THE BIOLOGY OF EPIPOGIUM ROSEUM (D. DON) LINDL.

by

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Epipogium roseum is a tropical, holosaprophytic orchid; it lacks chlorophyll, and its colour on the whole is pale yellow, occasionally somewhat brown. The flowers are also pale yellow, sometimes with pink dots on the lip. The flowering plant consists of a tuber and an inflorescence, roots are lacking. When the flowering is over and the fruits have dehisced, the plant dies. It grows in densely shaded places, rich in humus, in virgin forests, secondary woods, and in bamboo wildernesses. The plant is of frequent occurrence in the so-called forest-garden in the Botanic Gardens at Buitenzorg and in the lower parts of the mountain forest near Tjibodas, up to an altitude of about 1500 m above sea-level. For many years this plant has held my attention. BURGEFF used the photographs I made up to 1928 and part of the material I collected in his publication (1932, p. 77).

GROOM (1895—97, p. 149) and BURGEFF gave extensive descriptions of the anatomy and development, so that I may be brief as to these points. The tuber is flattened dorsi-ventrally, otherwise more or less cylindrical, and may be from 3 to 8 cm long, the transverse section being from 1 tot 2½ cm. On the outer side this tuber is ringed, but the bracts have developed but slightly. At the apical end develops a large bud, from which will grow up the inflorescence. The latter rises above the ground with a nodding top, and in this stage (see *Fig. 1*) the plant is very similar to a *Monotropa Hypopitys* L. that has just come up. Because of this nodding top BLUME (Bijdr. 1825, p. 416) called it *Galera nutans.*

Early in the flowering period the tuber is swollen and full of starch, but when flowering is over and the fruits have emptied themselves, then the tuber shrivels up and becomes hollow. It is a remarkable fact that there is no mycorrhizal fungus in the cells of the tuber. From this it may be concluded that the tuber does not constitute the only stage of development of the plant, see BURGEFF (1932, p. 78).

In Tjibodas in February 1927 I found the younger stage, that consists of a thick, coralloid rhizome with thick offshoots, about 3 cm in diameter. The latter swell up at their top and thus form the anthogenous tubers[1]), see the photographs 76 and 77 in the afore-mentioned study of BURGEFF. In the rhizome are cells with a mycorrhizal fungus. The fact that the offshoots do not become very long and are formed in great numbers explains why so many flowering plants are often found close together in groups, see *Fig. 2.* Isolated specimens are also found, and it is not clear how these develop. One may search the whole neighbourhood without finding another specimen. It may be a tuber which has not flowered together with the other plants, but has remained in the soil for a year. The plants flower mostly in the rainy season.

At first the coralloid rhizomes are closely covered with white hairs, but in the course of further development these disappear. By the side of the thick offshoots which at their top swell up to the anthogenous tubers, there are also thin offshoots, which are no more than 1 mm in diameter. These offshoots arise not only from the coralloid rhizome, but also develop from the anthogenous tubers. They grow above the soil under a covering layer of decaying leaves. They can grow to a length of many decimeters, and branch. They are also known from the European *Epipogium aphyllum* (SCHMIDT) SW., and have been described and figured by IRMISCH (1853, p. 47). But while in the latter they arise from the end-bud of the main and side-axes and rarely from the axils of the bracts, this is the rule in *Epipogium roseum.* In the case of *E. aphyllum* the end-bud of such an offshoot seems to develop immediately into a new rhizome, but in *E. roseum* the development is different. In this species the offshoots consist of internodes, some 1 to 2 cm long, with small bracts at the nodes. In the axil of such a bract arises a small tuber, so that we find series of these small tubers, connected with each other by means of the internodes of the thin offshoots. These tubers consist of short internodes and are ringed, resemble the young anthogenous tubers, and likewise contain much starch. Often they become fairly large, see figure 98 on p. 82 of BURGEFF's work. The tuber represented in the right top corner of the said figure was found with still a short piece of the thin offshoot at the basal end, but I have never been able to find a flowering tuber with still traces of the offshoot. Therefore it is very probable that the small tubers arising at

[1]) I owe thanks to Sir ARTHUR W. HILL, Director, Royal Botanic Gardens, Kew, who kindly helped me to this term.

Fig. 1.

Young and old plants of *Epipogium roseum* (D. DON) LINDL. in the forest-garden at Buitenzorg, November 1931 — Phot. Miss C. C. REIJNVAAN.

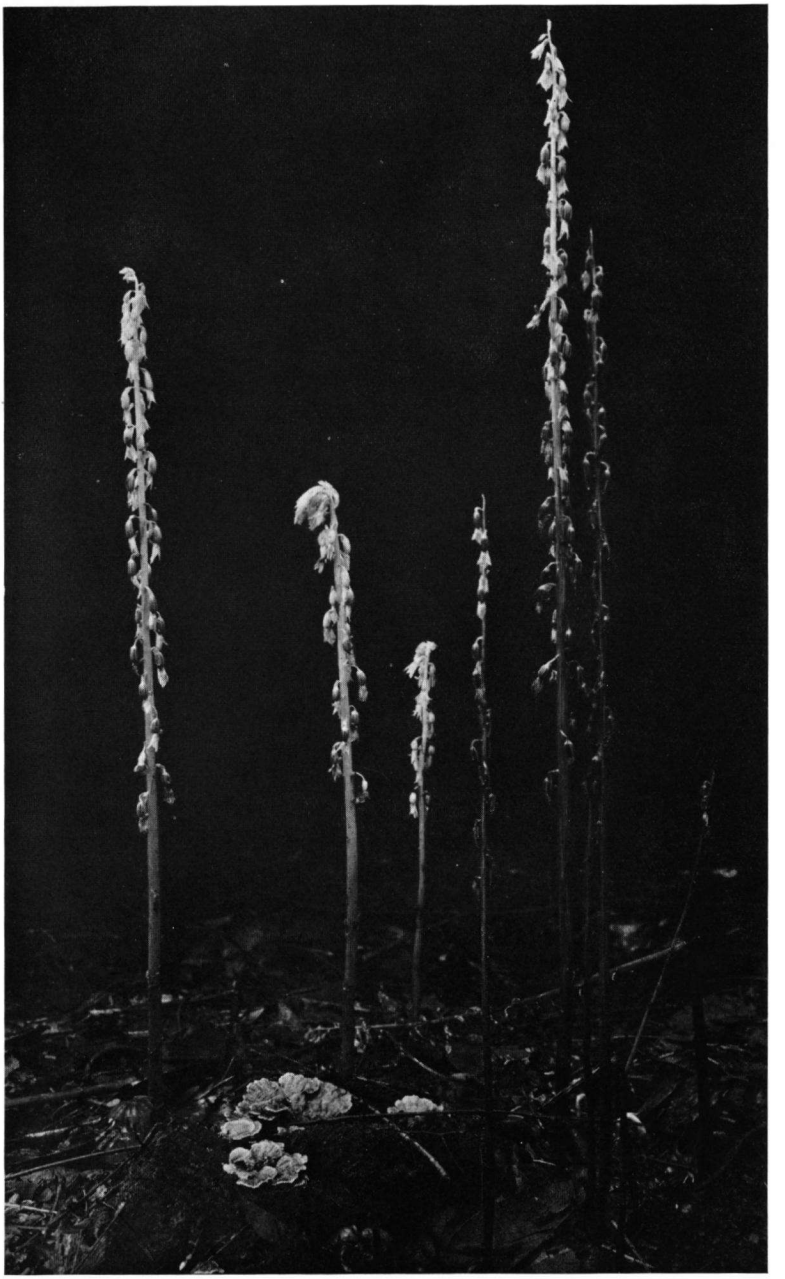

Fig. 2.

A group of older specimens round a tree-trunk, on which a *Polyporacea* has developed. The coralloid rhizome has probably arisen in or against the trunk and the offshoots of the anthogenous tubers have developed from this point.

Buitenzorg, November 1931 — Phot. Miss C. C. REIJNVAAN.

the nodes of the thin offshoots first develop into a coralloid rhizome, and that next the real anthogenous tubers are formed; the entire development, however, is not yet sufficiently clear since the intermediate stages are lacking.

The growth of the inflorescence is very rapid. As said above the inflorescence rises above the ground with the top curved downwards. The flowers are then still very small, and accumulated at the pendent part of the inflorescence. First elongates the erect basal part of the main-axis. Measurements have been made on a great number of specimens in the forest-garden at Buitenzorg as to the rate of growing. For demonstrating this rapid development one specimen will be discussed. The plant was found on the 16th of November 1931. The distance from the soil to the top of the nodding part was then 6 cm, one day later 8 cm, and on November 20th, or 3 days later, it measured 26 cm. At that moment the lower part of the flower-bearing end had stretched, and the distance from the soil to the undermost flower was 23 cm. Twelve flowers were open, and five of them had set fruit. The topmost flowers were still in bud, and attached to the nodding part of the inflorescence. Constantly the stem stretches itself until the whole inflorescence stands erect. On the 21th of November the distance from the soil to the top of the nodding part measured 32 cm, to the lowest flower 25 cm, 16 flowers were open, and 13 of them had set fruit. The growth of the basal part of the inflorescence has now pretty well ended, but with the rest of the plant it goes on for some time longer until all flowers are open. On November 22nd the distance from the soil to the top of the nodding part measured 38 cm, to the lowest flower 25½ cm. At that moment 22 flowers were open and 5 were still in bud. The course of the development is still clearer in the following table.

16	*17*	*20*	*21*	*22*	*November 1931.*
6	8	26	32	38	distance from the soil to the top of the nodding part in cm.
		23	25	25½	distance from the soil to the lowest flower in cm.
		12	16	22	number of open flowers.
		5	13	18	number of fruits.

One specimen that grew too far from the laboratory for regular observations was planted in a flower-pot on November 27th, and thus grown in the conservatory. That first day the distance from the soil to the top of the nodding part was 7 cm, the next day only 7½ cm,

which was probably owing to the transplanting. Two days later, on November 30th, the distance was 18.2 cm and 10 flowers were open. These two examples may suffice for showing how rapidly the development of the inflorescence takes place when once the top has made its appearance above the covering layer of leaves. Nothing is known as yet about the time passing between the arisal of the anthogenous tuber and the development of the inflorescence.

The measurements of the specimens vary considerably. The smallest plant I found was 17 cm high and bore 4 flowers, the largest specimen 65 cm with more than 70 flowers. Those plants have developed most luxuriously which grow in places with a thick layer of humus. Very large specimens were found at Buitenzorg in a pit containing swept-up leaves, and which, when full, had remained undisturbed for a long time.

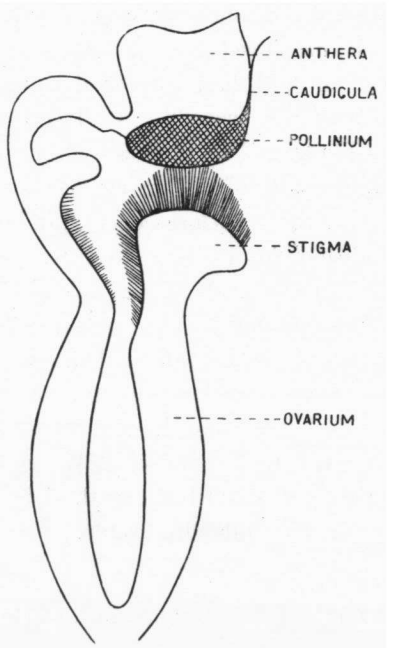

Fig. 3.

Median section of the sexual organs of *Epipogium roseum*, slightly schematic, 15 ×. The ovules have not been marked in the figure.

The flowers are placed in the axils of the bracts by means of filiform pedicels, some 7 mm long; when open they are pendulous and the sepals and petals remain connivent. The latter are linear-oblong, acute, and pale yellow as the rest of the plant. The labellum has a broad basis, which loosely surrounds the column; it is concave and on the upper-side it has two parallel, carunculate ridges. The spur is short and more or less swollen; it contains a small quantity of nectar.

The column is short and has a very convex back, the anther is large, fleshy, and movable since it is attached to the column by means of a short, thin filament. There are two pollinia, each with a long, curved caudicula. The pollinia consist of granular, yellow pollen. The stigma is close to the basis of the column, and consist of two diverging lobes, while a rostellum is wanting, see *Fig. 3*. The stigma is covered with long hairs, as the inside of the column. According to SMITH 1905, p. 62) this plant also occurs with peloric flowers, but I have

not examined this form, since my material only contains normal flowers. Mr M. L. A. BRUGGEMAN, Assistant-Curator of the Buitenzorg Gardens, sent me some fine, preserved material that served my examination well, and for which I tender him my cordial thanks.

The sexual organs represented in the text-figures were taken from a bud which would have opened two days later. One day before there is still a clear, though narrow slit between the underside of the pollinia and the hairs of the stigma-lobes. But as the plant grows older the anther moves towards the stigma, and finally they touch one another. When in this stage, i.e. two days before the flower will open, the anther is removed from the column the pollinia are removed simultaneously, but one day later part of them stick to the lobes of the stigma. The pollen grains are then recognizable by their yellow colour.

This communication has come about 1½ or 1 day before the flower will open. Microtomic sections, which Miss Dr J. A. LELIVELD was so kind as to prepare for me, gave a decisive answer. They showed that in this stage the wall at the underside of the pollinia has burst, and that the pollen grains are beginning to germinate on the moist hairs of the stigma, and that the pollen tubes grow over and across the hairs of the stigma lobes towards the canal of the style. First those grains germinate which lie nearest the hairs, later on also those which are farther away.

When the flowers expand the pollen tubes have penetrated into the cavity of the ovary, and the ovules have then for the greater part been fertilized. The pollination of this plant is consequently clearly autogamous. Although I have watched the flowers often and at all hours of the day I have never seen any visiting insects. Self-pollination of this flower has been mentioned by KING and PANTLING (1898, p. 25), they write: "In expanded flowers, the pollinia "rest directly on the stigma, and become absorbed in it as the plant gets "old." It is not quite clear to me what the writers mean by it. Self-pollination is presumed by SMITH (1928, p. 16) and by BURGEFF (1932, p. 90).

In the course of the first flowering day the ovaria are clearly beginning to swell, and the further development is uncommonly rapid. BURGEFF (1932, p. 90—91) published a table of the development of the flowers and the fruits, which I had made up in October 1918. Afterwards many such notes have been made by my assistant, Miss C. C. REIJNVAAN; they give the same outcome, so that I do not think it necessary to mention them here. The result is that most of the fruits dehisce and that the seeds are scattered on the 3rd or 4th day after the ex-

pansion of the flowers. Very few fruits open on the 5th day. As the pollen tubes begin to grow one day before the expansion of the flowers, there is consequently a period of 5 days between the fertilization and the dispersion of the seeds. The capsule dehisces by six valves.

RIDLEY (1930, p. 40) points to the fact that epiphytic orchids usually have pendulous, and terrestrial species erect capsules. "The "object of this difference between the position of ripe capsules in epi- "phytes and terrestrial plants is clear", he says. In case of terrestrial species a pendulous capsule, particularly when close to the ground, would easily simply drop the seeds on the soil. There are relatively few terrestrial orchids with pendulous fruits, and these are usually large plants with long pedicels, and mostly they occur in open country, so that the capsules are moved by the wind and the seeds can easily be blown away. So far RIDLEY. *Epipogium roseum* is thus an exception to the rule. The capsules of this species which grows in dark places are pendulous; partly they are even situated close to the soil, but the seeds are so very light that this is no drawback. They are easily carried away by the rising currents of air. The wide distribution area actually shows that the dispersal is very effective.

The development of the plant from the moment that the inflorescence comes up till the seed of the topmost fruit has been scattered is also very rapid. A plant with 32 flowers, and which became 42 cm long, lived from November 14th to the 30th. A smaller plant which had 13 expanded flowers and no more than 2 buds on November 16th had dropped on November 23rd. Indeed, a remarkable difference from the long time necessary for the development of the fruits with many other, particularly epiphytic, orchids. In many species this development takes up a whole year.

That the setting and the development of the fruits is a very rapid process in this species is proved by comparing it with the development of another saprophytic orchid, which is also a very tender construction, *Didymoplexis pallens* GRIFF. With this species the pedicel elongates considerably when the fruit is ripe. The development of a specimen is demonstrated in the following table.

2	*6*	*9*	*12*	*16*	*20*	*June 1931.*
7	7	7	7	7	7	length of the peduncle in mm.
1	1.8	2	2.2	2.2	empty	length of the capsule in mm.
1	1	2	2.8	7	drooping	length of the pedicel in mm.

The development of the capsule takes consequently from 17 to 18

days. According to BURGEFF (1936, p. 31) the seeds of *Didymoplexis pallens* weigh 0.45 γ, that is 4½ times as heavy as those of *Epipogium roseum*, and their fall through a tube used by BURGEFF (see below) took 32 seconds.

Although the mycorrhizal fungus has been cultivated by BURGEFF, the seeds of *Epipogium roseum* did not germinate. And thus nothing, indeed, is known about the germination. I looked in vain for seedlings in places where I had often found grown-up plants.

The seeds of *Epipogium roseum* are very small, and consist of a vesicular testa and an embryo, built up of 8 cells. BURGEFF (1936, p. 34, fig. 36) classes the seeds with the group of the net-bladder type ("Netzblasentypus"). The seeds are also uncommonly light. At Buitenzorg they were weighed by F. W. WENT, at that time assistant of the Botanic Gardens. They weighed 0.1 γ, i.e. 10.000.000 seeds to one gramm. BURGEFF (1936, p. 36) experimented as to the velocity of the fall of orchid-seeds. For this purpose he used a glass tube, 1.50 m long and 40 mm wide. The seeds were dropped in the upright tube, and then the time was measured wanted for the seeds to reach the lower end. Seeds of various tropical, terrestrial orchids fell through the tube in from 3.5 to 39 seconds, the seeds of *Epipogium roseum* taking from 90 to 120 seconds over it. BURGEFF stated that it was hardly possible to measure the velocity of the fall of these seeds, because they did not fall through the tube straightaway, but repeatedly got into currents of air by which they were carried upwards. In the habitats one can often observe that, even when the air seems to be completely motionless, after the fruits dehisce the seeds come out like a small cloud and then soon disperse.

Theoretically there is no distance on earth which cannot be bridged by the seeds. In this connection it is certainly noteworthy that *Epipogium roseum* belongs to the species with a wide distribution area.

Owing to the collaboration of the Directors of the Herbaria in Berlin-Dahlem, Buitenzorg, Kew, and Leyden I had the disposal of material collected in many places. To all of them I am grateful for their help.

The plant has been collected in West Africa (Angola, Cameroon), British India (Assam, Sikkim, Nepal, the Deccan, Khasia Hills), Ceylon, Siam, Philippine Islands (Luzon), the Netherlands' Indies, and Australia. In the Island of Malekula of the New Hebrides the plant was found for the first time in 1930. In the Netherlands' Indies the plant was

collected in Sumatra, Borneo, Java, Celebes, the Sangi and Talaud Islands, Boeroe, and New Guinea. It is also known as occurring in the Australian mandatory of this island. Most of the specimens originate from Java, particularly of the western part of this island. In the New Hebrides the plant grows at sea-level, but usually it occurs in the hills or in the lower part of the mountains. The highest place where it has been found in Tjibodas in Java, 1500 m above sea-level.

Unfortunately the labels of the older material do not bear any particulars about the habitat. I found statements about it on the new labels, especially of the material from Java. As habitat is mentioned virgin-forests, places rich in humus, dead tree-trunks, and bamboo-forests. Occasionally it has been noticed in incongenial habitats. J. JESWIET found the plant between grasses in shaded places near Nongkodjadjar (East Java). Miss C. C. RELJNVAAN collected it at the border of a canal in an open place in a wood near Selabintanah (Soekaboemi, West Java). And I saw it in a very uncommon place on Mt. Oengaran in Central Java. Here the plant grew between grass (*Imperata*) on a more or less stony slope, a long stretch away from the edge of the wood. Generally speaking, however, the plant occurs in shaded places, not too dry, and rich in humus.

RIDLEY (1888, p. 394) points at the fact that many autogamous orchids have a wide distribution area, and he and SMITH (1928, p. 5) say that autogamy is a common feature in species lacking the rostellum.

While *Epipogium roseum* occurs in the tropics of the Old World, not only in the warmer regions, but also in the cool mountain forests, there is another species of this genus, *Epipogium aphyllum* (SCHMIDT) Sw., which is indigenous in the temperate zones. It is found in Central and Southern Europe, as far north as Scandinavia, and furthermore in the Caucasus, in Siberia, and in Sikkim. The ranges of the two species overlap in Sikkim-Himalaya, see KING and PANTLING (1898, p. 252). The biology of this plant has been described by various authors, a.o. by IRMISCH (1853, p. 47), ROHRBACH (1866, p. 1), and ZIEGENSPECK (1928, p. 161). ROHRBACH gives an extensive description of the biology of the flower. According to him the pollen cannot reach the stigma without the help of insects; the flower is much larger, more fragrant, more colourful, and wider expanded than those of *Epipogium roseum*. Twice he saw *Bombus lucorum* L. visiting the flowers. But in many of the flowers he examined he rarely found the stigma pollinated. According to ZIEGENSPECK there is no fructification in this plant in

Germany. IRMISCH, who comes to the conclusion that there is never autogamy in this species, has not seen any visiting insects, and has rarely found any ripe fruits. The development seems, as in the case of *Epipogium roseum*, to take place mainly vegetatively.

The two species have many points in common, but as to the biology of the flower they vary considerably.

I am glad in rendering homage to my friend Dr J. J. SMITH with this short article on the special domain of this modest and profound scientist with whom I had the pleasure of collaborating so many years in the Botanic Gardens at Buitenzorg.

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