DANISH AND OTHER NORDIC PARASITIC PLANTS

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Contents

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Acknowledments

Cover

The hemiparasitic Toothwort, *Lathraea squamaria,* mostly parasitizes Hazel, *Corylus avellana.* Photo: H. S. Heide-Jørgensen.
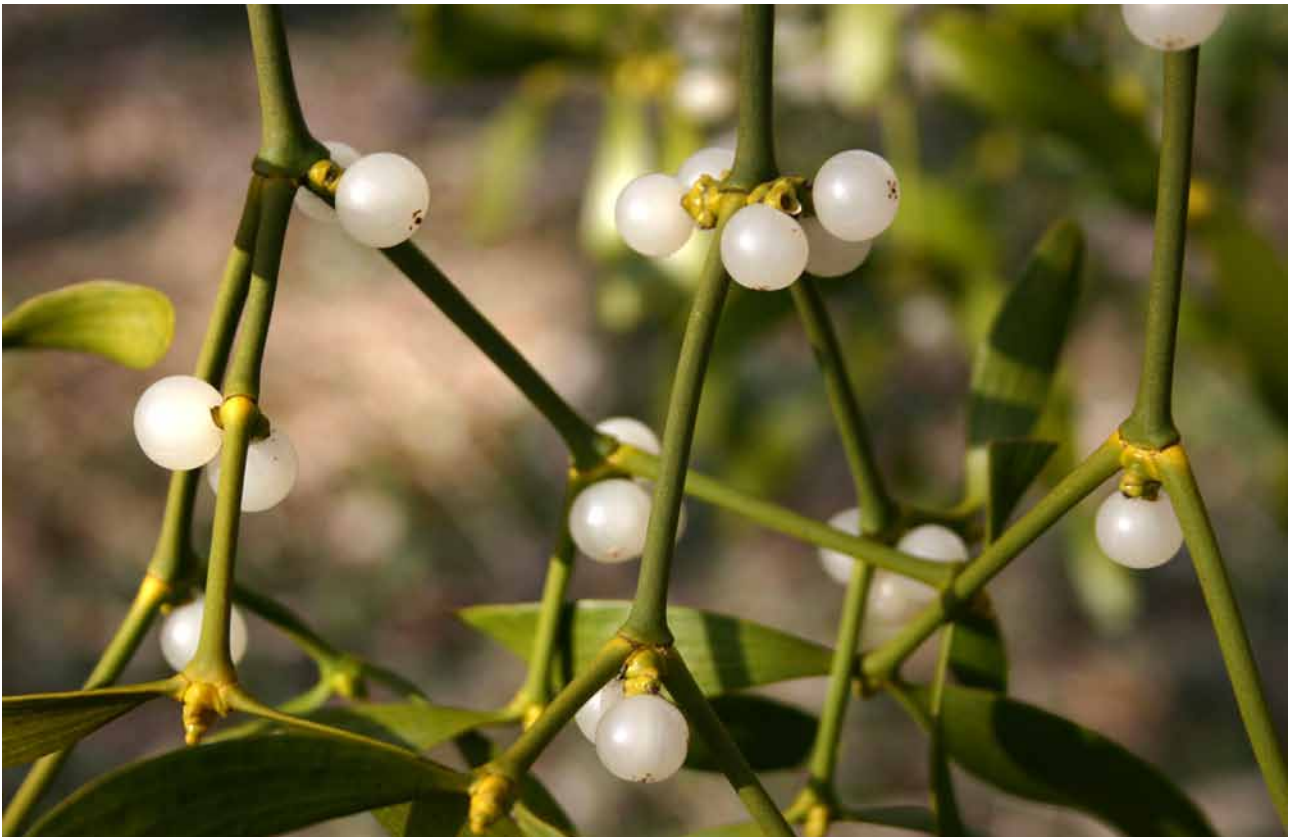
1. European Mistletoe, *Viscum album*, a rare but well known parasite in southern Scandinavia. Photo: H. S. Heide-Jørgensen.

In most people's minds, the term 'parasite' sounds as something very unpleasant and it must be acknowledged that even among flowering plants some of the most harmful weeds in the world in relation to agriculture and forestry are parasitic plants. However, in the Nordic countries parasitic plants cause no harm and that is also true for the majority of the about 4.500 species known worldwide. From another point of view, many parasitic plants exhibit flowers just as beautiful as those of orchids, and their nutrient uptake is as specialised as in carnivorous plants. Furthermore, they are as important elements in various ecosystems as any other organism. The present paper focuses on parasitic plants in the five Nordic countries: Denmark including the Faro Islands and Greenland, Norway, Sweden, Finland, and Iceland. Scandinavia refers to Norway, Sweden, and Denmark. The Scandinavian Peninsula to Norway and Sweden. If the reader wants to know more about harmful parasites, explosive flowers in some Loranthaceae (the mistletoe family) and their pollination and dispersal biology, or about the world's

largest single flower *Rafflesia*, and the smallest and most reduced ones in Balanophoraceae, there is a list of supplementary literature on page 40.

What is a parasitic plant?
Parasitic plants have evolved the ability to obtain water and nutrients from their host plants.They do so by exploiting the organs of the hosts and the most advanced parasites also benefit from the host's photosynthesis. Usually the exploited hosts will grow a little less and produce fewer and/or smaller fruits but in most cases the hosts does not suffer severely. If the host is drained so hard of water and nutrients that it dies, the parasite has removed the basis for its own existence. This, however, is not the case for annual parasites as discussed on page 35.

More precisely a parasitic plant can be defined as a plant that possesses a so-called physiological bridge used for transportation of water and nutrients from the host to the parasite. This bridge is called a haustorium, a term derived from the Latin 'to drink'. The structure and function of

2. Holdfasts of the climbing Japanese Ivy, *Parthenosissus tricuspidata,* attached to brick. Photo: H. S. Heide-Jørgensen.

3. English Ivy, *Hedera helix,* has climbing stems adhering to their support by adventitious roots secreting an adhesive substance. Photo: H. S. Heide-Jørgensen.

the haustorium are discussed on page 27. However, the term haustorium for the connection has through time been used in very different meanings. At first, it was used to describe the physical connection between a Dodder (*Cuscuta*) and its host. Irrespective of the organism in question there is the common feature for haustoria that they are used for the uptake and transport of water and nutrients.

Another problem is the fact that the haustorium is not always visible to the naked eye. After germination and penetration into the host all external signs of the presence of the parasites may have disappeared for a longer period. The entire vegetative body of the parasite may split into cellular strands which are completely embedded in host tissue. It may take months or years before flowers or inflorescences are produced and emerge on the surface of the host. This happens e.g. in Rafflesiaceae, and the most advanced species in the mistletoe family (*Viscaceae*) evolve in the same direction. In such cases a haustorium cannot be identified and one distinguishes between the parts hidden in the host (the endo-

phyte) and the visible part outside the host (the exophyte).

Yet another problem in relation to the parasitic plant definition is that some none-parasites are in tight physical contact with other plants but without absorbing anything from their supporting plant. This, for example, applies in the rain forests to a great number of orchids, many bromeliads (Bromeliaceae), and to other flowering plants besides a great number of lichens, mosses and ferns. Such plants which only use other plants for support are called epiphytes. In climbers such as the Japanese Creeper or Grape Ivy (*Parthenosissus tricuspidata,* Fig. 2) and English Ivy (*Hedera helix,* Fig. 3) special adhesive organs have developed which literally glue the plant to any supporting surface but lack the capability for water and nutrient uptake.

There is one more group of plants which may be mistaken for parasitic plants. These plants were earlier known as saprophytes. They have practically no chlorophyll and hence no photosynthesis. This means that the members depend on having all carbon nutrients supplied by other

4. Yellow Bird's nest (Monotropaceae) is a myco-heterotrophic plant free of chlorophyll. It occurs in beech and pine woods. Photo: H. S. Heide-Jørgensen.

5. Bird's Nest Orchid is not a parasitic plant but a myco-heterotrophic orchid. Photo: H. S. Heide-Jørgensen.

plants. The opinion was that carbon is delivered by fungi which decompose dead organic matter in the soil. The fungi have hyphae connections (mycorrhizae) to the parasite. Examples of this group of plants from the Nordic flora are Yellow Bird's nest (*Monotropa hypopitys,* Fig. 4) and the orchids Bird's Nest Orchid (*Neottia nidus-avis,* Fig. 5), Northern Coral-Root (*Corallorhiza trifida*), and Spurred Coral-Root (*Epipogium aphyllum*). It is possible that some plants are saprophytes in accordance with the original definition, i.e. plants that obtain organic carbon through mycorrhizal connections with fungi. However, the species so far investigated have shown to form mycorrhizae with different fungi that at the same time have mycorrhizae with green photosynthetic plants. The result is a chlorophyll-lacking flowering plant that has the fungal mycelium as a connecting link to a green plant supplying carbon and other important nutrients. Such chlorophyll-free

plants are now called myco-heterotrophic plants. There are about 400 species in nine families.

As mentioned there are about 4,500 species of parasitic flowering plants. They are placed in 20 families or 28 if a recent splitting up of Santalaceae in 8 families is accepted. They occur in all parts of the world except Antarctica and in practically all plant communities except in water. In the Nordic countries inclusive the Faro Islands and Greenland there are about 50 species in four families. In addition there are some introduced species and a number of subspecies.

Two main types of parasitic plants are recognized which each can be divided into two subtypes. The main types are either photosynthetic or non-photosynthetic and they are called hemiparasites and holoparasites respectively. The subtypes are either stem parasites having the haustoria on host stems or root parasites having their haustoria on host roots. Hemiparasites are the most numerous, while there are only about 390

6. Primary haustorium of Ivy Broomrape *Orobanche hederae*. **A**, Tubercle with primary haustorium (arrow) and the base of three inflorescences. The very short and thick roots may develop secondary haustoria. Note the host root is much reduced in thickness beyond the haustorium. **B**, Same tubercle cut parallel to the host root. A complicated vascular system shows faintly in the tubercle. Photo: H. S. Heide-Jørgensen.

6. Primary haustorium of Ivy Broomrape *Orobanche hederae*. **A**, Tubercle with primary haustorium (arrow) and the base of three inflorescences. The very short and thick roots may develop secondary haustoria. Note the host root is much reduced in thickness beyond the haustorium. **B**, Same tubercle cut parallel to the host root. A complicated vascular system shows faintly in the tubercle. Photo: H. S. Heide-Jørgensen.

species of holoparasites. In the Nordic countries the few holoparasites are all root parasites.

Some authors use the terms obligate and facultative parasitic plants. Obligate parasites are only able to survive if they have functional haustorial attachments to hosts. Hence all holoparasites are obligate parasites. The other group may survive without a host, but the parasite grows less vigorously and produces fewer viable seeds. There are some examples of hemiparasites grown under laboratory conditions without a host but since no facultative parasites able to reproduce have been shown in natural plant communities it does not make much sense to use the terms obligate and facultative in parasitic plants. Plants unable to provide themselves with sufficient amounts of important nutrients such as carbon, nitrogen, and phosphor are called heterotrophic plants in contrast to autotrophic plants that are self-sufficient if light, water, and carbon dioxide are available. It is clear that parasitic plants are heterotrophic plants.

Basics about haustoria

The haustorium is the parasite's connection to the host(s). In many parasitic plants and first of all in nearly all stem parasites and holoparasites the haustorium develops from the tip of the primary root. In the more advanced parasites this becomes the only haustorium called the primary haustorium. (Figs. 6-7). Haustoria may also

develop from lateral roots or adventitious roots, and in Dodder (*Cuscuta*) even from stems. Such haustoria are called secondary haustoria. Generally, a primary haustorium may live and function for a long time and often as long as the parasite is alive. By counting annual growth rings in the nearby host wood it has been shown that the American mistletoe *Phoradendron libocedri* may live at least 409 years. Usually secondary haustoria have a shorter life, mayby only a few months. Perennial parasites produce new secondary haustoria in the same or succeeding growth season.

The Nordic genera

There are about 50 species of parasitic plants in the Nordic countries. Their distribution is summarized on page 8. Subspecies are not included.

Thesium - Toadflax

Toadflax belonging to the Sandalwood family (Santalaceae) is a large genus with about 300 species all of which are hemiparasites and root parasites with a variety of hosts. Most species are located in Africa and around the Mediterranean Sea while only two species occur in Scandinavia. *Thesium ebracteatum* has been found near Jægerspris and in Brede Bakker on Zealand but has not been observed since 1900. This species has an eastern distribution in Europe and belongs to the wood-steppe. The other species Alpine Toadflax (*Thesium alpinum,* Fig. 8) was earlier present near Holstebro in Jutland, but occurs today only in southeastern Sweden. Both species prefer dry habitats. Since the nearest locality for *T. alpinum* is 500 km to the south in Germany and the main distribution is in the Alps, the Pyrenees, high levels in the Balkan, and farther East, this species can most likely be considered a relict from the Ice Age. The small white 4-merous flowers are supported by a bract which is displaced along the flower stalk. Each flower produces only one seed dispersed by ants.

8. Alpine Toadflax, *Thesium alpinum,* is a root parasite from the Sandalwood family Santalaceae. In the Nordic countries it is only known from Sweden. Photo: Carol Gracie.

Viscum - European mistletoe

The only other member of the Sandalwood order (Santalales) in the Nordic countries is the hemiparasite European Mistletoe (*Viscum album*) present by the subspecies *V. album* ssp. *album (*Fig. 1) belonging to the family Viscaceae. While *Thesium* has many secondary haustoria on different hosts, *Viscum* has only a primary haustorium.

In past centuries when Denmark was forested the Mistletoe occurred widely but today the original population has disappeared. The last member of this population parasitized a wild apple tree at Store Elmue, South Zealand but it disappeared when the host died about 30 years ago. A small population near Middelfart may be original but in recent years *V. album* has been a popular garden plant and dispersal from gardens by birds is increasing, particularly around Copenhagen. In Norway it is doing well on

Parasitic plants in Nordic countries (Some place names in local language)

Species, Figure	Distribution	Family
Thesium alpinum, 8	Eastern Götaland and Småland in dry habitats.	Santalaceae
Viscum album, 1	Fyn, Zealand, Oslo Fjord, E-Småland, Mälardalen, Gotland	Viscaceae
Cuscuta europaea, 11-13	Southern Scandinavia, not West-Jutland	Convolvulaceae
- epithymum, 54	Southern Scandinavia, but rare	-
- epilinum	Southern Scandinavia, very rare	-
- campestris and C. scandens are introduced and rare		-
Odontites verna	Denmark, South Sweden, and South Norway	Orobanchaceae
- vulgaris, 17	Like O. verna, but also in South Finland	-
- litoralis	Shorelines into the Bothnic Bay	-
Melampyrum pratense, 19, 21	Scandinavia and Finland	-
- sylvaticum, 18	Scandinavia + Finland + NE Iceland. In Denmark: East Jutland	-
- cristatum, 22	Southern Scandinavia + SW Finland, absent from West Jutland	-
- arvense, 23, 60	SW Finland, scattered in SE Scandinavia, absent from Jutland	-
- nemorosum, 20, 63	As M. arvense + a few localities in Jutland	-
Euphrasia rostkoviana	Sweden on calcareous soil - earlier also in Denmark	-
- arctica	West- and North Jutland + Faro Islands	-
- stricta, 15-16	Scandinavia and Finland, but rare in the north	-
- hyperborea	Scattered in Middle and North Scandinavia	-
- nemorosa	SE Scandinavia + Finland, but rare in Norway	-
- frigida, 14	Scandinavia highland + Iceland, Faro Isl., Svalbard and Bothnic Bay	-
- dunensis	Thy and Vendsyssel (Denmark)	-
- micrantha	South Scandinavia + Norway's west-coast, Fare Isl., SW Finland	-
- scottica	Western part of South Norway and Faro Island	-
- bottnica	Northern Bothnic Bay	-
- salisburgensis	Highland in Norway, mainly in the north + Gotland	-
- brevipila	Denmark (Further 3-4 species ? on Iceland and Faro Islands)	-
Parentucellia viscosa, 25	Introduced at Fil Lake, Jutland. Recently found on Zealand	-
Bartsia alpina, 24	North-Scandinavia, Finland, Gotland, Iceland, Faro Isl. + Greenland	-
Pedicularis sceptrum-carolinum, 31D-E	Northern Scandinavia and Finish highland	-
- hirsuta, 27	Northern Norway, Svalbard, and Greenland	-
- oederi, 31C	Highland in Middle Norway and West Sweden	-
- flammea, 28	North-Norway, Island, and Greenland	-
- palustris, 32	Scandinavia and Finland, but sparse in northern highland	-
- sylvatica, 33, 58	Southern Scandinavia	-
- lapponica, 30	Scandinavian highland and Greenland	-
- groenlandica, 26	Only one locality in Præstefjord, West-Greenland	-
- capitata	Inglefield Land in Norrth Greenland	-
- labradorica, 31B	Southern West Greenland	-
- lanata, 31A	Central West Greenland	-
- langsdorfii	Isolated in NW Greenland	-
- albolabiata, 29	Isolated in NW Greenland	-
Rhinanthus serotinus, 35	Southern Scandinavia and most of Finland	-
- minor, 34	South and Middle Scandinavia, Finland, Iceland and Faro Isl.	-
- groenlandicus	Scandinavia highland, Iceland, and SW Greenland	-
- alecterolophus	Introduced in Finland	-
Lathraea squamaria, 36-38	Southern Scandinavia + SW Finland	-
Orobanche purpurea	Öland and north Zealand	-
- alba	Öland and Gotland	-
- reticulata	Middle Sweden, Skåne and one locality on Fyn (Denmark)	-
- minor	South Zealand and Skåne	-
- elatior, 39, 53, 55	Zealand, East Jutland, and Skåne	-
- loricata	Fyn and SE Zealand?	-
- caryophyllacea	Southern Tröndelag (Norway)	-
- hederae, 52, 62 and O. flava, 40-41, 59	Introduced in Denmark	-
- lucorum	Introduced in Denmark on Berberis sp.	-

9. Two male flowers of European Mistletoe, *Viscum album*, with many open pollen sacs. The visiting Ichneumon Fly is loaded with pollen. Photo: H. S. Heide-Jørgensen.

10. A fly visits a female flower of European Mistletoe. Inset: Inflorescence with three female flowers. A liquid covers pistil and the green ring-shaped nectary. Photo: H. S. Heide-Jørgensen.

several islands in the Oslo Fjord and it also occurs in Småland and Øster Götaland, Sweden, where it is protected. In Scandinavia the northern limit is determined by winter temperature and studies of fossil pollen from the late glacial warm period more than 12,600 years ago show that *Viscum album* occurred more than 100 km further north. The present climate change may cause a spreading further north again.

The dichotomous construction of the shoot system with two opposite, leathery evergreen leaves per stem node gives the mistletoe a very distinctive appearance (Fig. 1). In winter, when the host trees are leafless, the Mistletoe lightens up with its green leaves and white berries, and it is no surprise that it has appealed to people's fantasy and superstition. As recent as in the early 19th century even botanists did not understand the biology of the Mistletoe. The view was the Mistletoe developed on twigs of trees almost similar to how warts occur on humans and it was denied the plant could germinate from bird droppings. We now know the seeds are dispersed by birds, the mistle trush in particular. However, the seeds do not pass the alimentary canal, they are wiped off from the beak and glued to the host twig by viscin which is part of the fruit meat.

V. album is dioecious, i.e. having female and male plants (Fig. 9-10), but many others of the about 150 species are monoecious. All species have unisexual flowers. There are four perianth members. In male flowers the anthers are joined with the perianth. The anthers have unusually many pollen sacs each opening with a pore (Fig. 9). The female flower has a single stigma surrounded by a nectar gland (Fig. 10), but the nectar contains very little sugar and the watery nectar may primarily serve to catch pollen which may end up on the stigma when the fluid dries. Pollination is mainly by different small insects but wind pollination may also play a role. The haustorrium, germination biology, and hosts are discussed on page 29-30 and 33, while the influence of the European mistletoe on man is discussed below.

The best known myth about *V. album* is that of Balder's death as told in the Icelandic Eddas (although, there has never been *Viscum* in Iceland). Balder was a son of Odin and Frigg and a favourite of the gods. One night Balder had an evil dream. When his mother heard about the dream she hurried to take into oath all plants, animals, and objects which might be used as a killing weapon. However, Frigg forgot to look up and therefore

11. Greater Dodder, *Cuscuta europaea* ssp. *europaea,* with long reddish twining stems on Tansy (*Tanacetum vulgare*), which is one of its many hosts. Photo: H. S. Heide-Jørgensen.

she overlooked the Mistletoe. The evil god Loki noticed the mistake and prepared an arrow (more likely an arrow head) of the Mistletoe. Afterwards Loki persuaded Balder's brother, the blind Oeder, to shoot the arrow towards Balder on a following day when the gods amused themselves with sport games. The arrow killed Balder but he got a chance to return from the land of the dead if only all would cry over his death. However, Loki refused to cry and the fate of Balder was sealed.

Viscum album also played a role for the Celtic people in the Iron Age. Their priests, the Druids, cut Mistletoes with golden sickles in connection with sacrificing ceremonies in mid-summer. We may here find the origin of the more recent tradition to kiss under the Mistletoe at Christmas. In Sweden one used to collect mistletoes to the mid-summer feast until 1910 when the plant became protected by law. It has also been proposed that the golden twig Aeneas used to open the door to the land of the dead in Vergil's Aneid was a Mistletoe. Instead, this may have been *Loranthus europaeus* since it grows

in Southern Europe. It has yellow fruits but the vegetative parts are similar to *V. album*.

There is a widespread medicinal use of *V. album* but this has often been based on superstition as for example when people in Austria believed a decoction of the berries was useful in contraception. In folk medicine Mistletoe has been used against practically any kind of illness. It may be that a lectin containing extract of the plant has a relieving but not curative effect on certain types of cancer and inflammatory joint diseases. As indicated earlier, mistletoe has a certain importance as merchandise at Christmas. In some places, e.g. in England, this has led to exploitation and has caused the plant to be locally wiped out.

Cuscuta - Dodder

The dodder genus contains more than 150 species. Dodder occurs all over the world except Antarctica and the largest deserts. Five species are found in the Nordic countries, although two of these occur irregularly when seeds are introduced with cultural plants

12. Greater Dodder, *Cuscuta europaea* ssp. *europaea*, with flowers in heads on the narrow windings where haustoria occur. Photo: H. S. Heide-Jørgensen.

13. Same Dodder as in Fig. 12. The flowers are 4-merous and 2 mm in diameter. Photo: H. S. Heide-Jørgensen.

(page 8). Dodder is now and then placed in its own family, Cuscutaceae, but most botanists place Dodder along with the Bindweeds in the Morning Glory family, Convolvulaceae, where Dodder then is the only genus of parasitic plants. All species are stem parasites and most are hemi- parasites but some species including Greater Dodder (*Cuscuta europaea*, Fig. 11-13), have so little chlorophyll that they are considered holoparasites. Their photosynthesis only provides a surplus under laboratory conditions.

The stems of Dodder have only a few small scale-like leaves supporting lateral shoots and inflorescences. The shoot tips perform nutation, i.e. circular movements used to search for hosts to twin around. When a host is found the growth pattern changes and a smaller number of tight coils around the host are produced. The haustoria develop from these coils. After the tight coils Dodder is once again producing loose coils searching for new places where haustoria can develop. It has recently been shown that the twining Dodder stems do not find suitable hosts by chance only. At least some Dodder seedlings can 'smell' in which direction a suitable host is located by detecting aetherial compounds released from the hosts. The American *Cuscuta pentagona* is even able to distinguish between wheat and tomato and prefers the last one as host.

In Nordic botany, it is a tradition to call Dodder left-coiling since the dodder stem turns left around the back of the host stem if you 'walk' along the Dodder stem in its direction of growth. According to the international opinion, Dodder is right-coiling since the stem bends to the right when looked upon in frontal view. The inflorescence of *Cuscuta europaea* is a dense head with 4- or 5-merous small flowers. The corolla is bell-shaped with free segments. The stamens have scale-shaped appendages with unknown function. There is no nectar but pollination is nonetheless assumed to be by small insects. Four seeds may be produced per flower but the number is usually smaller. Dispersal is partly by birds and partly by wind when the capsules open.

Greater Dodder (*Cuscuta europaea* ssp. *europaea,* Fig. 11-13*)* with 4-merous flowers is the most common Dodder species in southern Scandinavia although not present in West Norway and West Jutland. It is mostly found in nitrogen rich and humid habitats. Anoth-

14. Cold Eyebright, *Euphrasia frigida,* from Greenland. Photo: H. S. Heide-Jørgensen.

15. Glossy Eyebright, *Euphrasia stricta* var. *stricta*. Photo: H. S. Heide-Jørgensen.

er subspecies, *Cuscuta europaea* ssp. *halophyta,* with dark red stems and 5-merous flowers parasitizes beach plants in southern Sweden and Finland. Common Dodder is also 5-merous and occurs in two varieties. *Cuscuta epithymum* var. *epithymum* mostly parasitizes Heather, *Calluna vulgaris* (Fig. 54) and in southern localities also Creeping Thyme, *Thymus serpyllum*. The other variety (var. *trifolii*) is introduced from southern countries with Clover (*Trifolium*) seeds and seldom seen. *Cuscuta epilinum* is also introduced from the south. It has yellow stems and was earlier seen in Flax fields.

Broomrape family - Orobanchaceae
Gene-molecular studies in recent years have resulted in many changes in plant systematics. Earlier the Broomrape family (Orobanchaceae) was only represented in the Nordic countries by the genus *Orobanche*. Today all parasitic plants from the Figwort family (Scrophulariaceae) have been transferred to Orobanchaceae which now consists of both hemi- and holoparasitic species.

Orobanchaceae is by far the largest of all parasitic plant families. It has representatives in all cli-matic zones from Tierra del Fuego in South America to the northernmost Greenland. Most species are annuals. A primary haustorium is only produced in a few genera. In the Nordic genera this happens only in Broomrape (*Orobanche*). All other Nordic species produce countless numbers of secondary haustoria connecting to several different hosts. That is an advantage for the nutrition of the parasite since it gets nutrients from a larger root net. Furthermore, different hosts absorb different types and amounts of nutrients and often they produce different amino acids which also may be transferred to the parasite via haustoria. All species are root parasites. The first seven genera described below are hemiparasites with photosynthesis.

Euphrasia - Eyebright
There are about 200 species of eyebright (Figs. 14-15), but many should be considered subspecies since they look very much alike. Therefore the systematics becomes difficult and Danish species are often placed in a collective species *Euphrasia officinalis* sensu lato. The distribution of eyebright is bipolar, i.e. it occurs both on the northern and southern

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16. Glossy Eyebright, *Euphrasia stricta*, with pointed trigger spurs on the anthers. Wilted pistil and open pollen sacs in right flower. Photo: H. S. Heide-Jørgensen.

17. Red Bartsia, *Odontites vulgaris*, is a species closely related to Red Rattle, *O. verna*, with unilateral inflorescence. Bumblebee with yellow pollen basket. Photo: H. S. Heide-Jørgensen.

hemisphere but is absent from the warmer climatic zones. Eyebright occurs in all Nordic countries. The genus name refers to medicinal use against eye diseases in former time. The small flowers are two-lipped and the lower lip is often equipped with coloured stripes functioning as guides for insects towards the nectary and the sexual parts of the flower. The pollination mechanism is quite refined since the anthers are equipped with a spur-like trigger mechanism (Fig. 16). Touching a trigger cause pollen to sprinkle over the insect. Several species display season dimorphism. They occur with an early summer form which do not ramify or only ramifies at the top and a late summer form which ramifies mainly at the lower part of the main stem (Fig. 15). Season dimorphism is considered an adaptation to light condition and competition with other plants on for example grazed or hay meadows. Depending on opinion there are 3-6 species in Denmark and perhaps 15 species in the Nordic countries besides several subspecies and varieties. Species are distinguished mostly on their indumentum. Glossy Eyebright (*Euphrasia stricta* var. *brevipila*) is the most widespread followed by Arctic Eyebright (*Euphrasia frigida*, Fig. 14).

Eyebright can occur in almost any plant community but subspecies and varieties are often associated with specific ecological conditions in geographical small areas. Several species are known only from calcareous ground. As the most fastidious *E. salisbugensis* var. *schoenicola* may be mentioned since it grows on tussocks of Rush, *Schoenus ferrogineus,* in calcareous fens on Gotland. There are 5-6 species on the Faro Islands of which *E. atropurpurea* is endemic, i.e. it only occurs here.

Odontites - Rattle

There are about 30 species in the mainly European genus *Odontites*. The common name Rattle is also used for *Rhinanthus* (page 21). It is closely related to Eyebright (*Euphrasia*) but differ by the long dome shaped upper lip. The Nordic species are all annual herbs with unilateral arranged, paired reddish flowers. The parasite poses no problem in Nordic countries but in South Europe several species are harmful to vegetables. The most common species is Red Rattle (*Odontites vulgaris,* Fig 17). It prefers sunny habitats where, like most root parasites, it attacks many hosts. Beach Rattle (*Odontites litoralis* ssp.

18. Wood Cow-Wheat, *Melampyrum sylvaticum*, prefers shaded habitats. Photo: Niels Faurholt. Inset flowers, Peter Wind.

19. Common Cow-Wheat, *Melampyrum pratense,* with flowers in right angels to the stem. Photo: H. S. Heide-Jørgensen.

litorialis) has darker red flowers than the former species and as the name indicates it occurs along the coasts. It reaches the lowest portion of the Gulf of Bothnia. The subspecies ssp. *fennicus* occurs in Finland. A third species Red Rattle (*O. verna*) is now the rarest but was earlier a common weed in the fields.

Melampyrum - Cow-Wheat
Cow-Wheat contains 35 primarily European species but the genus is also present in North America and China. There are five species in Scandinavia of which Wood Cow-Wheat (*Melampyrum sylvaticum*, Fig. 18) also occurs in Iceland. The common name partly refers to Cow-Wheat being eaten by cows and partly to the resemblance of the seeds to wheat grains. All species are annuals and are considered poisonous due to the glycoside rhinanthin which occur at highest concentration in the seeds. Apparently, cows have no problem with the toxicity. Young plants are considered nutrient rich since they contain the sugar dulcite.

Cow-Wheat has been used to demonstrate that hemiparasites, if necessary, can cover all their needs for water and nutrients from the root system of their hosts. The parasite was established on a suitable host plant in a flowerpot. The roots of the host plant were allowed to grow through the hole in the bottom of the flower pot into another flowerpot. Hereafter only the lowermost flowerpot was watered. Through haustoria placed on host roots in the upper dry flowerpot the parasite received sufficient water and nutrients to complete its life cycle. In nature the roots of the hemiparasite will partly cover the needs for water and nutrients. Cow-Wheat also is an example of hemiparasites having many different hosts from both monocotyledons and dicotyledons.

Wood Cow-Wheat (*Melampyrum sylvaticum*, Fig. 18) and Common Cow-Wheat (*M. pratense*, Fig. 19) are the most common species and known from nearly all parts of Scandinavia. They occur in nearly the same kind of habitats but wood cow-wheat accepts the more shaded and wetter conditions. Common Cow-Wheat has larger, often whitish flowers arranged perpendicular to the stem while flowers are more erect in Wood Cow-Wheat. The other three species have a south-eastern distribution in the Nordic countries and have an outstanding appearance with coloured bracts in the inflorescence. In Denmark *Melampyrum nemorosum* (Figs. 20 and 63) is the rarest of the species and on disappearing. However, in Brede Bakker on Zealand it is recov-

20. *Melampyrum nemorosum.* Note the colour change from yellow to red in older flowers. Photo: H. S. Heide-Jørgensen.
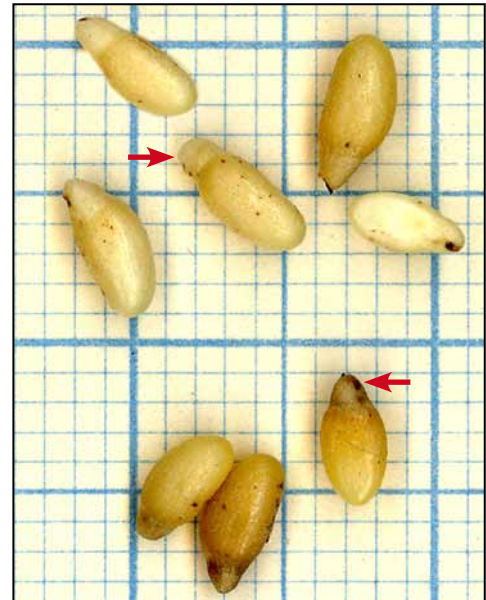
21. Common Cow-Wheat, *Melampyrum pratense.* Seeds with elaiosome (arrow). Photo: H. S. Heide-Jørgensen.

ering due to nature conservation. It demands well light-exposed woods. Field Cow-Wheat (*Melampyrum arvense*, Fig. 23) is a grassland species also occurring along road sides. Earlier it caused some harm in fields and if too many of the grain-like seeds occurred in the flour the bread turned sour and unhealthy to eat. Crested Cow-Wheat (*M. cristatum*, Fig. 22) occurs mainly in coastal undergrowth and, as the previous species, often on calcareous ground.

Cow-Wheat produces nectar in the flowers and in some species also in extra floral nectaries on the lower leaves. These nectaries may serve to keep away ants from the flowers. In several species a change in flower colours occur with age, in *Melampyrum nemorosum* and *M. cristatum* from yellow to red (Figs. 20 and 22). Such colour changes are interpreted as a signal to the pollinator that it is not worth visiting the flower since nectar production ceased after pollination has already taken place during a former visit. Both plant and pollinator take advantage of the system. The pollinator does not use unnecessary energy to visit a flower which no longer contain food, and the plant obtain improved security that the pollinator reaches more flowers in the optimal state for pollination. This will increase seed production. The single flower is also allowed to change its energy use from nectar production to seed development. The value of colour change is

22. Crested Cow-Wheat, *Melampyrum cristatum.* Note the colour change of the lip in older flowers. A Rattle, *Rhinanthus serotinus,* is seen in the background. Photo: H. S. Heide-Jørgensen.

23. Field Cow-Wheat, *Melampyrum arvense*, along a roadside. In the background Viper's Bugloss, *Echium vulgare*. Photo: H. S. Heide-Jørgensen.

particularly well documented in bird pollination. How relevant this is to *Melampyrum* is unknown.

The seeds are equipped with an elaiosome (Fig. 21), i.e. an oil-rich appendage attractive to ants. They transport the seeds to their nests and serve in this way for dispersal of the seeds. Germination takes place in the autumn when the radicle emerges and ramifies, but the cotyledons stay inside the seed coat until spring. As mentioned for Eyebright (*Euphrasia*), *Melampyrum, Rhinanthus*, and *Pedicularis* produce genetically based seasonal forms, so-called seasonal dimorphism.

Bartsia - Bartsia

The genus *Bartsia* has about 60 species with mainly arctic-alpine distribution. Therefore *Bartsia* is not present in Denmark today but occurs in the other Nordic countries and Greenland, however, only with one species *Bartsia alpina* (Fig. 24). This species is the most widespread in the genus. It is light demanding and occurs mainly above the tree-limit. An isolated population in Gotland is considered a late-glacial relict. Most

24. Alpine Bartsia, *Bartsia alpina*, is an arctic-alpine hemiparasite. Photo: Carol Gracie.

25. Yellow Bartsia, *Parentucellia viscosa*, is a rare, introduced plant in Scandinavia. Photo: Forest and Kim Starr.

26. The upper lip forms a twisted beak in the Elephant's Head, *Pedicularis groenlandica*. Photo: Carol Gracie.

likely it was the advance of the forest that drove away *Bartsia alpina* from Denmark.

Bartsia alpina is perennial with a branchy rhizome. It has different Sedges (*Carex*) and dicotyledonous species as hosts inclusive the Common Butterwort (*Pinguicula vulgaris*), which, however, has a weak root system as usual for carnivorous plants. It has been shown that the roots of *Bartsia alpina,* like other plants growing in unstable arctic soils, have a high degree of elasticity and tensile strength. The flowers produce nectar and are pollinated by different bumblebees. In Sweden, the seeds, while they still are inside the capsule, are attacked by larvae of the leaf roller *Aethes deutschiana* and the dung fly *Gimnomera dorsata*. In return, the larvae of both species are attacked by the parasitic wasp *Scambus brevicornis*.

Parentucellia - Yellow Bartsia
Yellow bartsia, *Parentucellia viscosa* (Fig. 25), is closely related to *Bartsia*, but it is annual as the

only other species in the genus *Parentucellia latifolia*, which occurs on sandy and gravelly localities from France to Turkey. Yellow Bartsia is native on nutrient pure soils in South- and Western Europe but it is introduced in many countries from Australia to Hawaii including a few localities on Zealand and in South Sweden.

Pedicularis - Lousewort
Lousewort is the largest genus in the broomrape family with nearly 800 species including many newly described species from China. Lousewort occurs only in the northern temperate and arctic zone and no other of our genura is represented as far north as the northernmost part of Greenland. The ability of Lousewort to survive in a high arctic climate may be related to the fact that it is the only parasitic genus with vegetative propagation from rhizomes. It is known that asexual reproduction becomes more and more important with increasing latitude, probably because the number of

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27. Hairy Lousewort, *Pedicularis hirsuta*, in high arctic Greenland. Photo: H. S. Heide-Jørgensen.

28. Upright Lousewort, *Pedicularis flammea*. See distribution page 8. Photo: H. S. Heide-Jørgensen.

suitable pollinators simultaneously decreases. The common name Lousewort alludes to its use as a decoction used to treat livestock for lice once in older times. The allusion to lice also appears from the scientific name *Pedicularis* since *pediculus* means lice in Latin.

In some species the flowers are strongly asymmetric, since the upper lip is prolonged into a more or less curved beak. The curve is most pronounced in the Elephant's Head, *Pedicularis groenlandica,* having a beak up to two cm long (Fig. 26). Therefore this species was earlier placed in a separate genus *Elephantella*. Since the valid Latin name is *Pedicularis groenlandica* one might think the species is characteristic for Greenland. However, it is only known from one locality, Præstefjord in West Greenland. The main distribution is in Canada and the northern US but the type specimen originates from Greenland.

Among the other arctic species Hairy Lousewort (*Pedicularis hirsuta*, Fig. 27) deserves mention. It

reaches the northernmost point of Greenland and Svalbard. It mainly occurs in dwarf-shrub heaths and species of Willow (*Salix*) are considered the most important hosts. Snow hares eat the infructescence but it is not known if they also disperse the seeds. Southern species of Lousewort are equipped with elaiosomes and adapted to ant dispersal. Little is known about the presence of elaiosomes in the arctic species. It is likely elaiosomes are reduced in arctic species or not developed since there are no ants in Greenland and high-arctic regions. However, ants were present in Greenland about 2.4 million years ago. Upright Lousewort, (*Pedicularis flammea*, Fig. 28) reaches the Thule district and similar latitude on the east coast. It is the only Lousewort in southernmost Greenland and the only one on Iceland. It prefers humid habitats and demands snow cover during winter. Both *P. hirsuta* and *P. flammea* occur in northernmost Scandinavia.

Snow Geese are most likely responsible for the dispersal of White Lipped Lousewort (*Pedic-*

29. This White Lipped Lousewort, *Pedicularis albolabiata,* was most likely dispersed from Canada to northern Greenland by Snow Geese in the 20th century. Photo: H. S. Heide-Jørgensen.

30. Lapland Lousewort, *Pedicularis lapponica,* occurs in the southern high arctic Greenland and in Scandinavian highlands. Photo: H. S. Heide-Jørgensen.

ularis albolabiata, Fig. 29) from Canada to NW-Greenland at places such as Qaanaaq, where the geese are nesting and foraging during migration. Lapland Lousewort (*Pedicularis lapponica*, Fig. 30) with relatively large flowers is fairly common in lush dwarf-bush heaths on both the west and east coast of the middle part of Greenland as well as in large parts of the Scandinavian Peninsula.

Woolly Lousewort (*P. lanata*, Fig. 31A) and Labrador Lousewort (*P. labradorica*, Fig. 31B) occur in Greenland only on the west coast. Woolly Lousewort has a particularly thick and stout yellow tap root which is edible. It occurs both on wet and dry soil and sometimes it appears so isolated that this species and perhaps other arctic Louseworts may not be real hemiparasites. This brings us back to the question if there are facultative parasites in nature but, as mentioned, none has so far been proven to exist (see page 5-6). Haustoria have not been demonstrated with certainty in all arctic species of

31. Different Louseworts. **A,** Woolly Lousewort, *P. lanata,* occurs in West Greenland. **B,** Labrador Louse-wort, *P. labradorica,* occurs in SW Greenland. **C,** Oeders Lousewort, *P. oederi*, Norway. **D-E,** The King's Sceptre, *P. sceptrum-carolinum* is the tallest species of Lousewort in Scandinavia (up to 80 cm high). The corolla tube is closed when the plant is blooming. Only large bumblebees can pollinate the flower. Photo: A-B, H. S. Heide-Jørgensen. C-E, Egil Michaelsen.

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32. Marsh Lousewort, *Pedicularis palustris* ssp. *palustris*, with a two-lipped calyx (inset) ramifies above. Photo: H. S. Heide-Jørgensen.

33. Marsh Lousewort, *Pedicularis palustris* ssp. *palustris*. Note inflated calyx in the fruiting stage (inset). Photo: H. S. Heide-Jørgensen.

Lousewort. The root system in Willow and Dwarf Birch (*Betula nana*) particularly are very extensive and since the haustoria of Lousewort generally are less than one mm in diameter and are placed on the finest host roots, they are easily overlooked.

Oeders Lousewort (*Pedicularis oederi*, Fig. 31C) is named after the botanist Georg Oeder. It occurs on calcareous ground in southern Scandinavia but is rare. The 80 cm high King's Sceptre (*Pedicularis sceptrum-carolinum,* Figs. 31D-E) is the tallest Lousewort in Scandinavia. The flowers are 3 cm long with a closed corolla tube when blooming. This means pollination can only be performed by powerful bumblebees. The King's Sceptre was present at a meadow in Jutland in the years before 1930 but has since disappeared from Denmark, while it is not uncommon on humid nutrient rich soils in Scandinavia.

Marsh Lousewort (*P. palustris* ssp. *palustris*, Fig. 32-33) is the most widespread Lousewort in Scan-

dinavia and this and *P. sylvatica* are the only Louseworts in Denmark. The two species can be recognized on their ramifications all along the main stem in *P. palustris* but only at the base in *P. sylvatica*. In the first the calyx is clearly two-lipped and the upper lip is short (Fig. 32 inset). In the last the calyx is inflated both in the flowering and fruiting stage. A few more species are mentioned on page 8.

Rhinanthus - Rattle

Rattle has got its common name from the rattling sound produced by the seeds within the dry capsule when wind is shaking the plant. There are about 45 species in Eurasia but only three and some subspecies in the Nordic countries. All species are annuals and root parasites with many secondary haustoria on several hosts. The winged seeds are dispersed by wind but released slowly from the capsule that opens only a little at the apex. The dominating 4-toothed calyx is a pro-

34. Yellow Rattle, *Rhinanthus minor,* with dark coulered calyx. Photo: H. S. Heide-Jørgensen.

35. Greater Hay Rattle, *Rhinanthus serotinus,* with light green calyx. Photo: H. S. Heide-Jørgensen.

nounced character of the genus. The yellow zygomorphic flowers, i.e., one plane of symmetry only, each have a short beak of a different colour on the upper lip. Pollination is primarily by bumblebees but self-pollination has also been established.

The Danish species Yellow Rattle (*Rhinanthus minor*, Fig. 34) and Greater Hay Rattle (*R. serotinus*, Fig. 35) are recognized among others by the colour of the calyx. In Greater Hay Rattle the style are longer than the corolla. Both species contain several subspecies and seasonal forms (seasonal dimorphism) occur as in Eyebright (*Euphrasia*). Yellow Rattle is the most widespread in the Nordic countries occurring to northernmost Norway and 65° N.Lat. in West Greenland. *Rhinanthus groenlandicus,* growing mainly in mountain regions, is often considered a subspecies of Yellow Rattle. Both *R. minor* and *R. serotinus* prefer humid soil but occur in many habitats from wood edges to grassland. *R. serotinus* is also seen in rye fields where it parasitizes the roots of the crop. The glycoside rhinanthin makes the plants slightly poisonous. The seeds have the highest concentration of this compound.

The following genera are holo- and root parasites and they lack chlorophyll and a fully developed root system. As holoparasites they are completely dependent on getting water and all nutrients from their hosts. However, toothwort has roots assumed to be able to absorb some water. All holoparasites avoid the need to compete with other plants for light.

Lathraea - Toothwort

Toothwort (*Lathraea squamaria*, Fig. 36) is found in humus rich deciduous forests in southern Scandinavia and has Hazel (*Corylus*), Alder (*Alnus*), and Beech (*Fagus*) as the favourite hosts. There are three of seven perennial species in Europe but only one species in Scandinavia. Contrary to all other investigated holoparasites toothwort does not have a primary haustorium and most of the secondary haustoria die in winter. New ones are produced in the spring. Likewise in contrast to other holoparasites the seeds are large (up to 2 mm, Fig. 37) containing enough nutrients for the underground seedling to develop roots able to produce secondary haustoria. Growth is slow and it may take up to ten
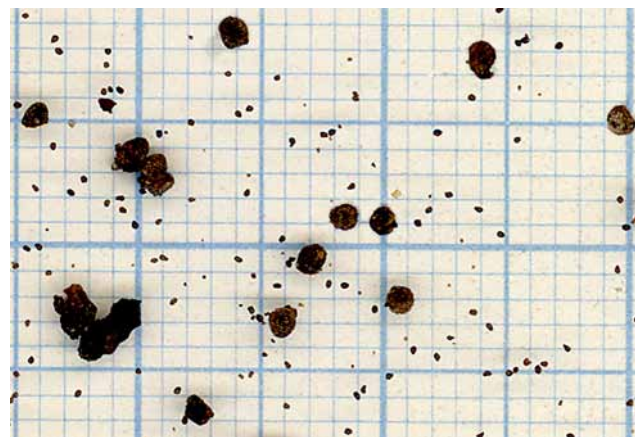
36. Toothwort, *Lathraea squamaria,* with thick, whitish scale-leaves on the rhizomes. The rhizomes are in this case placed just belove the litter. Photo: H. S. Heide-Jørgensen.

years before the plant is able to bloom. The inflorescence has unilaterally placed flowers (see cover) pollinated by bumblebees. When ripe, the seeds are hurled out of the capsule. The seeds are equipped with an oil and protein rich elaiosome attractive to ants which disperse the seeds. Elaiosomes are also present in *Melampyrum* (Fig. 21) and *Pedicularis*.

Toothwort has ramified rhizomes which may be seen under fallen leaves but normally they are placed deeper in the soil (Fig. 36). The rhizomes have scaly leaves formed by a re-curving of the leaf lamina with a labyrinthine cave system as a result. The caves are covered with glandular hairs known as hydathodes (Fig. 38). Because small invertebrates were found in the caves besides protein degrading enzymes and large numbers of energy producing mitochondria in the glandular hairs, the glands were interpreted as digestive glands and Toothwort was supposed to be a carnivorous plant. This has turned out to be wrong.

Hydathodes are primarily water secreting glands by use of an energy demanding pump. This explains the large number of mitochondria needed to provide the pump with energy in the form of ATP

(adenosine-triphosphate). The demand for active secretion of water is a result of the fact that Toothwort has no above ground vegetative parts with stomata. Evaporation through stomata is essential to keep water translocation going in the plants conductive tissue. This so-called transpiration stream transports most of the inorganic nutrients. Most land plants need to limit their water consumption

37. Large seeds (46 years old) af Toothwort, *Lathraea squamaria,* and small seeds of Ivy Broomrape, *Orobanche hederae*. Photo: H. S. Heide-Jørgensen.

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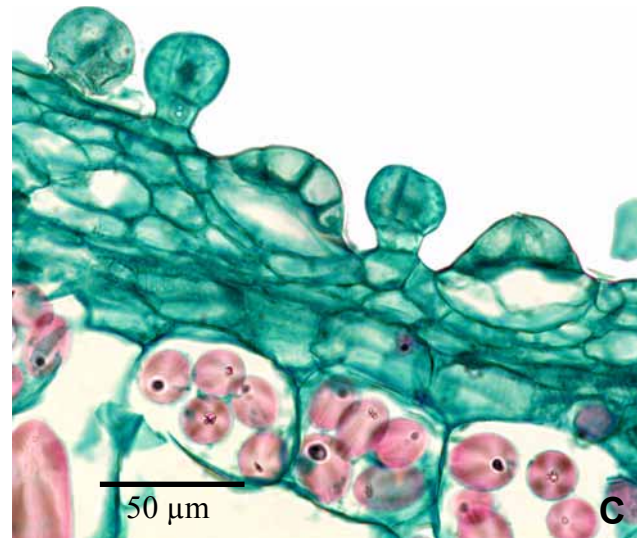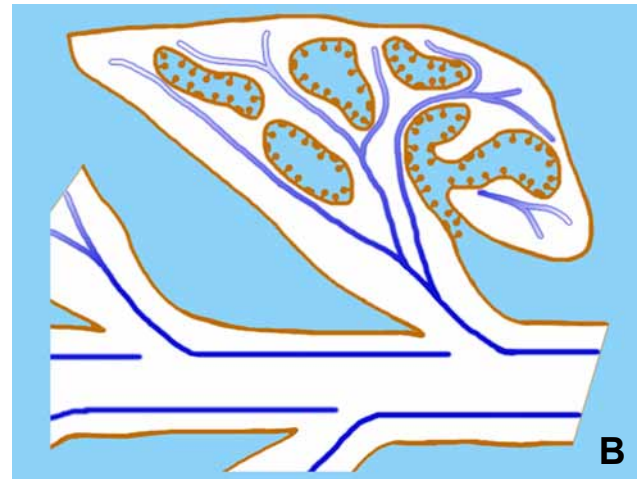
38. Toothwort, *Lathraea squamaria*. **A,** Longitudinal section of a rhizome covered with scale leaves and continuing in an inflorescence. **B,** Diagram of scale leaf in longitudinal section showing the entrance to the labyrinth-like cavities which are covered by epidermal hydathodes. **C,** Sectioned scale leaf with three stalked and two sessile hydathodes. Starch grains are coulered red. Photo and graphic: H. S. Heide-Jørgensen.

but some water translocation is necessary to keep the growing parts supplied with nutrients. Since the transpiration stream in Toothwort is not functional, the water with nutrients must be pumped through the plant and this is done by the hydathodes. It is uncertain why two structurally different types of hydathodes have developed as shown in Fig. 38C. It is possible that the very slow growth of toothwort is caused by the slow transport of nutrients.

Orobanche - Broomrape

Broomrape is a large genus with about 150 species some of which are widely distributed. In Scandinavia ten species are recognized all of which have a highly local distribution and generally they seem to

be on retreat. Three of the species are introduced. Systematics and species determination are difficult, some botanists tending to split *Orobanche* into several smaller genera.

Most species are annuals but exact knowledge is lacking about several species. All species produce a primary haustorium and some also have secondary haustoria, however, the root system is generally weakly developed, and in some species so reduced that development of secondary haustoria is not possible. A tubercle develops from the primary haustorium (Figs. 6 and 62). From growing points (meristems) within the tubercle one or several fast growing inflorescences emerge. The host is drained very effectively for nutrients and

39. Tall Broomrape, *Orobanche elatior* (= *O. major*). **A,** Two developing inflorescences growing several cm a day. The tallest is 30 cm high. **B,** Six days later the left inflorescence shown in A has doubled in hight. **C,** Visiting wasp but bumblebees are the most common pollinator. Photo: A-B, H. S. Heide-Jørgensen. C, Henrik Madsen.

the host root often dies beyond the haustorium (Fig. 6).

The inflorescence is a spike with zygomorphic, two-lipped flowers adapted to pollination by bees and wasps. The style is pressed against the upper lip and possesses a large downward bent stigma which in some species is bi-lobed (Fig. 40), while the four stamens are inserted on the corolla tube. The complete exophyte, flowers inclusive, are often strongly hairy which may keep away creeping insects from the flowers. The capsules contain an enormous number of seeds that are among the tiniest in the plant world (Fig. 37). One single inflorescence of Lesser Broomrape (*Orobanche minor*) may produce more than 100.000 seeds which are wind dispersed. In more southern countries Broomrape causes great harm on cultivated plants but the Nordic species are no threat at our latitudes. Broomrapes are fairly host-specific meaning that they only accept few species as host. This is reflected in popular names such as Thistle Broomrape (*O. reticulata*) and the introduced Ivy Broomrape (*O. hederae,* Fig, 52). Purple Broomrape (*O. purpurea*) having *Artemisia* as host is in Danish also named after the host genus.

40. Butterbur Broomrape, *Orobanche flava,* has a bi-lobed stigma with white surface (inset). Photo: H. S. Heide-Jørgensen.

41. Butterbur Broomrape, *Orobanche flava,* is introduced to Denmark but rare. It is primarily parasitic on Butterbur, *Petasites hydridus*. Photo: H. S. Heide-Jørgensen.
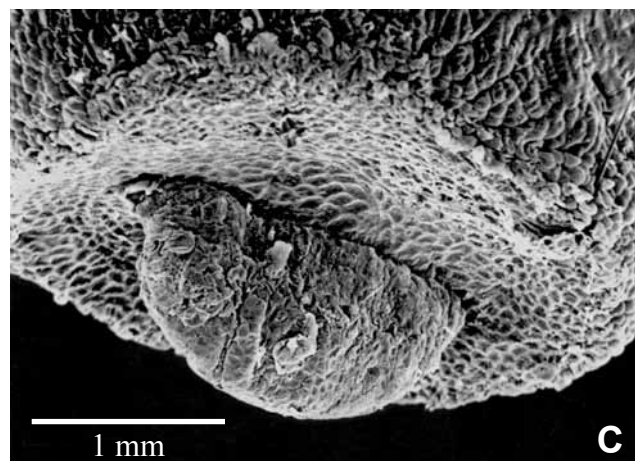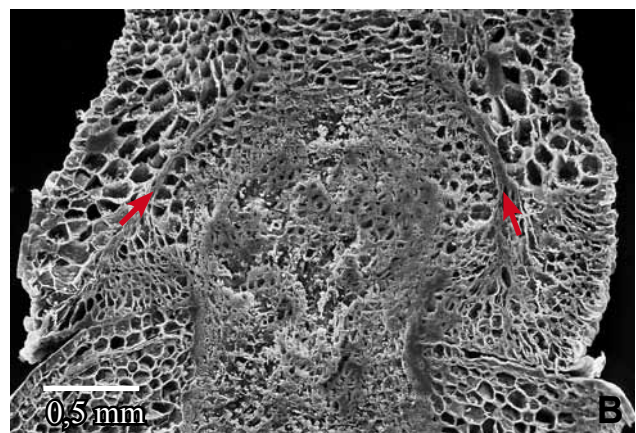
Haustoria

The presence of one or more haustoria is essential for a plant to be able to live as a parasite. The term haustorium was first used in 1813 to describe the structural connection between a Dodder (*Cuscuta*) and its host. Since then it has been used for many structures involved in nutrient uptake but without comparable origin or structure and only with its function as a common feature. Examples of such more recent practise for using the term haustorium are among others the protuberances of fungal hyphae into algae or higher plant cells, the foot in the embryo of Pteridophytes, and outgrowths from the embryo sacs of flowering plants. However, even the haustoria of parasitic plants have diverse origins.

Generally, the haustorium is interpreted as a modified root. This seems evident when it is the tip of the radicle that directly develops the primary haustorium, or when secondary haustoria show several common features with the initiation of lateral roots from a main root. However, in Dodder (*Cuscuta*) and *Cassytha,* the haustoria are initiated from the stems (Fig. 42A). It deserves mention in this context that dodder belongs to the Morning Glory family (Convolvulaceae) and that there is not a single known example of roots developing from stems in this family. Furthermore, the first cell divisions in haustorial initiation happens outside the starch sheet, that is a cell layer with the same position as the endodermis separating the conductive tissue from the rest of the root tissue. In contrast, lateral roots and adventitious roots are normally initiated from the cell layer just inside the endodermis. Therefore the Dodder haustorium can be interpreted as an organ without parallel.

Anatomy and function

There is considerable variation in haustorial anatomy both between different families and between several genera within a family. Some general features of haustorial structure appear from Figs. 42-43. *Cassytha* (Fig. 42) is a tropical-subtropical genus where the initiation and

42. Devil's twine*, Cassytha pubescens* (*Cassytha* is a genus of tropical-subtropical hemiparasites of similar general structure as Dodder, *Cuscuta*). **A,** Haustoria with holdfasts on *Pavonia praemorsa.* Three haustoria are placed on a *Cassaytha* stem, an example of self-parasitism. **B,** Longitudinal section through holdfast and intrusive organ. Arrow, Collapzed cell layers. **C,** Exposed young, wedge-shaped intrusive organ after removal of host. B and C are photographed in a scanning electron microscope. Photo: H. S. Heide-Jørgensen.
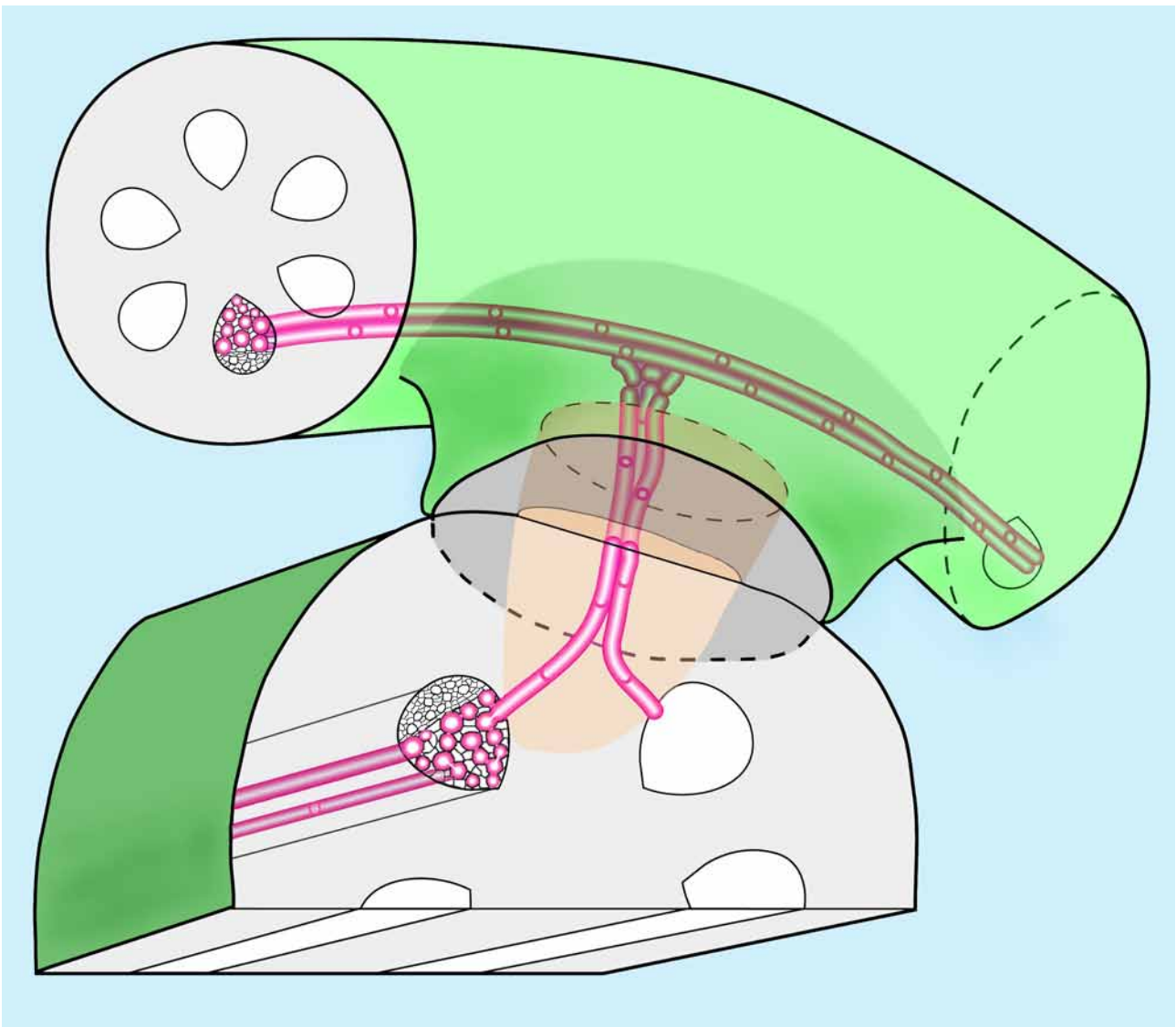
43. Diagram of a Dodder (*Cuscuta)* haustorium. The parasite stem with six vascular bundles is on top. Below is the host with four vascular bundles. Phloem is positioned towards the periphery and xylem towards the centre of the stems. The red 'tubes' are water conducting xylem elements. The darker green bulge on the parasite is the holdfast. The pale brown wedge is the intrusive organ (sinker). It establishes contact to the vascular bundles of the host and a xylem bridge of vessels develops as a water and nutrient transport fascility between host and parasite. Graphic: H. S. Heide-Jørgensen.

anatomy of the haustoria correspond closely to the haustoria of Dodder (*Cuscuta*). Generally, the haustorium consists of two main elements, a holdfast or adhesive disk which glues the parasite to the surface of the host and an intrusive organ (also called a sinker) that penetrates the host and establishes contact with the conductive tissue of the host. The intrusive organ is initiated from a growing point (meristem) within the holdfast. Therefore it must break through several cell layers of the holdfast before it can penetrate host tissue. The penetration occurs partly by enzymat-

ic dissolving of the pectin in the middle lamella between cells in front of the intrusive organ and partly due to a higher hydrostatic pressure in parasite cells compared to host cells.

When contact to a vascular bundle of the host is obtained, cells in the intrusive organ differentiate into xylem elements, usually vessel members. The differentiation begins from the parasite cell that made contact to host xylem and proceeds backwards to the vascular bundles of the parasite. The result is a bridge of vessels, named the xylem bridge that directly connects the xylem of the vas-

cular tissue of the two partners. It often occurs that the common wall of xylem cells at the place of parasite/host contact dissolves, and the resulting perforation reduces the resistance almost to zero against water and nutrient transport from host to parasite. The xylem bridge is the most general feature of haustorial anatomy.

In only two genera are the xylem bridge accompanied by phloem all the way from the parasite vascular bundle to the host. This advanced character is known from Dodder (*Cuscuta* Fig. 44) and some species of Broomrape (*Orobanche* Fig. 45). Dodder species are among the fastest growing parasitic plants and several Broomrapes are among the most harmful to their hosts. This may be explained by a more effective nutrient uptake due to the advanced phloem contact.

Traditionally, a haustorium is considered functional when the xylem bridge is established but in reality water and nutrient translocation occur across the contact surface (interface) already during growth of the intrusive organ. The area of the interface is enormous compared to the very modest part representing direct xylem contact with the host. In the tropical *Olax phyllanthi* (Olacaceae) it was calculated such xylem contacts made up only 1% of the total interface. In certain species of the Broomrape family the xylem bridge may even fail to develop in otherwise fully developed haustoria. *Olax* is a hemiparasite with a relatively simple wedge-shaped intrusive organ as in the diagram Fig. 43. In Dodder the front of the intrusive organ is split up in multicellular strands seeking towards different vascular bundles of the host. This increases the area of the interface considerably. The fragmentation can be much more pronounced than shown in Fig. 46. A similar fragmentation of the endophyte happens in Mistletoe (*Viscum*), where the so-called cortical strands run in the living cortex parallel to the host's vascular bundles (Fig. 47). From the cortical strands secondary sinkers grow into the host xylem. These sinkers are able to accomodate the secondary growth in thickness of the host.

The energy status of water in plant cells, the so-called water potential, is crucial for the direction the water and its dissolved nutrients will take. Usually parasitic plants have a lower water potential
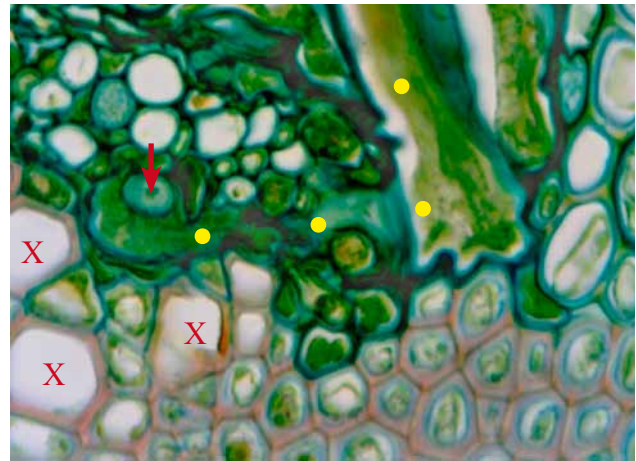
44. Phloem contact cell of Greater Dodder, *Cuscuta europaea*, embraces host sieve tube member (arrow) of host, *Pelargonium zonale*. X, vessel in host xylem. Yellow dots mark parasite phloem continuity. Photo: H. S. Heide-Jørgensen.
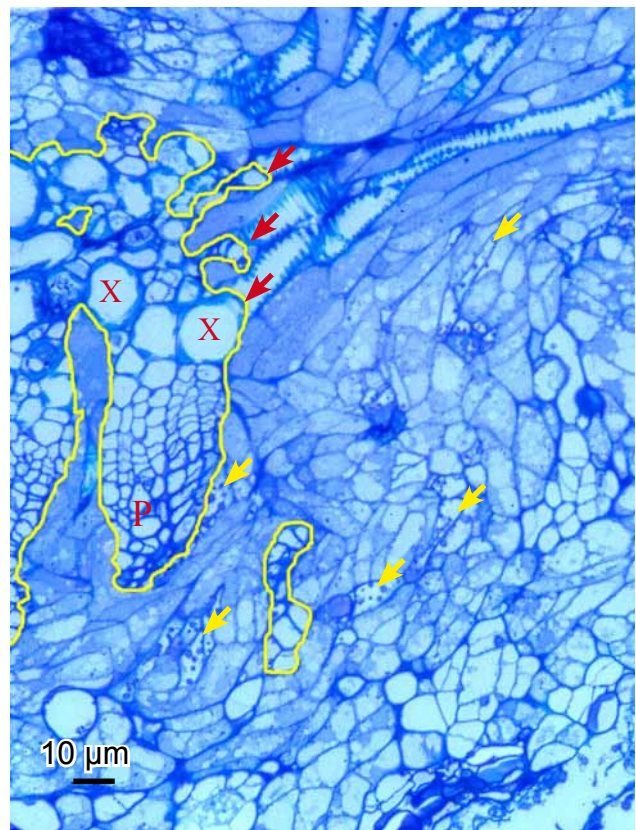
45. Transverse section of White Stonecrop, *Sedum album,* root with strongly displaced tissues caused by the North American Naked Broomrape, *Orobanche uniflora*. Yellow line, Host-parasite interface. Red arrow, Direct parasite/host ylem contact. Yellow arrow, Parasite phloem. P, Host phloem. X, Host vessel. Photo: H. S. Heide-Jørgensen.
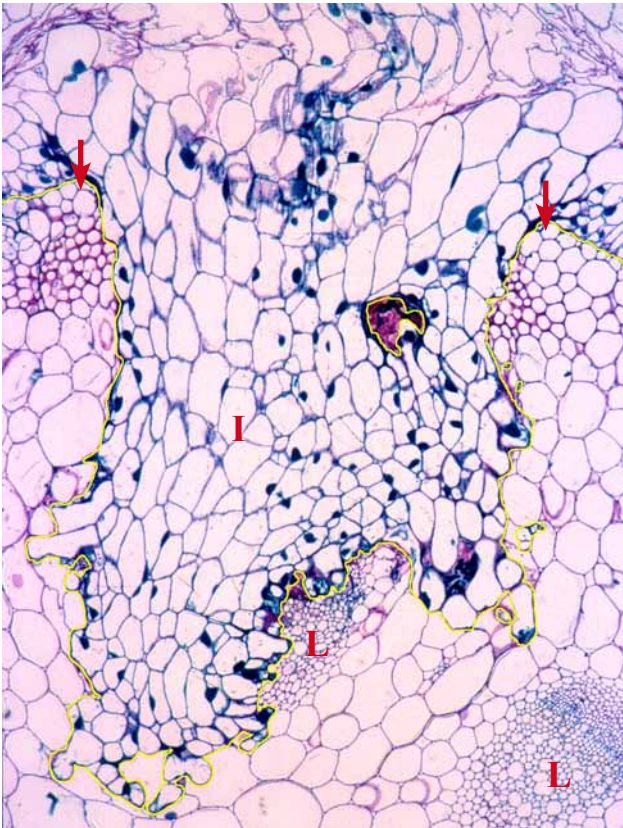
46. Longitudinal section of developing intrusive organ (I) of *Cuscuta reflexa,* into the stem of *Pelargonium zonale*. Yellow line marks the interface. L, Vascular bundles. The contact surface of the holdfast runs from the arrows to the edges of the photograph. Photo: H. S. Heide-Jørgensen.

47. European Mistletoe, *Viscum album,* with cortical strand (green of chlorophyll) running below the bark in an apple twig. Part of a primary (∗) and two secondary sinkers (arrows) are visible. Photo: H. S. Heide-Jørgensen.

and simultaneously a higher transpiration rate than their hosts. Therefore, water and nutrient transport is always from host to parasite. In root parasites the transport controlling endodermis (page 27) is disrupted by the intrusive organ, and this is no ob-

stacle to the free streaming of nutrients across the interface. An endodermis is only present in subterranean plant parts and stem parasites have no problems in this respect.

Establishment of the parasite

The first condition for a parasitic plant to become established on a suitable host is that the seedling must obtain contact with the host. This is achieved by different seed dispersal strategies. For the Nordic parasites only three of the strategies are relevant.

a) The parasite seed is relatively large and contain sufficient nutrients in the endosperm for the seedling to live as an autophyte long enough to reach the host and make contact. The seedlings of Greater Dodder (*Cuscuta europaea*) are able to survive for 3-4 weeks, but die if they have not been able to establish a functional haustorium during that period (Fig. 48). Other examples are Eyebright (*Euphrasia*), Rattle (*Rhinanthus*), and Cow-Wheat (*Melampyrum*).

b) The seeds are sticky and dispersed by birds that eat the fruit flesh. Mistletoe (*Viscum album*) is the only but clear example of this strategy. The Mistle Trush (*Turdus viscivorus*) is considered the main disperser but the Blackcap (*Sylvia atricapilla*) is also active. The behaviour of the birds is essential. The innermost fleshy layer of the fruit consists of the strongly adhesive and elastic tissue called viscin (Fig. 49). This part of the fruit flesh birds do not like. Therefore, they wipe off the viscin covered seeds on a twig and some seeds will end up on a suitable host. In the Nordic countries man may be the most effective disperser of mistletoe seeds.

c) The seeds are very small but numerous and spread by wind and water. Some seeds will accidentally land close to a suitable host root or the root will grow so close past a seed that chemical germination stimulants released from the root will start seed germination. Other stimulants will then direct the radicle towards the host root and a primary haustorium may be established. Under natural circumstances the different stimulants are only effective within a short distance, often less than two mm. Therefore it is important to produce large numbers of seeds. This strategy is used by all species of Broomrapes (*Orobanche*) as well as

48. Seedling of Greater Dodder, *Cuscuta europaea*. The radicle has withered (arrow) after establishment of haustoria from the first winding of the stem. Note the first coil is left winding opposite normal as in Fig. 12. Photo: Hans Tybjerg.

49. Seed of European Mistletoe (*Viscum album*). Fruit skin with scars from pistil and petals hanging in the elastic viscin. The green radicle is just emerging from the seed. The viscin hides the green endosperm. Photo: H. S. Heide-Jørgensen.

by Toothwort (*Lathraea*) although it has relatively large seeds and only secondary haustoria.

When the initial contact is obtained between the two partners further stimulation is needed to initiate a haustorium. In Dodder (*Cuscuta*) this stimulation is purely mechanical, and is caused by pressure when the Dodder stem winds around the host stem or any other object, live or dead. However, it is only in the Dodder stem's elongation zone just behind the shoot apex that it is receptive to a pressure stimulus.

In dodder the stimulation results in cell divisions in the inner part of the cortex, i.e. the cell layers between the epidermis and the endodermis. The divisions lead to the formation of a holdfast where the contact surface consists of glandular cells. The glands secrete an adhesive carbohydrate that, in collaboration with the tight windings of the Dodder stem, secures a stable

contact with the host during growth of the intrusive organ. If the holdfast is initiated on an inacceptable host or a dead subject, the development of the holdfast will usually stop before the intrusive organ is initiated.

In Mistletoe (*Viscum album*) the factor that stimulates haustoria initiation is unknown. It may be mechanical, but light dependence or chemical stimulation from the host has also been suggested. The embryo is green with chlorophyll already while in the seed (Fig. 49), and the hypocotyl/radicle bends towards the surface of the host during germination until the extremely short radicle obtains physical contact to the host (Fig. 50). As in Dodder, a holdfast develops but in this case the glandular cells secrete large amounts of a sticky lipid compound and not a carbohydrate.

In root parasites chemical stimulation to initiate haustoria is normal but in this case also, only the

50. Six month old seedling of European Mistletoe, *Viscum album*, with a primary haustorium. The coalesced cotyledons are emptied for nutrients and have turned yellow. Photo: H. S. Heide-Jørgensen.

51. Toothwort, *Lathraea squamaria* (arows), in front of an unusual host, the living fossil Dawn Redwood, *Metasequoia glyptostroboides,* grown in the Forest botanical Garden in Copenhagen, Denmark, but native to the Sichuan-Hubei region of China. Photo: H. S. Heide-Jørgensen.

elongation zone of the root is receptive to stimulation. Hemiparasites in the Broomrape family (Orobanchaceae) develop a kind of holdfast but it consists mainly of root hairs that cling to the host root. It is noteworthy that no root hairs occur in the normal position behind the elongation zone.

How many hosts?
(Host specificity)

Some parasitic plants are able to use only one or a few species as host. They are said to have a high degree of host specificity while others with low host specificity can use a broad selection of host species. A parasite's ability to use several different host species is often underestimated. This has several reasons. For example, the parasite is rarely collected together with the host for filing in a scientific herbarium. Also, it is often not possible to determine the host in the field because it can be difficult or impossible to follow a host root back to the mother plant. An acceptable host may therefore easily be overlooked, and negative observations may be misleading. Dispersal biology and geographical distribution must be taken into consideration. For example, in Denmark Toothwort (*Lathraea squamaria*) is parasitic on Hazel, Alder and Beech but introduced species from outside the distribution area of Toothwort may also function as host. This can be seen in the Forest botanical Garden in Copenhagen, where Toothwort are established on the roots of several specimens of the living fossil Dawn Redwood, *Metasequoia glyptostroboides,* native to China (Fig. 51). The occurrence of parasites dispersed by birds depends on the behaviour and distribution of those birds. Many bird species prefer the open land and wood edges and they do not appear in the woods which may contain species and individuals that could be hosts for parasitic plants. Even though Mistletoe (*Viscum album*) occurs in many Danish gardens there is only a modest dispersal to natural habitats. The reason is that the most important disperser, the Mistle Trush, rarely visits urban areas. Only a

52. Ivy Broomrape, *Orobanche hederae,* always has Ivy, *Hedera helix,* as host. Photo: H. S. Heide-Jørgensen.

53. Tall broomrape, *Orobanche elatior*, primarily has Great Knapweed, *Centaurea scabiosa*, as host. Four inflorescences of host and parastite are in flower. Photo: Henrik Madsen.

few parasitic plants parasitize a single host species. In the Nordic flora there are no examples outside the Broomrape genus (*Orobanche*). Ivy Broomrape (*O. hederae)* is only known from Ivy, *Hedera helix* (Fig. 52). Butterbur Broomrape (*O. flava*) parasitizes primarily Butterbur (*Petasites hybridus* Fig. 41) but is also found on Colts-foot (*Tussilago farfara*), while Tall Broomrape (*O. elatior*) prefers Great Knapweed, *Centaurea scabiosa* (Fig. 53) but it is also able to use other species of Knapweed. The introduced Barberry Broomrape (*O. lucorum*) is limited to species of Barberry (*Berberis*).

Hemiparasites which also are root parasites generally have the lowest host specificity. They can use hosts among both monocots and dicots, although dicots and grasses are the most common hosts. Hosts are fairly rare among certain groups of monocots such as orchids and among gymnosperms. Normally root parasites have many secondary haustoria on different host species simultaneously. This seems to pro-vide a greater security that all necessary nutrients are available to the parasite since different host species absorb more or less of different inorganic nutrients in relation to their own needs.

Hemiparasites, which at the same time are stem parasites, are more fastidious regarding host species. This generalisation is, however, not evident when only looking at the Nordic parasitic species. In Denmark, Mistletoe (*Viscum album*) is doing particularly well on apple trees but in Sweden it is most common on Small-Leaved Lime (*Tilia cordata*) and Sycamore (*Acer platanoides*). Nonetheless, *Viscum album* is registered from more than hundred genera. There are four subspecies of *V. album* but only *V. album* ssp. *album* occurs in the Nordic countries. The four subspecies are separated primarily on the basis of their host choice. Thus *V. album* ssp. *austriacum* limited to Pine (*Pinus*). It can be seen in the Botanic Garden in Copenhagen. *V. album* ssp. *album* is further segregated in several physiological races that only deviate from one another regarding the choice of host species. Conse-

54. Heather, *Calluna vulgaris*, sporadically parasitized by Common Dodder, *Cuscuta epithymum,* on a heath in Jutland. Photo: Inge Nagstrup.

quently, at this level host specificity becomes relatively high. Therefore, sowing *Viscum album* seeds originating from an apple tree as host is seldom successful when using *Sorbus*, Birch (*Betula*), or Poplar (*Populus*) as hosts, although these genera are registered as hosts for *V. album* ssp. *album.*

The above generalisation is not valid for Greater Dodder (*Cuscuta europaea*). It thrives excellent on Stinging Nettle (*Urtica dioeca*) but is able to use any other herb within its reach. The other Nordic Dodder species show greater discriminating taste in their choice of hosts. Common Dodder (*Cuscuta epithymum*) uses Heather (*Calluna vulgaris* Fig. 54), Thyme (*Thymus serpyllum*), and a few other woody dicotyledonous heath species. Clover Dodder (*Cuscuta trifolii*) prefers legumes as host including crop plants such as Clover (*Trifolium*) and Alfalfa (*Medicago sativa*), however, without doing any harm worth mention at our latitudes. Now and then a parasite may function as host for its own species. In the Nordic countries this is often seen in Dodder (*Cuscuta*) and sometimes in Mistletoe (*Viscum*). This phenomenon is called self-parasitism (Fig 42A).

Many plants have an effective biochemical defence against parasitic plants since establishment of a parasite naturally demands tissue compatibility between host and parasite. It is supposed that secondary metabolites in the host determine if there is tissue compatibility or not. Such metabolites are often considered waste products from the metabolism of the plant but in the case of parasitism they may be used to the advantage of a potential host. Experiments with establishing the South African Mistletoe *Viscum minimum* on a number of succulent Spurges (*Euphorbia)* indicate that metabolites in the latex determine if the parasite is accepted or rejected.

If tissue compatibility is present the host has not many possibilities to avoid attack from a parasite. However, it may happen that some haustoria of Greater Dodder (*Cuscuta europaea*) fail to become fully functional because the host produces a thicker layer of lignified cells which the intrusive organ fails to penetrate. Development of cork (phellem) may also reject an attack of e.g. Mistletoe (*Viscum*) and normally establishment is only possible on younger twigs with a thin layer of cork.

Further Ecological Relations

Attack from a parasitic plant nearly always causes a certain weakening of the host. Its growth is reduced and especially fruit and seed production decreases. However, perennial parasites only rarely weaken the host so much that they die because the parasite then will also die. Death of the host may result when many individuals grow on the same host. Naturally, the vigour of the host is in relation to how well developed the parasite may be. This is illustrated by comparing the vigorous Tall Broomrape (*Orobanche elatior*) in Fig. 39 and 53 with Fig. 55, where the host Great Knapweed (*Centaurea scabiosa*) grows in pure chalk that is very poor in inorganic nutrients.

For annual parasites it is often of lesser importance if the host dies because they may have set seed beforehand and the seeds can later on germinate on new hosts (Fig. 56). It may therefore be expected that the most harmful parasitic plants in agriculture and gardening are to be found among annuals such as Dodder (*Cuscuta*) and Broomrape (*Orobanche*). However now a days, damage of economic importance rarely occurs on cultivated plants in the Nordic countries. It is quite different in tropical and subtropical regions where attack of root parasites primarily by species of *Striga* and *Orobanche* from the Broomrape family (Orobanchaceae) may reduce yield with up to 100% for important crops such as mays, sorghum and a number of legumes.

In North America attack on conifers of certain species of the perennial Dwarf Mistletoe, *Arceuthobium*, cost enormous sums yearly in forestry due to losses in timber. Research stations in several countries are working solely on how to control parasites also by breeding of resistant strains of crop plants.

In plant communities parasites usually occur in a patchy pattern but they can also be a dominant element. In grassland and meadows Rattle (*Rhinanthus*) may obtain a high frequency (Fig. 57) but grazing can keep it down. The occurence of Yellow Rattle (*R. minor*) during the first year may favour dicoty-

55. Small specimen about 12 cm high of Tall Broomrape, *Orobanche elatior,* (compare with Fig. 53) on a weak host of Great Knapweed, *Centaurea scabiosa* (arrow). Photo: H. S. Heide-Jørgensen.

56. Dead Tansy, *Tanacetum vulgare*, after attack by the annual Greater Dodder, *Cuscuta europaea,* which has set seeds before killing the host. Photo: H. S. Heide-Jørgensen.

57. Meadow with Greater Hay Rattle, *Rhinanthus serotinus*. Grasses are supperessed where Rattle is abundant. Öland. Photo: H. S. Heide-Jørgensen.

58. Plenty of Lousewort, *Pedicularis sylvatica* ssp. *sylvatica,* near the coastline in Northern Jutland. Photo: Henning Adsersen.

ledonous herbs because the rattle primarily parasitizes grasses which it thereby suppresses. Similarly does Tall Broomrape (*Orobanche elatior*, Fig. 53) suppress its host Great Knapweed (*Centaurea scabiosa*) to the advantage of other non-host plants. It is said that even a vigorous Knapweed may succumb if it is attacked by Tall Broomrape for four years in a row. A similar situation has been suggested for the use of Butterbur Broomrape (*Orobanche flava*) in the biological control of the invasive host Butterbur (*Petasites hybridus,* Fig. 59). Species of Lousewort (*Pedicularis*, Fig. 58) and Cow-Wheat (*Melampyrum*) may also locally be dominant but there are no investigations showing what consequences this may have on species composition and dynamics in the plant communities where these parasites occur. Common Cow-Wheat (*Melampyrum pratense*) may be abundant in some years after forest clearing and fire and heath fires seem to facilitate the occurrence of Common Dodder (*Cuscuta epithymum*, Fig. 54).

Parasitic plants like other plants are included in diverse food chains. Seeds are eaten by birds and other animals. The author, e.g., has observed snow hares walking from plant to plant for a feast meal on the infructescence of Hairy Lousewort (*Pedicularis hirsuta,* Fig. 27). Species with fat rich elaiosomes on the seeds of Toothwort, Cow-Wheat, and Lousewort attract ants. Mammals and insects are grazing on vegetative parts. Larvae of the Mouse Moth *Amphipyra tragopoginis* (Noctuidae) and the butterfly

Eupithecia plumbeolata (Larentiinae) live among others on *Melampyrum pratense* (Fig. 19). See also about Leaf Roller larvae on *Bartsia alpina* page 17.

Subjects like self-parasitism, epi-parasitisme, where a parasite attacks another parasite, mimicry, where the vegetative parts or flowers to confusion resembles those of the host, and plant diseases are also relevant for a discussion of parasitic plants. Apart from self-parasitism often occurs in Dodder and now and then in Mistletoe, it is mostly in tropical and subtropical regions the evident examples are found. More knowledge on these subjects can be found using the literature list page 40.

59. Leaves and leaf stalks of Butterbur, *Petasites hybridus,* have lost turgidity after attack by Butterbur Broomrape, *Orobanche flava*. Photo: H. S. Heide-Jørgensen.

60. Field Cow-Wheat, *Melampyrum arvense*. Hemiparasites, which are also root parasites, are considered the most primitive parasitic plants. Photo: H. S. Heide-Jørgensen.

Evolution of parasites

It is a clear advantage if a plant develops a system allowing it to draw water and nutrients directly from other plants root net and/or other plant's photosynthetic apparatus. This is exactly what parasitic plants have succeeded in doing. However, there are no aquatic parasitic plants simply because in this environment water is always available, and therefore the lack of water does not become a driving force in evolution contrary to the situation for land plants.

It has not been possible to identify the earliest parasitic plants, partly because there is practically no fossil material. On the other hand, from morphological criteria one can state that parasitic plants have arisen independently at least 8 or 9 times. It becomes evident when comparing the haustorial anatomy and origin in Dodder, Mis-

tletoe and diverse root parasites that the evolution of parasitic plants has had different starting points and went in different directions in the systematic groups (taxa) where we find parasitic plants today. According to modern gene molecular investigations parasitic plants may even have evolved 12-13 times independently.

It is generally agreed that the most primitive parasitic plants are to be found among hemiparasites with secondary haustoria on the roots of the host. A Cow-Wheat (*Melampyrum,* Fig. 60) like plant could be the starting point. True enough, Eyebright (*Euphrasia*) has very simple constructed haustoria but the simplicity is thought to be a result of reduction of more complicated haustoria in the family. In the tropics there are a few parasites in Loranthaceae which both parasitize roots, rhizomes, and aerial stems. It seems clear from such examples that the first stem parasites brought their roots with them up into the trees. These so-called epicortical roots grow parallel with and in close connection to the host twigs and they develop secondary haustoria. In more advanced Loranthacean stem parasites the epicortical roots becomes reduced or

61. A false graft where the Virgin's Bower, *Clematis* virginiana, is caught in the angle between two twigs of a Cherry, *Prunus* sp. Photo: H. S. Heide-Jørgensen.

62. Same as in Fig. 60 seen in a longitudinal section. The Bower stems (arrow) are encapsulated by Cherry bark but exchange of water and nutrients does not occur. Photo: H. S. Heide-Jørgensen.

63. About 5 mm large seedling of Ivy Broomrape, *Orobanche hederae*. The primary haustorium has already brought the growth in thickness of the distal part of the Ivy (*Hedera helix)* host root to an end. Photo: H. S. Heide-Jørgensen.

seems to move inside the cortex (periderm) as the cortical strands mentioned for Mistletoe (*Viscum*, page 29 and Fig. 47). Development of the primary haustorium from the radicle (Fig. 63) means the time is reduced where the seedling is dependent of the nutrients in the endosperm and/or by photosynthesis in the cotyledons. In the order Santalales, which includes Loranthaceae and *Viscum,* many intermediate evolutionary stages lead to the most advanced species of the Mistletoe family (Viscaceae) but these species are not represented in the Nordic flora.

The evolution of the primary haustorium from the radicle is the most important prerequisite allowing a parasitic plant to give up photosynthesis and hence become a holoparasite. For root parasites it further seems essential that the potential parasite is able to take advantage of the growth stimulating compounds that many plants excrete from their roots. This secures that the growth of the radicle from the beginning becomes targeted directly towards a suitable host root. The next step is to develop a difference in hydrostatic pressure in host and parasite cells to allow the intrusive organ to mechanically penetrate the host tissue.

64. This Cow-Wheat, *Melampyrum nemorosum,* takes advantage of nature conservancy in Denmark. Photo: H. S. Heide-Jørgensen.

This event has further been facilitated by enzymatic dissolution of the middle lamella in host cell walls. Finally, the transpiration rate of the parasite should be higher than that of the host securing that water translocation through the haustoria is unidirectional from host to parasite.

Toothwort (*Lathraea*) may be seen as a relatively primitive holoparasite because it has only secondary haustoria and has kept leaves on the subterranean rhizomes. Its relatively large seeds are neither characteristic of holoparasites. Broomrapes, which like Ivy Broomrape (*Orobanche hederae*, page 6 and 34) are almost without roots and have a well-developed primary haustorium, are more advanced. In holoparasites it is no surprise that the superfluous leaves become reduced but there is also a strong reduction of endosperm and embryo since the primary haustorium very soon during germination becomes the central organ in the nutrition of the parasite.

An alternative evolution path could be a further development of natural grafts as they now and then are seen between tree roots in a wood. However, this explanation is unlikely because such root grafts mostly happen between individuals of the same species and in places far from the growth zones (meristems) where haustoria are initiated in all investigated species. False grafts as shown in Figs. 61-62 have hardly led to evolution of parasitic plants. Another theoretical possibility is that a mycorrhizal fungus was involved. The mycelium between a host and a potential parasite (e.g. a saprophyte or myco-heterotrophic plant, see page 5) could with time shorten and at last the two flowering plants could be joined. In New Caledonia a conifer, *Parasitaxus usta*, occurs that possibly in this manner is about to evolve to a parasitic plant in the traditional sense.

To finish this article it should be mentioned that several of the Nordic parasitic plants are protected. This is true first and foremost for all the wild Danish broomrapes but not for the introduced ones. Toothwort and several species of Cow-Wheat and Dodder occur so sparsely that they should be protected even though some of them may experience a short rise in number following forest clearing or fires. Protection has had a positive effect for example on the presence of *Melampyrum nemorosum* in a locality near Copenhagen (Fig. 64).

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http://www.iceland-nh.net/plants/   Flora of Iceland in English.

http://www.parasiticplants.siu.edu/   Comprehensive web site by D. Nickrent.

http://www.viscum.dk   The authors web site.