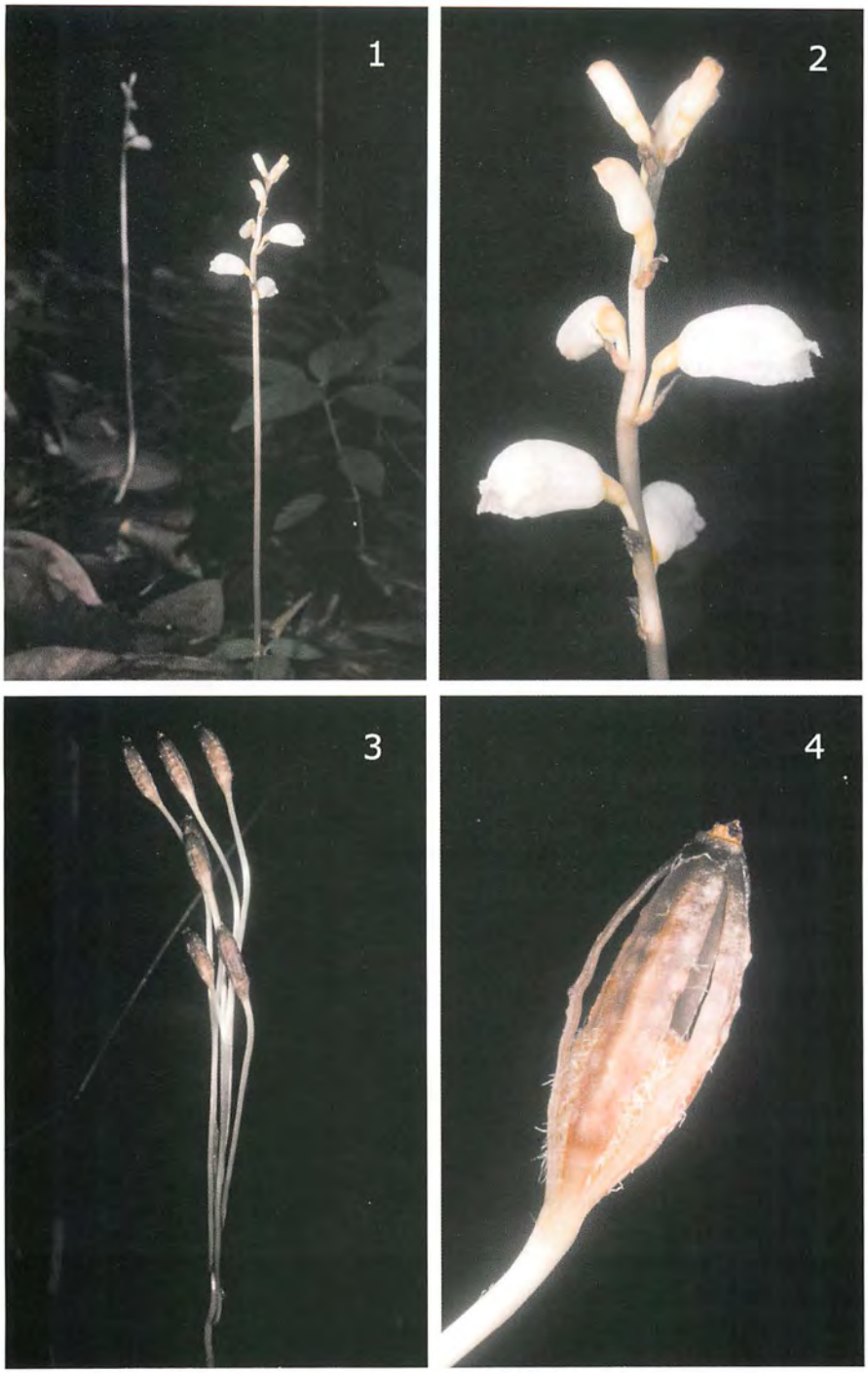
MATERIAL AND METHODS

Study Species and Population

G. exilis is known only from a few scattered localities in India (Kerala, Meghalaya) and Thailand (SEIDENFADEN, 1978: 181; JOSEPH *ET AL.*, 1980; SATHISH KUMAR & SURESH KUMAR, 2001). According to these, it grows among moist decaying leaves on the forest floor at 500–1300 m altitude and flowers during the monsoon.

G. exilis is a 5–30 cm high, delicate, leafless herb (Fig. 1). The 0.5–7 cm long rachis carries 2–13 fragile whitish flowers, each produced on a c. 5-mm long pedicel. The flowers do not emit any scent that can be perceived by the human nose, and they appear to offer no reward to potential pollinators. The sepals and petals are connate for almost their whole length to form a narrowly urn-shaped perianth with slightly erose margins (Fig. 2). The labellum is ovate with slightly erose margins, a pair of almost globose, swollen glands at its base (see transverse section in F. N. RASMUSSEN, 1982: Fig. 64F), and a pair of short keels close to its apex. It is firmly attached to a subclavate, distally winged column. The anther is incumbent and holds four sectile, granular pollinia. It is subtended by a well-developed rostellum ending in a minute viscidium. The receptive part of the stigma is proximal on the column. For informative sections through the column, see F. N. RASMUSSEN (1982: Fig. 64). The clearance between anther and labellum is c. 1(-2?) mm. Unpollinated flowers are soon shed from the nodes on the rachis. A pollinated flower looses its perianth, after which the pedicel elongates markedly (Fig. 3) until the ellipsoidal capsule dehisces by six longitudinal slits (Fig. 4).

The study population was situated near the summit of Doi Pui in northern Thailand, Chiang Mai Province (18° 49' 36.0" N, 098° 53' 15.9" E). The habitat can be characterized as a west-exposed, 10° slope in hill evergreen forest (cf. Table 1) at c. 1550 m altitude.



Figures 1–4. *Gastrodia exilis*. 1. Habit. 2. Rachis with flowers and buds. 3. Rachis with capsules on elongated pedicels. 4. Recently dehisced capsule. – Doi Pui, Northern Thailand, October-November 2002. Photograph by H. A. Pedersen.

Table 1. List of vascular plants occurring in the study area on Doi Pui, November 2002

TREES
Archidendron clypearia (Fabaceae)
Betula alnoides (Betulaceae)
Castanopsis acuminatissima (Fagaceae)
Castanopsis diversifolia (Fagaceae)
Cinnamomum iners (Lauraceae)
Engelhardtia spicata (Juglandaceae)
Eurya acuminata var. *wallichiana* (Theaceae)
Glochidion acuminatum (Euphorbiaceae)
Helicia nilagirica (Proteaceae)
Litsea verticillata (Lauraceae)
Olea salicifolia (Oleaceae)
Phoebe lanceolata (Lauraceae)
Pyrenaria cameliiflora (Theaceae)
Pyrenaria garrettiana (Theaceae)
Quercus semiserrata (Fagaceae)
Rapanea yunnanensis (Myrsinaceae)
Symplocos cochinchinensis s.str. (Symplocaceae)
Turpinia pomifera (Staphyleaceae)

SHRUBS
Ardisia virens (Myrsinaceae)
Daphne sureil (Thymelaeaceae)
Euodia triphylla (Rutaceae)
Maesa montana (Myrsinaceae)
Melastoma malabathricum s.str. (Melastomataceae)
Sarcandra glabra (Chloranthaceae)

SCANDENTS
Mussaenda parva (Rubiaceae)
Rubus ellipticus (Rosaceae)
Smilax sp. (Smilacaceae)

HERBS
Alpinia sp. (Zingiberaceae)
Commelina diffusa (Commelinaceae)
Curculigo gracilis (Hypoxidaceae)
Dendrobium falconeri (Orchidaceae)
Dianella ensifolia (Liliaceae)
Gastrodia exilis (Orchidaceae)
Ophiopogon intermedius (Liliaceae)
Otochilus albus (Orchidaceae)
Piper sp. (Piperaceae)
Polygonum sp. (Polygonaceae)
Strobilanthes consors (Acanthaceae)
Zeuxine nervosa (Orchidaceae)

The plants were growing in black, humus-rich soil with a neutral pH and overlayered with c. 5 cm of litter.

General Notes on Sampling and Data Analysis

The study population was examined on 27 October, 3, 9, 21, 28 November, and 6 December 2002. In an area of approximately 1000 m^2, 23 specimens of *G. exilis* were found and examined during the six days of study. However, since not all specimens were present (or discovered?) from the beginning, and since some of them were damaged (experimentally or by incidents unknown to us) before the end of the study, not all of them could be included in all calculations.

Statistical analyses were performed by the program PractiStat (ASHCROFT & PEREIRA, 2003). Prior to inclusion in statistical tests, all data sets were checked for normality. In cases where normality could not be confirmed, a non-parametric test was chosen.

Flowering and Fruit Set

For 20 specimens, the total number of flowers was established from the number of nodes in the raceme. By the end of flowering, the natural fruit set was determined as the number of capsules produced, and the relative fruit set was calculated. Spearman's rank correlation coefficient was used to test for correlation between the numbers of flowers and capsules produced. Additionally, the specimens were sorted in ascending order by the number of capsules they produced, and the cumulative percent of specimens was then plotted against that of the capsules to form a Lorenz curve (WEINER & SOLBRIG, 1984; CALVO 1990). Throughout the flowering time, we attempted to spot any insects visiting the flowers.

On 27 October, two other specimens, still in bud, were bagged (width of meshes: 1.0 x 1.5 mm). By the end of flowering, the fruit set was checked in order to test the possibility of spontaneous autogamy.

Phenology

The mode and sequence of flowering in a raceme was established by repeated observation of 20 specimens throughout the study period. In each of the 20 racemes, the numbers of flower buds, fresh flowers, and capsules + shed flowers were counted six times.

For each of the 24 capsules that completed development to seed dispersal, the approximate time of dehiscence was noted.

Morphological Size Relations

For each of the 23 specimens, the total number of flowers was established from the number of nodes in the raceme, and the maximum lengths of peduncle and rachis were scored. The three data sets were tested pairwise for correlations (Spearman's rank correlation coefficient), and the best-fitting curves were estimated by linear regression.

For each of the 24 capsules (distributed among 11 racemes) that completed development to seed dispersal, the maximum length of the pedicel was scored and correlated (Spearman's rank correlation coefficient) with the maximum lengths of the corresponding peduncles and rachises. The best-fitting curves were estimated by linear regression.

Post-pollination Growth

All measurements mentioned in this section were taken from plants that developed at least one ripe capsule, when all flowers had already withered. The growth studied thus represented post-pollination growth.

For each of those 11 specimens that developed at least one ripe capsule, the lengths of peduncle and rachis were measured repeatedly until the first day that a capsule was observed to have dehisced. This day was defined as "day 0", and the individual series of measurements were arranged accordingly. For both peduncle and rachis, this resulted in three series of measurements: (i) a series of specimens (n = 2) measured on "day 0" as well as 7 days before; (ii) a series of specimens (n = 4) measured on "day 0" as well as 12, 18, and 25 days before; (iii) a series of specimens (n = 5) measured on "day 0" as well as 8, 15, 27, and 33 days before. For each series, the mean was calculated for each date and, whenever applicable, Pearson's correlation coefficient was calculated to test for correlation between peduncle or rachis length, and time before dehiscence of the first capsule.

For each of the 24 capsules that developed to seed dispersal, the length of the pedicel was measured repeatedly to the day of capsule dehiscence. This day was defined as "day 0", as above, for the following series of measurements: (I) a series of pedicels (n = 3) measured on "day 0" as well as 7 days before; (II) a series of pedicels (n = 5) measured on "day 0" as well as 6 and 13 days before; (III) a series of pedicels (n = 5) measured on "day 0" as well as 12, 18, and 25 days before; (IV) a series of pedicels (n = 11) measured on "day 0" as well as 8, 15, 27, and 33 days before. For each series, the mean was calculated for each date and, whenever applicable, Pearson's correlation coefficient was calculated to test for correlation between pedicel length and time before dehiscence of the capsule.

Scanning Electron Microscopy of Pedicel and Seed

A pedicel from a young capsule that had just begun to develop as well as a pedicel from an old, dehisced capsule were collected and fixed in FAA. From each of these pedicels, a proximal, a median, and a distal section were critical point dried and examined by scanning electron microscopy (SEM). Additionally, two ripe capsules were collected and dried, after which seeds were examined by SEM. The SEM studies were carried out by a Jeol JSM 5410LV microscope after previous coating of the samples with gold.

Table 2. Phenological progression in *Gastrodia exilis* throughout the study period. For flower buds, fresh flowers, and capsules + shed flowers, the mean ± SD is indicated for each date

	27 Oct.	3 Nov.	9. Nov.	21 Nov.	28 Nov.	6 Dec.
# flower buds	1.00 ± 1.59	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
# fresh flowers	1.50 ± 1.79	0.20 ± 0.52	0.10 ± 0.45	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
# capsules + shed flowers	3.30 ± 3.64	5.60 ± 2.85	5.70 ± 2.77	5.80 ± 2.59	5.80 ± 2.59	5.80 ± 2.59
% capsules dehisced	0	13	33	54	54	100

RESULTS

Flowering and Fruit Set

The individual specimens of *G. exilis* produced 2-13 flowers (μ = 5.95; SD = 2.44) and developed 0–7 capsules (μ = 1.50; SD = 1.79). The relative fruit set ranged between 0.00 and 0.67 (μ = 0.25; SD = 0.23). No statistically significant correlation between the numbers of flowers and capsules produced was found ($P > 0.05$). The relative contribution of specimens to the capsule pool of the population can be seen from the Lorenz curve (Fig. 5). No insects were observed to visit the flowers.

The two bagged specimens of *G. exilis* had a relative fruit set of 0.00 and 0.50, respectively.

Phenology

The flowering universally started from the proximal part of the raceme and lasted up to c. 1 week. A survey of the overall progression in flowering is given in Table 2. At the bottom of the table is indicated the progression in fruit ripening, based entirely on those capsules that completed their development to dehiscence (see also Fig. 6).

Morphological Size Relations

The maximum length of peduncle varied between 6.0 and 27.7 cm (μ = 17.05; SD = 5.53), the maximum length of rachis ranged from 0.6 to 7.6 cm (μ = 3.68; SD = 1.93), and the individual specimens carried 2–13 flowers (μ = 5.57; SD = 2.50). All pairwise tests revealed significant, positive correlations ($P < 0.05$). The equations of the regression lines are given in Table 3.

The maximum length of pedicel varied between 2.9 and 16.0 cm (μ = 7.49; SD = 3.73). A significant, positive correlation ($P < 0.05$) was found between the maximum pedicel and peduncle lengths as well as between the maximum pedicel and rachis lengths. The equations of the regression lines are given in Table 3.

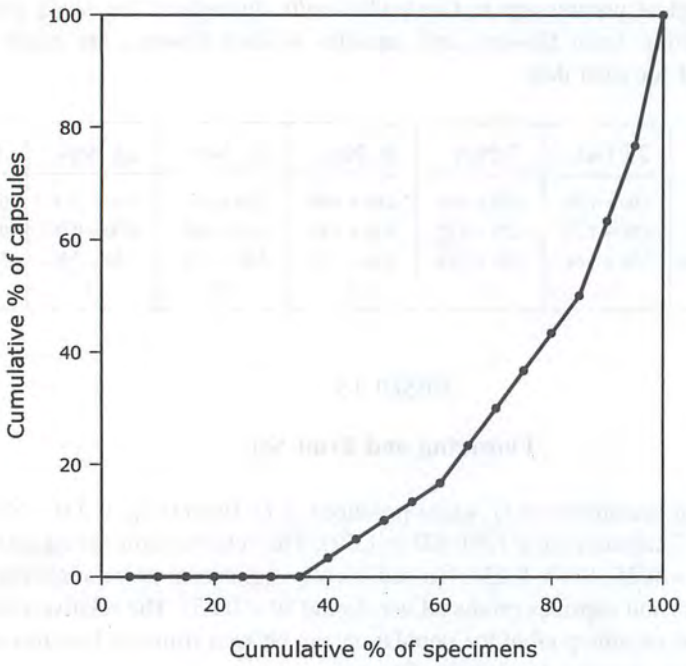


Figure 5. Lorenz curve for *Gastrodia exilis*. A diagonal line from the lower left to the upper right corner would indicate equal contributions of individuals to the capsule pool, while curves deviating from this diagonal line indicate inequality. Equality is usually associated with spontaneous autogamy.

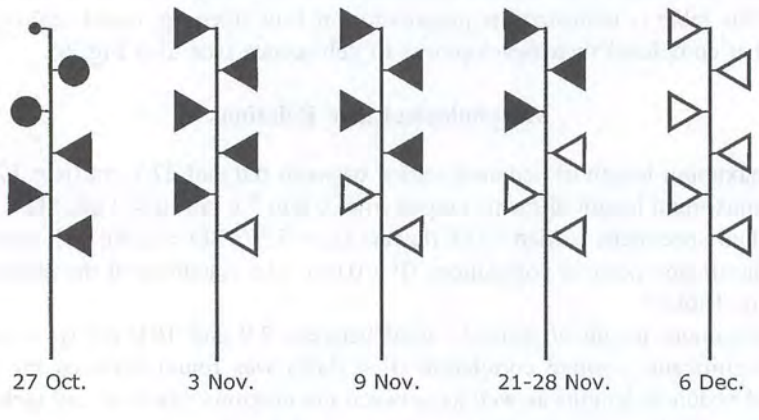


Figure 6. Phenological progression in *Gastrodia exilis* during the period of observation. Small closed circle: bud. Large closed circle: flower. Closed triangle: undehisced capsule. Open triangle: dehisced capsule. It should be borne in mind that this figure deals with phenology only and says nothing about the natural level of fruit set.

Table 3. Equations for linear regression lines – representing positive morphological size correlations in *Gastrodia exilis*

Abscissa (x)	Ordinate (y)	Regression line
Max. length of peduncle (cm)	Max. length of rachis (cm)	$y = -0.42 + 0.24x$
Max. length of peduncle (cm)	Total number of flowers	$y = -0.41 + 0.35x$
Max. length of rachis (cm)	Total number of flowers	$y = 1.94 + 0.98x$
Max. length of peduncle (cm)	Max. length of pedicel (cm)	$y = -3.58 + 0.53x$
Max. length of rachis (cm)	Max. length of pedicel (cm)	$y = 1.28 + 1.38x$

Post-pollination Growth

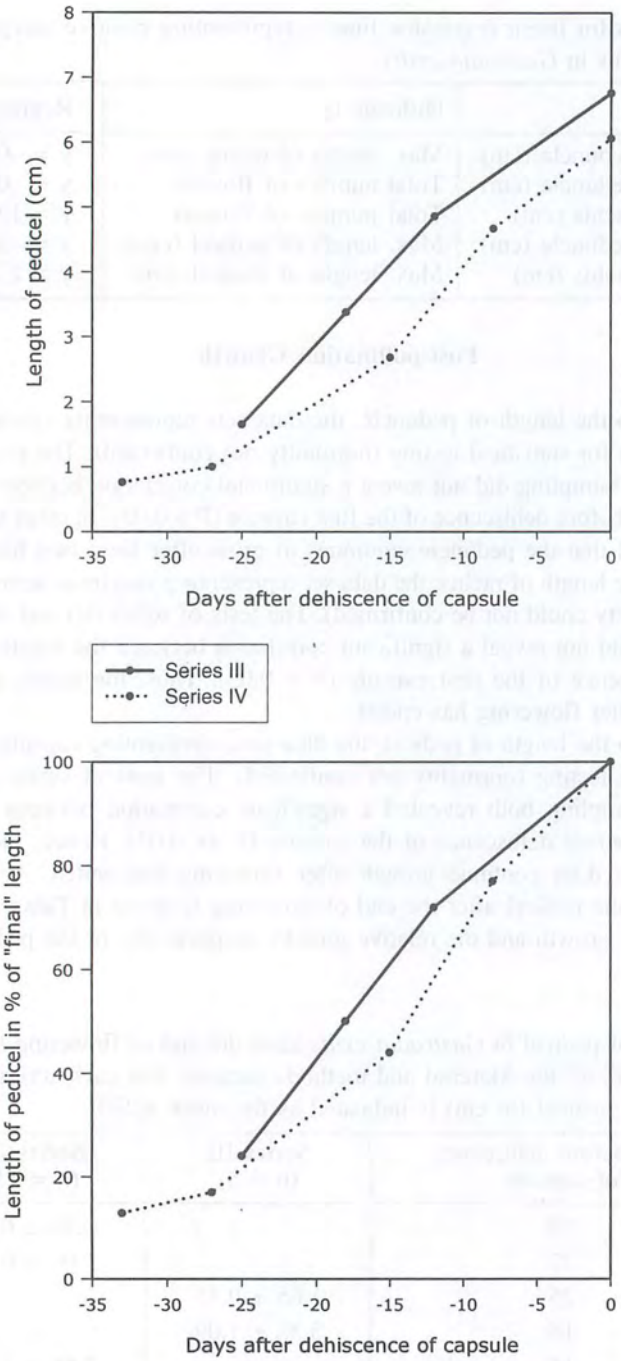
With regard to the length of peduncle, the data sets representing specimen series (i) and (iii) were unfit for statistical testing (normality not confirmed). The test of series (ii) against the time of sampling did not reveal a significant correlation between the length of peduncle and time before dehiscence of the first capsule ($P > 0.05$). In other words, it could not be documented that the peduncle continues to grow after flowering has ended.

Concerning the length of rachis, the data set representing specimen series (i) was unfit for testing (normality could not be confirmed). The tests of series (ii) and (iii) against the time of sampling did not reveal a significant correlation between the length of rachis and time before dehiscence of the first capsule ($P > 0.05$). Thus, the rachis appears not to continue growth after flowering has ended.

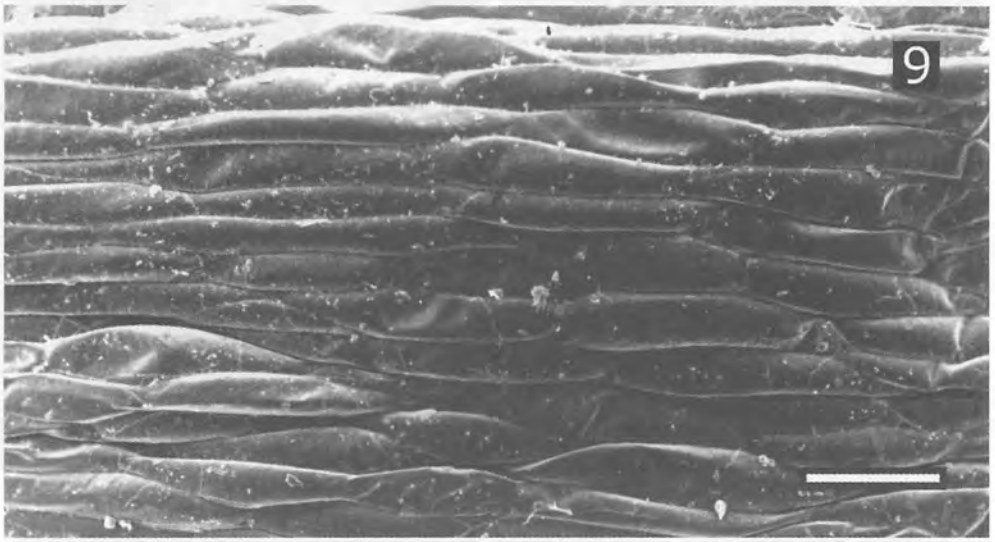
With regard to the length of pedicel, the data sets representing capsule series (I) and (II) did not permit testing (normality not confirmed). The tests of series (III) and (IV) against time of sampling both revealed a significant correlation between the length of pedicel and time before dehiscence of the capsule ($P << 0.05$). Hence, the pedicel of a developing capsule does continue growth after flowering has ended. A survey of the overall growth of the pedicel after the end of flowering is given in Table 4, and Figs. 7 and 8 illustrate the growth and the relative growth, respectively, of the pedicel for series (III) and (IV).

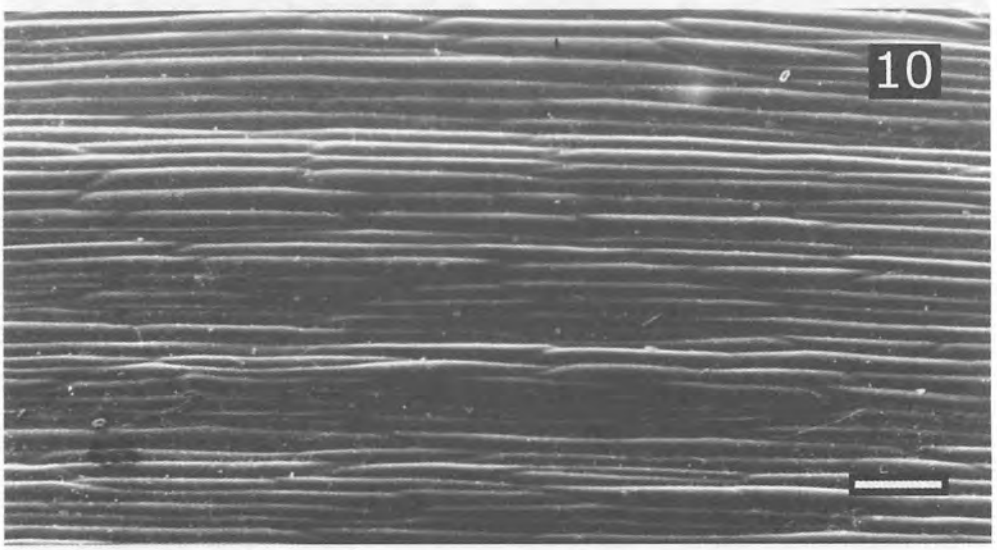
Table 4. Growth of pedicel in *Gastrodia exilis* after the end of flowering (capsule series III and IV, cf. the Material and methods section). For each series and date, the length of pedicel (in cm) is indicated as the mean ± SD

Days before dehiscence of capsule	Series III (n = 5)	Series IV (n = 11)
33	-	0.76 ± 0.34
27	-	1.00 ± 0.39
25	1.65 ± 0.51	-
18	3.38 ± 1.09	-
15	-	2.68 ± 2.19
12	4.86 ± 2.44	-
8	-	4.67 ± 2.55
0	6.76 ± 5.61	6.06 ± 2.23

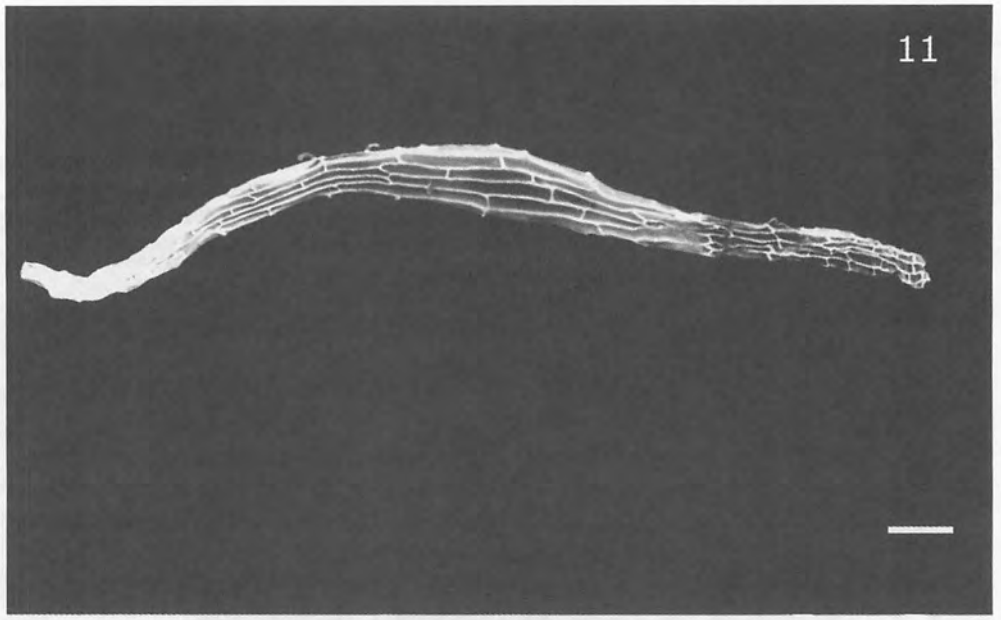


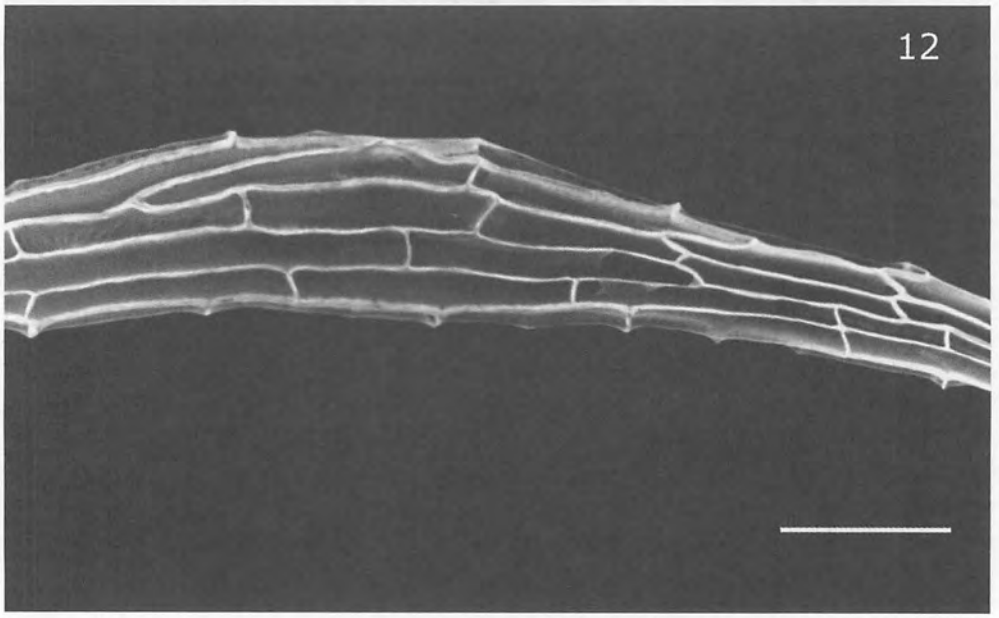
Figures 7–8. Growth and relative growth of pedicel in *Gastrodia exilis* after the end of flowering. 7. Length of pedicel (for each series indicated as means for each date) as function of time. 8. Relative length of pedicel (i.e. in percent of length at the time of capsule dehiscence) as function of time; for each series, the means plotted in Fig. 7 have been transformed to percentages.





Figures 9–10. Epidermis from pedicels of *Gastrodia exilis* depicted by SEM. 9. Young pedicel. 10. Old pedicel. – Scale bars = 100 μm.





Figures 11–12. Seed from *Gastrodia exilis* depicted by SEM. 11. Seed. 12. Median part of testa showing the weak reticulate thickenings of the periclinal cell walls. – Scale bars = 100 μm.

Scanning Electron Microscopy of Pedicel and Seed

The SEM comparisons of sections from a young and an old pedicel revealed the shape of the epidermal cells. The differences were identical for the young/old pairs of proximal, median, and distal sections. In most epidermal cells from the young pedicel, the periclinal wall was linear-oblong in outline (Fig. 9), while it was band-shaped in most epidermal cells from the old one (Fig. 10).

The light brown seed is c. 1.5 mm long and consists of a slenderly ellipsoidal embryo in a thin, papery testa which is slenderly fusiform and somewhat curved (Fig. 11). The testa cells are almost similar and rectangular with weak reticulate secondary thickenings on their periclinal walls (Fig. 12). The junctions of their anticlinal walls do not protrude significantly.

DISCUSSION

Breeding System

Very little is known about the diversity of breeding systems within the Gastrodiinae. CHRISTENSEN (1994: 433) presumed that most species of *Gastrodia* are pollinated by bees. However, bee pollination has only been observed in *G. sesamoides*, which is pollinated by a small xylocopid bee (*Exoneura* sp.) gathering pseudopollen from the labellum (JONES 1981, 1985). CARR (1928) observed fly pollination in *G. javanica* (Blume) Lindl. (sub syn. *G. malayana* Ridl.). Spontaneous autogamy has been described for *G. cunninghamii* Hook.f. (LEWIS & CRIBB, 1989: 48) and *G. verrucosa* Blume (CARR, 1929: 40, sub syn. *G. holttumii* Carr), while STEWART & HENNESSY (1980) noticed cleistogamous pollination in *Didymoplexis verrucosa* J. Stewart & E. F. Hennessy. KUSANO (1915) thoroughly examined the fertilization and embryology of *G. elata* Blume. He demonstrated that the flowers are fully self-compatible and that no parthenogenetic reproduction seems to take place.

G. exilis does not really fit any of the traditionally recognized pollination syndromes (e.g., VOGEL 1954; VAN DER PIJL & DODSON, 1966), but it shares the combination of connate perianth parts, a relatively short, winged column, and granular pollinia with a considerable number of other holomycotrophic species. MOLVRAY *ET AL.* (2000) suggest that this combination of features may well be recognized as a special "achlorophytic pollination syndrome". They regard fungus gnats (Diptera: Mycetophilidae) as the most likely pollinators, but also consider autogamy a possible alternative. The flowers of *G. exilis* correspond reasonably well with flowers of species that VOGEL (1978) reported to be pollinated by fungus gnats. However, no part of the *G. exilis* flower obviously mimicks a fungus, and there appears to be no olfactory mimicry either.

The brief span of flowering, the detection of fruit set in one of the bagged specimens, and the fact that no insect visitors were observed during our study of *G. exilis* indicate that this species might be autogamous. This is supported by the lack of a positive correlation between the number of flowers and capsules produced by the individual specimens. In species pollinated by insects, many-flowered specimens usually produce relatively more capsules than few-flowered ones. In *G. exilis* we even found a positive correlation between plant height (expressed by the lengths of peduncle and rachis) and the number of flowers

(Table 3)—which must further strengthen the floral advertisement in many-flowered specimens (though not towards geophilous insects such as fungus gnats).

On the other hand, a significant number of open flowers (and, hence, a realistic chance to encounter visiting insects) was only found on 27 October (Table 2; Fig. 6), and the well-developed rostellum as well as the basal position of the receptive stigma part (far removed from the anther) seem to obstruct rather than facilitate spontaneous autogamy. Additionally, the overall fruit set in the two bagged specimens was only 25% as opposed to the c. 100% expected for an autogamous species (e.g., CATLING, 1990). Finally, the Lorenz curve for our population of *G. exilis* (Fig. 5) is much more similar to the curves that CALVO (1990) provided for allogamous orchid species than for the autogamous *Oeceoclades maculata* (Lindl.) Lindl.

Our data do not unequivocally reveal the breeding system of *G. exilis*, but they favour a scenario of pollination by insects sufficiently small to force the 1.0 x 1.5 mm meshes surrounding the bagged specimens (a possibility that does not seem unlikely, cf. the very small clearance between anther and labellum). These small insects could be fungus gnats, but a more qualified guess would be thrips (Thysanoptera). Thus, thrips are generally smaller (most species 0.5–4 mm long) and streamlined and seem much better suited to sneak through fine mesh. In some species of thrips the males are known to mediate autogamy in some plants, while the females conduct allogamy. The latter process is usually associated with the females depositing eggs in the flower (e.g., O. HAGERUP, 1950, 1954; E. HAGERUP AND O. HAGERUP, 1953). Consequently, thrips and their eggs should be specifically searched for in flowers of *G. exilis*. Pollination by thrips might well explain the 25% fruit set in bagged specimens and would be consistent with the lack of morphological as well as olfactory mimicry of fungi.

Pedicel Elongation and Fruit Ripening

BURGEFF (1932: 93, 127) mentioned that the elongation of the pedicel in *D. pallens* and *G. callosa* J.J.Sm. is due to intercalary growth, but no information on the nature of this intercalary growth has been published. Our SEM studies of *G. exilis* clearly indicate that strong elongation of the individual cells plays an important part in the remarkably rapid post-pollination growth of the pedicel (Figs. 9–10)—at least as far as the epidermis is concerned. CARR (1929: 39) noticed that the elongate pedicel in *G. verrucosa* is hollow. We found the same condition in *G. exilis*, and suggest that it may be due to longitudinal lacunae appearing in the place of tracheary elements that are destroyed during elongation of the ground tissue.

The post-pollination growth of the pedicel in *G. exilis* seems to follow a more or less sigmoidal curve, i.e. with the growth rate accellerating by the end of flowering and decellerating shortly before dehiscence of the capsule (Figs. 7–8). The nice fit between cease of pedicel elongation and dehiscence of the capsule suggests that the post-pollination growth of the pedicel has an adaptive significance in relation to seed dispersal.

Seed Dispersal

The seed of *G. exilis* (Figs. 11–12) belongs to the so-called *Gastrodia* type (DRESSLER, 1993: 53), the morphology and anatomy of which correspond well with the majority of

orchid seeds. ARDITTI & GHANI (2000) find that the small size of most orchid seeds and their large internal air spaces make them well adapted to wind dispersal, but also recognize that the internal air spaces and the difficult-to-wet surface of the testa facilitates dispersal through small run-off rivulets that may follow rains.

Like most other holomycotrophic orchids, *G. exilis* usually grows in deep layers of decaying leaves, for which reason small run-off rivulets associated with rain are unlikely to occur. Consequently, we do not consider water-assisted dispersal important for this species. This leaves us with wind as the presumedly most important dispersal agent.

HEMSLEY (1883) suggested that the adaptive significance of the elongated capsule pedicel in *D. pallens* is that it "carries up the ripening fruit above the decaying vegetable matter in which the plant grows". CARR (1929: 39) more explicitly suggested that the elongation of the pedicel in *G. verrucosa* "ensures the dispersal of seed to much greater distances than would otherwise be possible, while during flowering the plant is rendered inconspicuous and thus less liable to attack". While it does seem logical that the ability of the species to disperse its seeds over longer distances will increase with increasing height of the point of seed release, the statements of Hemsley and Carr do not explain why each pedicel and not just the peduncle elongates after flowering. In *G. exilis*, post-pollination growth of the peduncle or rachis does not even contribute to the total height of the plant at the time of seed dispersal.

RIDLEY (1930: 16) described the concept of jactitation: "In most small plants the fruits are borne on long peduncles, standing well above the mass of foliage, and frequently the pedicels lengthen in fruit and stand stiffly out so as to expose the fruits more thoroughly to the wind as it sweeps over the open country, downs, meadows or mountain sides and carries the seed some distance. The springiness of the peduncle allows of its being jerked back, after the blast has passed, in such a manner that the seeds are liable to be thrown on all sides of the plant. This is well seen in such tall plants as the Foxglove (*Digitalis*), Evening Primrose (*Oenothera biennis*), and the Mulleins (*Verbascum*), where the tall racemes bend before the wind, throwing the light seed in the direction of the wind, and when the breeze drops and the raceme recovers its erect position, the seeds on the windward side are ejected in the opposite direction". The size and strength of *G. exilis* is evidently very different from the sturdy herbs above, but also the prevailing wind velocities in its habitat are very different—and we will argue that the features characterizing *G. exilis* and its habitat at the time of seed dispersal are consistent with a hypothesis of "miniature, low-power jactitation".

G. exilis (like most other Gastrodiinae) grows under sheltered conditions on the forest floor. Consequently, wind is not a prevailing phenomenon, and even when a breath of air comes around, its velocity is usually very modest. This must be a problem for a small, wind-dispersed herb as *G. exilis*. However, by markedly elongating the pedicels after flowering (Fig. 3), the plant "sets sail" by maximizing the exposure of its distal part to the wind. Due to the delicate, flexible nature of the peduncle and pedicels, this will, on a miniature and low-power scale, bring about the same "jactitation" as described by RIDLEY (1930) for large, rigid herbs from windy habitats (an effect that could not have been achieved to the same extent by elongation of the peduncle). Naturally, the limited elasticity of the delicate peduncle and pedicels does not allow the seeds to be thrown for a long distance, but the process should be seen in coherence with the tiny, balloon-like seeds that (unlike the the large, heavy seeds of the herbs above) are perfectly adapted to wind-

dispersal once they have been ejected from the capsule. It should also be remembered that the height of the point from where the seeds are released is increased by the elongated pedicels.

It is obvious that our hypothesis of "miniature, low-power jactitation" should be tested experimentally. At the same time it should be checked if the physical influence of individual rain drops falling on dehisced capsules or their pedicels can bring about ejection of seeds. Indeed, we suspect that increased exposure of the capsules to rain is an additional adaptive feature of the elongated pedicels—if they were not prolonged, the lower capsules would be placed in rain shelter below the uppermost ones (and the elasticity of the short pedicels would be negligible).

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REFERENCES

ARDITTI, J. AND A. K. A. GHANI. 2000. Tansley review no. 110. Numerical and physical properties of orchid seeds and their biological implications. *New Phytol.* 145: 367–421.

ASHCROFT, S. AND C. PEREIRA. 2003. *Practical Statistics for the Biological Sciences. Simple Pathways to Statistical Analyses.* Palgrave Macmillan, Basingstoke and New York.

BURGEFF, H. 1932. *Saprophytismus und Symbiose. Studien an tropischen Orchideen.* Verlag von Gustav Fischer, Jena.

CALVO, R. N. 1990. Inflorescence size and fruit distribution among individuals in three orchid species. *Amer. J. Bot.* 77: 1378–1381.

CAMPBELL, E. O. 1962. The mycorrhiza of *Gastrodia cunninghamii* Hook.f. *Trans. Roy. Soc. New Zealand, Bot.* 1: 289–296.

CAMPBELL, E. O. 1963. *Gastrodia minor* Petrie, an epiparasite of manuka. *Trans. Roy. Soc. New Zealand, Bot.* 2: 73–81.

CAMPBELL, E. O. 1964. The fungal association in a colony of *Gastrodia sesamoides* R.Br. *Trans. Roy. Soc. New Zealand, Bot.* 2: 237–246.

CARR, C. E. 1928. Orchid pollination notes. *J. Malayan Branch Roy. Asiat. Soc.* VI: 49–73, Pl. V-XVII.

CARR, C. E. 1929. Some Malayan orchids. *Gard. Bull. Straits Settlem.* V: 1–50, Pl. I-XVIII.

CARR, C. E. 1935. Two collections of orchids from British North Borneo Part I. *Gard. Bull. Straits Settlem.* VIII: 165–240.

CATLING, P. M. 1990. Auto-pollination in the Orchidaceae. Pages 121–158 *in* J. Arditti (ed.), *Orchid Biology: Reviews and Perspectives, V.* Timber Press, Portland Oregon.

CHRISTENSEN, D. E. 1994. Fly pollination in the Orchidaceae. Pages 415–454 *in* J. Arditti (ed.), *Orchid Biology: Reviews and Perspectives, VI.* John Wiley and Sons, New York.

COGNIAUX, A. 1893-1896. Orchidaceae. Tribus I. Cypripedilinae, tribus II. Ophrydinae, tribus III. Neottiinae, tribus IV. Liparidinae, tribus V. Polystachyinae, tribus VI. Pleurothallidinae. Pages 1–671, Pl. 1–133 *in* C. F. P. de Martius, A. G. Eichler and I. Urban (eds), *Flora Brasiliensis enumeratio plantarum in Brasilia hactenus detectarum quas suis aliorumque botanicorum studiis descriptas et methodo naturali digestas partim icone illustratas III(IV).* Munich and Leipzig.

DRESSLER, R. L. 1993. *Phylogeny and Classification of the Orchid Family*. Cambridge University Press, Cambridge, U.K.

FREUDENSTEIN, J. V. AND M. W. CHASE. 2001. Analysis of mitochondrial *nad1* b-c intron sequences in Orchidaceae: utility and coding of length-change characters. *Syst. Bot.* 26: 643–657.

FREUDENSTEIN, J. V. AND F. N. RASMUSSEN. 1999. What does morphology tell us about orchid relationships? – A cladistic analysis. *Amer. J. Bot.* 86: 225–248.

GARAY, L. A. AND H. R. SWEET. 1974. *Orchids of Southern Ryukyu Islands*. Botanical Museum, Harvard University, Cambridge Mass.

HAGERUP, E. AND O. HAGERUP. 1953. Thrips pollination of *Erica tetralix*. *New Phytol.* 52: 1–7.

HAGERUP, O. 1950. Thrips pollination in *Calluna*. *Biol. Meddel. Kongel. Danske Vidensk. Selsk.* XVIII(4): 1–16.

HAGERUP, O. 1954. Thrips-pollination in *Hypochoeris radicata*. *Nytt Mag. Bot.* 3: 55–58.

HALLÉ, N. 1977. Orchidacées. Pages 1–565 *in* A. Aubréville and J-F. Leroy (eds), *Flore de la Nouvelle Caledonie et dépendances 8*. Múseum National d'Histoire Naturelle, Paris.

HEMSLEY, W. B. 1883. On the synonymy of the orchidaceous genus *Didymoplexis*, Griffith, and the elongation of the pedicels of *D. pallens* after flowering. *J. Linn. Soc., Bot.* XX: 308–311, Pl. 28.

HOEHNE, F. C. 1945. *Flora Brasílica XII, II (completo). Orchidaceas* [p.p.]. Secretaria da Agricultura, Indústria e Comércio, São Paulo.

HUNT, P. F. 1984. *Auxopus*. Pages 265–267 *in* R. M. Polhill (ed.), *Flora of Tropical East Africa. Orchidaceae (part 2)*. A. A. Balkema, Rotterdam.

JONES, D. L. 1981. The pollination of selected Australian orchids. Pages 40–43 *in* L. Lawler and R. D. Kerr (eds), *Proceedings of the orchid symposium held as a satellite function of the 13th International Botanical Congress, Sydney, Australia 1981*. Orchid Society of New South Wales, Sydney.

JONES, D. L. 1985. The pollination of *Gastrodia sesamoides* R.Br. in southern Victoria. *Victoria Naturalist* 102: 52–54.

JOSEPH, J., N. R. ABBAREDDY, AND K. HARIDASAN. 1980. *Gastrodia exilis* Hook.f. – a rare and interesting orchid from Khasi and Jaintia Hills, Meghalaya, India. *Bull. Bot. Surv. India* 22: 203–205.

KURZ, S. 1866. On the orchidaceous genus *Didymoplexis*, Griff. *J. Bot.* IV: 40–41.

KUSANO, S. 1911. *Gastrodia elata* and its symbiotic association with *Armillaria mellea*. *J. Coll. Agric. Imp. Univ. Tokyo* IV: 1–66, Pl. I–V.

KUSANO, S. 1915. Experimental studies on the embryonal development in an angiosperm. *J. Coll. Agric. Imp. Univ. Tokyo* VI: 7–120, Pl. V–IX.

LEWIS, B. A. AND P. J. CRIBB. 1989. *Orchids of Vanuatu*. – Royal Botanic Gardens, Kew.

LEWIS, B. A. AND P. J. CRIBB. 1991. *Orchids of the Solomon Islands and Bougainville*. Royal Botanic Gardens, Kew.

LINDER, H. P. AND H. KURZWEIL. 1999. *Orchids of Southern Africa*. A. A. Balkema, Rotterdam and Brookfield.

MCLENNAN, E. I. 1959. *Gastrodia sesamoides* and its endophyte. *Austral. J. Bot.* 7: 225–229 and 4 pl.

MOLVRAY, M., P. J. KORES, AND M. W. CHASE. 2000. Polyphyly of mycoheterotrophic orchids and functional influences on floral and molecular characters. Pages 441–448 *in* K. L. Wilson and D. A. Morrison (eds), *Monocots: systematics and evolution*. CSIRO, Melbourne.

MONTFORT, C. AND G. KÜSTERS. 1940. Saprophytismus und Photosynthese I. Biochemische und physiologische Studien an Humus-Orchideen. *Bot. Arch.* 40: 571–633.

PEARCE, N. R. AND P. J. CRIBB. 2002. *Flora of Bhutan including a record of plants from Sikkim and Darjeeling 3(3). The Orchids of Bhutan*. Royal Botanic Gardens, Edinburgh and Royal Government of Bhutan, Thimphu.

RASMUSSEN, F. N. 1982. The gynostemium of the neottioid orchids. *Opera Bot.* 65: 1–96.

RASMUSSEN, H. N. 1995. *Terrestrial Orchids from Seed to Mycotrophic Plant*. Cambridge University Press, Cambridge, U.K.

RIDLEY, H. N. 1930. *The Dispersal of Plants throughout the World*. L. Reeve & Co., Ashford.

SATHISH KUMAR, C. AND P. C. SURESH KUMAR. 2001. *Gastrodia exilis* Hook.f. (Orchidaceae), a new genus and species record for South India. *Rheedea* 11: 49–52.

SEIDENFADEN, G. 1978. Orchid genera in Thailand VI. Neottioideae Lindl. *Dansk Bot. Ark.* 32(2): 1–195.

SMITH, J. J. 1905. *Die Orchideen von Java. Band VI der Flora von Buitenzorg*. E. J. Brill, Leiden.

SMITH, J. J. 1920. Orchidaceae novae Malayenses, IX. *Bull. Jard. Bot. Buitenzorg* 3, II: 15–127.

STEWART, J. AND E. F. HENNESSY. 1980. *Didymoplexis verrucosa* – a new saprophytic orchid from South Africa. *Amer. Orchid Soc. Bull.* 49: 836–842.

SUMMERHAYES, V. S. 1953. African orchids: XXI. *Kew Bull.* 1953: 129–162.

SUMMERHAYES, V. S. 1956. *Didymoplexis africana* Summerhayes. Orchidaceae. Tribus Neottieae. *Hooker's Icon. Pl.* 5, VI: Pl. 3563.

VAN DER PIJL, L. AND C. H. DODSON. 1966. *Orchid Flowers. Their Pollination and Evolution.* The Fairchild Tropical Garden and University of Miami Press, Coral Gables.

VOGEL, S. 1954. Blütenbiologische Typen als Elemente der Sippengliederung dargestellt anhand der Flora Südafrikas. *Bot. Stud.* 1: I-X, 1–338, and 5 pls.

VOGEL, S. 1978. Pilzmückenblumen als Pilzmimeten. *Flora* 167: 329–398.

WEINER, J. AND O. T. SOLBRIG. 1984. The meaning and measurement of size hierarchies in plant populations. *Oecologia* 61: 334–336.

WOOD, J. J., R. S. BEAMAN AND J. H. BEAMAN. 1993. *The Plants of Mount Kinabalu 2. Orchids.* Royal Botanic Gardens, Kew.