

Some notes on *Epipactis helleborine* (L.) Crantz ssp. *neerlandica* (Vermeulen) Buttler and *Epipactis renzii* K. Robatsch

JEAN CLAESSENS, JACQUES KLEYNEN & RUUD WIELINGA

Key words:

E. pipactis, *E. helleborine* ssp. *neerlandica*, *E. renzii*, *E. helleborine* ssp. *neerlandica* var. *renzii*, autogamy.

Samenvatting

Epipactis helleborine ssp. *neerlandica* wordt in zijn typische vorm gevonden in kruipwilgvegetaties in de Nederlandse duinen. In dennenbossen in de duinen kunnen planten worden gevonden, die nemen naar *Epipactis helleborine*.

In 1997 vonden de auteurs autogame *Epipactis helleborine* ssp. *neerlandica*. De autogamie werd veroorzaakt door aanhoudend extreem warm zomerweer. In de literatuur wordt vaak verwezen naar het feit dat orchideeën, als de omstandigheden ongunstig zijn, over kunnen schakelen op autogamie. Daardoor kunnen ook veranderingen optreden in de vorm van het zuiltje, die echter als onbelangrijk moeten worden beschouwd. Om die reden wordt een autogame variëteit van *Epipactis helleborine* ssp. *neerlandica*, beschreven als *E. renzii*, teruggezet in de rang van variëteit.

Summary

Epipactis helleborine ssp. *neerlandica* in its most typical form, is found in the *Salix repens*-scrub in the dutch dunes. In the pinewoods plants can be found that show a tendency towards *E. helleborine*. In 1997 the authors found autogamous *E. helleborine* ssp. *neerlandica*. The autogamy was caused by the extremely hot weather during summer. Numerous mentionings in literature indicate, that many orchids are capable of autogamy if condi-

tions are unfavourable. This may also cause changes of the column structure, that must be regarded as of only little importance. Therefore an autogamous variety of *Epipactis helleborine* ssp. *neerlandica*, described as *E. renzii*, is lowered to the varietal rank.

Zusammenfassung

Typische Exemplare von *Epipactis helleborine* ssp. *neerlandica* finden sich vor allem im *Salix repens*-Gebüsch in den niederländischen Dünen. In den Fichtenwäldern der Dünen wachsen Pflanzen die nach *E. helleborine* neigen. Im Jahre 1997 fanden die Autoren autogame *E. helleborine* ssp. *neerlandica*. Die Autogamie wurde verursacht durch das extrem heiße Wetter während des Sommers. In der Literatur gibt es viele Hinweise, daß viele Orchideen auf autogame Vorgänge übergehen können, wenn die Bedingungen für sie zu ungünstig sind. Deshalb können auch Veränderungen in der Struktur des Säulchens auftreten, die als unwichtig betrachtet werden müssen. Deshalb wird eine autogame Varietät von *E. helleborine* ssp. *neerlandica*, beschrieben als *E. renzii*, in den Rang der Varietät verschoben.

1. Introduction

Epipactis helleborine is a species, well known for its broad ecological amplitude as well as for the great variety in shape and form under which it appears. During the last few years there is a tendency for splitting up *E. helleborine* in smaller entities, based on morphological, ecological or pollination biological criteria.

The ecological viewpoint has lead to the description of species or the evolution of the originally given rank. Newly described or rediscovered spe-



Salix repens-scrub in the dunes of Holland.

cies are *Epipactis lusitanica* Tyteca and *E. distans* Arvet-Touvet. The latter species is only recently brought down to the rank of subspecies; its name then is *E. helleborine* ssp. *orbicularis* (Klein 1997).

"Older" taxa are *Epipactis helleborine* ssp. *tremolii* (Pau) Klein, *E. helleborine* ssp. *latina* Rossi & E. Klein and *E. helleborine* ssp. *neerlandica* (Vermeulen) Buttler.

Table 1. Characteristics of *E. helleborine* ssp. *neerlandica*.

	<i>E. helleborine</i> ssp. <i>neerlandica</i> Cl., Kl., & Wie. n = 25	Tyteca n = 16	<i>Epipactis helleborine</i> Cl., Kl. & Wie.	Tyteca
Plant height	(14) 24-44 (50)	19-39	60.9	58
Height 1st leaf-soil	(0.3) 4.4-11.6 (16.4)	0.6-3.6	9.4	9.6
Number of leaves	5-7	5-9	7.7	5-9
Length 2nd leaf	(3.4) 4.2-2.6 (7.2)	3.6-5.2	10.3	7.6
Width 2nd leaf	(2) 2.2-3.6 (4.2)	2.2-3.2	5.2	4.5
Length largest leaf	(3.9) 5.1-8.3 (11.6)	4.3-6.9	12.4	10.4
Width largest leaf	(2) 2.1-3.9 (5.3)	2.1-3.5	4.4	4.6
Inflorescence length	(3.6) 5.8-15.4 (23.3)	7-17	16.7	19
Number of flowers	(10) 15-34 (44)	12-44	36.2	30
Length of 1st bract	(1.4) 1.6-2.8 (4.2)		2.2	

Intervals indicate the mean plus or minus 1 standard deviation, the values between brackets are the lowest and highest value measured.



Epipactis helleborine ssp. *neerlandica* in the *Salix repens*-scrub in the Waterleiding dunes.

We tend to regard all taxa as subspecies of *Epipactis helleborine*, because they are quite distinct in the center of their area of distribution, but there can be found transitional stages towards the nominate species.

The differences between the taxa are mainly morphological, and concern above all the habitus of the plant. On the whole the form of the flowers and the gynostemium is the same, with only one exception. A variety of *Epipactis helleborine* ssp. *neerlandica* that grows in an extreme biotope and that shows a change in column structure, was described as *E. renzii* (K. Robatsch 1988). We will return to this taxon later on.

2. *Epipactis helleborine* ssp. *neerlandica*

Epipactis helleborine ssp. *neerlandica* was originally described as a variety of *E. helleborine* (Vermeulen 1949), then raised to the rank of subspecies (Buttler 1986 in Greuter, W. & Th. Raus ed.) and finally given the specific rank (Delforge, Devillers-Terschuren & Devillers 1991). Little has been published about *E. helleborine* ssp. *neerlandica*, and the elevations of the rank were published without comments.

Kapteyn den Boumeester (1989) critically examined the characteristics of *Epipactis helleborine* ssp. *neerlandica* as given by Vermeulen (1949) as well as some newly added characteristics (Buttler 1986, Kreutz 1987). These characteristics were also adopted by Delforge (1994). In their preliminary key to the species in the *E. helleborine* - *E. atrorubens* group, Tyteca & Dufrêne (1994) use geographical and phenological features and say only very little about the morphology of *E. helleborine* ssp. *neerlandica*.

The uncertainty about what really is *Epipactis helleborine* ssp. *neerlandica* is reflected in the description of a finding of *E. helleborine* ssp. *neerlandica* in sand plains and *Salix repens*-scrub.

Table 2. Comparison between *E. helleborine* ssp. *neerlandica* growing in pine woods and plants growing in sand and *Salix repens*-scrub.

	pine woods		sand plains and <i>Salix repens</i> -scrub	
	n=16		n=6	st. dev.
	mean	st.dev.		
Plant height	38.7	7.5	29.6	12.4
Height 1st leaf-soil	9.6	2.7	5.9	4
Length largest leaf	7.6	1.7	5.4	0.9
Width largest leaf	3.4	0.9	2.5	0.7
Inflorescence length	11	4.3	10.7	5.9
Number of flowers	25	7	22	11

Table 3. Comparison between *E. helleborine* and *E. helleborine* ssp. *neerlandica*.

	<i>E. helleborine</i> n = 16		<i>E. helleborine</i> ssp. <i>neerlandica</i> n = 25	
	average	st.dev.	average	st.dev.
Plant height	60.9	17.8	34.0	9.8
Height 1st leaf-soil	9.4	3.6	8.0	3.5
Number of leaves	7.7	1.2	5.3	0.8
Length 2nd leaf	10.3	2.2	5.4	1.2
Width 2nd leaf	5.2	1.5	3.0	0.6
Length largest leaf	12.4	2.3	6.8	1.6
Width largest leaf	4.4	1.5	3.0	0.9
Inflorescence length	16.7	4.3	10.5	4.7
Number of flowers	36.2	12.4	24.6	9.1
Length of 1st bract	4.9	1.0	2.2	0.6

dica on Usedom (Germany) (Peterek & Todt 1991). The taxon that is described and illustrated in this article, is not identical to the *E. helleborine* ssp. *neerlandica* as it can be found in *Salix repens*-scrub of the dutch dunes. The measures of those plants exceed in all aspects those of the typical *E. helleborine* ssp. *neerlandica*: height 40 - 90 cm; leaves 4-9 cm long, 2-6 cm large; number of flowers 25-60; bracts up to 6 cm long and 2 cm large.

In order to be able to delimitate the typical *Epipactis helleborine* ssp. *neerlandica*, we measured 25 plants from different biotopes. The data were collected from different localities in the Oostduinen and the Waterleidingduinen, two dune complexes between Scheveningen and Haarlem.

In table 1 we compare our findings with those of Tyteca (1995).

When comparing our findings with those of Tyteca, there are above all two characters that differ: the length of the second and of the largest leaf, and the height first leaf - soil. A possible explanation is that Tyteca only examined plants growing in *Salix repens*-scrub, being the most typical (Tyteca & Dufrêne 1994), whereas we also examined plants in pinewoods.

The character: height first leaf - soil seems of very little value, as it is influenced by the herbs in which the plants grow, or by the absence of surrounding vegetation (sand plains). The influence of the biotope is reflected in the values that were obtained, varying from 0,3 up to 16,4 cm!

In table 2 we compare the plants of the typical *neerlandica*-biotopes (open sandplains, *Salix repens*-scrub) with those found in more transitional biotopes (pine forests).

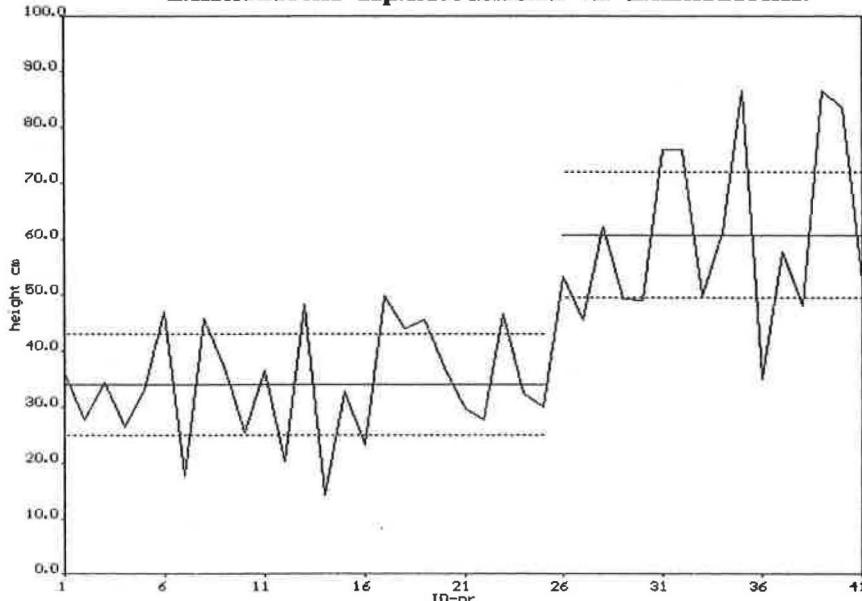
Table 2 demonstrates, that the plants in pine woods and those growing in sand plains and *Salix repens*-scrub differ above all in plant height, length and width of the largest leaf. This conclusion is quite obvious, because plants growing in the shade of trees need a larger leaf surface to ensure an optimal photosynthesis. A quality, not to be found in the table, is the texture and position of the leaves. The typical *neerlandica*-leaves are firm, sloping and often undulate, whereas the plants from the pine-woods have less firm leaves that tend to be placed more horizontally (but still differing from typical *Epipactis helleborine*) and which can be less undulate. They form the transition between *E. helleborine* ssp. *neerlandica* and *E. helleborine*, as pointed out before (Claessens & Kleynen 1991).

In table 3 we compare *Epipactis helleborine* and *E. helleborine* ssp. *neerlandica*. The *E. helleborine* plants were found in parks in the surroundings of The Hague and Zoetermeer.

When comparing the findings there are two characters that differ: the plant height and the length and width of the second leaf.

With a statistical computer programme we made a cusum analysis of the different sets of observations. With a cusum analysis, a number of obser-

E. helleborine ssp. neerlandica vs. E. helleborine.



plant 1 - 25 *E. helleborine* ssp. *neerlandica*
 plant 26 - 41 *E. helleborine*

Area from	Area till	Mean	standard deviation	number of observations	outliers
1	25	34.02	9.96	25	0
26	41	60.88	16.12	16	0

vations can be divided in different groups/areas, which differ significantly of each other.

The graph shows a significant difference between the height of *Epipactis helleborine* and *E. helleborine* ssp. *neerlandica*.

We also used this computer programme to review the other sets of observations. From all the other sets of observations we found significant differences between the length and width of the second leaf only.

The form of the papillae on the leaf margin is a characteristic seldom used. It was recently taken up by Delforge (1997) as a means to separate various taxa. It was also used by Vermeulen as a dis-

criminative feature between *Epipactis helleborine* and *E. helleborine* ssp. *neerlandica*. As it appears from our photographic comparison, there is indeed a clear difference: the papillae of *E. helleborine* ssp. *neerlandica* are smaller ($30 \times 60 \mu$) and form an equilateral triangle whereas the papillae of *E. helleborine* are larger ($60 \times 160 \mu$) and often have their top pointing towards the leaf apex (see page 60). But the comparison of the papillae of all the leaves of one plant shows that even within one plant there is quite a great range. The form of the papillae can help to distinguish between *Epipactis helleborine* and the ssp. *neerlandica*, but the conclusions should be based on a sufficient large number of observations and do not have an absolute character.

Results of the cusum analysis of a number of observations of the height of *E. helleborine* and *E. helleborine* ssp. *neerlandica*.

Epipactis helleborine ssp. *neerlandica*
3 augustus

pine wood, Berkheide - Katwijk
papilles on the leaf margin (125x)



leaf 8



leaf 7



leaf 6



leaf 5



leaf 4



leaf 3



leaf 2



leaf 1

Epipactis helleborine
25 juli 1997

park, The Hague
papilles on the leaf margin (125x)



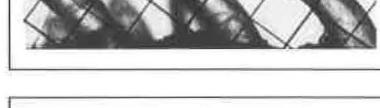
leaf 7



leaf 6



leaf 5



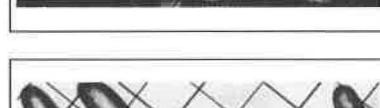
leaf 4



leaf 3



leaf 2



leaf 1



Linksboven:
E. helleborine ssp. *neerlandica* autogamous; pollinies desintegrating.
Pollen grains falling left and right of the viscidium onto the stigmatic surface.
Noordwijkerhout, 16-8-1997
(Jean Claessens)

Rechtsboven:
E. helleborine ssp. *neerlandica* autogamous; anther cap dried out and flattened.
Noordwijkerhout, 16-8-1997
(Jean Claessens)

Linksmiddelen:
E. helleborine ssp. *neerlandica* *Gymnostemium*, old stage, perianth and anther cap dried out. Desintegrated pollinies are lying in the clinandrium as well as scattered over the stigmatic surface.
Noordwijkerhout, 16-8-1997
(Jean Claessens)

Linksonder:
E. helleborine ssp. *neerlandica*
Plant growing in plain sand
flowers partially autogamous
Detail of autogamous flower
Wassenaar, 16-8-1997
(Jean Claessens)

The plants that grow in *Salix repens*-scrub are often difficult to find, because their colour shows a large similarity with that of *Salix repens*: both show a dull, greyish-green colour.

Characteristic are also the firm gutter-shaped, grooved sloping leaves that are often more or less undulate and stem-embracing.

It is obvious that these characteristics are an adaption to the extreme biotope in which *Epipactis helleborine* ssp. *neerlandica* grows. *E. helleborine* ssp. *neerlandica* distinguishes itself in its phenology (late flowering: august up to october).

Epipactis helleborine ssp. *neerlandica* is known up to now to grow with certainty in Holland, Belgium, France (Pas de Calais) and Denmark (Hansen 1963). Findings from Germany are to be examined.

3. Autogamy

Epipactis helleborine ssp. *neerlandica* is normally well visited and pollinated. Up to now only pollinators of the genus *Dolichovespula* were observed (Kapteyn den Boumeester 1989, Peterek & Todt 1991).

The summer of 1997 was extremely hot and dry, and those extreme conditions caused autogamy in *Epipactis helleborine* ssp. *neerlandica*. We were able to observe this phenomena in several plants of different growing places. The tetrads comprising the pollinia lost their coherence and fell left and right of the viscidium onto the stigmatic surface (see color photo's).

A similar process happens e. g. in *Epipactis helleborine* ssp. *orbicularis*. In more temperate regions this taxon is allogamous and well visited by insects (Wucherpfennig 1993). In xerophilous regions it is facultatively autogamous even before anthesis (Claessens & Kleynen 1997).

Other reports of autogamy in *Epipactis helleborine* are to be found in e. g. Hagerup (1952), Reineke (1987), Franz (1995) or Delforge (1996).

Autogamy only takes place incidentally in *Epipactis helleborine* ssp. *neerlandica*, but our observations show that even a plant, well adapted to extreme conditions, can change its mode of pollination if required. Here we have an example of a taxon that moves over towards autogamy, but there are also reports of cases where exactly the



Epipactis helleborine ssp. *neerlandica*.

opposite takes place: now and then plants of *E. muelleri* or *E. leptochila* are found, that possess a well-developed and functional viscidium (Reinhard 1977). In fact, both allogamous and autogamous flowers can be found on one plant. This was also observed in *E. helleborine* (Delforge 1996). Due to Darwins views, autogamy was for a long time considered to be unnatural. But meanwhile there have been numerous reports of autogamy in the orchid family (Reinhard 1977). Most orchids are capable of autogamy under certain conditions; the harder the conditions are (biotope, presence of pollinators), the sooner a plant turns to autogamy as a survival or a conquering strategy. Independence of pollinators offers an opportunity to conquer an ecological niche.

4. *Epipactis renzii*

As mentioned before, a deviant variety of *Epipactis helleborine* ssp. *neerlandica* was described as

E. renzii (K. Robatsch 1988). In his introduction the author questions himself whether changes in the construction of the gynostemium, that cause obligatory or facultative autogamy, justify the description at the specific rank. An other objection, as pointed out by the author, lies in the fact that *E. renzii* and *E. helleborine* ssp. *neerlandica* show great concordance as to their vegetative appearance.

In fact, both taxa actually grow in the same region, *Epipactis renzii* being limited to the extreme biotopes. *E. renzii* can be found in the extreme north of Jutland (Denmark), in a region called the "Danish Sahara". The constantly moving sanddunes and omnipresent winds constitute for insects as well as for plants extremely hostile conditions. Therefore it is not surprising that *E. renzii* has changed to autogamy. This has not only affected the coherence of the pollinia but also the construction of the gynostemium.

The clinandrium is reduced, so that in combination with a large filament, the anther is brought in a position above the stigmatic surface. Thus the pollinia can easily contact the stigma.

There are more cases known where the clinandrium is incompletely developed or disintegrated, as described in e. g. King & Pantling 1898 or in Kirchner 1922a. Catling (1990) states that "in most auto-pollinated orchids, the rostellum (= viscidium - *remark authors*) either does not develop, develops incompletely, or in a few cases disintegrates during flowering, allowing the pollinia and stigma to come in contact".

There are many examples of species that can be both pollinator-dependant or auto-pollinating, depending on various factors of the natural environment.

Well known is the example of the genus *Viola*, where during spring normal chasmogamic flowers are produced, but autogamous as well as cleistogamous flowers are formed during summer.

Among the tropical orchids, *Dendrobium densiflorum* is capable of producing normal chasmogamic flowers as well as more or less cleistogamic ones, both types growing on the same plant at the same time (Uphof 1968). According to the same author "a characteristic of the cleistogamic orchid flower is a very rudimentary rostellum or its absence".

Schlechter (1992) gives a striking example of the changes in the structure of the gynostemium, cau-

sed by cleistogamy: the tropical orchid *Encyclia odoratissima* grows in two varieties. The variety *odoratissima* is allogamous and possesses a monandrous gynostemium, whereas the autogamous and cleistogamous variety *serroniana* shows a triandrous gynostemium.

The changes in the structure of the gynostemium as described above, can be regarded as minor, since they do not involve the creation of an entirely new structure, but only the loss of a structure or the appearance of a primitive condition (Catling 1990). Autogamy is most frequent in relatively primitive groups (Dressler 1993), so it is not surprising to find many autogamous forms among the genus *Epipactis*. Drought and poor nutritions can cause autogamy and even cleistogamy (Uphof 1968), and are in the case of *E. renzii* factors that, together with the quasi-absence of pollinators can cause autogamy. In this process structural changes of the gynostemium are quite logical and of little value.

Species growing near the borders of their range of distribution or growing in an area where insect pollinators are scarce, may reverse to autogamy as a means of survival (Van der Pijl & Dodson 1966, Proctor & Yeo 1973), whereas they have allogamous forms in other areas.

During the last few years new species have been described mostly on the basis of a different column morphology: most plants described were autogamous. It seems to us that too much weight is put upon these changes, whereas there are many examples of changes of column structure within species.

Therefore it seems us more appropriate to describe the taxon from the "Danish Sahara" as a variety of *Epipactis helleborine* ssp. *neerlandica*.

Epipactis helleborine (L.) Crantz ssp. *neerlandica* (Vermeulen) Buttler var. *renzii* (K. K. Robatsch) Claessens, Kleinen & Wielinga comb. et stat. nov.

Basionyme: *Epipactis renzii* K. Robatsch

Linzer Biol. Beitr. 20 (1): 164, 1988.

Literature:

Catling, P. M., 1990. Auto-pollination in the Orchidaceae: p. 123-158 in: Arditti, J. (ed). *Orchid Biology*. Re-

vieuws and Perspectives, V. Timber Press, Portland, Oregon.

Claessens, J., 1992. Enige opmerkingen over de orchideën in Andalusië (Spanje). *Euroorchis* 4:37-51.

Claessens, J. & J. Kleynen, 1991. Het geslacht *Epipactis* in de Benelux: bloembiologische beschrijvingen en soorttypische kenmerken. *Euroorchis* 3: 5-38.

Claessens, J. & J. Kleynen, 1997. Quatre *Epipactis* de la flore de France, 1^o partie. *L'Orchidophile* (128): 167-172.

Claessens, J. & J. Kleynen, 1997. Quatre *Epipactis* de la flore de France, 2^o partie. *L'Orchidophile* (129): 225-229.

Delforge, P., J. Devillers-Terschuren & P. Devillers, 1991. Contribution taxonomique et nomenclaturales aux Orchidées d'Europe (Orchidaceae). *Les Naturalistes belges* 72 (3): 99-101.

Delforge, P., 1994. Guide des Orchidées d'Europe, d'Afrique du Nord et du Proche-Orient. Delchaux & Nestlé, Lausanne-Paris.

Delforge, P., 1996. Note sur deux *Epipactis* de la Région bruxelloise. *Les Naturalistes belges* 77: 218-223.

Delforge, P., 1997. *Epipactis phyllanthes* G. E. Smith en France et en Espagne - Données nouvelles, révision systématique et conséquences taxonomiques dans le genre *Epipactis*. *Les Naturalistes belges* 78: 233-256.

Dressler, R., 1993. Phylogeny and classification of the orchid family. Cambridge University Press.

Franz, G., 1995. *Epipactis helleborine* lus. *flavescens* auf einer Schwermetall-halde in Stolberg (Rheinland). *Ber. Arbeitskr. Heim. Orchid.* 12 (1): 102-105.

Greuter, W. & Th. Raus (ed), 1986. Med-Checklist Notulae 13. *Wildenowia* 16: 103-116.

Hagerup, O., 1952. Bud autogamy in some northern orchids. *Phytomorphology* 2: 51-60.

Hansen, A., 1963. *Epipactis helleborine* var. *neerlandica* in Danmark. *Bot. Tidskr.* 59: 334-337.

Kapteyn den Boumeester, D. W., 1989. *Epipactis helleborine* var. *neerlandica* Vermeulen - problematiek, veldwaarnemingen, bestuivers. *Euroorchis* 1: 93-112.

King, G. & R. Pantling, 1898. The orchids of Sikkim-Himalaya. *Ann. Roy. Bot. Gard. Calcutta* 8: 1 - 342.

Klein, E., 1997. *Epipactis helleborine* (L.) Crantz subsp. *orbicularis* (Richter) Klein comb. nova, eine xerophile Unterart (Orchidaceae - Neottieae). *Phytom* 37(1): 71-83.

Kirchner, O. von, 1922a. Über Selbstbestäubung bei den Orchideen. *Flora* 115: 103-129.

Kreutz, K., 1987. De verspreiding van de inheemse orchideën in Nederland. *Thieme-Zutphen*.

Peterek, M. & K. H. Todt, 1991. Zum Vorkommen von *Epipactis helleborine* (L.) Crantz ssp. *neerlandica* (Vermeulen) Buttler auf Usedom (Nordostdeutschland). *Mitt. Bl. Arbeitskr. Heim. Orch. Baden-Württ.* 23 (3): 510-515.

Pijl, L. van der & C. Dodson, 1966. Orchid flowers. Their pollination and evolution. University of Miami Press, Coral Gables.

Proctor, M. & P. Yeo, 1972. The pollination of flowers. Taplinger Publishing company, New York.

Reineke, D., 1987. *Epipactis helleborine* - ein Beispiel für die Unzulänglichkeit der heutigen Evolutionstheorien? *Mitt. Bl. Arb. Heim. Orchid. Baden-Württ.* 19 (4): 822-834.

Reinhard, H. R., 1977. Autogamie bei europäischen Orchideen. *Die Orchidee* 28: 178-182.

Robatsch, K., 1988. Beiträge zur Kenntnis europäischer *Epipactis*-Arten. *Linzer Biol. Beitr.* 20 (1): 161-172.

Schlechter, R., 1992. Die Orchideen, 3rd Edition. Editors: F. Brieger, R. Maatsch & K. Senghas. Paul Parey, Berlin.

Tyteca, D., 1995. Multivariate analyses of western European allogamous populations of *Epipactis helleborine* (L.) Crantz s.l., with special emphasis on *Epipactis tremolsii* Pau in southeastern France. *Ber. Arbeitskr. Heim. Orchid.* 12(1): 4-49.

Tyteca, D. & M. Dufrêne, 1994. Biostatistical studies of western european allogamous populations of the *Epipactis helleborine* (L.) Crantz species group (Orchidaceae). *Systematic Botany* 19 (3): 424-442.

Uphof, J., 1968. Cleistogamic flowers. *Bot. Rev.* 4: 21-49.

Vermeulen, P., 1949. *Epipactis helleborine* var. *neerlandica* Vermeulen. *Ned. Kruidk. Arch.* 56: 240.

Wucherpfennig, W., 1993. Beobachtungen an vier wenig bekannten autogamen *Epipactis*-Arten Mitteleuropas. *Ber. Arbeitskr. Heim. Orchid.* 10 (2): 9-24.

Jean Claessens
Moorveldsberg 33
6243 AW Geulle

Jacques Kleynen
Pr. Constantijnlaan 6
6241 GH Bunde

Ruud Wielinga
Laan van Poot 262
2566 DB Den Haag