The Mistletoe Viscum album



Female fruiting plant of *Viscum album* ssp. *album*, February 2008.

Henning S Heide-Jørgensen 2015 - www.viscum.dk



Fig. 1. Flowering male plant of European Mistletoe (*Viscum album* ssp. *album*), early April 2011.

The author

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Introduction

The present paper on the European mistletoe is based on 'Danish and other Nordic parasitic plants' published at the web-site www.viscum.dk in 2014. The paper is mainly expanded on illustrations, discussions on vegetative morphology, pollination, and dispersal. Figures can be enlarged 200-300%.



Fig. 2. *Viscum album* in its first year where the radicle has produced a holdfast. The shrunken remains of the cotyledons are still visible. If both a radicle and a hypocotyl are present, is unclear.



Fig. 3. Young *Viscum album* 4-5 years after seed deposition. The holdfast of the primary haustorium can still be seen (long arrow) while the cotyledons and the first set of foliar leaves are lost. Short arrow, scar of cotyledon located 90° from scar after 1st foliar leaf.

The European mistletoe, *Viscum album* L. (Front page and Fig.1), is a fascinating parasitic plant and a pleasure to follow year round if one is so lucky to have it growing just outside the window. It has its own family Viscaceae together with six other genera, all of which were earlier placed in Loranthaceae. Viscaceae is regarded as the most advanced family in the sandalwood order (Santalales). If the reader is looking for more scientific information than provided in this article the following are recommended: Tubeuf 1923, Thoday 1951, Polhill & Wiens 1998, Büssing 2000, Watson 2011, Kuijt 1969, and Kuijt 2015.

Mistletoes are hemi-parasites having trees as hosts. Hemiparasites are characterized by containing the green matter chlorophyll which performs photosynthesis after addition of water, carbon dioxide, and solar energy. This means the plant by itself is able to produce all the carbon compounds needed for its growth. However, since mistletoes grow on tree branches without having direct root connections to the soil they are dependent on receiving water and all inorganic nutrients from the host. Therefore the European mistletoe is called a hemi-parasite since it approximately provides only about half the nutrients on its own.

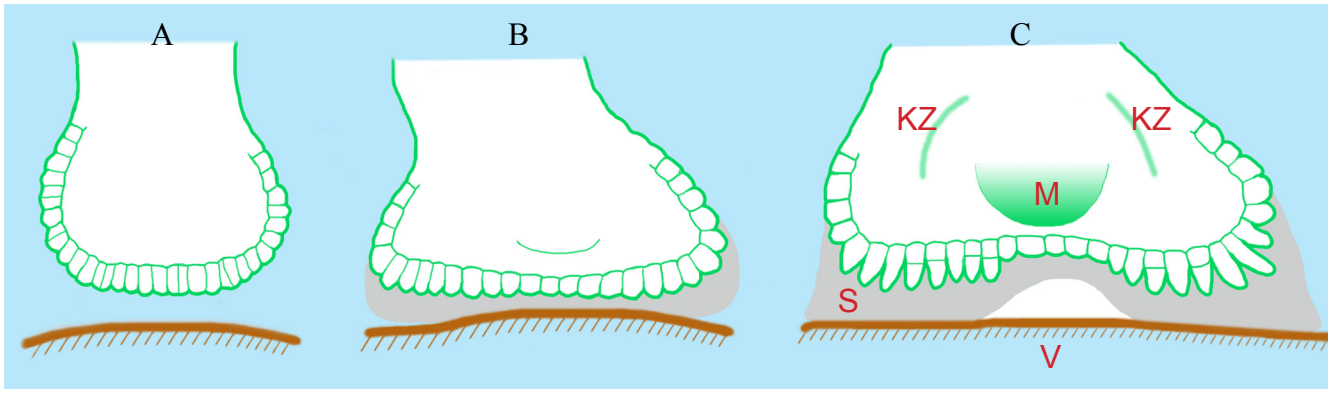
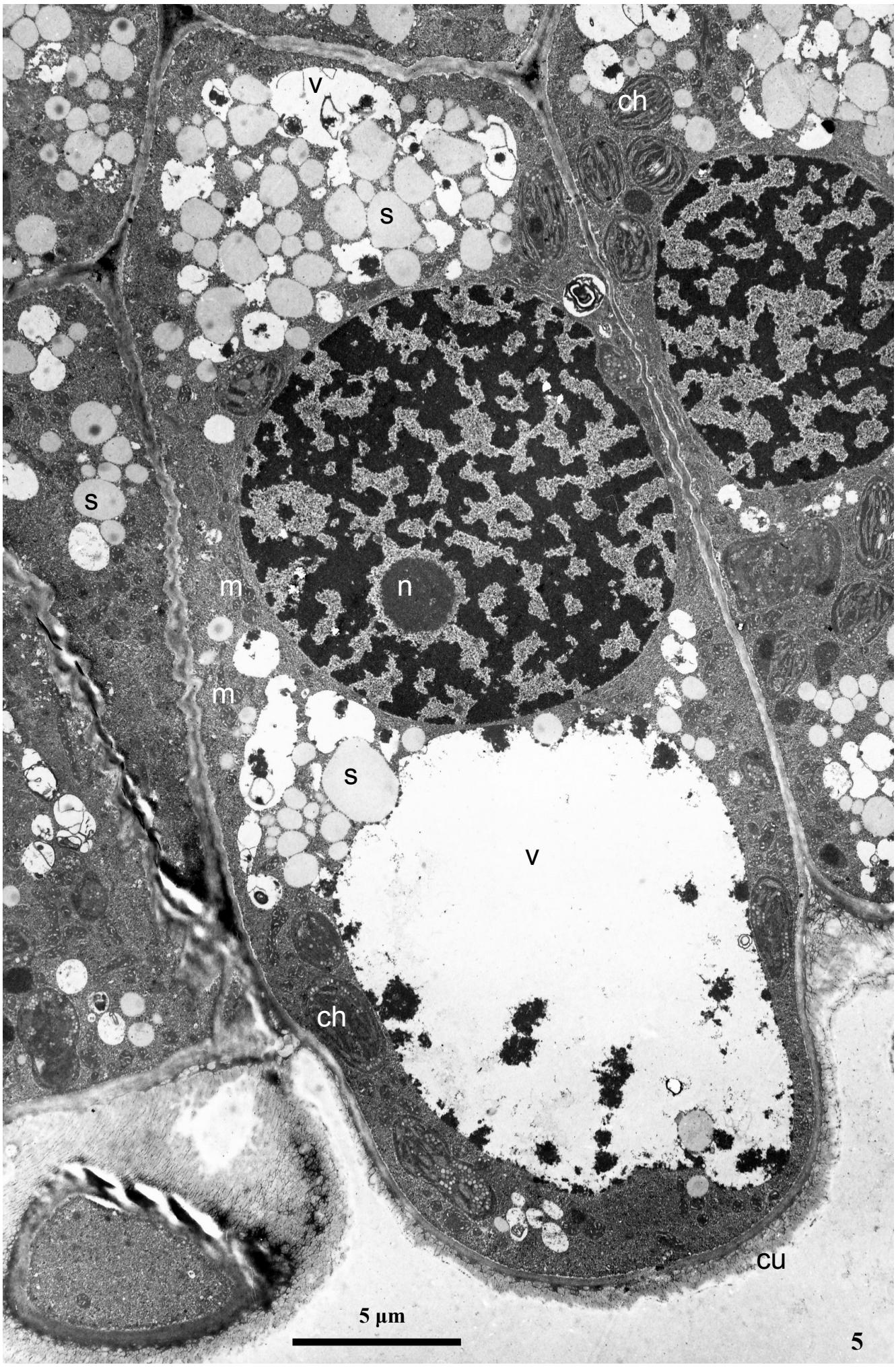
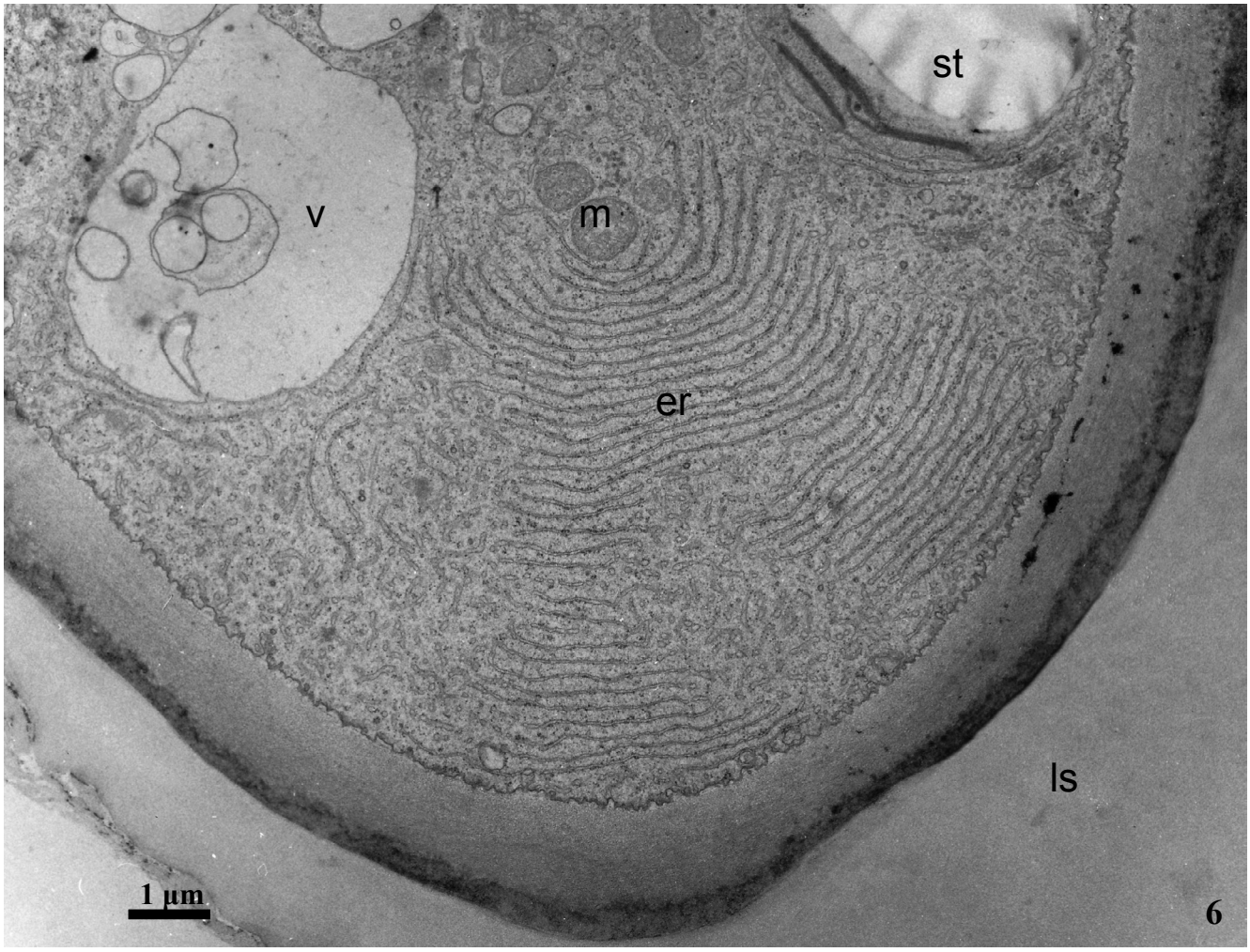
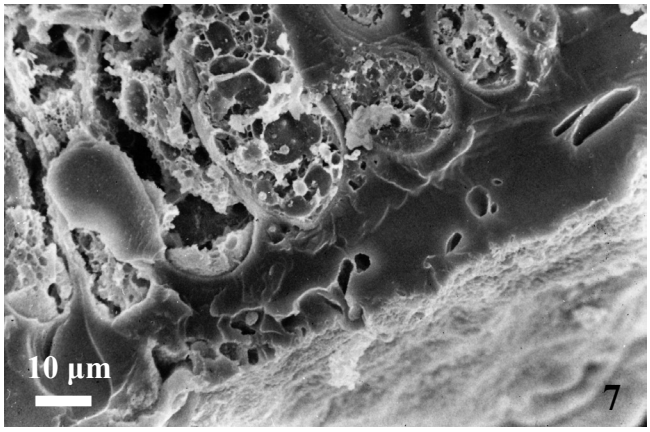


Fig. 4. Establishment of the holdfast of *Viscum album*. A, the tip of the radical expands and flattens. B, Epidermis in the contact zone differentiates to glandular cells secreting a lipid containing a adhesive compound (S). C, meristem (M) producing the intrusive organ. KZ, collapsed zones. V, host surface.


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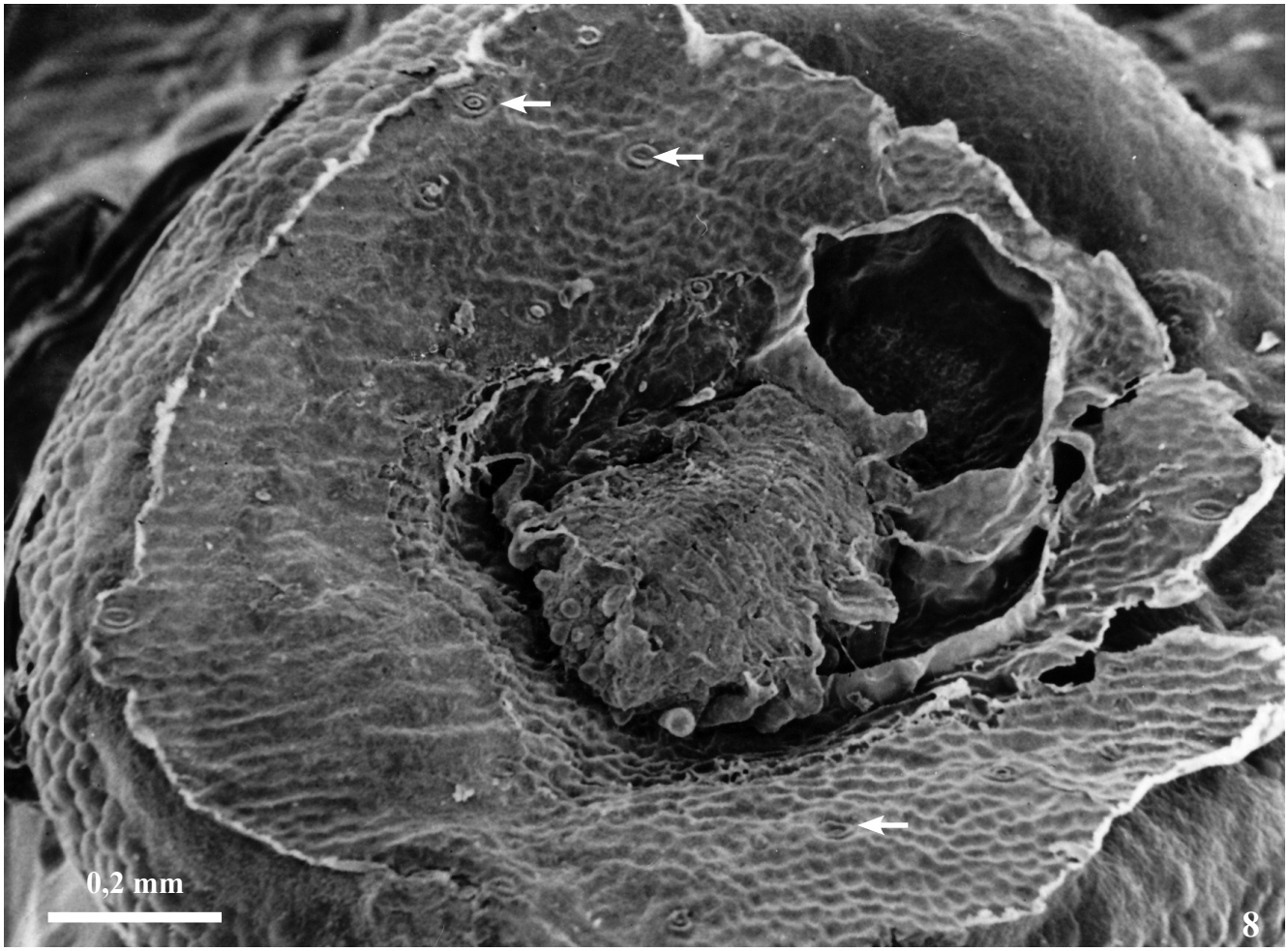


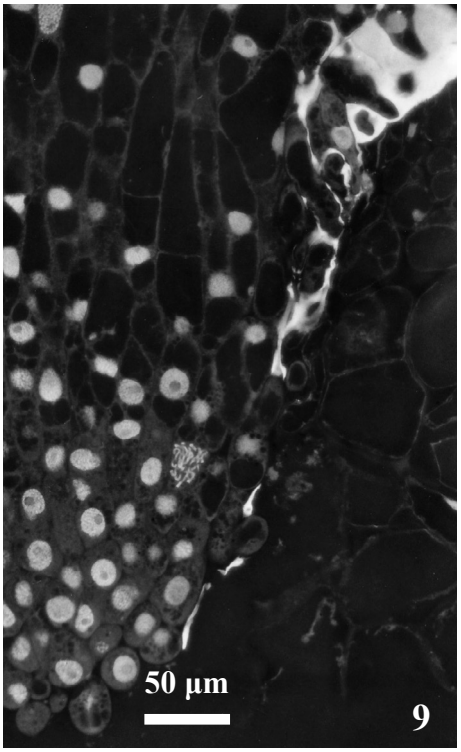


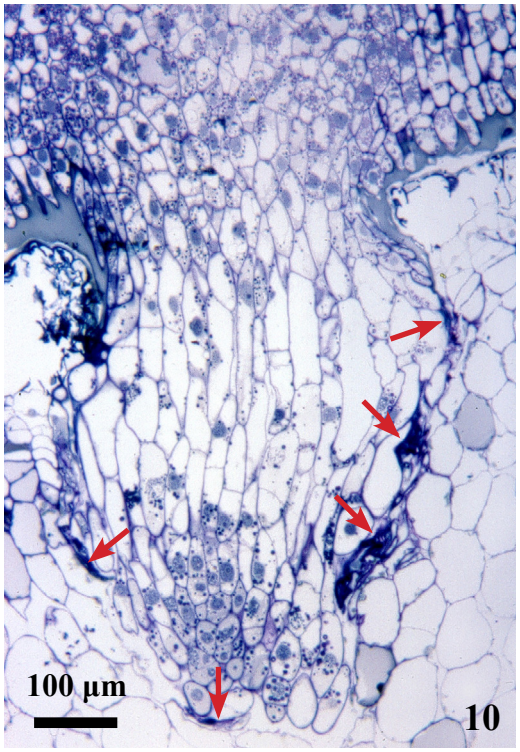
Figs. 5-7. *Viscum minimum*. **Fig. 5 page 4.** Longitudinal section as seen in a transmission electron microscope of immature epidermal cells from a young holdfast before contact to the host is achieved. ch, chloroplast. cu, cuticle. m, mitochondrion. n, nucleolus in cell nucleus with strongly condensed chromatin. s, sphaerosome (lipid body). v, vacuole. 1µm = 1/1000 mm. **Fig. 6.** Transmissions electron microscopy of the tip of an epidermal cell from the holdfast secreting lipid containing adhesive material (ls). er, endoplasmic reticulum. m, mitochondrion. st, plastid with starch grain. v, vacuole. **Fig. 7.** Scanning electron microscopy of holdfast epidermal cells after contact to the host is established, but the holdfast is artificially separated from the host. A thick layer of adhesive secret (ls) with cavities possibly containing cell-wall degrading enzymes is visible.

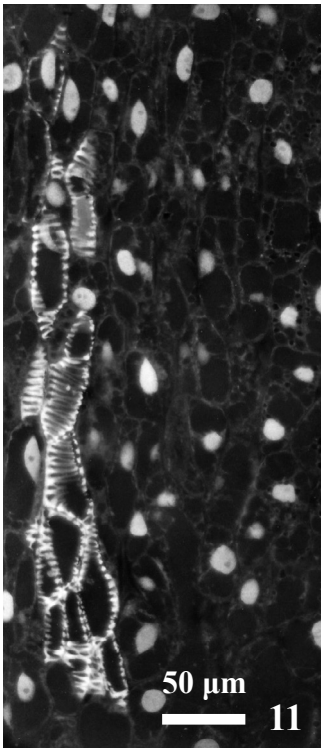
The haustorium

Viscum album is attached to a host branch by means of a primary haustorium (Fig. 2-3) which is interpreted as a modified radicle. In addition many other parasitic plants also have secondary haustoria. Some have only secondary haustoria which develop from side roots or adventitious roots. During germination the tip of the radicle, upon contact to the host surface, becomes expanded and flattened to form a holdfast also named an adhesive disk (Fig. 4). The development of the adhesive disk has been investigated for the small South African *Viscum minimum* (Heide-Jørgensen 1989) and it is illustrated in Figs. 5-10. When contact to the host is obtained the outermost cell layer (the epiderm) functions as gland cells secreting a lipidic compound. The compound glues









Figs. 8-11. *Viscum minimum.* **Fig. 8.** Scanning electron microscopy of holdfast loosened from the host to show the front of the wedge shaped intrusive organ as well as imprints of the host epidermis with stomata (arrow). The hole to the right is caused by some of the adhesive stayed attached to the host. **Fig. 9.** Epi-fluorescence microscopy of a young intrusive organ. Nuclei, chromosomes and the lipid-adhesive lit up and some secrete is drawn into the host. **Fig. 10.** Light microscopy of a young intrusive organ. Lipid-secrete is grey. Cell walls and nuclei are blue. Arrow, compressed cells. **Fig. 11.** Cell nuclei and tracheids of the xylem bridge lit up.

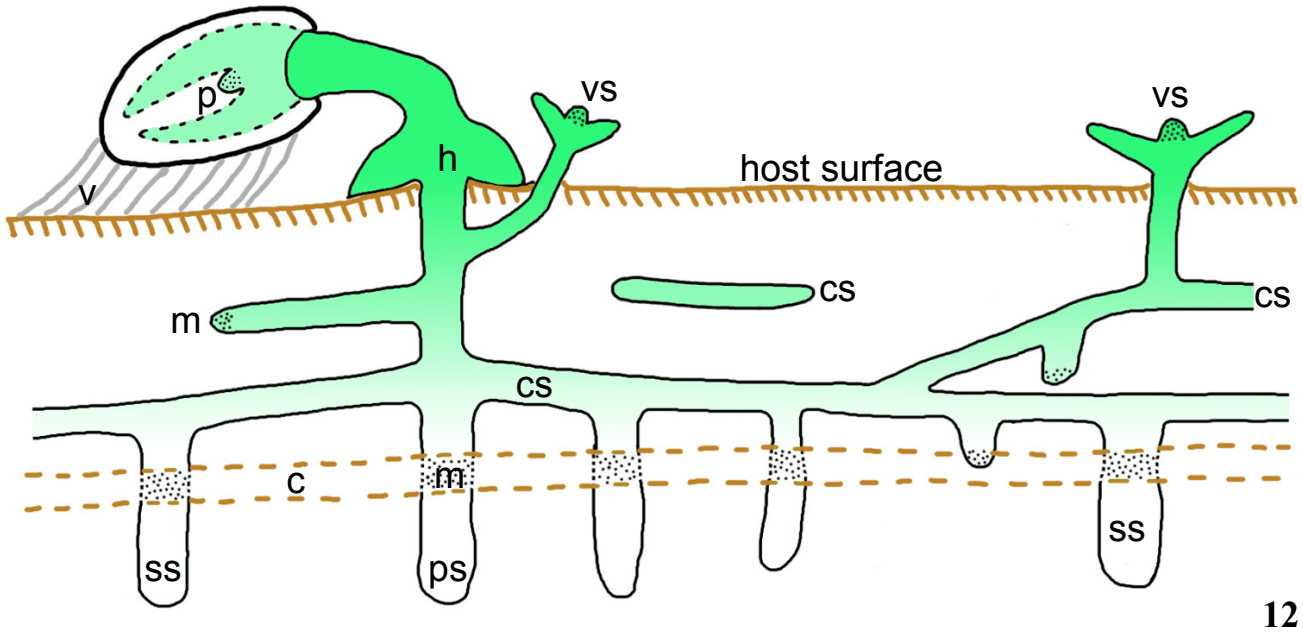




Fig. 12. General diagram of a *Viscum* haustorium. The holdfast (h) is first established, then develops the intrusive organ which after contact to the xylem of the host is called the primary sinker (ps). Then the cortical strands (cs) develop followed by secondary sinkers (ss). At last the vegetative (vs) shoots appear which flower 3-4 years later. c, cambium. m, meristem (growth point). p, plumule. v, viscin.

Fig. 13. *Viscum album* mother plant with a one year old vegetative shoot sprouting from a cortical strand.

the holdfast to the host (Figs. 4-7). Inside the holdfast a growing point (meristem) develops. By cell divisions, the meristem produces a so-called intrusive organ which penetrates the host tissue (Figs. 4 and 8-10). First, the intrusive organ has to break through several cell layers in the holdfast. Its growth also causes some of the holdfast cells to collapse in zones (Fig. 4). The tip of the intrusive organ is wedge shaped (Fig. 8), and it penetrates the host partly by enzymatically dissolving the pectic middle lamella between host cells and partly by compressing the host cells. The latter is possible since the hydrostatic pressure in parasite cells always is greater than in host cells (Fig. 9-10). The parts of the parasite seen outside the host are called the exophyte, while the parts inside the host are called the endophyte.

When the intrusive organ (also named primary sinker) reaches the water transporting vessels and tracheids in the wood of the host (xylem), the same kind of vessels and/or tracheids differentiate in the intrusive organ (Fig. 11). Thereby a xylem bridge is formed between the host and the mistletoe stem and water and nutrients can stream freely from host to parasite. Furthermore, the intrusive organ ramifies in the living part of the bark (cortex) outside the phloem. These ramifications are called cortical strands (Fig. 12), and from here secondary sinkers grow into the host xylem (Fig. 12). When these sinkers pass the host's growth layer (the cambium) they develop a meristem at the level of the cambium. Thereby the sinkers are able to accomodate the increase in thickness of the host. In *Viscum* the xylem bridge is not accompanied by phloem.

In addition to the primary shoot cortical strands also produce flowering shoots (Fig. 12-13). In *Viscum album* the strands are relatively short and













Fig. 14. New shoots of *Viscum album* sprouting from cortical strands in an old apple tre (*Malus domesticus*) at relatively short distance from the mother plant seen at right.

Fig. 15A-E. Longitudinal section of apple branch and a *Viscum album* with 8 shoot innovations (approx. 11 year old). **A.** The following pictures (B-E) are photographed from the opposite side and mirrored vertically so the left exophyte is not visible in the section series. Also note the host twig is dead distally (right) to the mistletoe. This is caused by drainage of the host for water and nutrients by the haustorium. The thickening close to the haustorium consists mainly of host tissue. **B-E.** The cortical strands (arrow) are green since the cells contain chlorophyll. The strands grow in all directions in the cylindrical area between the conductive tissue and the cortex (primary bark) of the host. Therefore the strands are cut in transverse, longitudinal, and oblique positions. **D-E.** Some secondary sinkers are also visible.

rarely more than a few cm long. However, in old plants they may exceed ten cm in length as indicated in Fig. 14 where new shoots sprout in a row from a deep furrow in the host's bark. The ramified endophyte in *Viscum album* is illustrated in Fig. 15 showing longitudinal sections through a host branch with a haustorium from a plant with eight shoot innovations. As it appears in Figs. 12 and 15 the cortical strands contain chlorophyll. It is assumed



Fig. 16. The locality in southern Sealand near the village Store Elmue where a descendant of the last wild specimen in Denmark of *Viscum album* ssp. *album* is growing on a young apple tree (right and ind-set). A very old apple tree with a dead main trunk and no mistletoes is seen in the center. At lower right is a dead stump which may have been the original protected host for V. *album*. It is assumed someone has transplanted seeds from the original wild V. *album* to the young apple tree which now is host for a female plant (arrow) at least 10 years old. How this plant is pollinated is so far a mystery. A request to the Nature Conservation Authorities has so far not given any result.

enough light reaches the strands to allow a modest degree of photosynthetic activity, but most likely it is only sufficient to compensate for the respirational loss within the cortical strands themselves.

Distribution in Scandinavia

The European mistletoe occurs from Western Europe to Japan. Earlier when Denmark was heavily forested it was a common species but today wild populations are considered extinct. The last extant wild specimen grew on an apple tree at Store Elmue, South Sealand. The host and consequently also the mistletoe died several years ago. Seeds were transferred to a young apple tree which today hosts a more than 10 years old female plant of *Viscum album* (Fig. 16). A population near Lillebælt (Kauslunde) may also be original. In recent years *V. album* has become a popular garden plant. In Copenhagen the presence of the mistletoe along a number of roads and in other public places has recently been counted to 858 specimens, 177 of which are assumed to be spread by birds. However, these numbers represent far from all occurrences (Gjøl Sørensen 2013).

In Norway *Viscum album* thrives on the islands in the Oslo Fjord and in Sweden it also occurs naturally in several localities in Småland and Östergötland, where it is protected. The northern limit in Scandinavia is determined by winter temperature. The mean temperature must be higher than -5°C, but the lesser the winter temperature is the higher July mean temperature is needed. Fossil pollen findings show the northern limit for *V. album* in the relatively warm Late-glacial interstadial about 12.600 years ago was more than 100 km further north (Iversen 1944). The ongoing climate change may mean *V. album* may again spread further north.





Fig. 17. *Viscum album* ssp. *album* on *Robinia pseudacacia*. **Fig. 18.** *Viscum cruciatum* has red berries. © H. A.

Hosts and taxonomy

Viscum album ssp. *album* is registered parasitic on more than 100 different genera and 230 different species. In Denmark it grows among others on apple, crab apple, *Crataegus* sp, *Populus* sp, *Acer platanoides*, *Ulmus minor*, *Tilia platyphyllos*, and *Robinia pseudacacia* (Fig. 17). In Southern Europe it occurs on many other species, and in Poland alone on 194 species (Stypiński 1997). However, it is not possible to collect seeds of *V. album* growing on an apple tree and get the parasite successfully established on anyone of the other hosts mentioned. The reason is, *V. album* consists of a number of physiological races which look alike morphologically but are physiologically different in such a way that each race can only accept a limited number of the total number of registered hosts. I have collected *V. album* seeds from domestic apple and got the parasite established on red hawthorn and crab apple. In Europe four of these races have the status of subspecies. Besides *V. album* L. ssp. *album*, which parasitise broad leaved trees the following are recognized: *V. album* ssp. *abietis* (Wiesb.) Abromeit having *Abies alba* as host, *V. album* ssp. *austriacum* (Wiesb.) Vollmann having *Pinus* and *Larix* as hosts, and *V. album* ssp. *creticum* (subsp. nova) which are only known from *Pinus halepensis* ssp. *brutia*. The only other species in Europe is *Viscum cruciatum*, which has red berries (Fig. 18). It prefers olive trees but is also found on *Crataegus*.

The shoot system

Viscum album has a characteristic bifurcated construction (Fig. 19). Each annual increment consists of one internode. The yearly internode ends with two or more rarely 3(-4) leaves (Fig. 21-22). Each leaf supports a bud which produces next year's growth increment resulting in the basic dichotomy. The number of subsequent internodes reveals the approximate age of the parasite, although, 2-4 years should be added for the time it takes from germination and establishment of the endophyte to the first leaf bearing shoot is developed. The leaves are evergreen but are shed after about 1½ year. Therefore it is surprising that the Flora Danica plate of *Viscum album* (Knudsen 2014) shows a plant with leaves on three successive nodes. In older plants 3-6-(8) innovations may develop from the same node (Fig. 20), although only two are expected according to the basic ramification scheme. The reason is that two tiny leaves named prophylls (Fig. 23-24) are located at the base of each internode. Each of the prophylls supports a bud and in older plants in good growth condition these buds produce an internode. The prophylls are so tiny (<½ mm) and partly translucent that they have only recently been described in the scientific literature by Job Kuijt in 2013. When wilted the prophylls become black.













Figs. 19-24. *Viscum album.* **Fig. 19.** Bifurcate shoot system where each internode represents one year's growth ending with two leaves and a terminal bud. **Fig. 20.** Many shoots originate from the same node. **Fig. 21.** Male plant internode with three leaves in a whorl. **Fig. 22.** Female plant internode with three leaves in a whorl. **Fig. 23.** Internode with two leaves and a terminal male flower. Each leaf supports a new internode which has just begun to grow. At the base of the internodes two filamentous prophylls are located of which one is visible per internode (arrow). Each of the prophylls supports a bud which the following year may develop a shoot (new internode) or an inflorescence. **Fig. 24.** Turned 90° in relation to Fig. 23. The reader is looking directly on the brown scar after a leaf which has supported the middle internode. The prophylls supporting the two lateral internodes are barely visible (long arrow) while their prophylls (short arrow), on the reader's side, do not support visible buds. On the opposite side, however, they support an inflorescence.



Fig. 25. *Viscum album* male plant with a terminal inflorescence and two lateral inflorescences on the two preceeding internodes.

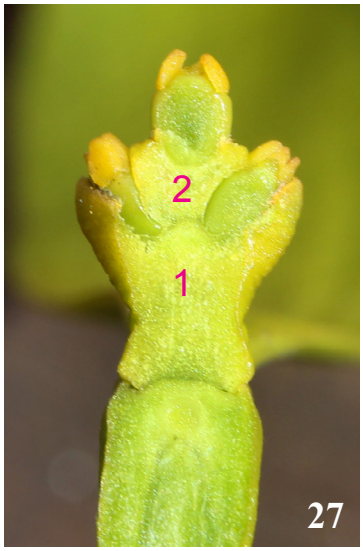
When the exophyte is in its third or fourth year each internode terminates into an inflorescence besides the two leaves. The buds in the corners of the prophylls may also produce inflorescences (Fig. 24). The result is that a several year old branch may simultaneously have one terminal inflorescence and two lateral inflorescences plus further 1-4 lateral inflorescences on up to two older internodes (Fig. 25). Both female and male flowers are produced but placed on different plants and therefore *Viscum album* is dioecious. The male inflorescence consists of a short internode ending with two small scaly bracts which embrace three flowers (Fig. 26). The female inflorescence consists of 1-3 successive very short internodes each of which ending in a pair of small scaly bracts. The uppermost bracts embrace a terminal flower, while the other bracts below each support a lateral flower (Figs. 27-30). The inflorescence may be seen as a three-flowered cyme or as a very short spike. All bracts are equipped with short hairs on the edges but they are most visible on the female inflorescence (Figs. 28-30). The function of these hairs is unknown but they may participate in attracting pollinators.

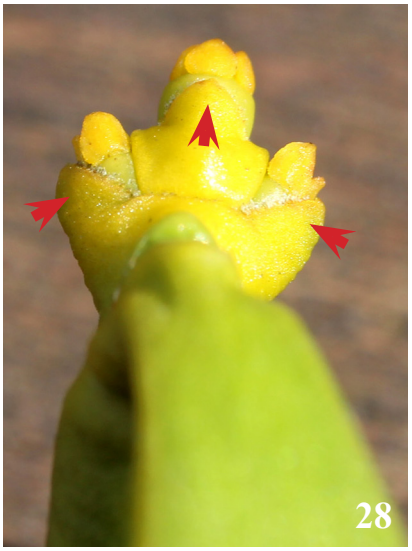


Fig. 26. *Viscum album* male inflorescence. The two lateral flowers are each supported by a bract (arrow). Green algae are seen on the tepals.

Flowering and pollination

In Northern Europe *Viscum album* flowers in March-April. The flowers are 4-merous (rarely 3-merous) with only one whorl of yellowish-green tepals which are 4 mm long in male flowers (Fig. 26) but only about 1 mm in female flowers (Fig. 31). In the male flowers the anthers are united with the tepals. Each anther usually contains more than 20 pollen sacs, each opening by a pore (Fig. 32-33). The female flower is epigynous with a single stigma which appears as a small bump at the top of the ovary. The stigma is surrounded by a green nectary (Fig. 31) which in the closely related *Viscum cruciatum* (Fig. 18) produces 0.05 mg nectar per day (Aparicio *et al.* 1995), but with a low sugar content. It has been suggested the watery nectar in *Viscum* helps in collecting airborne pollen.











Figs. 27-31. *Viscum album* female inflorescence. **Fig. 27.** Longitudinal section through a three-flowered cyme. The yellow-green internodes are marked 1 and 2. Two bracts are seen on the first internode. On the second internode is one bract cut away while the other is hidden behind the stem. Three green ovaries are visible. **Fig. 28.** Same inflorescence as in Fig. 27. The arrows point to the bracts. **Fig. 29.** Spike with three internodes and five flowers. **Fig. 30.** The remains of last year's terminal 3-flowered cyme are seen centrally. Two circular scars after the two lateral fruits are visible as well as their bracts. An oblong brown scar is seen centrally after the terminal flower's stalk. The flower was most likely un-pollinated and a fruit has not developed. **Fig. 31.** Four-merous female flowers with one whorl of tepals and a domed stigma surrounded by a ring-shaped nectar.

There are no comprehensive investigations of the pollination but both wind- and insect pollination are suggested. The pollen production is large and amounts to 58,000 pollen grain per male flower in *V. cruciatum* (Aparicio *et al.* 1995). The pollen grains are round with small spikes and no equipment to facilitate wind pollination. They have a tendency to stick together in small lumps (Fig. 32). Therefore wind pollination plays only a minor role but can occur according to experiments where shoots of *V. cruciatum* are enclosed in net-bags with different mesh sizes (Aparicio *et al*. 1995). The flowers of *V. album* are visited, as shown in Figs. 34-46, by many different insects. Flies in particular seem to be effective pollinators. Bees are pollen collectors and they often visit male flowers (Figs. 34-36) but are more rarely seen on female flowers and they are not considered important pollinators. The common house fly is often seen on both sexes, and Figs. 38-41 show it brings pollen to the female flowers. Other flies,





Figs. 32-33. Male flowers of *Viscum album*. **Fig. 32.** Newly opened flowers filled with globular pollen grains which have a tendency to huddle together. **Fig. 33.** The flowers have been open in several days and most of the pollen are collected by bees. The many open pollen sacs of the anthers are visible.





Figs. 34-35. Honey bees visiting newly opened male flowers of *Viscum album* to collect pollen.

bugs, beetles, and mosquitoes also visit the flowers according to Figs. 37 and 42-46. As mentioned, *V. album* is dioecious and self-pollination cannot occur. Some Angiosperms are able to develop fruits and seeds without pollination but a simple experiment provides some indication that *V. album* must be pollinated to produce seeds. A few female shoots with flower buds were enclosed in a translucent plastic bag with a small hole in the two lower corners to allow the leaves to obtain both light and carbon dioxide for photosynthesis and drain water from transpiration (Fig. 47). The bags were removed two months later when the male flowers were wilted and emptied for pollen and fruit development had started in the female flowers (Fig. 48). There was no sign of fruit development on the shoots from the bag hence the flowers had not been pollinated (Fig. 49).

Fruit, seed, and seed dispersal

The fruit is a single seeded berry. It ripens during winter where the color changes from green to white or yellowish. Hence the parasite has ripened fruits simultaneously with flowers (Fig. 51). On top of the about 1 cm large round berry scars after the stigma













Figs. 36-41. Insects visiting *Viscum album* flowers. **Fig. 36.** Honey bee with filled pollen basket on male flower. **Fig. 37.** Fly on male flower. **Figs. 38-41.** Flies on female inflorescences. **Fig. 38.** Pollen grains on the thorax. **Fig. 39.** Pollen on foreleg and abdomen. **Fig. 40.** Pollen on wing. **Fig. 41.** Pollen lump on foreleg.











Figs. 42-46. Insects visiting *Viscum album* flowers. **Fig. 42.** The insect is powdered with pollen from male flower. **Fig. 43.** Same kind of insect on female inflorescence but without pollen and sign of a preceding visit to male flowers. **Fig. 44.** Tick on male flower and at least five pollen grains on the wings. Pollen are also seen catched on spiders threads which may indicate wind pollination. However, wing movements and other insect activities in the flower may also explain the presence of pollen on the spider's web. **Fig. 45.** Unidentified mosquito on female flower. **Fig. 46.** Beetle powdered with pollen on male flower. (Notice the Figures can be enlarged considerably).







Figs. 47-49. Pollination is a must for fruit development in *Viscum album*. **Fig. 47.** Several shoots are enclosed in a plastic bag before flowering. **Fig. 48.** Fruit development in freely exposed pollinated flowers. **Fig. 49.** The plastic bag is removed after three months. No fruits developed due to lack of pollination.

and the four tepals remain visible (Fig. 50). In most plants the fruit and seeds are independent morphological entities, but in *Viscum* no seed coat is formed since the integuments are lacking. The outermost layer of the endosperm is thus united with the innermost layer of the fruit wall.



Fig. 50. The *Viscum album* fruit is a one-seeded berry. A scar is seen on the top of the berry after the stigma surrounded by four scars from the tepals.

The structure of the fruit corresponds to other investigated species in Viscaceae and Loranthaceae such as *Arceuthobium tsugense* (Paquet el al. 1986), *Phoradendron californicum* (Gedalovich *et al.* 1988), and *Passovia (Phthirusa) pyrifolia* (Gedalovich & Kuijt 1987) but with lesser differences in the chemical composition of the viscin. The fruit wall is three-layered. The outermost layer (exocarpium) is a tough membranous, white layer with vascular bundles (Figs. 51 and 53-54). This layer is easily separated from the middle layer (mesocarpium) which is a limpid and sticky/slimy layer constituting by far the main part of the fruit wall (Fig. 53). The innermost layer (endocarpium) is a very thin tough, white layer which, as mentioned, is united to the seed body. This layer also contains vascular bundles (Figs. 53 and 71). The sticky substance of the middle layer is called viscin or viscin tissue. It consists of two cell types. Long degenerated cells with an inner spiralized wall of cellulose surrounded by a cylinder of pectin are found innermost in contact with the endocarpium. Strongly vacuolated globular cells surrounded by polysaccharide material (most likely also pectins) are found towards the exocarpium (Fig. 53) (Sallé 1983). The other Viscacean species with bird dispersal have a similar construction of the mesocar-

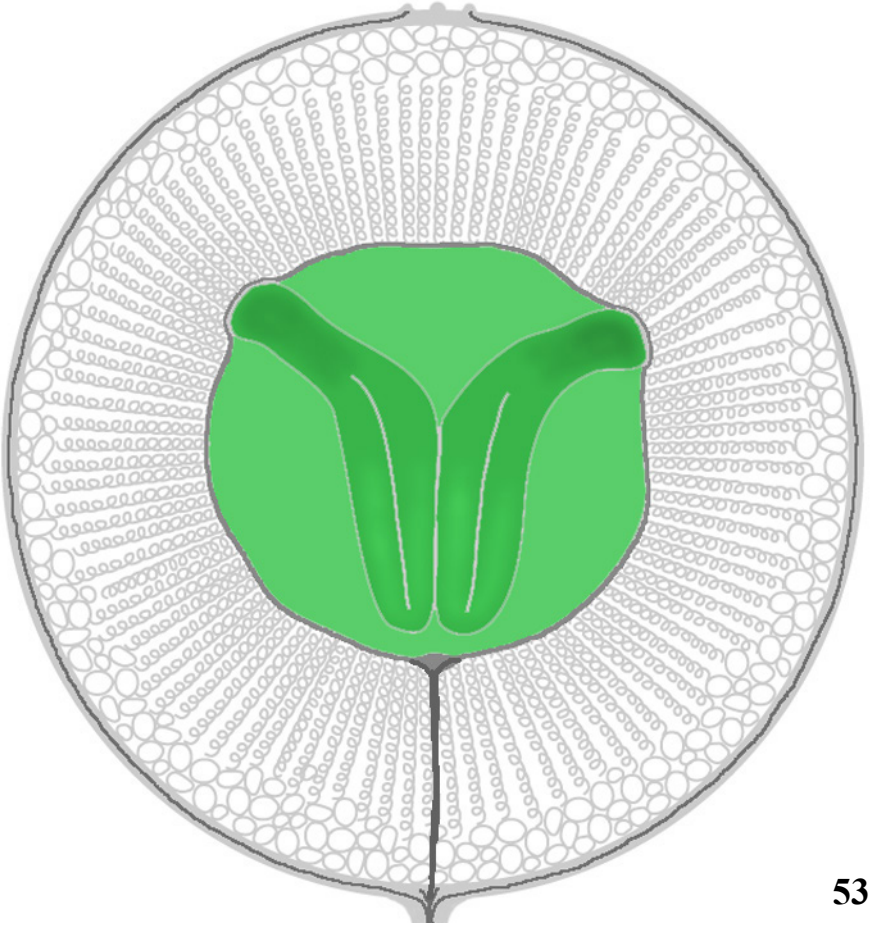




pium. The complex chemical composition of the viscin has been analyzed in *Phoradendron californicum* (Gedalovich *et al.* 1988). The viscin has both sticky and elastic qualities. The latter is ascribed to the cells with the spiralized wall. The elasticity is illustrated in Figs. 52 and 54. The weight of the seed in combination with rain and wind is able to stretch a viscin-strand up to 75 cm or even more (Fig. 52). It is remarkable that the viscin in the two subspecies *Viscum album* ssp. *abietis* and ssp. *austriacum*, both having conifers as hosts, lacks the elastic quality (Grazi & Urech 1981). The sticky quality secures that the seed, after dispersal by birds, is able to glue to a potential host. When the seed is deposited on a host twig, the viscin is wet and jelly-like, a condition which is particularly distinct in rainy weather (Fig. 55). If a seed is deposited on the upper surface of a branch, the jelly-like condition will usually make the seed slide down to the underside of the branch where it is protected in a better way. As soon as the viscin dries, it becomes hard and it cannot become jelly-like again during a future shower (Fig. 56). The seeds are remarkable by often containing two (Fig. 53) or occasionally even three embryos. All of the embryo as well as the complete endosperm are green of chlorophyll and able to perform photosynthesis (see later).

Viscum album is spread by birds, but in Denmark man has in recent years had the greatest influence on the dispersal by sowing seeds on potential hosts in gardens and public places. The birds handle the berries in two very different manners. Some birds swallow the berry and the seed is expelled with their droppings. Other birds separate the fruit skin (exocarpium) from the seed and the viscin, and the birds only eat the skin and some of the globular viscin cells. Looking at the total distribution of *V. album* in Europe the mistle trush (*Turdus viscevorus*) is the most important disperser except in Denmark. The reason is the mistle trush is a forest bird which rarely appears in gardens where the majority of the parasites are found. The mistle trush belongs to the group of berry-eating

Fig. 51. Ripe fruits on *Viscum album* are seen in the early spring simultaneously with flowers. Vascular strands in the fruit wall are seen on the berry to the right. **Fig. 52.** Viscin threads are stretched up to 75 cm by weight of the seed, rain drops and wind. The middle seed hangs in a strand which above consists of two coalesced strands.



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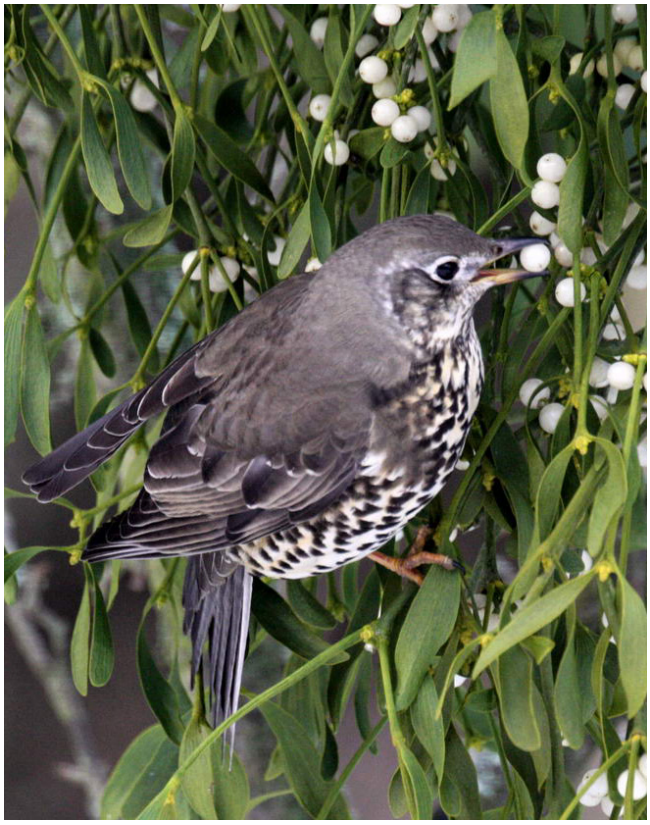
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Figs. 53-56. Fruits and seeds of *Viscum album*. **Fig. 53**. Schematic section through one-seeded berry. The outermost thin layer (exocarpium) of the fruit wall is shown grey with black vascular strands. The middle layer (mesocarpium = viscin tissue) consists outwardly of globular cells and inwardly of cells with a spiralized wall. The innermost layer (endocarpium) is marked as a thin grey line in direct contact with the green chlorophyll containing endosperm. Two green embryos are seen each with two cotyledons and a radicle. **Fig. 54**. Seed deposited on a branch with the exocarpium hanging in a viscin thread. **Fig. 55**. Seed deposited on a branch in rainy weather. The viscin is jelly-like. Notice the green endosperm. **Fig. 56**. Same seed as in Fig. 55 photographed two days later when the viscin has dried and the seed is firmly anchored to the branch.

birds that swallow the entire berry (Figs. 57-58). The bird primarily exploits the fruit skin while most of the viscin and the seed are defecated. The viscin has a double function. First, the jelly-like condition makes a meal of 16-18 berries to pass the alimentary canal in only 15-20 min. (Lütken 2009) and 3 min. for a single seed (Steindl 1935). In the Australian mistletoe bird (*Dicaeum hirundinaceum*), which spreads *Amyema* species, a seed passes the bird on average in 14 minutes (Watson 2011). The second function is





Figs. 57-58. The mistle trush, *Turdus viscivorus*, eats berries of *Viscum album*. **Fig. 57**. A berry has just been picked. **Fig. 58.** The berry is on its way down the throat in undamaged condition. Photo © Emil Lütken.



connected to the adhesive quality of the viscin which secures the seed adheres to the host branch.

Since the mistle trush usually eats several berries rapidly the seeds are also expelled similarly fast and often as pearls on a string where the string consists of viscin (Fig. 59). Such a pearl string is called a rosary and rosaries are characteristic for a great number of bird dispersed species in Viscaceae and Loranthaceae (Heide-Jørgensen 2008). A rosary delivered by a mistle trush is beautifully illustrated by Lütken (2009), who also notes that although it eats other berries, the mistle trush is highly dependent on *V. album* berries in severe winters. Therefore the bird establishes territories around trees with many mistletoes which it defend against other fruit eating birds. Droppings in the form of rosaries are an advantage for *V. album* compared to seeds defecated one by one, since rosaries increase the chance that some of the seeds will hit an acceptable host when the rosary

Fig. 59. 'Rosary' with three seeds of *Viscum album*, however, not produced by the mistle trush but formed when seeds deposited by a blackcap slides down a common viscin thread in rainy weather.



Fig. 60. Bohemian waxwing eats *Viscum* berries but here it has gorged oneself with drupes of *Crataegus*.





falls to the ground. Since the mistle trush in Northern Europe predominantly is a migrating bird and since the digestion of a meal takes up to about 20 minutes the mistle trush is of decisive importance for long distance dispersal of *V. album*.

Bohemian waxwing (*Bombycilla garrulus*) is an irregular winter guest in Denmark. In certain years it arrives in large flocks while it is almost absent in other years. It occurs in both woods and gardens and eats berries of *Viscum album* using the same method as the mistle trush but it prefers other berries such as *Sorbus* or e.g. drupes of *Crataegus* (Fig. 60). Its importance for dispersal of *V. album* in Denmark is considered minimal.

The Eurasian blackcap (*Sylvia atricapilla*) is an eager consumer of *Viscum album* berries and it occurs in both woods and gardens in the general distri-

Figs. 61-62. Female blackcap eats *Viscum album* berry. **Fig. 61.** The berry in the beak has just been picked. **Fig. 62.** The bird has moved to a nearby branch on the host apple tree where the seed and viscin are smeared onto the branch. The arrow points to a seed deposited about a month earlier by another blackcap. The two embryos are germinating.









bution area of *V. album* until Caucasus. The Danish blackcaps usually migrates south during winter, but in mild winters some will stay and then *V. album* berries become an important food source. I have seen a male blackcap eat many hundred berries in a few days in January and February. The blackcap uses the technique of separating the seed from the fruit skin (exocarpium) (Figs. 61-66). The bird picks a berry and flies to a twig just a few meters from the food source. It then clamps the beak and causes the fruit skin to crack and the seed and most of the viscin are partly squeezed out. Then the bird swings its body and head from side to side across the twig to wipe of the seed and viscin on the twig, and finally it swallows the nutritious fruit skin with remains of the globular viscin cells. The process is repeated 4-5 times before the blackcap takes a break between meals. The longest distance I have observed between a food source and a seed deposited by a blackcap is 12 m. Hence the blackcap is only responsible for short distance dispersal of *V. album*. It is most likely the main cause that a host tree or a group of closely standing trees with time becomes plastered with the mistletoe. It happens that a blackcap loses a fruit and it does not pick it up again. However, the common blackbird (*Turdus merula*) may pick up such a lost fruit when food is sparse in winter.

Dispersals of *Viscum album* in Denmark with other birds than the mistle trush, Bohemian waxwing, and Eurasian blackcap are rare exceptions, but does not exclude the possibility that other berry eating birds such as song trush, fieldfare, bullfinch, and hawfinch exceptionally spread *V. album*. Tits (Paridae) and the European robin (Fig. 67) visit *V. album* but do not eat or spread the fruits/seeds. One reason is the berries are too large to be swallowed. Another reason is the birds have not learned the technique of the blackcap. However, the great tit (Fig. 68) may search for un-germinated seeds glued to a twig. By doing so the great tit reduces the number of mistletoe plants. Most likely Figs.

Figs. 63-66. The four Figures illustrate how a blackcap (male) handles a fruit of *Viscum album*. First it clamps the beak to make the fruit skin (exocarpium) burst to press out viscin and seed (63 and 64). Then the beak is wiped fourth and back across the branch to smear off the viscin and seed onto the branch (65 and 66) before the fruit skin is swallowed.









Fig. 67. European robin, *Erithacus rubecula*. **Fig. 68.** Great tit, *Parus major*. **Fig. 69.** A Great tit most likely has eaten the remains of the cotyledons and endosperm of at least two of the four *Viscum album* seedlings and thereby damaged the plumule, although it may also have aborted. **Fig. 70.** The plumule is dead and vegetative growth has started from the intrusive organ immediately below the holdfast.

69-70 illustrate the result of a great tit visit where the bird during seed germination has eaten remains of the endosperm and cotyledons and thereby damaged the plumule. In such a case the exophyte may develop shoots from the holdfast or the upper part of the intrusive organ as shown in Fig. 70. A corresponding situation occurs when the plumule aborts which is the normal case in *Viscum minimum* (Kuijt 1986), but is less common in *V. album*.

Embryo and germination

About 50% of the seeds contain not just one but two embryos (Figs. 53 and 71-73) and a few seeds even three embryos (Fig. 77). Both the endosperm and the entire embryo contain chlorophyll (Figs. 53 and 71-73), and the ability to perform photosynthesis has great importance during germination until the primary haustorium is functional. Until then the parasite is on its own without supply of water and nutrients from the host. *Viscum album* loses the ability to germinate a few days after the berry has been picked but if the seed is glued to a potential host in due time germination will normally proceed. If the support is not an acceptable host branch germination will stop before or as soon as the holdfast is established. The holdfast does not develop on completely smooth surfaces such as glass (Fig. 74) or metal (Thoday 1951, Sallé 1977). There are different opinions if the embryo besides cotyledons and plumule consists of both a radicle and a hypocotyl and if so where the transition is located. Some researchers tend to mean the hypocotyl is lacking, while all agree the haustorium is produced by the radicle. In this article the Salomonical expression radicle-hypocotyl is used.

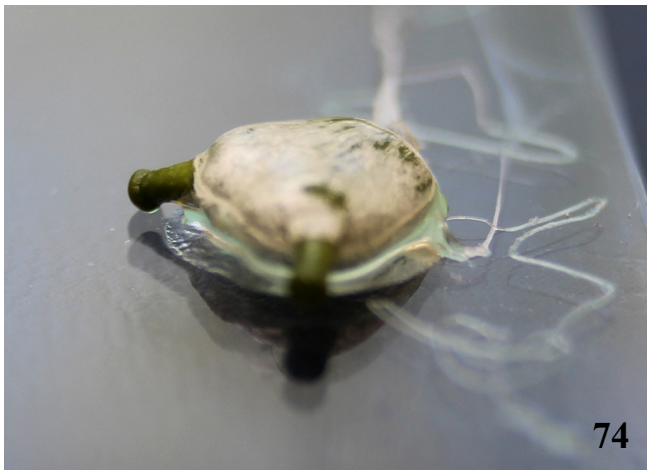
The germination is dependent on light (Heinricher 1916, Tubeuf 1923) and temperature, where 15-







Figs. 71-73. Fruit with seed of *Viscum album*. **Fig. 71.** Transverse section of berry showing seed with two embryos (compare Fig. 53). Vascular strands in the endocarpium and green endosperm are clearly visible. **Fig. 72.** The fruit skin (exocarpium) and viscin tissue (mesocarpium) are removed. **Fig. 73.** Same as Fig. 72 but cut so the lighter green cotyledons from the two seeds are partly visible.





18°C is optimal (Sallé 1983). The radicle-hypocotyl is both negative phototropic and negative geotropic. Therefore it always bends towards the host branch independent of how the seed is placed (Figs. 75-76 and 79). When a seed is placed on a glass plate and illuminated equally from both sides the phototropic and geotropic reaction fail to appear (Fig. 77). The passage through the bird's alimentary canal has no influence on the germination ability (Sallé 1983).

The cotyledons are emptied of nutrients and are lost rapidly after the holdfast is established (Fig. 79), but it takes a minimum of two and usually three years before the endophyte is so well developed that the first pair of foliage leaves develop from either the plumule (Fig. 80) or the endophyte (Fig. 70). According to Weber (1993) the seedling dies shortly after penetration of the host, and the exophyte develops from callus-like outgrowths breaking through the bark of the host from the endophyte (Fig. 78). This seems more the exception than the rule. A further 3-4 years passes before the plant is able to bloom and it becomes visible if it is a male or

Fig. 74. Germination stops in *Viscum album* before the holdfast is fully developed when the seed is deposited on a completely smooth surface such as glass.

Fig. 75. The radicle-hypocotyl is negatively phototropic in *Viscum album* and bends away from light and towards the host branch.













Figs. 76-81. Germination and seedlings in *Viscum album*. **Fig. 76.** Newly germinated seeds. The radicle-hypocotyl bends away from light (negative phototropic) and against gravitation (negative geotropic). **Fig. 77.** Seed with three embryos germinated on glass illuminated equally from both sides. The negative phototropic reaction fails to appear. **Fig. 78.** Older plant with callus-like primordia breaking through host bark. From here one to more shoots develop (arrow). **Fig. 79.** Two germinated seeds each with two embryos. The holdfast is established, and the nutrients in cotyledons and endosperm are used. **Fig. 80.** Three year old seedling where the two first leaves is growing. Arrow, scar after cotyledon. **Fig. 81.** Young plant six years after germination.









Fig. 82. Thickened host branch around *Viscum album* haustoria. The distal part of the host branch (right) is dying. **Fig. 83.** The outermost part of this apple host branch is dead since *V. album* has drained it for water and nutrients. **Fig. 84.** Apples on the branch with *V. album* are smaller and less well developed than apples on uninfected branches seen above and at lower left. **Fig. 85.** Fifteen years old and 1½ m long *V. album* male exophyte on an apple tree.

female. In my garden where far the most individuals have the same mother plant there is a considerable majority of female plants. In Poland the proportion between male and female *Viscum album* plants is 1:7.55 in a population of 900 plants (Stypiński 1997). The vegetative growth starts slowly in late April after the flowering, speeds up in May-June (Fig. 81), and is finished during July.

Host reactions and self-parasitism

Viscum album is a parasite that drains the host for water and nutrients, but in the northern part of its distribution it is not considered harmful to its hosts, and the hosts have not developed any real defense against the parasite, although, germination on older branches with a thick bark usually fails. However, the hosts do react to an attack of the mistletoe. It is common to see the host branch become thicker around the haustorium (Fig. 82). The thickening develops partly due to increased formation of bark (periderm) and partly because the endophyte takes up space in the host tissue (cortex). As the mistletoe grow older and bigger the part of the host branch located outside (distally to) the haustorium will suffer more and more from lack of water and inorganic nutrients, the yearly growth increase becomes lesser, and finally that part of the branch may die (Figs. 82-83). If the entire branch or the host tree dies, *V. album* will also die. Generally, an apple branch bearing *V. album* produces fewer and smaller apples than a branch on the same tree without







Fig. 86. *Viscum album* seed with two embryos germinated on kiwi (*Actinidia* sp.) The host has rejected the radicle-hypocotyl's normal negative phototropic reaction. **Figs. 87-88.** Self-parasitism in *Viscum album.* **Fig. 87.** Male plant on female plant. **Fig. 88.** Female plant on female plant.

a mistletoe (Fig. 84). Further, *V. album* may become so large and heavy that the host branch breaks in a storm. A 15 years old *V. album* exophyte may reach a length of 1½ m (Fig. 85), and I have seen *V. album* plants more than 2 m long.

Many species refuse attack from *Viscum album.* Some of these have developed an effective defense by tissue incompatibility causing the intrusive organ to die while others refuse the parasite already during its germination. This seems the case when seeds are sown on kiwi (*Actinidia* sp.), wine (*Vitis vinifera*), and Chinese wisteria (*Wisteria sinensis*). The phototropic reaction of the radicle-hypocotyl fails to appear on kiwi and germination stops before contact to the branch is achieved (Fig. 86). On wine and Chinese wisteria the growth stops when the holdfast is established. In South Europe *V. album* does some harm, particularly when it invades fruit plantations









Fig. 89-91. Self-parasitism in *Viscum album*. **Fig. 89.** The host has lifted the holdfast on two young seedlings from the original surface of the host stem. Below, germinated seed with two embryos. **Fig. 90.** Same situation in older self-parsite as in Fig. 89. **Fig. 91.** Self-parasitic male flowering already from the second internode of the exophyte. **Fig. 92.** Deciduous Loranthus europaeus with yellow berries. © I. Drozdowski.

and it can only be controlled by cutting infected branches.

As mentioned, *Viscum album* ssp. *album* is parasitic on more than 230 species and among these are *V. album* itself. This is called self parasitism. In my garden the blackcap is responsible for a considerable number of self parasitic plants with both male and female individuals on the same host mistletoe (Figs. 87-88). It appears the *Viscum* host stem only expands immediately below the holdfast (Figs. 87-90), and no cases are observed where the host branch is thickened as in Fig. 82. This may mean cortical strands are not developed during self parasitism but only a xylem bridge is established connecting to the vascular tissue of the host stem. It is interesting to see if in this case phloem continuity also occurs. Self parasites flowers 1-2 years earlier than if the host is not a *Viscum* (Fig. 91). This probably happens because the self parasite receives flowering hormones from the host. *V. album* also parasitizes the closely related deciduous *Loranthus europaeus* (Fig. 92, Loranthaceae), and it has been suggested that *V. album* may be used in biological control of *L. europaeus* on oak trees in Austria (Grazi & Urech 1985).

Myths, superstition and medicine

The bifurcate construction of the shoot system with two opposite leathery, evergreen leaves per in-



Fig. 93. During winter *Viscum album* lightens up with green leaves and white berries on the leaf-less host.

ternode gives *Viscum album* a very characteristic appearance (Fig. 1). When during winter the parasite moreover lightens up with white berries (Fig. 93) on a leaf-less host it is understandable *V. album* has appealed to people's fantasy and lead to myths and superstition. As late as at the beginning of the 19th century even botanists did not understand the biology of mistletoes. One imagined *V. album* sprouted on tree branches much in the same way as warts appear on humans, and one denied the parasite could germinate from a bird dropping. The popular plant is not surprisingly introduced to North America. The horticulturist Luther Burbank brought it to Sonoma County in California about year 1900 where it since then has spread considerably (Hawksworth *et al*. 1991). Around 1945 it was also introduced to Victoria, Vancouver Island, where it however has not spread to any notable extension.

The best known myth seems to be that of Baldur's death from the Nordic mythology before 1000 A.D. and told in the Icelandic Eddas. Baldur was a son of Odin and Frigg and a favorite of the gods. One night Baldur had an evil dream. When his mother heard about the dream she hurried to take all plants, animals, and objects which could be used for killing into oath. However, Frigg forgot to look up and the mistletoe escaped her attention. The evil god Loki noticed that, and he prepared an arrow (or more likely and arrowhead) of *Viscum album*. Then Loki persuaded Baldur's blind brother Oeder (Øder) to shoot the arrow towards Baldur on a day when the gods enjoyed themselves with sport games. The arrow killed Baldur but he got a chance to return from the land of the dead if everybody would shed a tear over his death. However, Loki refused to cry and the fate of Baldur was sealed.

Viscum album has also played a role in other religious communities. The Celtic priests named druids cut the parasite with golden sickles in con-



Fig. 94. *Viscum album* suspended in a Danish living room at Christmas signaling it is allowed to kiss a girl standing under it.



Fig. 95. Swedish Midsummer Eve in this case celebrated in Maine, US.

nection with sacrifications at mid-summer (Tubeuf 1923, Kuijt 1969). It may be here we shall look for the root to the more recent Christmas tradition of kissing under a mistletoe (Fig. 94). If a girl is kissed under a mistletoe she will be married within a year. In Sweden one used to collect *V. album* for the Midsummer Eve feast (Fig. 95) until 1910 when the plant was protected by law (Walldén 1961). Further, it has been interpreted by J G Frazer (1890), the golden bough Aeneas used to open the door to the land of the death in Vergil's The Aeneid was a *V. album*, or it may more likely have been *Loranthus europaeus*, (Fig. 92) since it occurs in South Europe. It has yellow berries but vegetatively looks completely like *V. album*.

There is an extensive use of *Viscum album* in medicine but often it is only based on superstition. For example in parts of Austria people believed eating berries of *V. album* was useful in contraception. (Tubeuf 1923, Kuijt 1969). In folk medicine *V. album* has been used against almost any kind of illness and as an aphrodisiacal. The most reliable seems to be that a lectin-containing extract have relieving but not curing effect on certain kinds of cancer and inflammatory joint diseases (Hänsel 1999). More than hundred organic compounds have been found in *V. album* (Stypiński 1997), thus there seems to be a considerable potential for research based medicinal use. Beyond this, at Christmas *V. album* is of certain importance as an article of commerce. In certain parts of England this has led to ruthless exploitation and local extinction of the parasite. Finally, in South Europe the viscin has been used as bird-lime, i.e. the viscin has been smeared on twigs to catch small songbirds.

With this the article on the European mistletoe, *Viscum album* ends, but space is allowed for one more illustration of germinating plants dispersed by the blackcap over several years (Fig. 96). However, the subject of evolution has not been touched on, but one very recent discovery deserves mention since it seems to be unique for the genus *Viscum*. It has been shown *Viscum scurruloideum* from Java has an unusual small mitochondrial genome with none nad-genes and it lacks Complex 1 (NADH dehydrogenase) of the respiratory electron-transfer chain. All other investigated plants possess Complex 1 encoded by nine mitochondrial nad-genes and many nuclear genes. It seems these highly unusual evolutionary reductions in *Viscum* are closely related to its parasitic lifestyle (Skippington *et al.* 2015).



Fig. 96. A blackcap has deposited these seeds and seedlings of *Viscum album* on an apple branch over several years.

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