Chapter 1
Introduction: The Parasitic Syndrome in Higher Plants

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1.1 Parasitism in Plants

In vascular plants, parasitism is found only in the eudicotyledonous angiosperms, although the gymnosperm *Parasitaxus usta* may be considered a borderline case, because it develops graft-like attachments with roots of another conifer, rather than haustoria, and has only direct water relations with its host while carbon trafficking from the host is mediated by mycorrhiza fungi (Feild and Brodribb 2005; Heide-Jørgensen 2008). Parasitic plants have been able to adapt to all types of plant communities in all environments where flowering plants occur, except the aquatic environment. Competition for water is one of the main driving forces in the evolution of land plants. In an aquatic environment, water is no limitation to plant growth, and there is no advantage in being a parasite removing water from a host. On the other hand, if a land plant, especially during its establishment, exploits another plant's root system and photosynthetic apparatus, it obtains a clear competitive advantage. It is this advantage that has been exploited by terrestrial parasitic plants and enabled them to be represented in nearly all ecosystems from the high arctic to the driest deserts. This is particularly true for the group of parasites that are dealt with in this book, the Orobanchaceae.

The physical connection organ between parasite and host is called a **haustorium**. The term was introduced by A. P. de Candolle (1813) to describe the connection between *Cuscuta* and its hosts. Since then, it has been used for a variety of structures that are involved in nutrient absorption from species to species or from generation to generation, as exemplified by fungal hyphae, sporophyte of mosses and pteridophytes, and embryo of some seed plants. In parasitic angiosperms, the haustorium is "the essence of parasitism" as Job Kuijt (1969) has put it. At first, the haustorium serves as an attachment organ. Then it develops as an intrusive structure

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that penetrates host tissues. It later becomes a water and nutrient absorption organ. Its most characteristic anatomical feature, which can be seen in all parasitic plant families, is a **xylem bridge**, connecting the xylem of the parasite to host xylem. A few parasites also develop **phloem connection** (see Sect. 3.9.3). Haustorial morphology and anatomy varies greatly among families and taxa. In some parasites, such as Rafflesiaceae, no haustorial parts are visible outside the host. The internal parts in these parasites form cellular strands within the host tissues and become so diffuse that it no longer makes sense to use the term haustorium (Heide-Jørgensen 2008). In such cases, the vegetative part of the parasite within the host is often referred to as the **endophyte**, while the external parts, which are sometimes limited to flowers or flowering stems, as the **exophyte**. The haustorial variation among major taxa reflects the generally agreed opinion that parasitic plants have evolved independently about a dozen times (Nickrent 2008; see Chap. 14).

Traditionally, parasitism has been recognized in 20 dicotyledonous families (Fig. 1.1a), but recently Olacaceae and Santalaceae were split into several smaller families based on molecular studies (Malécot and Nickrent 2008; Nickrent et al. 2010). Parasitic plants may now be found in up to 28 dicotyledonous families (see Sect. 1.7). Based on the presence of mature haustoria, all families consist solely of parasites except for Orobanchaceae that includes the non-parasitic genus *Lindenbergia* (see Chap. 14) and Lauraceae and Convolvulaceae where only *Cassytha* and *Cuscuta* are parasitic. The total number of parasitic species is close to 4,500, in 270–275 genera. That is about 1 % of all known 260,000 seed plants (Thorne 2002). The majority or 90 % of all parasites are hemiparasites, and root parasites represent 60 % of all parasitic plants (Fig. 1.1a).

Although some parasitic plants have been known since the days of Theophrastus (372–287 B.C.), botanists did not pay much attention to this life form until the nineteenth century. Some members of Rafflesiaceae, Balanophoraceae, and Cynomoriaceae were classified as fungi or placed in a separate class for bizarre excrescences, named Sarcophytae (Trattinick 1828; Kuijt 1969). It was the introduction of the very harmful witchweed *Striga asiatica* (Fig. 18.3b) to maize fields in the eastern USA in the early 1950s that stimulated research in parasitic plants. The first comprehensive scientific treatment of parasitic plants was published by Job Kuijt in 1969, and more recent thorough treatments of major parasite taxa or aspects of the parasitic syndrome include Kuijt (1977, 2003), Calder and Bernhardt (1983), Bhandari and Mukerji (1993), Weber (1993), Press and Graves (1995), Polhill and Wiens (1998), Geils et al. (2002), Joel et al. (2007), Carlón et al. (2008), Heide-Jørgensen (2008), and Mathiasen et al. (2008). Following a series of scientific meetings on parasitic plants since 1973, the International Parasitic Plant Society (IPPS; http://www.parasiticplants.org/default.asp) was founded in 2001. Besides organizing congresses and symposia on parasitic plants, the society publishes the newsletter “Haustorium” that is an excellent source on recent published literature on parasitic plants.

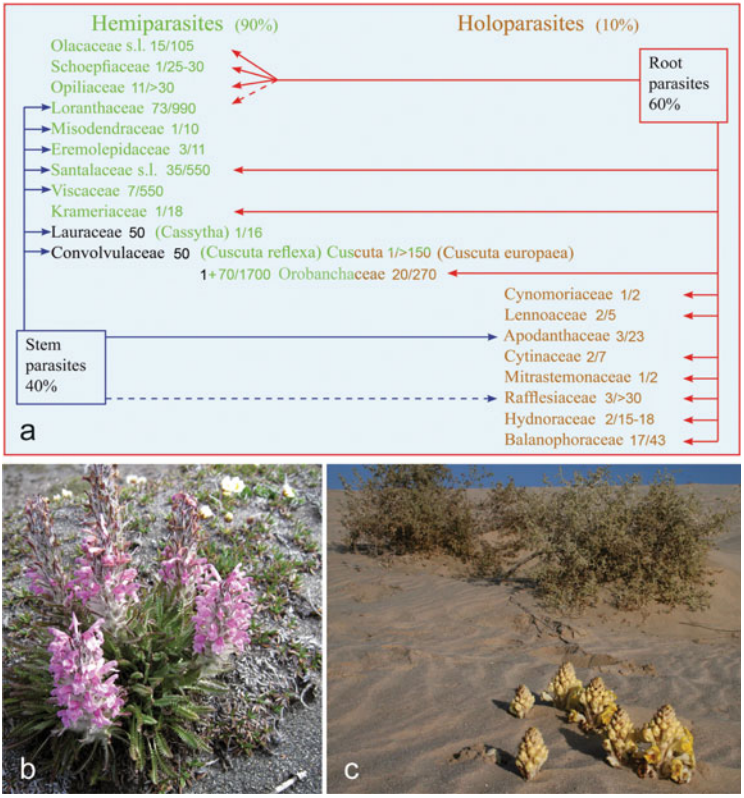

Fig. 1.1 (**a**) Parasitic families arranged according to parasitic types. Family names are followed by a number of genera and species. Broken lines indicate a few exceptions from main type: black, non-parasites; green, hemiparasites; brown, holoparasites; percentages are in relation to the total number of parasitic plants. Apodanthaceae, Cytinaceae, and Mitrastemonaceae used to be in Rafflesiaceae. Orobanchaceae includes the former parasitic Scrophulariaceae and the non-parasitic genus Lindenbergia (modified from Heide-Jørgensen 2008 and 2011). (**b**, **c**) The two main types of parasitic plants. (**b**) The hemiparasitic *Pedicularis lanata* (Orobanchaceae), between plants that serve as its host; high arctic Greenland. (**c**) The holoparasitic *Cistanche tubulosa* (Orobanchaceae) with the host in the background; desert, Qatar (photos: part **b** by Helene Heide-Jørgensen; part **c** by KK Kristiansen)

1.2 Hemi- and Holoparasitism

Two main types of parasitic plants are recognized (Fig. 1.1b, c): (a) **hemiparasites** that are able to photosynthesize although they are not necessarily self-sufficient with carbon and (b) **holoparasites** that have no photosynthetic abilities (dePamphilis and Palmer 1990; Hibberd et al. 1998). Unlike some hemiparasites, when holoparasites have a root system, it is highly reduced and all or the major part of their needs for water and nutrients is derived from their hosts.

Interestingly, in the genus *Cuscuta* (Convolvulaceae), some species have no chlorophyll and are holoparasites (e.g. *C. europaea*; Fig. 1.2a), and others are hemiparasites (e.g. *C. reflexa*; Revill et al. 2005). A third group of species including *C. gronovii* seems to be intermediary having disturbed chloroplast ultrastructure and so little chlorophyll that photosynthesis is insufficient to sustain growth (Van der Kooij et al. 2000). In other families that are dominated by hemiparasites, a single or a few species have also lost most of the photosynthetic ability and may be close to becoming holoparasites. Examples are *Tristerix aphyllus* (Loranthaceae), certain *Arceuthobium* spp. (Viscaceae), and *Phacellaria* spp. (Santalaceae). This evolutionary line is accompanied by a strong reduction of the exophyte (Kuijt 1969).

Both hemiparasites and holoparasites may connect either to the shoot system of the host (stem parasites, aerial parasites) or to host roots (root parasites). It is generally agreed that the former were derived from parasites attacking roots, and in Santalaceae, there are a few species such as *Exocarpos cupressiformis* and *E. pullei* that occur both on roots and on stems (Coleman 1934; Lam 1945). Further, in Orobanchaceae some species may penetrate both roots and rhizomes (Weber 1976, 1993; see Sect. 3.6.1); therefore, the terms root and stem parasites should be used with caution.

Some authors also distinguish between facultative and obligate parasites. **Facultative parasites** may survive without haustorial connection to a host but productivity is better with hosts. Naturally, only hemiparasitic root parasites can be facultative parasites. However, so far no parasitic plant has been documented to complete its lifecycle in a natural environment without haustorial connection to a host. In nature, competition from other plants may eliminate a potential facultative parasite. Therefore, these terms should only be used for parasites grown under artificial conditions (Kuijt 1969). Nonetheless, for a shorter or longer period after germination, some parasites are autophytes nourished by nutrients stored in the seed and/or manufacturing some carbohydrates from photosynthesis in cotyledons. Others at maturity may live for some time from nutrients in storage organs, as suggested for *Nuytsia floribunda* (Fineran and Hocking 1983).

1.3 The Haustorium

Two main types of haustoria are recognized (Kuijt 1969) (see Chap. 3). The **terminal haustorium** (= primary haustorium; Fig. 1.2b, c) develops directly from the apex of the primary root, while **lateral haustoria** (= secondary haustoria; Fig. 1.2d) develop laterally on young lateral or adventitious roots (see Sect. 3.3 for description of terminal and lateral roots of the Orobanchaceae).

In many parasitic plant families, the terminal haustorium is the largest and usually serves as the main functional haustorium throughout the life of the parasite, while lateral haustoria are in most species short-lived and are functional only for a few months or a growing season. In perennials, new haustoria develop each season.

Fig. 1.2 Parasites of the various parasitic plant families. (**a**) Flowering *Cuscuta europaea* (Convolvulaceae) with red achlorophyllous twinning stems; Denmark. (**b**) Terminal haustorium of the hemiparasitic stem parasite *Erianthemum ngamicum* (Loranthaceae) forming a woodrose; most of the tissue is produced by the host *Burkea Africana*; Shakati Nature Reserve, South Africa. (**c**) Tubercle of the holoparasite *Orobanche hederae* (Orobanchaceae) with base of three flowering stems attached to host root (light colour) by terminal haustorium; the host root is wilting distally to the haustorium. (**d**) Rhizome of the holoparasite *Hydnora visseri* (Hydnoraceae) with three lateral haustoria attached to short adventitious roots occurring in rows between buds; lighter host root is *Euphorbia dregeana*; SE of Port Nolloth, South Africa. (**e**) Coiling stems of the hemiparate *Cassytha pubescens* (Lauraceae) with several lateral haustoria attaching its host *Pavonia praemorsa*; Botanical Garden, Copenhagen. (**f**) Self-parasitism in the hemiparasitic stem parasite *Viscum album* (Viscaceae); two young plants have established on a parasite internode after dispersal by the bird *Sylvia atricapilla*. (**g**) Terminal haustorium (asterisk) of the stem parasite *Plicosepalus kalachariensis* (Loranthaceae) and two epicortical roots with lateral haustoria (arrows); South Africa. (**h**) Directional explosive buds and open flower of bird-pollinated *Agelanthus gracilis* (Loranthaceae); Shakati Nature Reserve, South Africa (photos: parts **b**, **c**, **e**, **f**, **h** by HS Heide-Jørgensen; part **d** by LJ Musselman; part **g** by C Calvin)

The numbers of lateral haustoria may amount to several thousands per plant, especially in hemiparasites (Fineran 1963a). Some parasites have both types of haustoria, while others only one. *Cassytha* (Fig. 1.2e) and *Cuscuta* are exceptional by developing haustoria laterally from the stems (see Chap. 3 for detailed description of Orobanchaceae haustoria).

The structure of the mature haustorium varies greatly among families. Both haustorial types may produce an attachment organ, often named a holdfast or adhesive disc. This is particularly important in aerial parasites, where the parasite seedling is not supported by soil particles. In these plants, its function is to glue the young haustorium to the host by secretion of lipidic or pectic substances (Dobbins and Kuijt 1974; Heide-Jørgensen 1989, 1991). In Santalaceae and Loranthaceae, the holdfast often develops a mantle clasping the host, and in the most extreme cases, the clasping folds meet one another on the opposite side (Weber 1980; Fineran and Hocking 1983; Calladine and Pate 2000).

Along the **interface** (the border between parasite and host cells), which often increases tremendously with the splitting up of the haustorium within the host tissues, the cell walls are often thicker (Dobbins and Kuijt 1973) and in some cases labyrinthine walls may also develop (Gedalovich-Shedletzky and Kuijt 1990; Heide-Jørgensen and Kuijt 1993; Fineran and Calvin 2000).

The xylem bridge was once assumed to be the main transport route for water and nutrients from host to all parasites. However, apoplastic markers demonstrated the existence of an apoplastic continuum along the interface of some parasites (Coetzee and Fineran 1987). Pate et al. (1990) demonstrated that only 1 % of the interface cells of *Olax phyllanthi* are xylem-to-xylem connections, while the other interface cells face host parenchyma cells rather than conductive cells. In *Triphysaria pusilla* (Orobanchaceae), many haustoria have no xylem bridge at all or a bridge with incomplete xylem strands, but all haustoria have a well-established intrusive organ and hence a considerable interface area for apoplastic nutrient translocation (Heide-Jørgensen and Kuijt 1995) (see Chap. 6).

The most advanced haustoria from both an anatomical and physiological points of view are those containing phloem with sieve elements, occurring close to or in connection with host sieve elements. This has been demonstrated with some *Cuscuta* and *Orobanchaceae* species (see Sect. 3.9.3). The presence of phloem with fully differentiated sieve tubes so close to host sieve tubes may explain *Cuscuta* being one of the fastest growing parasites. Phloem is known from haustoria in other taxa as well, including stem parasites of Loranthaceae (Calvin 1967), but it never comes as close to host phloem as in the examples above.

1.4 Dispersal and Germination Strategies

Five different strategies for seed dispersal are recognized in parasitic plants and relate to their parasitic syndrome (Kuijt 1969; Heide-Jørgensen 2008).

- The seeds are sticky and in most cases dispersed by birds eating the fruits. By wiping the sticky seeds off the beak or by defecation, the seeds are often placed directly on a branch of a suitable host (Kuijt 1969). Rodents and marsupials may also participate in such seed dispersal (Amico and Aizen 2000). These seeds are relatively large with enough nutrients to produce a large terminal haustorium, while photosynthesis in the endosperm may provide additional nutrients until a vascular connection is established with the host (Kuijt 1969). This strategy is common in stem parasites in Santalaceae *s.l.*, Loranthaceae, and Viscaceae. Dispersal of mistletoes by birds is thus strongly correlated with the behaviour of the birds, which prefer free-standing trees, hedges, and wood edges but avoid the interior of woods.
- Fruits of *Misodendrum* (Misodendraceae) are dispersed by wind and by hygroscopic movements. Long hairy setae (Fig. 1.3b) secure some fruits to the host (Hooker 1847).
- *Arceuthobium* (Viscaceae) has explosive fruits and some seeds may land on suitable hosts 20 m away (Hinds et al. 1963). Explosive fruits are also known from a few species of *Korthalsella* (Santalaceae) (Sahni 1933).
- The parasite seeds contain enough nutrients to sustain the seedling for some weeks. For example, *Cuscuta gronovii* may live for 7 weeks on seed reserves and reach a length of 35 cm before parasitizing a host (Spisar 1910). The young *Cuscuta* stem is guided by volatile oils as shown for *Cuscuta pentagona* (Runyon et al. 2006). This strategy also applies to *Cassytha*, to root parasitic members of Santalales, and to several hemiparasitic Orobanchaceae.
- The seeds are small and numerous with very little nutrient reserves, as in most holoparasitic root parasites. In some holoparasitic Orobanchaceae, seed output per plant is often in the range of 10,000–1,000,000 (Molau 1995). The seeds germinate only when receiving a chemical signal from an adjacent host root (see Chap. 8).

1.5 Host Range

Most parasitic plants, hemiparasitic root parasites in particular, have a wide host range (Kuijt 1979; Gibson and Watkinson 1989; Nilsson and Svensson 1997). Some parasites, like hemiparasitic Orobanchaceae, may attach to several hosts simultaneously. This may provide an ecological advantage since different hosts supply the parasite with different types and amounts of nutrients as shown for *Odontites verna* (Govier et al. 1967). Some stem parasites also have many hosts, such as *Dendrophthoe falcata* (Loranthaceae) that is known from about 400 different host species (Narasimha and Rabindranath 1964). As noted by Kuijt (1979), the relatively few examples of narrow host range (high host specificity) are found among parasites having a terminal haustorium only. *Viscum cruciatum* is known mainly from *Olea europaea*, while the closely related *V. album* is known from more than hundred genera. **Epiparasitism**, which occurs when one parasitic species

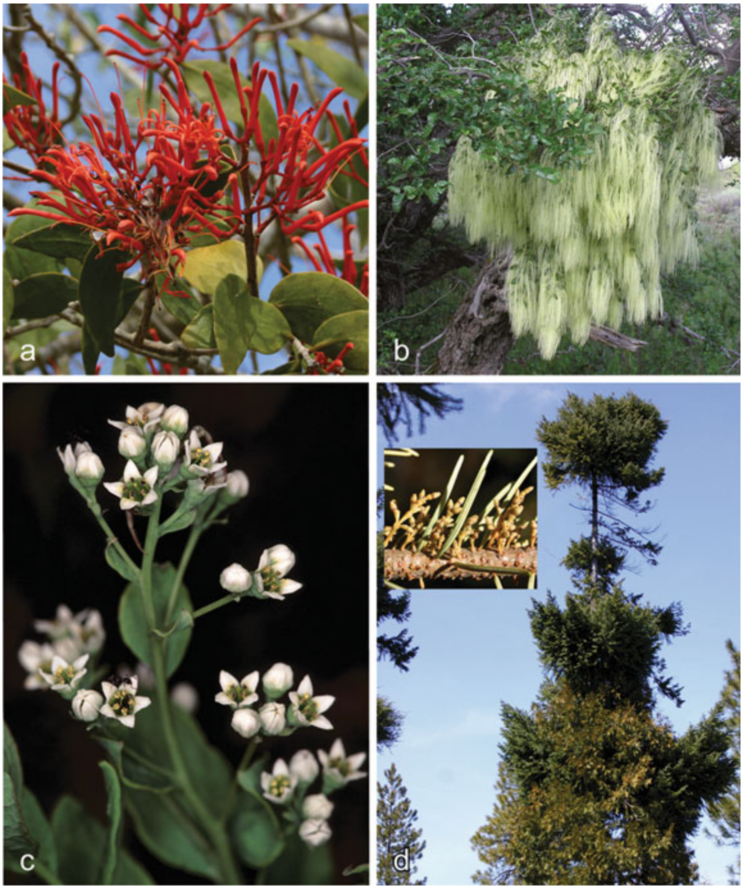

Fig. 1.3 Parasites of various parasitic plant families. (**a**) *Psittacanthus calyculatus* (Loranthaceae) with large showy bird-pollinated flowers; Yucatan, Mexico. (**b**) Female inflorescences of *Misodendrum* cf *oblongifolium* (Misodendraceae) on *Nothofagus antarctica* with persistent staminodes used for wind dispersal; Alumine, Patagonia. (**c**) *Comandra umbellata*, a perennial root parasite of the Santalaceae; Albany Pine Bush, New York. (**d**) The tree *Pseudotsuga menziesii* heavily damaged by *Arceuthobium douglasii* (Viscaceae), Oregon, USA; Inset: fruiting female *Arceuthobium* exophytes between needles of the host tree (photos: part **a** by H Adsersen; part **b** by V Thomsen; part **c** by C Gracie; part **d** by HS Heide-Jørgensen)

parasitizes another parasite species, is most common among members of Santalales (Kuijt 1969; Calvin and Wilson 2009). **Self-parasitism**, occurring when haustoria form between different parts of the same plant, is also known (Fig. 1.2f), mainly in *Cuscuta*, *Cassytha*, and the Orobanchaceae (see Sects. 3.4.2 and 3.5).

1.6 Geographical Distribution

Parasitic plants occur in all climatic zones from northern Greenland to Tierra del Fuego and on all continents except Antarctica. Some plants are resistant to certain parasites (see Chap. 7). However, if a parasite is not found on certain plant species, they are not necessarily resistant and the species may still be an acceptable host. The absence of the parasite may also have ecological causes such as the lack of a suitable dispersal agent (e.g. birds), or the light conditions may be insufficient for the parasite. Some plant groups such as ferns, water plants, and orchids are rarely or never parasitized. Genetics and tissue incompatibility determine the maximum number of acceptable hosts, but in practice, host range is mainly influenced by geographical (host distribution) and ecological (dispersal biology and environmental factors) relationships.

1.7 The Parasitic Plant Families (Fig. 1.1a)

Families recently revised based on molecular studies are treated as *sensu lato* (s.l.) (Nickrent 2010). The families are arranged in about 12 orders, indicating that parasitism has evolved independently several times. All families are illustrated including distribution maps in Heide-Jørgensen (2008) and Nickrent (2010).

Santalales

This plant order comprises at least the following eight families:

Olacaceae s.l. is a tropical–subtropical family of root parasitic shrubs, trees, or lianas. A terminal haustorium has not been observed, and the family is considered the most primitive in Santalales. *Olax* is the largest genus and its lateral haustoria may serve as a model for haustoria in the order. For characteristic haustorial features such as the mantle, collapsed zones, interrupted zones, and graniferous tracheary elements, see Fineran (1985, 1991) and Fineran et al. (1987). According to Nickrent (2010) Erythropalaceae, Strombosiaceae, Coulaceae, Octoknemaceae, Ximeniaceae, and Aptandraceae, which are related to the Olacaceae, are independent families. The first three families are assumed to be non-parasitic.

Schoepfiaceae with the single genus *Schoepfia* was earlier included in Olacaceae (Werth et al. 1979; Nickrent and Malécot 2001). Life form, parasitic mode, and distribution are similar to Olacaceae, but the family is not represented in Africa.

Opiliaceae is a small pan-tropical family of root parasitic evergreen trees and lianas (Hiepko 1979, 1982). Lateral haustoria resembling those of Olacaceae are the only type known.

Loranthaceae is the largest family in Santalales with close to 1,000 species of hemiparasitic stem parasites and three root parasites mainly from tropical and subtropical regions. All species are shrubs except the best-known root parasite, the Australian *Nuytsia floribunda*, which is a tree. The holdfast of its numerous lateral haustoria may completely encircle the roots of grasses. The intrusive organ develops a knife-like sclerenchymatic cutting device which is pushed through the host roots, cutting the vascular bundle (Fineran and Hocking 1983; Beyer et al. 1989; Calladine and Pate 2000). The majority of species have both terminal and lateral haustoria. The latter are located on epicortical roots (Fig. 1.2g) that run parallel with host branches (Kuijt 1969; Calvin and Wilson 2006). The most advanced stem parasites have only a terminal haustorium (Fig. 1.2b), and in some species, intrusive runners may develop within host branches. Host range is generally wide. Some of the larger Loranthaceae have become serious pests in plantations of teak, cocoa, and rubber trees, particularly in India and West Africa (Parker and Riches 1993). Most flowers of the Loranthaceae are large, showy, and bisexual nectar-producing flowers (Figs. 1.2h and 1.3a), and some species show remarkable co-evolution with pollinating birds (Kuijt 1969, 2009; Polhill and Wiens 1998; Ladley and Kelly 1995; Kirkup 1998). The fruit is fleshy including a viscid layer which serves to glue the seed to host branches when wiped off the beak, regurgitated, or dropped after passing the digestive canal (Kuijt 1969, 2009; Polhill and Wiens 1998; Watson 2001).

Misodendraceae with the single shrub genus *Misodendrum* (Fig. 1.3b) occurs in the coldest part of South America south of 33° S Lat. Misodendrum does not occur in the high Andes. These stem parasites on *Nothofagus* spp. have only a terminal haustorium. The first origin of stem parasitism may have occurred in this family (Vidal-Russell and Nickrent 2007).

Eremolepidaceae is another small family with three genera of shrubs found from Mexico and southwards. The terminal haustorium corresponds to *Misodendrum*. In addition, *Antidaphne* has epicortical roots with lateral haustoria (Kuijt 1988). According to molecular analysis, the family is closely related to Santalaceae (Der and Nickrent 2008).

Santalaceae s.l. Root parasites comprising both perennial herbs (Fig. 1.3c) and woody species with many lateral haustoria. A few genera are stem parasites with terminal haustoria or both types (Fineran 1963b, 1991; Toth and Kuijt 1976, 1977; Tennakoon and Cameron 2006). The distribution is similar to Loranthaceae, but it extends farther to the north. Flowers are usually less than 1 cm across, regular, and insect pollinated. Fruits of some species are dispersed by birds, as in Loranthaceae. Of the about 35 genera, *Thesium* is the largest with approximately 350 species. *Santalum* is the only genus where several species are of economic value as a source of hard timber and essential oils. Therefore, *S. album*, which is grown in India, has been introduced to a number of Pacific Islands (Kuijt 1969; Thomson 2006). *Okoubaka aubrevillei*, a tree to 40 m from tropical Africa, is the largest known parasitic plant (Veenendaal et al. 1996). Commandraceae, Thesiaceae, Cervantesiaceae, Nanodeaceae, and Amphorogynaceae, which were regarded part of the Santalaceae, are considered independent families by Nickrent et al. (2010).

Viscaceae consists of hemiparasitic stem parasites with only terminal haustoria. Geographical distribution is similar to Loranthaceae but extends farther north in the temperate zone. The most advanced genera have an extensive endophyte, which in *Arceuthobium douglasii* (Fig. 1.3d) can reach the shoot tips of the host *Pseudotsuga menziesii* (Lye 2006). The flowers are small and mostly insect pollinated.

The viscid fruits are dispersed by birds except in *Arceuthobium* (see Sect. 1.4). *Arceuthobium* species are the most damaging parasites on conifers in North America (Fig. 1.3d) (Tubeuf 1923; Calder and Bernhardt 1983), and *Arceuthobium minutissimum* is perhaps one of the tiniest parasites. *Phoradendron* with at least 234 species is the largest genus (Kuijt 2003). *Viscum album* (Fig. 1.2f) is the most common mistletoe in Europe.

Each of the following families belongs to a separate order:

Krameriaceae (Zygophyllales) is a small New World family. *Krameria* is the only genus and all species are root parasites and small shrubs or semi-shrubs mainly from semiarid to arid communities. There is only one report of a terminal haustorium. The fruits have spines aiding in adherence to fur of mammals (Kuijt 1969; Simpson 1989).

Convolvulaceae (Solanales) includes mainly autotrophic non-parasitic genera, except for the parasitic genus *Cuscuta* (Fig. 1.2a), where all species are annual twining stem parasites with only lateral (lateral) haustoria (Yuncker 1932). There are diverse hosts for most species but often difficult to determine, since many haustoria only develop a holdfast and do not penetrate host tissues (Dörr 1972; Wolswinkel 1974; Dörr and Kollmann 1995). Some *Cuscuta* species are troublesome in agriculture; the North American *C. campestris* is an invasive weed in many countries (Parker and Riches 1993; Heide-Jørgensen 2011).

Lauraceae (Laurales) genera are also autotrophic except for *Cassytha*, which is a perennial stem parasite (Weber 1981). *Cassytha* (Fig. 1.2e) and *Cuscuta* (Fig. 1.2a) are similar morphologically, with twining stems and leaves reduced to vestigial scales, and in their mode of parasitism. They are a classical example of convergent evolution (Kuijt 1969).

Orobanchaceae (Lamiales) is by far the largest family of parasitic plants (Fig. 1.1a) after inclusion of the hemiparasitic root parasites (see Chap. 14), which were earlier placed in Scrophulariaceae (Young et al. 1999; Olmstead et al. 2001). One non-parasitic genus, *Lindenbergia*, is also included in this family (Bennett and Mathews 2006). The family is represented in all climatic zones and on all continents except Antarctica. All species are annual or perennial herbs. Most species have numerous lateral haustoria and many hosts, but some advanced species such as *Striga hermonthica* (Fig. 18.3a) and some holoparasites have only a terminal haustorium (see Sect. 3.3; Kuijt 1969; Dörr 1997). Flowers are bilaterally symmetrical and mostly insect pollinated. Some are self-pollinating, like *Orobanche cumana*, or facultative selfers (Teryokhin et al. 1993; Satovic et al. 2009). The hemiparasite *Pedicularis* (Fig. 1.1b) is the largest genus (numbers of species vary from 150 to 800 in the literature; see Chap. 14). *Hyobanche sanguinea* is noteworthy as the only known species attaching to host roots by haustoria which developed in soil from scale leaves of its rhizomes (see Sect. 3.6.2; Kuijt et al. 1978). Orobanchaceae contains some of the most serious agricultural parasites (see Chaps. 17 and 18).

Cynomoriaceae (Saxifragales, but uncertain) is one of seven small families with just 1–3 genera each, representing some of the most remarkable holoparasites regarding reduction of the exophyte, dissection and wide distribution of the

Fig. 1.4 Various holoparasites. (**a**) Inflorescence of *Cynomorium coccineum* (Cynomoriaceae); Algarve, Portugal. (**b**) Exophyte of Apodanthes caseariae (Apodanthaceae) consisting of female flowers with dark stigma on top of fruit; Costa Rica. (**c**) *Cytinus hypocistis* (Cytinaceae) pollinated by a bee (to the left); Southern France. (**d**) *Rafflesia keithii* flower with diameter up to 80 cm (Rafflesiaceae); Sabah, Borneo. (**e**) Flowering *Hydnora johannis* (Hydnoraceae); reproductive parts of the flower are subterranean; South Africa. (**f**) Rhizomes (earlier called pilot roots) of *Hydnora triceps* with short haustorial roots and flower buds in four rows; East of Port Nolloth, South Africa. (**g**) Female inflorescence of *Balanophora latisepala* (Balanophoraceae); Rongla National Park, Thailand (photos: part **a** by FN Rasmussen; part **b** by P Maas; part **c** by HS Heide-Jørgensen; part **d** by P Ø Larsen; parts **e**, **f** by LJ Musselman; part **g** by T Læssøe)

endophyte, and unusual flower construction. In the Mediterranean *Cynomorium* flowers on the succulent axis are so reduced (Fig. 1.4a) that the plants were erroneously considered fungi. There is a perennial rhizome, and lateral haustoria develop from adventitious roots. A terminal haustorium is expected but has not been described (Lanfranco 1960; Kuijt 1969).

Lennoaceae (Boraginales) is mainly Central American and interesting by showing root dimorphism: pilot roots search for host roots and when found they develop short haustorial roots connecting to the host. The species are perennial and succulent. A terminal haustorium is expected (Kuijt 1966, 1969).

Mitrastemonaceae (Ericales) contains South-East Asian root parasites that were previously included in the Rafflesiaceae. The main part of the perennial parasite is embedded in host roots, and only the flowers emerge out of the roots and can be seen above soil. After pollen release, the 16 stamens form a mitre-shaped tube, which is pushed off by the growing pistil and prevents self-pollination (Kuijt 1969; Meijer and Veldkamp 1993).

Apodanthaceae (Cucurbitales, formerly regarded as Rafflesiales or Malvales) represents some of the smallest stem parasites. The exophyte consists only of the flowers, which are 2–3 mm wide (Fig. 1.4b). The three perennial closely related genera have a highly disjunctive distribution on five continents assumed to originate from the disintegration of Gondwanaland (Kuijt et al. 1985; Blarer et al. 2004; Filipowicz and Renner 2010).

Cytinaceae (Malvales) are perennial root parasites in two genera occurring in Central America, Europe, and South Africa. The endophyte is composed of rows of parenchyma cells that grow through host pericyclic derivatives and reach both phloem and xylem (De Vega et al. 2007). The exophyte (Fig. 1.4c) consists only of the inflorescence of male and female flowers (Kuijt 1969; Nickrent 2007).

Rafflesiaceae (Malpighiales) is Southeast Asian. They are perennial and mainly root parasites (Fig. 1.4d), but a few species of *Rafflesia* may occasionally occur as stem parasites (Heide-Jørgensen 2008). All vegetative parts are embedded in the host, and flower capacity is transferred to the endophyte (Kuijt 1969). *Rafflesia arnoldii* produces the largest flower in the plant kingdom with a diameter of almost 1 m (Meijer 1984; Bänziger 1991; Wurdack and Davis 2009).

Hydnoraceae (Piperales) is African and South American. The perennial plant body consists of highly modified succulent rhizomes producing short exogenous outgrowths having the potential to develop lateral haustoria or new branches (Figs. 1.2d and 1.4f). The endophyte contains both xylem and phloem (Tennakoon et al. 2007). Flowers (Fig. 1.4e) and fruits are partly or completely subterranean (Musselman and Visser 1989; Tennakoon et al. 2007).

Balanophoraceae (Balanophorales but Santalales has been suggested) occurs throughout the more humid tropical–subtropical regions. It includes 17 genera of root parasites (Hansen 1972; Nickrent and Franchina 1990), which produce only a terminal (primary) haustorium, which develops into a tuber (occasionally up to 60 cm) that partly consists of host tissue. The inflorescence arises from the tuber, and specialized conductive cells connect the vascular system of the inflorescence with the endophyte (Gedalovich-Shedletzky and Kuijt 1990; Hsiao et al. 1995). The flowers are highly reduced and several species were earlier considered to be fungi (Fig. 1.4g).

1.8 Parasite Look-Alikes

Some plants, like epiphytic orchids and bromeliads, may look as if they are parasites (Heide-Jørgensen 2008). But these plants only attach to other plants for support and do not acquire any water or nutrients from their supporting plant. Other flowering plants, the myco-heterotrophs, lost all or nearly all chlorophyll and are involved in a three-part relationship with a mycotrophic fungus that indirectly connects them to an autotrophic vascular plant from which they obtain nutrients (Leake 1994, 2004; Imhof 2010).

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