Taxonomy and Classification

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2.1 Introduction

Fully mycoheterotrophic plants share only one particular feature—the obligation to obtain carbon from fungi. The plants that fall within this definition do not necessarily have to be evolutionarily related and therefore mycoheterotrophic plants consist of a wide variety of taxa. Although mycoheterotrophy is relatively rare in nature, multiple independent origins of the mycoheterotrophic mode of life have produced a remarkable array of mycoheterotrophic species in almost every major group of land plants. Furman and Trappe (1971) and particularly Leake (1994) presented excellent overviews of mycoheterotrophic plant species. Here we provide an updated list of all putatively fully mycoheterotrophic plant species, excluding initial and partial mycoheterotrophs, with details on their morphology, distribution, and ecology. This list covers 17 plant families, 101 genera, and ca. 880 species.

Fern and lycophyte species were included when there is evidence for the lack of chlorophyll in the gametophytic phase. For "higher" plants we considered all leafless, achlorophyllous plant species that are not holoparasitic (i.e., physically connected to a host plant) as "putative" full mycoheterotrophs (but see *Parasitaxus*). In some cases we also included species that retain at least some chlorophyll, but in these cases mycoheterotrophy is suspected on the basis of their extremely reduced leaves. However, to determine the trophic status of a species careful investigation is needed. Since these data are lacking for the great majority of putative mycoheterotrophs, the presence of mycorrhizas and the absence of both chlorophyll and a direct physical link to a host plant are probably the best indications for full mycohetertrophy. Nevertheless, it is important to

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keep in mind that the "full mycoheterotrophy" status of many species listed here remains speculative until a careful physiological analysis has been carried out.

Partial and initial mycoheterotrophs were not included in our overview, although we tried to mention confirmed partially mycoheterotrophic species where appropriate. Partial mycoheterotrophy has been detected in green Orchidaceae, Ericaceae, and Gentianaceae but may occur in several other plant families (Selosse and Roy 2009). In addition, probably all Orchidaceae species are initial mycoheterotrophs (Leake 1994; Chaps. 1 and 5) and this group includes over 20,000 species. Furthermore, many species that produce small dust-like seeds (e.g., Pyroleae in Ericaceae) may depend on a mycorrhizal fungus during early development and are thus initial mycoheterotrophs (Chap. 1). Currently, we know little about the phylogenetic range of partial and initial mycoheterotrophy in most plant lineages, but the chlorophyllous relatives of full mycoheterotrophs are the prime candidates to discover more partial and initial mycoheterotrophs, and we hope that this overview may be a valuable tool in search of new mycoheterotrophs.

The taxonomic affinities of many groups of mycoheterotrophs have puzzled systematists for almost three centuries. Many mycoheterotrophic plants are rare or at least very difficult to find, and in extreme cases particular species are known only from one or two collections. Obtaining study material is therefore often the first obstacle to be tackled when trying to unravel the evolutionary history of these intriguing plants. In addition, mycoheterotrophic plants have evolved convergent adaptations in their morphology and anatomy as a result of their peculiar mode of life, making identification of the close relatives of mycoheterotrophic plants in many cases a taxonomic challenge. The application of DNA data has offered new opportunities to elucide the relationships of mycoheterotrophic plant groups, although scarcity of study material and elevated DNA substitution rates have prevented an accurate inference of phylogenetic relationships of many mycoheterotrophic lineages to date (see Chap. 5). This overview has been compiled using the latest taxonomic and phylogenetic insights of the groups in question. For information on species numbers and distributions the International Plant Names Index (IPNI 2011), the World Checklist of Selected Plant Families (2011), and Tropicos (2011) were of great value, although in some cases we adopted information from alternative sources. In a few cases the choice between contradicting taxonomical classifications was made entirely arbitrarily. As mentioned above, the taxonomic status of many groups of mycoheterotrophs remains doubtful and it is likely to change, as new data will become available. Moreover, new species and even genera are still being identified and there is no doubt that more species are waiting to be discovered.

2.2 Liverworts

Liverworts (Marchantiophyta) are postulated to be the sister lineage to all other land plants and to have had a Late Ordovician origin (Heinrichs et al. 2007). Together with mosses and hornworts, they comprise a paraphyletic grade of the embryophytes in which the haploid gametophyte is the persistent autotrophic generation and the diploid sporophyte is short-lived, unbranched, and permanently matrotrophic. In liverworts the gametophyte can be either a thalloid or a leafy plant and the sporophyte is enclosed by tissues of the gametophyte until sporogenesis is completed.

Liverworts consist of approximately 8,000 species in nearly 500 genera. The gametophyte phase of many liverworts forms an association with endophytic fungi, including mucoromycetes, glomeromycetes, ascomycetes, and basidiomycetes (Pressel et al. 2010). In contrast to ferns, this association has never been observed in the sporophyte phase (Ligrone et al. 1993). Considering the huge number of taxa and the antiquity of the lineage, it is surprising that only a single fern taxon, namely *Aneura mirabilis* (Malmb.) Wickett & Goffinet (=*Cryptothallus* Malmb.), has ever been demonstrated to be fully mycoheterotrophic. This taxon, described by von Malmborg (1933) as *Cryptothallus mirabilis*, was first recorded from France by Denis (1919) who regarded it as an achlorophyllous form of *Aneura pinguis* and compared it with gametophytes of the clubmosses *Lycopodium selago* and *L. phlegmaria* (=*Huperzia phlegmaria*). Recent molecular analysis by Wickett and Goffinet (2008) has not supported its recognition as an autonomous genus, rather showing it to be *Aneura*, as Denis had originally suggested. It is interesting that *Tulasnella*, the basidiomycete fungal symbiont of the photosynthetic *Aneura pinguis*, is the same genus found in the mycoheterotrophic liverwort *Aneura mirabilis*. Although a second species of *Cryptothallus*, *C. hirsutus*, was described from Costa Rica (Crum and Bruce 1996), this problematic taxon was never proven to be mycoheterotrophic and subsequent efforts to collect this liverwort from the type locality proved to be unsuccessful.

2.2.1 Aneuraceae

Aneuraceae H. Klinggr., Höh. Crypt. Preuss.: 11 (1858).
Riccardiaceae Sanborn, Univ. Oregon Publ., Pl. Biol. Ser. 1(1): 33 (1929).

Persistent gametophyte plants thalloid, with the thallus often fleshy, 1–10 cm long, 0.2–12 mm wide, lacking a strongly differentiated midrib; vegetative branching monopodial or absent; ventral slime papillae 2-celled, in 2 rows or dispersed; oil bodies small and numerous or large and 1 to 3 per cell, finely granular; monoicous or dioicous; antheridia sunken in chambers on abbreviated lateral branches (on the main thallus in *Verdoornia*); archegonia in clusters, with paraphyses, on abbreviated lateral branches (on the main thallus in *Verdoornia*); sporophytes enclosed by a fleshy shoot calyptra or coelocaule; capsules ellipsoidial to cylindric, with the wall 2 cells thick, usually opening by 4 valves, with an apical elaterophore; elaters 1(2)–spiraled; gemmae usually endogenous (exogenous, but rare in *Aneura*).

Number of genera and species—The family comprises 4 genera with fewer than 150 accepted species. *Riccardia* is the largest genus with ca. 100 species while *Aneura* includes 10 to 20 species. *Lobatiriccardia*, with eight species, was formerly regarded as a subgenus of *Riccardia*. *Verdoornia* is a monotypic New Zealand endemic.

Distribution and habitat—Aneuraceae are distributed worldwide, from the High Arctic to Fuegia and the islands of the Sub-Antarctic. Populations can be found from sea level to over 4,000 m elevations, growing on moist rotting wood and bark, wet rocks, and over moist soil or boggy ground. The single mycoheterotrophic taxon, *Aneura mirabilis*, is a northern oceanic disjunct from Greenland and Europe.

Classification—Molecular phylogenetic analyses have consistently resolved two backbone lineages of simple thalloid liverworts, recognized as the subclasses Pelliidae and Metzgeriidae of the Jungermanniopsida (Forrest et al. 2006; He-Nygrén et al. 2006; Crandall-Stotler et al. 2009). Aneuraceae form a monophyletic lineage that is sister to the Metzgeriaceae within the Metzgeriidae. A recent phylogenetic hypothesis of relationships within the family resolves each of the four genera as monophyletic and strongly supports a sister group relationship between *Aneura* and *Lobatiriccardia*, with *Riccardia* and *Verdoonia* forming successive sister groups (Preußing et al. 2010).

Evolutionary history—Members of the Aneuraceae are absent from the fossil record, but calculations of divergence times from chloroplast sequence data estimate an origin of the family in the mid Jurassic, about 170 Ma (Heinrichs et al. 2007). Recent molecular analyses evince considerable cryptic speciation, especially in *Aneura* (Wachowiak et al. 2007), and morphological character reconstructions support recognition of the family as a crown group in liverwort phylogeny (Crandall-Stotler et al. 2005).

Mycoheterotrophy—Associations between liverworts and fungi are very common, and Aneuraceae is no exception. Typically, the fungal partner in these associations is either an ascomycete or glomeromycete (Davis and Shaw 2008; Bidartondo and Duckett 2010) or, in the earliest diverging lineage, a mucoromycete (Pressel et al. 2010); however, Aneuraceae is unique among liverworts in having an intracellular association with the basidiomycete genus *Tulasnella* (Kottke and Nebel 2005). Preußing et al. (2010) suggest that the well developed, tulanelloid mycothallus may have opened up novel habitats, which subsequently contributed to this being the most speciose group of simple thalloid liverworts. In *Riccardia*, the mycothallus, if present, is epidermal, whereas the remaining Aneuraceae are characterized by a parenchymal mycothallus. With a fleshy thallus composed almost entirely of parenchyma, *A. mirabilis* is the most intensely colonized species, and derives its fixed atmospheric carbon from its endophyte by way of either *Pinus* or *Betula* upon which the fungal partner is simultaneously ectomycorrhizal (Bidartondo et al. 2003). In all cases, the fungus enters the thallus at the base of the rhizoids and colonizes the interior of the host cells after penetrating the cell walls; there is no intercellular growth of the fungus (Preußing et al. 2010).

2.2.1.1 *Aneura* (Fig. 2.1a)

Aneura Dumort., Comment. Bot.: 115 (1822).
Cryptothallus Malmb., Ann. Bryol. 6: 122 (1933).

Thalli large, 1–5 cm long, 2–10 mm wide, thick and fleshy, sparingly and very irregularly branched, occasionally simple; oil bodies small, numerous, 6 to 40 per cell; dioicous, heteromorphic, with male plants somewhat smaller; antheridia in 2 to 6 rows on lateral branches; archegonia clustered in small lateral notches of the thallus margin.

The number of accepted *Aneura* species is problematic, ranging from as few as 6 to as many as 20. Apart from *A. mirabilis*, which is easily distinguished from other species by its lack of chlorophyll, morphological diagnoses of *Aneura* haven proven to be difficult to reconcile with patterns of DNA sequence variation; it has often been acknowledged that this genus is in need of intense morphological and molecular study in order to understand species level relationships. *Aneura mirabilis*, which is the only fully mycoheterotrophic member of the genus, is nested within the chlorophyllose *Aneura pinguis* complex (Wickett and Goffinet 2008; Preußing et al. 2010). It is predominantly found in oceanic Europe with a distribution covering the United Kingdom, Germany, France, Portugal, Russia, Sweden and Norway (Schuster 1992). Additionally, a disjunct locality has been reported from the western Greenland (Peterson 1972), and ecological models have predicted that its range should include Spain (Sérgio et al. 2005). In its northern localities, *A. mirabilis* is generally found buried up to 20 cm beneath the surface of *Sphagnum* dominated peat bogs (pH ± 3.8), occurring in proximity to birch trees from which the liverwort derives its fixed atmospheric carbon by way of its mycobiont. It is associated closely with pines in its more southern localities (e.g., Portugal) where it is frequently covered by mats of pleurocarpous mosses. It was initially suggested that *A. mirabilis* was saprophytic, harboring a fungal partner different from surrounding tree roots. However, clear transfer of carbon fixed by the associated tree to the liverwort via the fungal hyphae has been demonstrated (Bidartondo et al. 2003) and fungi with identical genotypes have been collected from *A. mirabilis* and a neighboring tree (Bidartondo and Duckett 2010). It appears that the mycobiont of *A. mirabilis* is species-specific given that it will not invade chlorophyllose *Aneura* (Duckett et al. 2004).

Unlike its sister species *Aneura pinguis*, it appears that *A. mirabilis* develops in response to temperature, rather than day length (Benson-Evans 1961). Fertilization occurs in June or July, followed by the development of the sporophyte, within a protective calyptra, with the seta elongating the following spring (Benson-Evans 1952, 1960). The elongation of the seta pushes the capsule nearer to the surface of the overlaying vegetation, allowing the spores to be dispersed in sufficient light. Various experimental conditions have been tested to determine optimal conditions for spore germination and suggest that diffuse light is required for, and frost exposure increases the rate of germination. Fungi do not colonize either the spores themselves or the sporophytes and gametangia (Ligrone et al. 1993), and spores germinated in culture do not mature beyond a 20- to 30-celled stage that follows the initiation of rhizoids (Benson-Evans 1960). This suggests

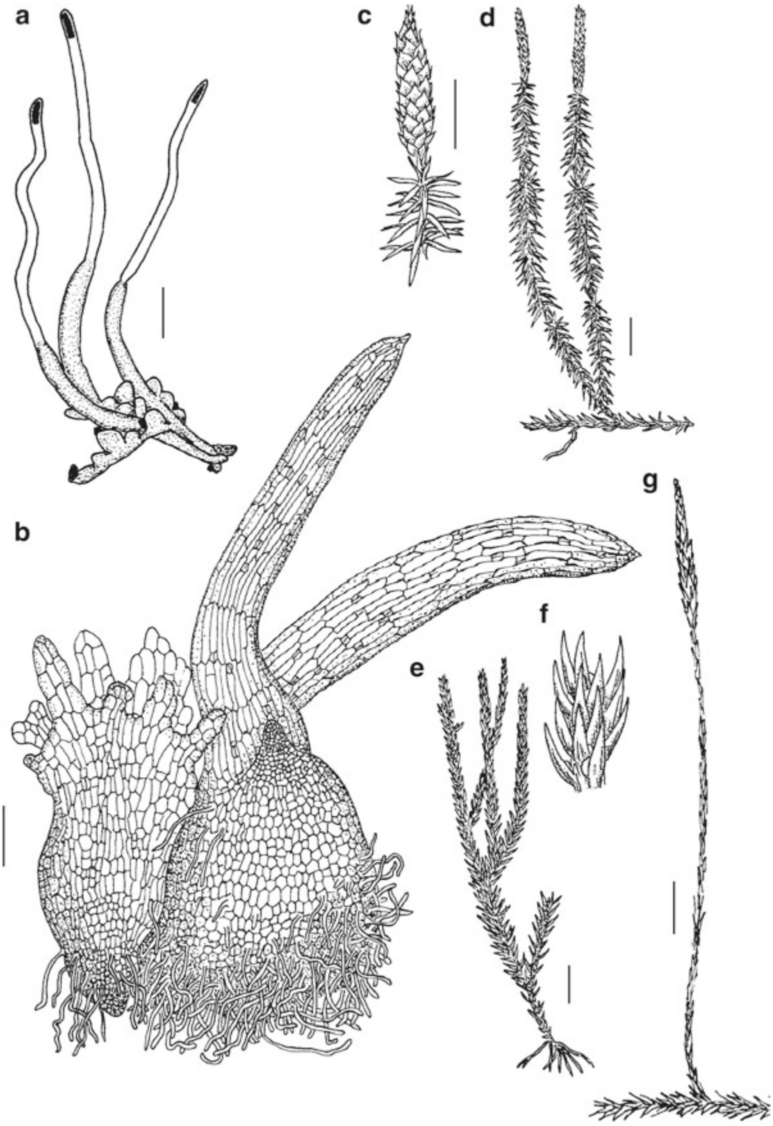

Fig. 2.1 Aneuraceae and Lycopodiaceae. (**a**) Fully mycoheterotrophic gametophyte of *Aneura mirabilis* (Aneuraceae). Drawn from Vanderpoorten and Goffinet (2009). (**b**) Mycoheterotrophic gametophyte (*left*) and emerging sporophyte (*right*) of *Huperzia phlegmaria* (Lycopodiaceae). Redrawn from Haig (2008). (**c**, **d**) Sporophyte of *Lycopodium annotinum*: (**c**) strobilus, (**d**) habit. (**e**, **f**) Sporophyte of *Huperzia selago*: (**e**) habit, (**f**) detail of microphylls. (**g**) Sporophyte of *Lycopodiella appressa*. (**c**–**g**) Redrawn from Wagner and Beitel (1993). Bar = 1 cm, except (**b**) bar = 0.1 cm

Tulasnella must colonize the thallus at this early stage of development. It is important for rhizoids to form pre-colonization as the fungal hyphae penetrate through the rhizoids and proceed to form dense, intracellular coils (Preußing et al. 2010). The liverwort appears to mediate the spread of the fungus, as evidenced by the clear demarcation of the mycothallus (limited to non-reproductive parenchyma), and the ability of a cell to persist (and be subsequently re-colonized) following the death of its intracellular hyphae (Ligrone et al. 1993). While its morphology clearly places it in *Aneura*, *A. mirabilis* is unique in that it is strongly sexually dimorphic and has reticulately ornamented spores that are permanently retained in tetrads (Schuster 1992). Though speculative, it is tempting to invoke the subterranean habitat of *A. mirabilis* as a selective force in the evolution of this divergent spore morphology. Given that the thalli of *A. mirabilis* can be found up to 20 cm beneath the surface of *Sphagnum* peat, it is unlikely that any photosynthesis occurs in this liverwort. Wickett et al. (2008a, b) demonstrated that photosynthesis is likely impossible due to the pseudogenization of, and relaxation of purifying selection on several of the plastid genes that encode structural subunits of the photosynthetic apparatus.

2.3 Ferns and Clubmosses

Of some clubmosses (Lycopodiopsida) and ferns (Polypodiopsida), the sexual stage or gametophyte is achlorophyllous and subterraneous. Many fern and clubmoss gametophytes have mycorrhizal associations as have many fern sporophytes, but in the cases where chlorophyll is absent, the prothallus is entirely dependent on the fungus for survival. These mycoheterotrophic gametophytes are widespread in Lycopodiaceae, Ophioglossaceae, and Psilotaceae, and are also known in *Actinostachys* (Schizaeaceae) and *Stromatopteris* (Gleicheniaceae). In other fern families they are not known to occur.

2.3.1 The Life Cycle of Ferns and Clubmosses

Under normal circumstances there is a regular alternation between a gametophyte (sexual) phase and a sporophyte (asexual) phase. The sporophyte is the dominant generation in ferns (in contrast, the gametophyte is dominant in mosses). It soon becomes independent of the gametophyte and grows to a much greater size and anatomical complexity than the gametophyte. These sporophytes produce haploid spores through meiosis, which, when germinated (usually under warm and moist conditions), form a sexual, free-living, haploid gametophyte. Gametophytes (prothalli) often resemble a liverwort or alga and form the gametes. The male gametes, produced in numbers by antheridia are known as antherozoids or spermatozoids, because they are flagellated and able to swim in water. The female gametes (or egg cells) are non-motile and are borne singly in flask-shaped archegonia. Under humid circumstances a fusion between an egg-cell and an antherozoid may result in the formation of a zygote, containing the combined nuclear material of the two gametes (diploid). The zygote develops through mitotic division into the diploid sporophyte. When mature, the sporophyte produces non-motile, haploid spores that are formed through meiosis, completing the life cycle.

The complexity of the sporophyte in comparison with the gametophyte allows the sporophyte to live under a much wider range of environmental conditions than the gametophyte. The sporophyte is however dependent to grow in places where the gametophyte can survive long enough for fertilization to take place. This is limiting species whose gametophytes are lacking a cuticle and are thus susceptible to dehydration, but not all gametophytes are limited that way: some make associations with fungi, are subterranean, and others are retained within the resistant spore wall (e.g., in heterosporous species).

2.3.2 Gametophytes and Mycoheterotrophy

Gametophytes of ferns are usually chlorophyllous, but in some cases the gametophyte is formed underground and lacks chlorophyll. This is especially the case in Lycopodiaceae (clubmosses) and early branching ferns like Ophioglossaceae and Psilotaceae. These gametophytes are assumed to be mycoheterotrophic, but studies have not been carried out to establish the intricate relationship between the achlorophyllous gametophytes of ferns and clubmosses and the fungus that it associates with.

2.3.3 Clubmosses

The clubmosses (Lycopodiopsida) consists of three families in three orders within the subclass

Lycopodiidae (Christenhusz et al. 2011a) that together form the sister lineage to all other vascular plants and are not closely allied to ferns. Only Lycopodiaceae show mycoheterotrophy at the gametophyte stage. The other two families, Isoëtaceae and Selaginellaceae are both heterosporous and have endosporic gametophytes that do not produce fungal associations. In all families mycorrhizal associations are known to occur at the sporophytic stage.

2.3.4 Lycopodiaceae

Lycopodiaceae P.Beauv. ex Mirb. in Lam. & Mirb., Hist. Nat. Vég. 4: 293 (1802).

Terrestrial or epiphytic plants. Habit erect, trailing or pendent. Stems usually branched, densely clothed nearly throughout with numerous small, simple, 1-nerved leaves, these all similar or dimorphic. Sporophylls similar to other leaves or modified and aggregated to form compact spikes (strobiles). Sporangia axillary, monolocular. Spores all alike, minute, very numerous. Gametophytes (hemi-)mycoheterotrophic, fleshy or tuberous, with or without chlorophyll, monoecious.

Number of genera and species—The Lycopodiaceae comprise 3 genera and ca. 300 species. The largest genus is *Huperzia* with ca. 200 species, followed by *Lycopodium* with ca. 40 species and *Lycopodiella* with ca. 40. Because of the varied growth forms of species within these genera, some authors have adopted a system with more genera, accepting *Phlegmariurus* for epiphytic *Huperzia*, *Palhinhaea* for the *Lycopodiella cernua* complex, and *Diphasiastrum* for *Lycopodium* with flattened branchlets (the cypress clubmosses).

Distribution and habitat—Lycopodiaceae occur worldwide in a variety of habitats. They can be terrestrial or epiphytic, erect or pendent, creeping or climbing plants, and are usually confined to habitats that are at least humid during some part of the year. *Huperzia drummondii* is peculiar in surviving dry periods by forming underground tubers.

Classification—Traditionally Lycopodiaceae was treated as a family of two genera *Lycopodium* and *Phylloglossum* (e.g., Sporne 1962; Bierhorst 1971; Tryon and Tryon 1982). Further division of *Lycopodium* led to as many as 12 genera (Rothmaler 1964; Holub 1983), mainly based on habit morphology. Øllgaard (1987) proposed a consensus classification, which I (MJMC) recommend to be followed, dividing the genus into four genera, but keeping many of the names proposed by Holub at subgeneric levels. Recent molecular studies (Wikström and Kenrick 1997; Wikström et al. 1999) supported Øllgaard's classification in which Lycopodiaceae consist of three major clades: *Lycopodiella* and *Lycopodium* s.s., the pair being sister to an enlarged *Huperzia* (including *Phylloglossum*). To maintain *Phylloglossum*, *Phlegmariurus* will have to be redefined, but in that case it has few morphological characters that separate it from *Huperzia* s.s., and thus inclusion of *Phylloglossum* in *Huperzia* appears to be a better alternative. Further division of *Lycopodiella* and *Lycopodium* is possible (as validated by Holub (1983); Øllgaard (2012)), but has only created confusion in the past, and should therefore be avoided.

Evolutionary history—Lycopods are only a fraction of the present-day vascular plant diversity, but their peak of evolution happened about 300 million years ago (Ma). During the Carboniferous, lycopods were a conspicuous and abundant element of the land flora (Kenrick and Crane 1997). Several groups have now become extinct, and the once dominant clade of rhizomorphic species that included arborescent species of the Carboniferous coal swamps, have been reduced to the few small herbaceous species of *Isoëtes*.

Because of the long fossil record lycopods were recognized as descendents of early divergences in the land plant evolution. Molecular studies have supported this view and place the lycopods as sister to all other vascular plants (Raubeson and Jansen 1992).

Mycoheterotrophy—In some species spores germinate without delay while on the surface of the ground, and then form chlorophyllous gametophytes (*Lycopodiella*). In other species there may be delay of many years in germination, by which time the spores may have been buried and they will become colorless and dependent on a mycorrhizal association. An arbuscular mycorrhizal association appears to occur in all species growing under natural circumstances (Sporne 1962; Winther and Friedman 2008 and references therein).

Photosynthetic (putative partially mycoheterotrophic) gametophytes of *Lycopodiella* and some *Huperzia* are cone-shaped, and have an upper green part, and a colorless lower part with fungal hyphae, whereas in mycoheterotrophic gametophytes the green part is missing and fungal hyphae occur throughout the gametophyte. In both cases the archegonia and antheridia are restricted to the upper part. Epiphytic species of *Huperzia* also have colorless prothalli, but they are slender, branching, and show a pronounced apical growth (Sporne 1962).

2.3.4.1 *Huperzia* (Fig. 2.1b, e, f)

Huperzia Bernh., J. Bot. (Schrader) 1800(2): 126 (1801).
Phylloglossum Kunze, Bot. Zeit. 1 (1843).
Urostachys Herter, Beih. Bot. Centralbl. 39 Abt. 2: 249 (1922).
Phlegmariurus (Herter) Holub, Preslia 36: 17 (1964).

Terrestrial, lithophytic or epiphytic plants. Roots in distal parts of shoots, but sometimes branches rooting near their tips or along prostrate shoots. Sometimes (*H. drummondii*) forming a subterraneous tuber on a leafless geotropic branch. Shoots clustered, dichotomously branching, erect or pendent, clothed with numerous monomorphic or dimorphic leaves, these imbricate or not, sometimes bearing gemmiferous branchlets and gemmae, or all leaves clustered in a basal rosette (*H. drummondii*). Sporangia reniform, borne singly in the axils of undifferentiated or highly differentiated sporophylls. Gametophytes achlorophyllous, mycoheterotrophic (but green in a few species), cylindrical, with pluricellular uniseriate hairs among gametangia.

A genus of over 200 species, but due to numerous species complexes the number is uncertain (Tryon and Tryon 1982). The genus is cosmopolitan extending from the tropics (there mainly epiphytic) to the Arctic and Subantarctic. The peculiar *Huperzia drummondii* (formerly in the monotypic genus *Phylloglossum*) has green mycorrhizal gametophytes and is the only Lycopodiaceae that produces tubers as a survival strategy for dry seasons. Its morphology is highly derived, but phylogenetically it is embedded within the genus *Huperzia* (Wikström and Kenrick 1997). *Huperzia selago* (which is the type of *Huperzia*, and which was found to be sister to *H. drummondii*) can have either colorless or green gametophytes (hemimycoheterotrophic), and can thus be considered a transition from mycoheterotrophic towards independent gametophytes. Most other *Huperzia* (such as the epiphytic *H. phlegmaria*) have mycoheterotrophic gametophytes. Mycoheterotrophic gametophytes of *Huperzia hypogeae* were found to grow with *Glomus* Group A fungi (Winther and Friedman 2008).

2.3.4.2 *Lycopodiella* (Fig. 2.1g)

Lycopodiella Holub, Preslia 36: 20 (1964).
Palhinhaea Franco & Carv., in Carv. Vasc. & Franco, Bol. Soc. Brot. Ser. 2, 41: 24 (1967).
Lateristachys Holub, Folia Geobot. Phytotax. 18(4): 440 (1983).
Pseudolycopodiella Holub, Folia Geobot. Phytotax. 18(4): 441 (1983).

Terrestrial plants with indeterminate main stems (rhizomes) which can be subterraneous, scrambling or creeping, indeterminate. Side branches determinate, simple to much-branched, arising dorsally along main stems. Leaves monomorphic or dimorphic. Strobili erect to nodding or pendulous, terminating simple (rarely forked) branches or much-branched branchlet systems. Sporophylls subpeltate, medially basiscopically winged or with membranes almost enclosing the sporangia. Sporangia axillary or on the base of sporophylls. Spores rugose. Gametophytes green, tuberous, lobed above, living on the surface, hemimycoheterotrophic, lacking pluricellular hairs.

A genus of ca. 40 species widespread in moist-temperate and tropical regions. Especially diverse in the New World.

2.3.4.3 *Lycopodium* (Figs. 2.1c, d and 4.1a)

Lycopodium L., Sp. Pl. 1100 (1753).
Lepidotis P.Beauv. ex Mirb. in Lam. & Mirb., Hist. Nat. Vég. 3: 477; 4: 311 (1802).
Diphasium Rothm., Feddes Repert. Spec. Nov. Regni Veg. 54: 64 (1944).
Diphasiastrum Holub, Preslia 47: 104 (1975).
Lycopodiastrum Holub ex R.D.Dixit, J. Bombay Nat. Hist. Soc. 77(3): 540 (1980 publ. 1981).
Pseudolycopodium Holub, Folia Geobot. Phytotax. 18(4): 441 (1983).
Pseudodiphasium Holub, Folia Geobot. Phytotax. 18(4): 440 (1983).
Austrolycopodium Holub, Folia Geobot. Phytotax. 26(1): 91 (1991).
Dendrolycopodium A.Haynes, Fam. Huperziac. Lycopodiac. New England 84 (2003).
Spinulum A.Haynes, Fam. Huperziac. Lycopodiac. New England 85 (2003).

Terrestrial or lithophytic plants. Main stems trailing along the ground, sometimes climbing, indeterminate, rooting on the underside, usually long-creeping or arching and rooting. Erect determinate shoots scattered along horizontal stems, unbranched or dichotomously or irregularly branched. Leaves spiral to subverticillate, or distinctly flattened and in rows, monomorphic or dimorphic. Strobili erect, sessile or pedunculate or pendulous to nodding. Sporophylls peltate, subpeltate or paleate. Sporangia attached to sporophyll base or axillary, reniform. Gametophytes subterranean, tuberous, mycoheterotrophic, lacking hairs among gametangia.

A genus of ca. 40 species widespread in temperate and tropical (montane) regions.

2.3.5 Ferns

Ferns (Polypodiopsida) or sometimes informally called monilophytes (to include the former “fern allies” Psilotaceae and Equisetaceae) are the second diverging lineage of vascular cryptogams. They consist of 45 families in 11 orders (Christenhusz et al. 2011a). Mycoheterotrophy of the gametophyte is relatively rare and only known with certainty in Ophioglossaceae, Psilotaceae, *Actinostachys* (Schizaeaceae) and *Stromatopteris* (Gleicheniaceae). There may be cases of mycoheterotrophy in Polypodiales (containing the bulk of ferns with ca. 15,000 species), but this is yet to be confirmed. The majority of ferns have chlorophyllous heart- or butterfly-shaped gametophytes, although rarely other shapes (strap-shaped or filamentose) occur. Partly subterraneous kinds are also reported (Sporne 1962), but are extremely rare. Further study on subterraneous gametophytes is needed, but it is complicated because they are difficult to find. Many families are known to have arbuscular mycorrhizal associations (e.g., Marattiaceae, Schizaeaceae, Gleicheniaceae), but while many species seem to be dependent on their fungal association, mycoheterotrophy at the gametophyte phase seems to be occur in only a few species.

2.3.6 Ophioglossaceae

Ophioglossaceae Martinov, Tekhno-Bot. Slovar: 438 (1820).
Helminthostachyaceae Ching, Bull. Fan Mem. Inst. Biol., Bot. 10: 235 (1941).

Terrestrial or epiphytic plants consisting of a fleshy rhizome bearing numerous fleshy roots, and one to several leaves. The growth is not circinnate as in most other ferns but the parts are folded or bent in bud. Leaves erect or pendent, consisting of a petiole bearing at the apex a simple or variously divided blade. Part of the blade may be fertile, and form erect or divergent sporangia-bearing spikes. Sporangia in two rows, naked, each opening by a slit. Gametophytes subterranean, very small, tuber-like, usually without chlorophyll.

Number of genera and species—The Ophioglossaceae comprise four (or five) genera with 60 or more species. *Mankyua* and *Helminthostachys* are monotypic, whereas *Botrychium* includes about 25 species and *Ophioglossum* 25–30.

Distribution and habitat—The Ophioglossaceae occur worldwide from the tropics to the Arctic and Antarctic. They grow epiphytically or in moist woodland or grassland settings.

Classification—The Ophioglossaceae is an early branching lineage of ferns, not closely related to any other group of vascular plants. Together with Psilotaceae it forms the sister group to all other ferns. Stevenson and Loconte (1996) concluded that *Ophioglossum* and *Botrychium* are sister taxa based on their transverse dehiscence of the sporangia. *Helminthostachys* has vertical dehiscence and they therefore considered this genus "ancestral" and segregated it into Helminthostachyaceae. It is however better pertained within Ophioglossaceae, because the genus is certainly allied to *Botrychium* and *Ophioglossum*. The placement of *Mankyua* is uncertain but it has transverse sporangia dehiscense and is thus probably most closely related to *Ophioglossum*.

Evolutionary history—The fossil history of Ophioglossaceae is very limited. Only a single macrofossil is known of the family, which is from the Palaeocene (Rothwell and Stockey 1989), but the family certainly is much older. This lack of fossils is probably due to the soft tissue decaying swiftly and the habitats where these plants grow providing little chance for fossilization. Nevertheless the family must have an ancient origin because of their large number of plesiomorphic characters. Kato (1990) suggested that the "three-dimensional construction of ophioglossoid fertile leaves with epiphyllous sporophores may be a hypothetical archetype for angiosperm carpels with adaxial ovules."

Mycoheterotrophy—The prothallus of all genera is mycorrhizal, the appropriate arbuscular mycorrhizal fungus is needed for the growth of the prothallus (Winther and Friedman 2007; Smith and Read 2008). In most cases the prothallus is subterraneous and lacks chlorophyll, although cases of superficial green prothalli have been reported (Sporne 1962).

Prothalli are tuberous bodies; flattened in *Botrychium*, cilindrical and elongated in *Ophioglossum*, not unlike rhizome parts. Often a large part of the mycorrhizal fungus is located in an enlarged bulbous base in *Ophioglossum*. The antheridia appear first and are deeply sunken, producing very large numbers of antherozoids. The archegonium is stalked in *Botrychium* and sunken in *Ophioglossum*. The prothalli of *Helminthostachys* and *Mankyua* are not known, but are presumably similar to those of *Ophioglossum* or *Botrychium*.

2.3.6.1 *Botrychium* (Figs. 2.2a and 4.1d)

Botrychium Sw., J. Bot. (Schrader) 1800(2): 8 (1801).
Botrypus Michx., Fl. Bor.-Amer. 2: 274 (1803).
Sceptridium Lyon, Bot. Gaz. 40: 457 (1905).
Japanobotrychium Masam., J. Soc. Trop. Agric. 3: 246 (1931).
Osmundopteris (Milde) Small, Ferns Southeast. States 377, 482 (1938).

Perennial terrestrial ferns. Rhizome subterranean, short, erect, usually unbranched. Leaves 1 or 2, the younger enclosing the buds or succeeding leaves in the sheathing petiole base, consisting of a petiole and a blade divided into a sterile and a fertile part. The sterile blade pinnate to deltate-decompound, the fertile portion being equivalent to the basal two divisions of the blade that have fused and bear sporangia on simple or paniculate branches. Sporangia globose, not immersed in the tissue. Spores trilete, thick-walled, exospore verrucose or reticulate. Gametophytes cylindric or oblong and flattened, unbranched, mycoheterotrophic, entirely without chlorophyll.

A genus of ca. 25 species widely distributed throughout the world in boreal, temperate and tropical regions (in the tropics mostly in mountain areas). The mycoheterotrophic gametophytes and autotrophic sporophytes (which are initially mycoheterotrophic) of *Botrychium lanceolatum* and *B. crenulatum* are associated with *Glomus* Group A fungi (Winther and Friedman 2007). The autotrophic sporophyte of *B. virginianum* is able to associate both with *Glomus* Group A and Gigasporaceae fungi (Kovács et al. 2007).

2.3.6.2 *Helminthostachys* (Fig. 2.2b)

Helminthostachys Kaulf., Enum. Filicum 28 (1824).
Botryopteris C.Presl, Rel. Haenk. 1: 76 (1825), non B.Renault (1875 = Botryopteridaceae fossil).
Ophiala Desv., Mém. Soc. Linn. Paris 6: 195 (1827).

Perennial terrestrial ferns with creeping rhizomes bearing thick fleshy roots. Leaves

Fig. 2.2 Ophioglossaceae, Psilotaceae, Gleicheniaceae, and Schizaeaceae (**a**) Sporophyte of *Botrychium lunaria* (Ophioglossaceae). Redrawn from Wagner and Wagner (1993). (**b**) Sporophyte of *Helminthostachys zeylanica*. Redrawn from Shieh and DeVol (1994). (**c**) Sporophyte of *Ophioglossum nudicaule* (Ophioglossaceae). Redrawn from Wagner and Wagner (1993). (**d**) Sporophyte of *Mankyua chejuense* (Ophioglossaceae). Redrawn from Sun et al. (2001). (**e**) Sporophyte of *Tmesipteris tannensis* (Psilotaceae). Redrawn from McLintock (1966). (**f**) Sporophyte of *Psilotum nudum* (Psilotaceae). Redrawn from Castroviejo (1998). (**g**) Sporophyte of *Stromatopteris moniliformis* (Gleicheniaceae). Redrawn from Diels (1902). (**h**) Sporophyte of *Actinostachys pennula* (Schizaeaceae). Redrawn from Wagner (1993). Bar = 1 cm

consisting of a common basal petiole with two rounded stipules at the base, a palmately divided sterile lamina and an erect sporophore projecting above the lamina and consisting of numerous crowded short lateral sporangiate branches. Sporangia large, globose, opening by a vertical slit. Spores granular, yellow. Gametophytes not sufficiently known.

Helminthostachys is a monotypic genus—*H. zeylanica* being the only species—extending from India and Sri Lanka through Malesia and New Guinea, north to southern Japan and south to Australia and New Caledonia. It grows in forest edges usually in alluvial soils by streams or rivers, or in rich organic soil in swamps (Chinnock 1998b).

2.3.6.3 *Mankyua* (Fig. 2.2d)

Mankyua B.-Y.Sun, M.H.Kim et C.H.Kim, Taxon 50: 1020 (2001, publ. 2002).

Perennial terrestrial ferns. Rhizomes tuberous, short, horizontally creeping, unbranched, Roots fleshy, cylindrical, sparsely branched, without root hairs, producing buds. Leaves usually 1, rarely 2, consisting of a common petiole, a thin sterile blade that is terately divided in several ovate to lanceolate lobes, margins dentate, the segments sessile. Sporophores spike-like, arising from top of a common stalk, placed at the base of the sterile blade, the spikes held above these, the spikes simple or branched. Sporangia sunken in fleshy sporophore, horizontally dehiscent. Spores yellowish white. Gametophytes unknown.

The single species *M. chejuense* is the only species in the genus and is only known from Cheju island south of the Korean Peninsula in a lowland swampy area under evergreen broad-leaved forest (Sun et al. 2001). Only 20 plants are reported and thus the species is of conservation concern.

Mankyua shares fertile characters with *Ophioglossum* in the structure of the sporophyll, but resembles in habit a small *Helminthostachys*.

2.3.6.4 *Ophioglossum* (Fig. 2.2c)

Ophioglossum L., Sp. Pl. 1062 (1753).
Ophioderma (Blume) Endlicher, Gen. 66 (1836).
Rhizoglossum C.Presl, Suppl. Tent. Pteridog. 47 (1845), non Kylin (1924, Rhodophyceae, Delesseriaceae).
Cheiroglossa C.Presl, Suppl. Tent. Pteridogr. 56 (1845).
Cassiopteris H.Karst., Linnaea 20: 437 (1847), nom. inval.
Holubiella Škoda, Preslia 68(4): 345 (1996, publ. 1997).

Perennial or annual, terrestrial or epiphytic herbs. Rhizomes short, usually erect, terminating in an erect exposed bud. Leaves erect or pendent, glabrous, somewhat fleshy or leathery, consisting of a petiole and separate sterile and fertile portions of the blade. Sterile blade simple or palmately lobed, sessile or short-stalked, venation reticulate, the primary areoles enclosing free veinlets and sometimes secondary areoles. Fertile portion (sporophore) one or several, simple, stalked spikes. Sporangia sunken, subglobose, more or less coalescent in two marginal rows. Spores yellowish, thick-walled. Gametophytes small, cylindric or ovoid, simple or branched, mycoheterotrophic, without chlorophyll.

About 25–30 species occurring almost throughout the world, except for very cold Arctic or Antarctic regions. It is a taxonomically difficult genus due to the plasticity of the species and lack of morphological characters. *Ophioglossum reticulatum* is known to be the plant with the highest number of chromosomes of $n=720$ (Khandelwal 1990). The epiphytic *O. palmatum* is sometimes maintained in its separate genus *Cheiroglossa* (Christenhusz et al. 2011a).

2.3.7 Psilotaceae

Psilotaceae J.W.Griff. & Henfr., *Micrgr. Dict.*: 540 (1855).
Tmesipteridaceae Nakai, Chosakuronbun Mokuroku [Ord. Fam. Trib. Nov.]: 206 (1943).

Epiphytic, lithophytic or sometimes terrestrial plants. Rhizomes without roots, beset with short hair-like rhizoids. Stems green, simple and provided with small two-ranked leaves or several times dichotomously branched and appearing leafless (the leaves being minute, scale-like and far apart). Sporangia bilocular or trilocular, attached on the adaxial base of minute bifid sporophylls, dehiscing vertically. Spores reniform, all similar. Gametophytes tuberous, subterranean or embedded in humus, mycoheterotrophic.

Number of genera and species—The Psilotaceae consists of two genera and ca. 17 species.

Distribution and habitat—Pantropical, extending into warm temperate areas, epiphytic on trees and tree ferns in peat bogs and in crevices of rocks and on walls.

Classification—The placement of Psilotaceae has always been disputed. Because of the protostele and lack of roots it has a superficial similarity to Psilophytopsida/Rhyniopsida—an extinct group of Devonian plants—but these are more likely to be secondary plesiomorphic characters.

The family consists of two genera that are sister to each other. This clade pairs distantly with Ophioglossaceae as sister to the rest of the ferns (incl. Equisetaceae). The Psilotaceae and Ophioglossaceae share several characters of the sporangia, leaf division into a fertile and sterile part, a reduced root system and mycoheterotrophic gametophytes.

Evolutionary history—Apart from an early Tertiary macrofossil of *Tmesipteris* (Carpenter 1988), the Psilotaceae are without a macrofossil record. The family has traditionally been compared with an early Devonian group of land plants, the Psilophytales (which includes the superficially similar *Rhynia*) or with the lycopods.

Bierhorst (1977) noted affinities with Schizaeales and Gleicheniales. This affiliation has since been rejected (Voirin and Jay 1997; Fineran and Ingerfeld 1985; Brownsey and Lovis 1987). However molecular studies showed Psilotaceae to be sister to Ophioglossaceae (Hasebe et al. 1995).

Mycoheterotrophy—Few botanists have had the good fortune to see living specimens of the gametophyte of either *Psilotum* or *Tmesipteris*, but all remark on their similarity and their resemblance to portions of sporophytic rhizome. They are irregularly dichotomizing colorless, cylindrical structures, covered with rhizoids, and they are packed with mycorrhizal fungus hyphae. Archegonia and antheridia are borne together on the same prothallus (monoicous), but because of their small size it is impossible to distinguish gametophytes from bits of sporophyte rhizomes in the field (Sporne 1962). Both the gametophytes and sporophytes of Psilotaceae form arbuscualr mycorrhizal associations (Wang and Qiu 2006 and references therein).

2.3.7.1 *Psilotum* (Figs. 2.2f and 4.1g)

Psilotum Sw., J. Bot. (Schrader) 1800(2): 8 (1801).
Bernhardia Willd. ex Bernh., J. Bot. (Schrader) 1800(2): 132 (1801).

Erect or pendent plants, epiphytic in crevices of cliffs or old walls or (rarely) terrestrial in peat, humus or on gravel. Rhizome short-creeping, dichotomously branched, beset with small, brown, hair-like rhizoids. Stems loosely clustered, the lower unbranched part more or less elongate, dichotomously branched above into numerous narrow divisions. Leaves alternate, 2- or 3-ranked, minute, gradually tapering to a sharp thin point. Sporangia depressed-globose, sessile, trilocular, 3-lobed. Spores hyaline. Gametophytes subterraneous or in humus, mycoheterotrophic.

A genus of two species: *Psilotum nudum* has a pantropical distribution extending into warm-temperate areas, occurring in a wide range of habitats, whereas *P. complanatum* also has a pantropical distribution, but is restricted to montane rainforests. The mycoheterotrophic gametophytes and autotrophic sporophytes (which are initially mycoheterotrophic) of *Psilotum nudum* are associated with *Glomus* Group A fungi (Winther and Friedman 2009).

2.3.7.2 *Tmesipteris* (Fig. 2.2e)

Tmesipteris Bernh., J. Bot. (Schrader) 1800(2): 131 (1801)

Usually epiphytic plants. Rhizome short-creeping, dichotomously branched, with brown rhizoidal hairs. Shoots pendent or erect, unbranched, or rarely a few branched, beset with leaves. Sterile leaves scale-like at the base of the shoot, large and leaf-like above, decurrent, 1-veined, entire, spirally or distichously arranged. Fertile leaves bifid but otherwise similar in size and form to sterile ones or somewhat smaller, produced basally, in distinct zones, or irregularly along a shoot. Sporangia fused into synangia, these large, bilobed, brown. Gametophytes subterraneous, mycoheterotrophic.

A genus of about 15 species extending from the Philippines to Australia, New Zealand and New Caledonia, and east to Samoa, Fiji, French Polynesia and the Marquesas Islands (Chinnock 1998a).

2.3.8 Gleicheniaceae

Gleicheniaceae C.Presl, Reliq. Haenk. 1: 70 (1825).
Mertensiaceae Corda, Fl. d. Vorwelt: 89 (1845).
Stromatopteridaceae Bierh., Phytomorphology 18: 263 (1968).

Terrestrial ferns with long-creeping rhizomes. Leaves pinnate or more complex, indeterminate, usually pseudodichotomously forked (except *Stromatopteris*), the leaves often branching through axillary buds. Veins free. Soria abaxial, not marginal, exindusiate. Sporangia 5–15(–20), each with a complete transverse medial annulus, opening by a longitudinal slit. Gametophyte green, costate, with club-shaped hairs, or, in the case of *Stromatopteris*, mycoheterotrophic, subterranean and cylindrical.

Number of genera and species—The family consists of six genera (*Dicranopteris*, *Diplopterygium*, *Gleichenella*, *Gleichenia*, *Sticherus*, *Stromatopteris*), with ca. 130 species. Only *Stromatopteris* has mycoheterotrophic gametophytes.

Distribution and habitat—Tropical and Southern Hemisphere, with species reaching Japan. It shows a Gondwana distribution, with centers of diversity in Australasia and South America.

Classification—The Gleicheniaceae (including Stromatopteridaceae) are placed together with the Dipteridaceae and Matoniaceae in the Gleicheniales. The Gleicheniales are placed between Schizaeales and Hymenophyllales among the leptosporangiate ferns, but their exact phylogenetic position is not yet clear.

Evolutionary history—The family is obviously of Antarctic origin, where many fossils dating back to the Cretaceous have been found. Older fossils, such as *Antarctipteris* and *Gleichenipteris*, may be ancestral Gleicheniaceae, but are more likely belonging to extinct lineages of Gleicheniales.

Mycoheterotrophy—Bierhorst (1969) discussed mycoheterotrophy in *Stromatopteris*. Because of the similarities in gametophytes between *Stromatopteris* and *Psilotum* he assumed that the two genera were related. It is now known that the similarities are likely due to convergence rather than to true affinity (Kato 1983). The gametophytes of *Stromatopteris* are subterranean, cylindric, non-green, mycoheterotrophic, bearing rhizoids and superficial gametangia and resemble the rhizome of the sporophyte. The antheridia are large, many-celled and produce numerous spermatozoids. The archegonia are long-necked and variously oriented.

2.3.8.1 *Stromatopteris* (Fig. 2.2g)

Stromatopteris Mett., Ann. Sci. Nat. IV 15: 84 (1861).

Rhizomes creeping, horizontal, protostelic, with vertical, slender unequally dichotomous branches bearing the leaves. Young parts scaly. Leaves several, rigidly erect; petiole long, dark. Lamina erect, 1-pinnate, with numerous, imbricate, simple, ovate-rounded, entire or slightly lobed, coriaceous pinnae, adnate to the dark, sulcate rachis, the margin more or less revolute. Venation obscure, anadromous, free. Sori usually 1 per pinna, roundish, consisting of 15–20 large sporangia, intermingled with small irregularly shaped scales. Sporangial stalk uniseriate, annulus oblique to nearly transverse. Spores monolete, ellipsoidal, rugulose-reticulate.

A genus with a single species *Stromatopteris moniliformis*, endemic to New Caledonia, where it is frequent on serpentine, ultrabasic soils in the southern third of the island, mostly in open places and macchia-like vegetation (Brownlie 1969).

2.3.9 Schizaeaceae

Schizaeaceae Kaulf., *Wesen Farrenkr.*: 119 (1827).

Terrestrial ferns with short-creeping or erect rhizomes. Leaves erect, simple or fan-shaped, lamina and petiole hardly distinguised in some species. Blades flabellate and entire or dichotomously incised to strongly reduced, straplike and similar to the green petiole. Veins dichotomous, free. Sporangia sessile, on marginal, compact, pectinate-pinnate or pseudodigitate, branched or unbranched projections at blade tips, not in discrete sori, exindusiate; spores bilateral, monolete. Gametophytes filamentose, partly green with special rhizoid-bearing cells, antheridia on short branches and archegonia on the filaments or on anchegoniophores (in *Schizaea*), or subterranean, fleshy, tuber-like, achlorophyllous and mycoheterotrophic (in *Actinostachys*).

Number of genera and species—The small family Schizaeaceae is now confined to the two genera *Actinostachys* and *Schizaea*, with a total of ca. 30 species.

Distribution and habitat—Pantropical America and Asia, and southern warm-temperate (in Africa only in the South), one outlying species (*Schizaea pusilla* Pursh) occurs in the temperate zone from New Jersey to Newfoundland. The species are always terrestrial, often on substrates poor in minerals, or on decaying wood.

Classification—Formerly the genera *Lygodium* (Lygodiaceae) and *Anemia* (Anemiaceae) were included in Schizaeaceae, but they diverge significantly and are thus placed into their own families within Schizaeales.

Evolutionary history—*Schizaeopsis*, a Cretaceous fossil is the oldest one assigned to this lineage (Wikström et al. 2002).

2.3.9.1 *Actinostachys* (Fig. 2.2h)

Actinostachys Wallich, Num. List 1. 1829.

Actinostachys differs from *Schizaea* in having a pseudodigitate fertile segment, sporangia in four rows (instead of two) and tuberous mycoheterotrophic gametophytes. Because of the similarities (the digitate fertile segments are essentially pinnate as in *Schizaea*), the genus *Actinostachys* is sometimes considered to be part of *Schizaea*. The differences are clear-cut and thus it is maintained at the level of genus.

2.4 Gymnosperms

The existence of mycoheterotrophy in Gymnosperms is under debate and the discussion revolves around the enigmatic plant *Parasitaxus usta*, which is a member of the Podocarpaceae and has a purple reddish appearance. The plant contains chlorophyll but is incapable of measurable photosynthetic electron transport (Feild and Brodribb 2005). *Parasitaxus usta* is always found sprouting from roots and (rarely) trunks of another podocarp, *Falcatifolium taxoides*, and is therefore often regarded as a holoparasitic plant (de Laubenfels 1959; Köpke et al. 1981). However, a typical haustorium is not formed and the connection to the "host" has been described as an "obligate root graft" (Köpke et al. 1981). Moreover, both *P. usta* and *F. taxoides* are associated with arbuscular mycorrhizal fungi, which are closely associated with the *Parasitaxus*–*Falcatifolium* union (Woltz et al. 1994; Feild and Brodribb 2005). Stable carbon isotopic measurements indicate that carbon transport from *F. taxoides* to *P. usta* most likely involves this fungal partner (Feild and Brodribb 2005). The situation seems unique in land plants (but see de Vega et al. 2010) and differs from "normal" mycoheterotrophic plants that are not directly linked to another plant (but see *Exochaenium* in Gentianaceae). Despite its doubtful classification as a mycoheterotrophic plant, we included this species in our overview.

In addition to *P. usta*, achlorophyllous specimens of *Sequoia sempervirens* (Taxodiaceae) are known. These plants obtain nutrients by grafting their root system with that of surrounding autotrophic specimens (Davis and Holderman 1980). Because there seem to be no fungi involved in the interaction these "albino" redwood trees are probably not mycoheterotrophic and can best be categorized as parasitic plants.

2.4.1 Podocarpaceae

Podocarpaceae Endl., Synopsis Coniferarum 203 (1847).

Phyllocladaceae Bessey, Nebraska Univ. Stud. 7: 325 (1907).
Phyllocladaceae E.L.Core ex H.Keng, Taiwania 18: 142 (1973), nom, illeg.
Pherosphaeraceae Nakai, Tyosen-Sanrin158: 15 (1938).
Nageiaceae D.Z.Fu, Acta Phytotax. Sin.: 522 (1992).
Acmopylaceae Melikian & A.V.Bobrov, Proc. Intern. Conf. Plant Anat. Morph. (St. Petersburg) 1997: 93 (1997).
Saxegothaeaceae Gaussen ex Doweld & Reveal, Phytologia 84: 365 (1999).
Microcachrydaceae Doweld & Reveal, Phytologia 84: 365 (1999).
Bracteocarpaceae Melikian & A.V.Bobrov, Bot. Zhurn. (Moscow & Leningrad) 85: 60 (2000).
Dacrycarpaceae Melikian & A.V.Bobrov, Bot. Zhurn. (Moscow & Leningrad) 85: 59 (2000).
Falcatifoliaceae Melikian & A.V.Bobrov, Bot. Zhurn. (Moscow & Leningrad) 85: 61 (2000).
Halocarpaceae Melikian & A.V.Bobrov, Bot. Zhurn. (Moscow & Leningrad) 85: 60 (2000).
Lepidothamnaceae Melikian & A.V.Bobrov, Bot. Zhurn. (Moscow & Leningrad) 85: 63 (2000).
Microstrobaceae Doweld & Reveal, Novon 11: 396 (2001).
Parasitaxaceae Melikian & A.V.Bobrov, Bot. Zhurn. (Moscow & Leningrad) 85: 61 (2000).
Prumnopityaceae Melikian & A.V.Bobrov, Bot. Zhurn. (Moscow & Leningrad) 85: 58 (2000).

Evergreen shrubs or trees, usually with straight trunk and more or less horizontal branches. Branching typically with extra, weaker branches along the trunk between the main tiers of 3 and 5 major branches. Leaves usually spirally arranged, or in pairs radiating around the twig, or arranged distichously on more or less flat rows on either side of predominantly horizontal branchlets, needle-like, or broader leaves, usually with a single vein. Plants monoecious or dioecious. Pollen cones usually catkin-like; stamens numerous, close together, imbricate, each with two sporangia; pollen grains usually winged. Female cones maturing in 1 year, much reduced to a few fleshy bracts or scales, pendant, usually borne on a thin peduncle, containing a single inverted ovule. Seeds completely covered by a fleshy structure referred to as an epimatium, wingless. Epimatium and integument sometimes connate and forming a leathery testa. Cotyledons 2, with 2 parallel vascular bundles.

Number of genera and species—Nine genera and ca. 180 species (Christenhusz et al. 2011b). The sole species in *Parasitaxus* is entirely reddish purple and has a heterotrophic mode of life. All other Podocarpaceae species are evergreen trees or shrubs (Eckenwalder 2009).

Dictribution and habitat—Podocarpaceae are widespread in the southern hemisphere and reach their northern distribution limits in Mexico, the West Indies (25ºN), East Africa (35ºN) and Japan (35ºN) (Eckenwalder 2009). Most members of the family are trees native to wet tropical or subtropical forests. A few are small trees or shrubs native to forest understory environments (Earle 1997).

Classification—There has been some debate about the position of the genus *Phyllocladus* either within the Podocarpaceae or as an independent family Phyllocladaceae (Tomlinson et al. 1997; Bobrov et al. 1999; Sinclair et al. 2002). Recent molecular analyses link *Phyllocladus* to Podocarpaceae and suggest that *Phyllocladus* forms a distinct lineage that diverged early in the evolutionary history of Podocarpaceae (Wagstaff 2004). Christenhusz et al. (2011b) classified Podocarpaceae in Araucariales and provided a full synonymy.

Evolutionary history—The current distribution of Podocarpaceae and their fossil record suggests that the family had an extensive distribution over southern Gondwana but also occurred in Laurasia. South America and Antarctica are possibly the cradle of much of the modern Podocarpaceae diversity, and while Malesia and Australasia have the greatest diversity of living podocarps these distributions are regarded as the result of secondary radiations (Mill 2003).

Ecology—All investigated Podocarpaceae are associated with arbuscular mycorrhizal fungi (Wang and Qiu 2006). Like all conifers, Podocarpaceae are wind-pollinated. Podocarpaceae seeds are associated with fleshy parts, and are presumably dispersed by birds. Seed dispersal by streams and rivers has been suggested as well (Page 1990).

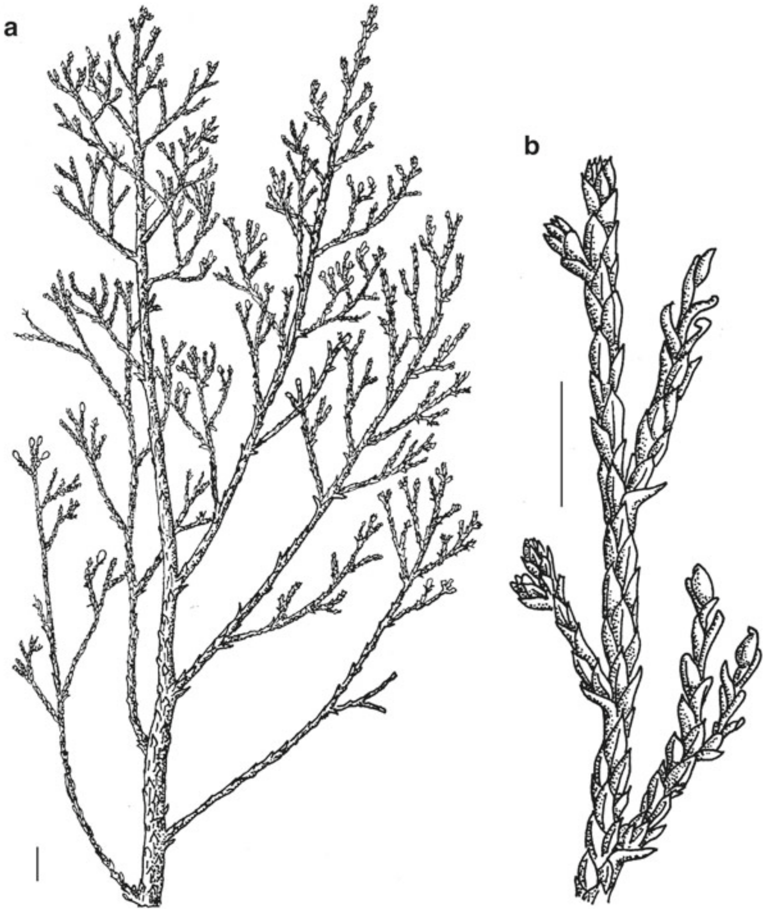

Fig. 2.3 *Parasitaxus usta* (Podocarpaceae): (**a**) habit, (**b**) branch with pollen cones. Redrawn from de Laubenfels (1972). Bar = 1 cm

2.4.1.1 *Parasitaxus* (Fig. 2.3)

Parasitaxus de Laub., Fl. N. Caledonia 4: 44 (1972).

Coral-like, red or purple shrub, 1–1.8(-3) m tall. Roots absent. Stems erect, repeatedly branched, emerging from the roots or lower stems of the host plant. Leaves dense, spirally inserted, scale-like. Plants monoecious. Pollen cones single, at the end of branchlets or in the axils of foliage leaves. Seed cones on a short, leafy stalk to 5 mm long. Combined seed coat and epimatium fleshy, becoming wrinkled when dry, pale bluish white with a thick coating of wax over a reddish purple skin, nearly spherical, 2.5–4 mm in diameter, with a tiny beak at the tip that becomes more pronounced while drying.

Parasitaxus contains a single species, *P. usta*. Its distribution is slightly more restricted than its host plant *Falcatifolium taxoides* (Podocarpaceae), but both species are found in wet montane cloud forests on serpentine soils across New Caledonia and on Île des Pins (Feild and Brodribb 2005; Eckenwalder 2009). Morphological observations suggest that arbuscular mycorrhizal fungi are involved in the interaction between *F. taxoides* and *P. usta* (Woltz et al. 1994), but molecular identification studies are needed to confirm this. Pollination and seed dispersal mechanisms remain to be studied.

2.5 Angiosperms

Mycoheterotrophy occurs in ten families of angiosperms and in terms of species numbers most angiosperms capable of mycoheterotrophy are monocots. We identified ca. 515 angiosperm species that are putatively fully mycoheterotrophic, 468 in monocots (in 7 families) and 47 in eudicots (in 3 families). Full mycoheterotrophy has evolved at least 45 times independently in angiosperms (Chap. 5). The existence of partial mycoheterotrophy has been demonstrated in several species of Orchidaceae and Pyroleae (Ericaceae). Probably all orchid species (>20,000 spp.) are initial mycoheterotrophs and initial mycoheterotrophy may also occur in *Pyrola* (Ericaceae) (Smith and Read 2008) and all other plant species that produce dust-like seeds as well (Eriksson and Kainulainen 2011; Chap. 5).

2.5.1 Petrosaviaceae

Petrosaviaceae Hutch., Fam. Fl. Pl. 2: 36 (1934).
Petrosavieae Engl. In Engl. & Prantl, Nat. Pflanzenfam. Nachtr.: 71,72 (1897).
Miyoshiaceae Nakai, J. Jap. Bot 17: 190 (1941).
Japonoliriaceae Takht., Bot. Zhurn. (Moscow & Leningrad) 79: 97 (1994).
Japonolireae (Takht.) M. N. Tamura in Kubitski, Fam. & Gen. Vasc. Pl. 3: 390 (1998).

Achlorophyllous and mycoheterotrophic (*Petrosavia*) or autotrophic (*Japonolirion*) herbs. Rhizome slender, creeping to erect, with scale-like leaves. Roots filiform. Stems erect, simple. Leaves cauline, reduced to scales and distichous (*Petrosavia*) or basal, linear, and spiral (*Japonolirion*). Inflorescence a terminal bracteate raceme, sometimes corymbiform; each flower subtended by a well-developed bract and possessing a single bracteole in the same radius as one of inner tepals. Flowers bisexual, actinomorphic. Tepals 6, in 2 whorls, those of the outer whorl smaller than those of the inner whorl; tepals erect to patent, persistent, basally connate (*Petrosavia*) or free (*Japonolirion*). Stamens 6; filaments linear, adnate to base of tepals (*Petrosavia*) or free (*Japonolirion*); anthers ovoid, dorsifixed (*Petrosavia*) or basifixed (*Japonolirion*), introrse. Ovary half-inferior (*Petrosavia*) or superior (*Japonolirion*), tricarpellate; carpels in *Petrosavia* postgenitally fused only near their bases (also fused peripherally due to formation of a semi-inferior ovary); carpels in *Japonolirion* postgenitally connate up to the stylar region; ovules numerous (*Petrosavia*) or 4–5 per carpel (*Japonolirion*). Septal nectaries present in both genera; in *Japonolirion* mostly located below the level of the ovary locules (infralocular). Styles 1 per carpel, short, stigmata subcapitate (*Petrosavia*) or linear and recurved (*Japonolirion*). Fruit dry, composed of 3 horizontally patent capsules dehiscing longitudinally and septicidally to the upper side (*Petrosavia*) or 1 ellipsoid, 3-carpellate capsule, dehiscing septicidally (*Japonolirion*). Seeds ellipsoid to broadly ellipsoid, more or less winged (*Petrosavia*) or wingless (*Japonolirion*) (Tamura 1998; Rudall 2002; Cameron et al. 2003; Remizowa et al. 2006a, b).

Number of genera and species—Petrosaviaceae comprise two genera (*Japonolirion* and *Petrosavia*) and four species. All three species of *Petrosavia* are fully mycoheterotrophic.

Distribution and habitat—Petrosaviaceae occur in Southeast Asia and Japan (Cameron et al. 2003). The only species of *Japonolirion* is restricted to serpentine swamps in central and northern Japan (Tomimatsu et al. 2004; Tamura 1998), while *Petrosavia* occurs in forests in Southeast Asia and southern Japan (Chen and Tamura 2000; Ohashi 2000).

Classification—Both genera of Petrosaviaceae have been placed in various groups. For *Petrosavia*, relationships with Melanthiaceae (Beccari 1871), Liliaceae (Engler 1888), Alismatales (Hutchinson 1959), Tofieldiaceae and Nartheciaceae (Tamura 1998), Triuridaceae (Cronquist 1981, 1988), and other families have been suggested (see Cameron et al. 2003 for an overview). *Japonolirion* has been placed in Liliaceae (Nakai 1930; Ohwi 1965), Melanthiaceae (Brummitt 1992; Mabberley 1997), Nartheciaceae (Tamura 1998), and Japonoliriaceae (Takhtajan 1996, 1997). Molecular phylogenetic analyses using plastid and/or nuclear DNA sequences suggest that

Petrosavia is the sister-group of *Japonolirion* (Caddick et al. 2000b; Chase et al. 2000; Fuse and Tamura 2000; Soltis et al. 2000) and that these two genera are phylogenetically isolated within the monocots, not closely related to any of the aforementioned families. Based on this molecular evidence, Cameron et al. (2003) proposed recognition of the family Petrosaviaceae, consisting of *Petrosavia* and *Japonolirion*, and its placement in its own order, Petrosaviales, which was adopted by the APG classification (APG 2009). Although a close relationship between *Petrosavia* and *Japonolirion* was unexpected due to their different mode of life, there are many similarities in their morphology (Cameron et al. 2003; Remizowa et al. 2006a, b; Tobe 2008; Tobe and Takahashi 2009).

Evolutionary history—Petrosaviaceae are sister to the liliid/commelinid clade (Chase 2004; Tamura et al. 2004; Chase et al. 2006; Givnish et al. 2006; Graham et al. 2006). Molecular clock analyses suggest that the Petrosaviaceae diverged during the Early Cretaceous, and the split between *Japonolirion* and *Petrosavia* also occurred in the Early Cretaceous (Janssen and Bremer 2004; Magallón and Castillo 2009).

Ecology—*Petrosavia* is associated with arbuscular mycorrhizal fungi (Yamato et al. 2011b). *Petrosavia* is capable of both cross-pollination and self-pollination (Takahashi et al. 1993). Seed dispersal agents are unknown.

2.5.1.1 *Petrosavia* (Figs. 2.4 and 2.5a)

Petrosavia Becc., Nuov. Giorn. Bot. Ital. 3: 7 (1871).
Protolirion Ridl., Ann. Bot. 9: 56 (1895).
Miyoshia Makino, Bot. Mag. 17: 144 (1903).

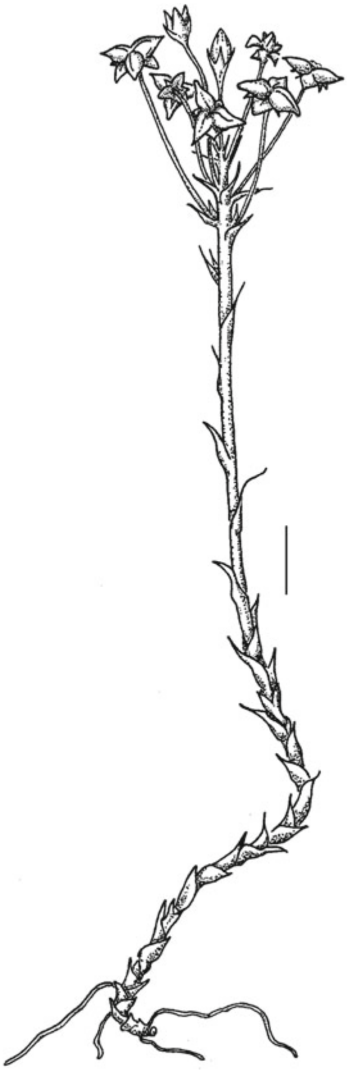

Fig. 2.4 *Petrosavia stellaris*. Redrawn from Tamura (1998). Bar = 1 cm

Mycoheterotrophic herbs, cream-colored, 4–30 cm tall. Leaves cauline, reduced to scales and distichous. Inflorescence a sometimes corymbiform raceme, 4- to more than 25-flowered. Flowers funnel-shaped, small, white to yellow, arising from the axil of a small bract, often subtended by a bracteole. Tepals 6, basally connate, inner ones larger than outer ones. Stamens 6, filaments adnate to base of the tepals, anthers dorsifixed. Ovary half-inferior, carpels 3, connate for 1/4–1/2 their length and distally apocarpous, with three separate styles, sometimes only basally connate; ovules numerous. Septal nectaries present. Stigmata subcapitate or slightly 2-cleft. Fruit almost apocarpous, composed of three horizontally patent capsules dehiscing to the upper side. Seeds brown, more or less winged.

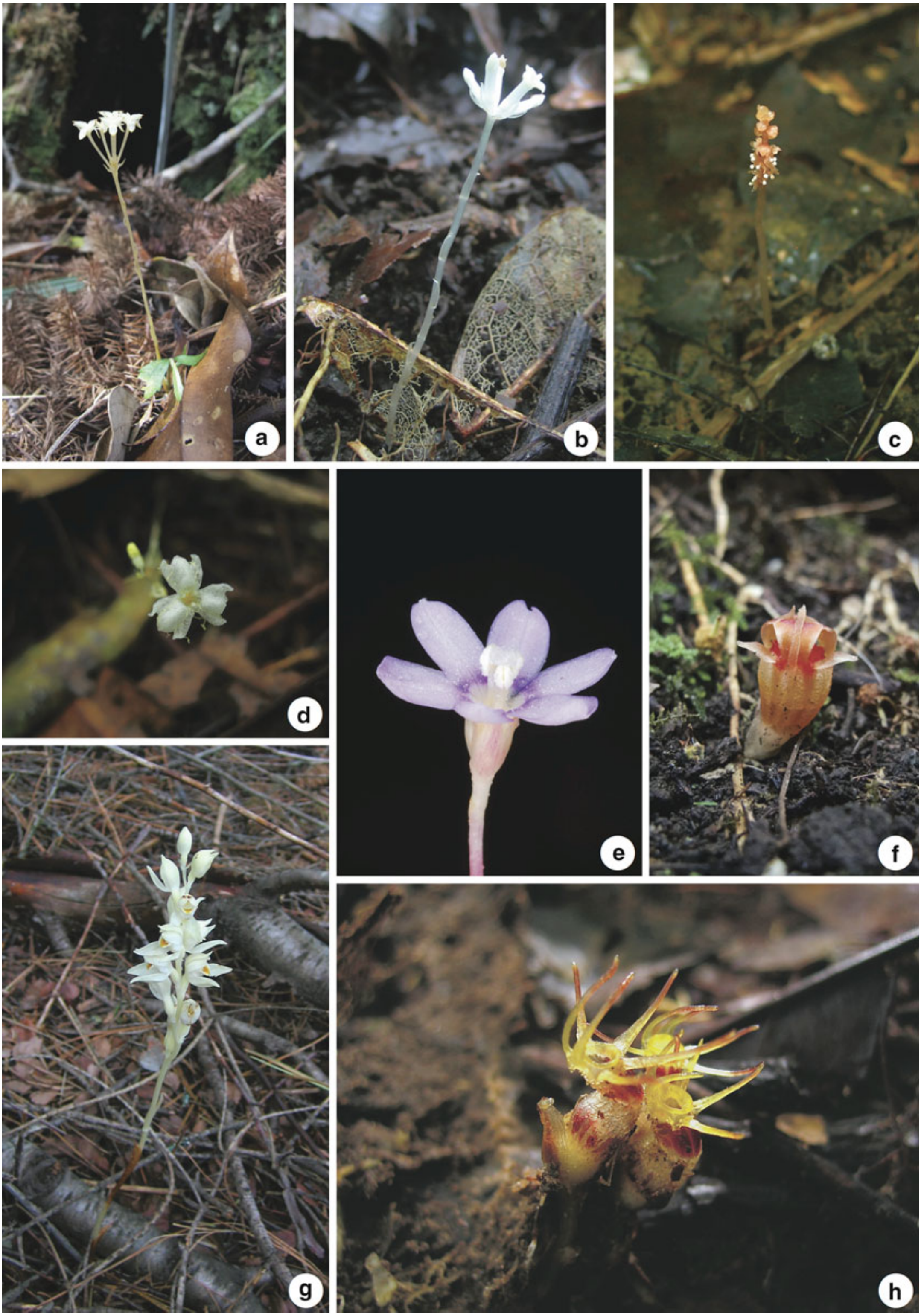

Fig. 2.5 Fully mycoheterotrophic species in monocots: (**a**) *Petrosavia stellaris* (Petrosaviaceae) pictured in Borneo. (**b**) *Campylosiphon congestus* (Burmanniaceae) from Cameroon. (**c**) Male plant of *Kupea martinetugei* (Triuridaceae) growing at Diongo Community forest in Cameroon. (**d**) *Gymnosiphon longistylus* (Burmanniaceae) from Cameroon. (**e**) Flower of *Geosiris aphylla* (Iridaceae). Photo by Ehoarn Bidault. (**f**) *Thismia rodwayi* (Thismiaceae) growing on Mount Wellington, Tasmania. (**g**) *Cephalanthera austinieae* (Orchidaceae) photographed in northern California. (**h**) *Afrothismia hydra* (Thismiaceae) from Korup National Park in Cameroon.

Petrosavia comprises three species: *P. sinii*, *P. sakuraii*, and *P. stellaris*, although some authors reduce *P. sinii* to *P. sakuraii* (Ohashi 2000; Cameron et al. 2003; Tobe and Takahashi 2009). *Petrosavia sinii* is endemic to China, *P. sakuraii* is fairly widespread in Southeast Asia (with records from China, Taiwan, Indonesia, Japan, Myanmar, and Vietnam), while *P. stellaris* occurs in Malesia (Chen and Tamura 2000; Ohashi 2000). *Petrosavia* grows in rain forests, mixed forests, bamboo forests, and coniferous forests, from sea level up to 1,800 m (Takahashi et al. 1993; Ohashi 2000; Chen and Tamura 2000).

The pollination biology of *P. sakuraii* was studied by Takahashi et al. (1993). They concluded that the plants are primarily self-pollinating (including insect mediated self-pollination), but cross-pollination by bees and other insects may occur as well. *Petrosavia sakuraii* is associated with a narrow clade of arbuscular mycorrhizal fungi (Yamato et al. 2011b). Dispersal agents remain unknown.

2.5.2 Burmanniaceae

Burmanniaceae Blume, Enum. Pl. Javae 27 (1827).

Achlorophyllous, mycoheterotrophic or autotrophic herbs. Rhizome cylindrical, rarely tuberous or absent, densely covered with scale-like leaves and filiform roots. Stems erect, usually unbranched, leaves alternate, sessile, simple, entire, in achlorophyllous species small and scale-like, in autotrophic species larger and often rosulate. Inflorescence a terminal, bracteate, usually bifurcate, 1-many-flowered cyme, or reduced to a single flower. Flowers syntepalous, actinomorphic, variously colored, campanulate, funnel-shaped, salverform, or tubular. Flower tube wingless, 3- or 6-ribbed, or broadly 3-winged, sessile or pedicellate. Tepals 6, free, entire or sometimes 3-lobed. Stamens 3, erect, inserted in the flower tube just below and opposite the inner tepals, without interstaminal lobes; thecae superposed, transversely dehiscent, connective often bearing apical and basal appendages. Ovary inferior, 1- to 3-locular, with parietal or axile placentation, nectarial glands often present in the septa or on top of the ovary; style equaling the flower tube; stigma variously shaped, sometimes provided with tortuous, filiform appendages; ovules numerous, anatropous. Fruit a capsule, longitudinally or transversely dehiscent, crowned by various flower remnants. Seeds numerous, dust-like, fusiform to subglobose.

Number of genera and species—Burmanniaceae consist of eight genera and ca. 96 species. With respectively 56 and 32 species *Burmannia* and *Gymnosiphon* are the largest genera. The other genera comprise one or two species only. All species, except for 37 species of *Burmannia*, are fully mycoheterotrophic.

Distribution and habitat—Burmanniaceae have a pantropical distribution. The distributions of *Apteria* and a few *Burmannia* species extend into the subtropics. Fully mycoheterotrophic Burmanniaceae species mainly occur in evergreen forest, but *Apteria* sometimes grows in wet savannas. Most species grow at low elevations, but some species occur at 2,000 m and above. Chlorophyllous *Burmannia* species prefer wet savannas or swamps, or grow occasionally in gallery or savanna forests (Maas et al. 1986).

Classification—Burmanniaceae were traditionally associated with the orchids (Lindley 1846; Karsten 1858; Engler 1888; Cronquist 1970; Rübsamen 1986) or other mycoheterotrophic families such as Corsiaceae and Geosiridaceae (now in Iridaceae) (Cronquist 1970; Dahlgren et al. 1985). However, use of molecular data, has shed new light on the position of Burmanniaceae among the monocots. In a phylogenetic analysis of 172 monocot *rbcL* sequences, a *Burmannia* species was sister to *Dioscorea* and *Tacca* (Chase et al. 1995). All subsequent molecular analyses with additional data and sampling recovered a monophyletic family of Burmanniaceae sister to Dioscoreaceae, and therefore part of Dioscoreales (Caddick et al. 2000b, 2002a, b; Soltis et al. 2000; Davis et al. 2004). Only the 26S rDNA analyses by Neyland (2002) and Neyland and Hennigan

(2003) revealed a different hypothesis, with Burmanniaceae (and Corsiaceae) sister to almost all other monocot groups. Analyses using sequence data from the nuclear and mitochondrial genome suggest that Thismiaceae are not part of Burmanniaceae (Merckx et al. 2006; 2009).

Evolutionary history—Burmanniaceae are the second diverging lineage in Dioscoreales (Merckx et al. 2008, 2009). There are no known Burmanniaceae fossils, but molecular clock analyses indicate that the family originated in the Cretaceous (ca. 100–120 Ma). The extant lineages share a common ancestor origniated in West Gondwana during the Late Cretaceous. The diversification rate in Burmanniaceae increased during the warm Eocene, when *Burmannia* and *Gymnosiphon* were able to migrate from the New to the Old World supposedly via boreotropical migration routes (Merckx et al. 2008).

Ecology—The mycorrhizas of only few species of Burmanniaceae have been studied. Morphological observations suggest that they are growing with arbuscular mycorrhizal fungi (Van der Pijl 1934; Terashita and Kawakami 1991; Imhof 1999c). Molecular sequencing detected *Glomus* Group A fungi, and sometimes also Acaulosporaceae fungi, in the roots of *Apteria*, *Burmannia*, *Campylosiphon*, *Gymnosiphon*, and *Hexapterella* species (Leake 2005; Franke et al. 2006; Merckx and Bidartondo 2008; Courty et al. 2011; Merckx et al. 2012). Except for a few *Burmannia* species, pollination has not been studied. The colorful, variously shaped flowers with septal nectaries, indicate insect pollination (Henderson and Stevenson 2004), but in some species of *Burmannia* there is strong evidence for selfpollination (Ernst and Bernard 1912; Wood 1983; Zhang and Saunders 1999, 2000). The tiny seeds are probably dispersed by wind or water (Maas-van de Kamer 1998).

2.5.2.1 *Burmannia* (Figs. 2.6e, f and 4.7g)

Burmannia L., Sp. Pl.: 287 (1753)
Vogelia J.F.Gmel., Syst. Nat. 2: 107 (1791).
Tripterella Michx., Fl. Bor.-Amer. 1: 19 (1803).
Maburnia Thouars, Gen. Nov. Madagasc.: 4 (1806).
Gonianthes Blume, Catalogus: 19 (1823).
Gonyanthes Nees, Ann. Sci. Nat. (Paris) 3: 369 (1824), orth. var.
Tetraptera Miers in J.Lindley, Veg. Kingd., ed. 2.: 172 (1847).
Tripteranthus Wall. ex Miers in J.Lindley, Veg. Kingd., ed. 2.: 172 (1847).
Cryptonema Turcz., Bull. Soc. Imp. Naturalistes Moscou 21(1): 590 (1848).
Nephrocoelium Turcz., Bull. Soc. Imp. Naturalistes Moscou 26(1): 287 (1853).

Mycoheterotrophic, or autotrophic herbs, 5–50 cm tall. Rhizome mostly absent, roots filiform. Leaves green and often rosulate, or without chlorophyll and scale-like. Inflorescence a 1-many- flowered, bifurcate cyme. Flowers erect, often 2-colored, white, yellow, and/or blue, tubular to salverform. Flower tube 3-winged, or 3- or 6-ribbed. Tepals 6, entire, inner tepals smaller than outer ones. Stamens 3, sessile. Ovary 3-locular, with axile placentation, septal nectaries sometimes present; style 3-branched at the apex. Fruit erect, dehiscing longitudinally, transversely, or irregularly, crowned by the persistent perianth. Seeds brown, ellipsoid or rarely narrowly fusiform.

The genus *Burmannia* comprises 19 achlorophyllous mycoheterotrophic species and 37 chlorophyllous species. Some chlorophyllous species are rather robust and have numerous well-developed leaves (e.g., *B. longifolia*, *B. kalbreyeri*, *B. foliosa*). These species are supposedly fully autotrophic. Other chlorophyllous species have reduced vegetative parts and are presumably partial mycoheterotrophs (Leake 1994; but see Merckx et al. 2010b). Full mycoheterotrophy has evolved many times independently in the genus (Merckx et al. 2008). *Burmannia* has a widespread distribution in the tropical and subtropical parts of both the Old and the New World. Nineteen chlorophyllous and one mycoheterotrophic species are found in Central and South America. In Africa (including Madagascar) four chlorophyllous species and one mycoheterotrophic species occur. In Asia, 15 species are chlorophyllous and 17 species are fully mycoheterotrophic. Mycoheterotrophic species grow in rain forests, while chlorophyllous species prefer wet grasslands and swamps (Maas-van de Kamer 1998). All species are terrestrial, except for the chlorophyllous *B. kalbreyeri* from Central and South America, which is an epiphyte growing on various trees

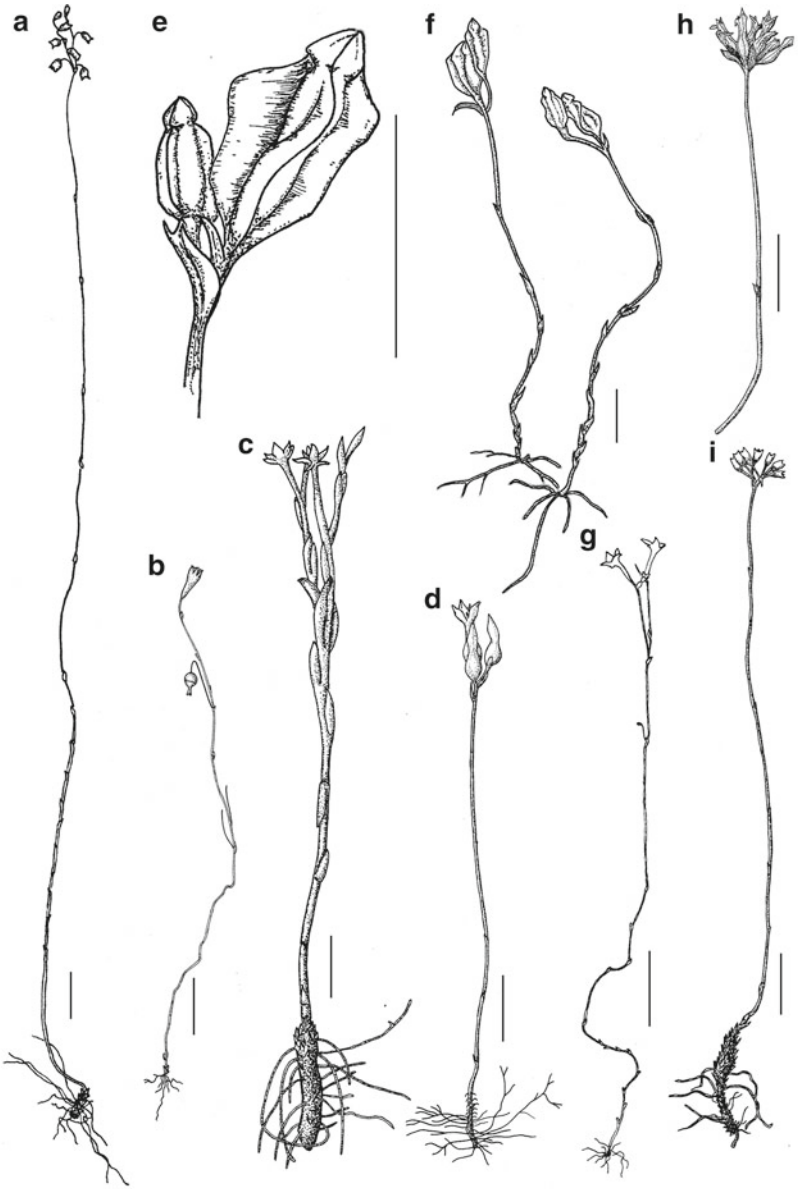

Fig. 2.6 Burmanniaceae. (**a**) *Dictyostega orobanchoides*. (**b**) *Apteria aphylla*. (**c**) *Campylosiphon purpurascens*. (**d**) *Hexapterella gentianoides*. (**e**, **f**) *Burmannia cryptopetala*: (**e**) flower, (**f**) habit. (**g**) *Gymnosiphon divaricatus*. (**h**) *Marthella trinitatis*. (**i**) *Miersiella umbellata*. Bar = 1 cm. Redrawn from Maas et al. (1986), except (**e**, **f**) redrawn from Hsu et al. (2005)

(Maas et al. 1986). *Burmannia* species generally occur at low elevations, but a few species prefer higher elevations of 1,000 m and higher (Jonker 1938; Maas et al. 1986). The Peruvian species *Burmannia stuebellii* has been found up to 4,100 m (León 2006).

Burmannia species are growing with arbuscular mycorrhizal fungi (Van der Pijl 1934; Terashita and Kawakami 1991; Imhof 1999c) belonging to the *Glomus* Group A clade (Franke et al. 2006; Merckx and Bidartondo 2008; Merckx et al. 2010b). Both self-pollination and cross-pollination have been suggested for species of *Burmannia*. Many species of *Burmannia* have strongly colored flowers with prominent wings, presumably to attract pollinators (Maas et al. 1986). Septal nectaries are present (Maas et al. 1986; Caddick et al. 2000a) and the stamens often have glandular apical appendages (Maas et al. 1986). Kato (1996) and Momose et al. (1998) reported that the flowers of *B. lutescens* were visited by mosquitos, suggesting cross-pollination. However, cleistogamy has been observed in the chlorophyllous species *B. capitata* with anther dehiscence in pre-anthesis flowers, and the presence of germinating pollen on the stigmas (Wood 1983). Premature opening of the anthers in pre-anthesis flowers, followed by pollen germination in situ within the anther, and subsequent penetration of the stigma by the pollen tube has furthermore been recorded for the mycoheterotrophic species *B. candida* (Ernst and Bernard 1912), *B. championii* (Ernst and Bernard 1912), and *B. stuebelii* (Spitmann 1975 *fide* Zhang and Saunders 2000). Zhang and Saunders (1999) note that the throat of *B. larseniana*, as with many species in the genus, is blocked by the three stigmatic branches, preventing cross-pollination. The only detailed study on the pollination biology of a *Burmannia* species, concluded that the mycoheterotrophic *B. wallichii* is primarily selfing (Zhang and Saunders 2000). *Burmannia* species have tiny dust-like seeds, which are presumably dispersed by wind or water (Maas et al. 1986).

2.5.2.2 *Campylosiphon* (Figs. 2.5b and 2.6c)

Campylosiphon Benth. in Hooker, Ic. Pl. Ser. 3 14(4): 65 (1882).
Dipterosiphon Huber, Bol. Mus. Paraense Hist. Nat. Ethnogr. 2: 502 (1898).

Mycoheterotrophic herbs, up to 35 cm tall. Rhizome tuberous, cylindrical. Leaves scale-like. Inflorescence a bifurcate 1-many-flowered cyme, flowers sessile or pedicellate. Flowers erect, salverform, blue to white. Flower tube narrowly 3-ribbed. Tepals 6, entire, subequal in length. Stamens 3, sessile. Ovary 1-locular, with 3 parietal placentas in its upper part, 3-locular with axile placentation in its lower part, septal nectaries present; style 3-branched at the apex. Fruit erect, dehiscing irregularly by withering of the fruit wall between the ribs, crowned by the marcescent perianth. Seeds brown, flattened, triangular in outline.

Campylosiphon has a disjunct distribution and contains *C. purpurascens*, which is widely distributed in tropical South America (including Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil, and Peru) (Maas et al. 1986), and *C. congestus* from West Africa (Guinea, Liberia, Ghana, Nigeria, Cameroon, Gabon, Central African Republic, Angola, and DR Congo) (Bamps and Malaisse 1987; Cheek 2006). Growing in rain forests, often along margins of streams and creeks.

Campylosiphon is dependent on arbuscular mycorrhizal fungi from the *Glomus* Group A clade and the Acaulosporaceae (Franke et al. 2006; Merckx et al. 2012). Pollination syndrome and dispersal agents are unknown.

2.5.2.3 *Hexapterella* (Figs. 2.6d and 4.6f, h)

Hexapterella Urb., Symb. Antill. 3(3): 451 (1903).

Mycoheterotrophic herbs, up to 20 cm tall. Rhizome cylindrical, slightly tuberous. Stems purplish. Leaves scale-like. Inflorescence a bifurcate 1–8-flowered cyme. Flowers erect, salverform, white to purple. Flower tube slightly 6-winged or 6-ribbed. Tepals 6, entire, inner ones much smaller than outer ones, sometimes 3-dentate, soon falling off. Stamens 3, filaments present. Upper part of ovary 1-locular, lower part 3-locular, with 3 parietal placentas, 3 septal nectaries present; style 3-branched at the apex. Fruit erect, dehiscent by transverse slits and/or withering of the fruit wall, crowned by the persistent part of the flower tube. Seeds brown, subglobose to ovoid.

Hexapterella contains two species, *H. steyermarkii* from Venezuela and *H. gentianoides* occurring in lowland forests in Trinidad and northern South America (Colombia, Venezuela, Guyana, Suriname, French Guiana, Brazil) (Maas et al. 1986; Maas and Maas 1989). A specimen of *Hexapterella gentianoides* from French Guiana was found to grow with *Glomus* Group A fungi

(Merckx et al. 2012). Self-pollination seems to occur in *Hexapterella* (Rübsamen 1980). Dispersal agents are unknown.

2.5.2.4 *Dictyostega* (Figs. 2.6a and 4.5a)

Dictyostega Miers, Proc. Linn. Soc. Lond. 1: 61 (1840).

Mycoheterotrophic herbs, 1–50 cm tall. Rhizome cylindric, slightly tuberous. Leaves scale-like. Inflorescence a bifurcate 3-many-flowered cyme. Flowers nodding, tubular, whitish. Flower tube wingless. Tepals 6, entire, inner ones smaller than the outer ones. Stamens 3, sessile. Upper part of ovary 1-locular, with 3 parietal placentas, lower part 3-locular, 3 septal nectaries present, style 3-branched at the apex. Fruit nodding, longitudinally dehiscent, crowned by the persistent perianth. Seeds white, narrowly fusiform.

Dictyostega contains a single, morphological variable species: *D. orobanchoides*. Maas et al. (1986) recognize three subspecies. Widely distributed in the Neotropics, from Mexico in the north to southeastern Brazil in the south, but absent from the West Indies. Growing in rain forests up to 2,600 m (Maas et al. 1986). *D. orobanchoides* is growing with various *Glomus* Group A fungi (Imhof 2001; Merckx et al. 2010b). *Dictyostega* is probably self-pollinating (Miers 1841; Warming 1901). Dispersal agents are unknown.

2.5.2.5 *Miersiella* (Fig. 2.6i)

Miersiella Urb., Symb. Antill. 3(3): 439 (1903).

Mycoheterotrophic herbs, 5–20 cm tall. Rhizome cylindrical, slightly tuberous. Leaves scale-like, almost peltate. Inflorescence a contracted, umbelliform, 4–10(-22)-flowered cyme. Flowers erect, tubular, deep lilac to white. Tepals 6, entire, inner tepals smaller than outer ones. Flower tube wingless. Stamens 3, sessile. Ovary 1-locular, with 3 parietal placentas, and three 2-lobed glands on the top of the ovary; style 3-branched at the apex. Fruit erect, dehiscence longitudinally and loculicidally, crowned by the persistent perianth. Seeds brown, narrowly ellipsoid to ovoid.

Miersiella comprises a single species, *M. umbellata*, growing in dense evergreen rain forests in southeastern and eastern Brazil and the Amazonian parts of Colombia, Venezuela, Guyana, and Peru (Maas et al. 1986; Tropicos 2011). Relationship to the other Burmanniaceae genera remains to be inferred. Pollination syndrome, dispersal agents, and mycorrhizal fungi are unknown.

2.5.2.6 *Gymnosiphon* (Figs. 2.5d and 2.6g)

Gymnosiphon Blume, Enum. Pl. Javae 1: 29 (1827).
Cymbocarpa Miers, Proc. Linn. Soc. London 1: 61 (1840).
Ptychomeria Benth. in Hooker's J. Bot. Kew Gard. Misc. 7: 14 (1855).
Benitzia H. Karst., Linnaea 28: 420 (1857).
Desmogymnosiphon Guinea, Ensayo Geobot. Guin. Continent. Espan.: 264 (1946).

Mycoheterotrophic herbs, up to 30 cm tall. Rhizome cylindrical, slightly tuberous. Leaves scale-like. Inflorescence a bifurcate 1–50-flowered cyme. Flowers erect, salverform, white, occasionally partly yellow or blue, flower tube wingless, upper part very soon falling off. Tepals 6, outer tepals mostly 3-lobed, inner tepals very small often somewhat swollen, inserted in the flower tube below the insertion of the outer tepals. Stamens 3, sessile. Ovary 1-locular, with 3 parietal placentas, septal nectaries present; style 3-branched at the apex, each branch with or without 2 apical, tortuous, filiform appendages. Fruit erect, longitudinally, loculicidally, or irregularly dehiscent, crowned by the persistent part of the flower tube. Seeds greyish-black, ellipsoid or fusiform.

Gymnosiphon has a pantropical distribution, with 16 species in the Neotropics, 8 in Africa (including Madagascar and the Comores), and 8 in Asia. The tiny flowers with soon falling upper parts trouble identification and taxonomy in this genus (Jonker 1938). Species of *Gymnosiphon* occur in lowland rain forests, but some species grow in montane forests up to 2,300 m (Maas et al. 1986). Molecular sequence data suggests that *Gymnosiphon* is the sister clade of *Hexapterella* (Merckx et al. 2008).

Glomus Group A and Acaulosporaceae fungi were detected in the roots of *Gymnosiphon* specimens of various species (Leake 2005; Courty et al. 2011; Merckx et al. 2012). Self-pollination occurs (Maas et al. 1986). Dispersal agents are unknown.

2.5.2.7 *Apteria* (Figs. 2.6b and 4.6b)

Apteria Nutt., J. Acad. Nat. Sci. Philadelphia 7: 64 (1834).
Nemitis Raf., Fl. Tellur. 4: 33 (1838).
Stemoptera Miers, Proc. Linn. Soc. London 1: 62 (1840).

Mycoheterotrophic herbs 5–70 cm tall. Rhizome cylindric, slightly tuberous. Leaves scale-like. Inflorescence a 1–5-flowered cyme. Flowers erect to nodding, funnel-shaped to campanulate. Flower tube wingless. Tepals 6, entire, subequal in length. Stamens 3, filament basally decurrent into a crescent-shaped pouch. Ovary 1-locular, with 3 parietal placentas, 3 septal nectaries present; style 3-branched at the apex. Fruit nodding, longitudinally dehiscent, crowned by the persistent perianth. Seeds brown, ellipsoid to subglobose.

Apteria contains a single species: *A. aphylla*. This species has a very wide distribution, and can be found from southern USA and the West Indies in the north to Peru, Bolivia, Paraguay, and South Brazil in the south (Maas et al. 1986). *Apteria aphylla* grows in rain forests, among decaying leaves or on rotten wood, between mosses and shrubs, or sometimes in savannas.

Apteria is able to associate with *Glomus* Group A and Diversisporales mycorrhizal fungi (Courty et al. 2011; Merckx et al. 2012). There is evidence for self-pollination in *Apteria*, perhaps mediated by flower mites (*Frankeliniella* spp.) (Warming 1901; Ernst and Bernard 1912; Uphof 1929; Maas et al. 1986). Dispersal agents are not known.

2.5.2.8 *Marthella* (Fig. 2.6h)

Marthella Urb., Symb. Antill. 3(3): 447 (1903).

Mycoheterotrophic herbs, up to 10 cm tall. Rhizome cylindric, slightly tuberous. Leaves scale-like. Inflorescence a 2–9-flowered contracted, bifurcate cyme. Flowers erect, tubular, yellowish. Flower tube wingless. Outer tepals entire, inner ones absent. Stamens 3, alternating with the tepals, filament basally decurrent into a crescent-shaped pouch. Ovary 1-locular, with 3 parietal placentas and 3 short-stipate, 2-lobed glands on top of the ovary; style 3-branched at the apex. Fruit erect, crowned by the persistent perianth, dehiscence unknown. Seeds brown, ellipsoid to broadly ovoid.

Marthella is a monotypic genus, only known from Mount Tucuche, Trinidad, growing in rain forests on rotten wood and decaying leaves. The only species, *M. trinitatis*, was last collected in 1898 and may be extinct (Maas et al. 1986). Observations on the biology of this species are lacking.

2.5.3 Thismiaceae

Thismiaceae J. Agardh, Theor. Syst. Pl. Fam. Phan. 99 (1858).

Achlorophyllous, mycoheterotrophic herbs. Underground part tuberous, or a cluster of coralloid or vermiform roots, or creeping cylindrical roots, or a rhizome bearing clumps of small root tubercles. Stems unbranched, leaves alternate, simple, sessile, reduced to scale-like. Flowers terminal, solitary or sometimes in few-flowered monochasial inflorescence, or rarely a panicle composed of few-flowered cincinni. Flowers actinomorphic or zygomorphic, variously colored. Flower tube urceolate or cylindric or obconical, sometimes more or less 2-chambered, sometimes bent in the middle. Tepals 6, free or the inner ones connate into a miter. Stamens 6 or rarely 3, inserted opposite the tepals, pendent or reflexed (*Oxygyne*), thecae dehiscing longitudinally to the abaxial side or latrorse (*Tiputinia*). Ovary inferior, 1-locular with 3 parietal placentae, septal nectaries absent; ovules numerous; style short and thick, sometimes with 3 stigmatic branches or stigma capitate or funnelform. Fruit fleshy and cup-shaped, or a dry capsule (*Haplothismia*). Seeds numerous, dustlike.

Number of genera and species—Thismiaceae comprise five genera and ca. 63 species. All species have a fully mycoheterotrophic mode of life. The largest genus is *Thismia*, with ca. 45 species. A remarkable common feature of most Thismiaceae is their extreme scarcity (Stone 1980; Maas et al. 1986; Franke 2004). The majority of species are known exclusively from the type collection, which in some cases was made more than a century ago (Stone 1980; Maas et al. 1986).

Distribution and habitat—Thismiaceae are widely distributed in the tropical regions of the world, but some species are known from subtropical and even temperate areas (Jonker 1938). The genus *Oxygyne* and several species of *Thismia* have disjunct distribution patterns (Stone 1980; Maas et al. 1986; Abe and Akasawa 1989). Most species occur in the leaf litter of dense tropical rainforest and can only be spotted during the flowering and fruiting period when aboveground organs appear (Maas et al. 1986; Franke 2007).

Classification—Not surprisingly, due to the strong reduction of vegetative organs and the rarity of most species involved, Thismiaceae taxonomy has been the subject of much debate. Most classifications included Thismiaceae, as a subtribe "Thismieae," in a broadly defined Burmanniaceae (Miers 1847; Schlechter 1921; Jonker 1938; Maas et al. 1986; Maas-van de Kamer 1998; Caddick et al. 2002b; APG 2009) while other authors favored the recognition of a separate family of Thismiaceae closely related to the mycoheterotrophic Burmanniaceae (Hutchinson 1934, 1959; Dahlgren et al. 1985; Takhtajan 1997; APG 1998). Thismiaceae or Burmanniaceae (including Thismieae) on their part were linked to various other families, including other mycoheterotrophic groups such as Triuridaceae, Geosiridaceae, Corsiaceae, and Orchidaceae (see Maas et al. 1986 for an overview). However, these relationships are now completely discredited based on convergence of character states involved, due to the mycoheterotrophic mode of life (Soltis et al. 2005). DNA-based phylogenetic analyses place Thismiaceae in Dioscoreales (Caddick et al. 2000b; Caddick et al. 2002a; Davis et al. 2004), but outside Burmanniaceae (Merckx et al. 2006, 2009). Nuclear and mitochondrial DNA data suggest that Thismiaceae are paraphyletic, due to the inclusion of *Tacca* (Merckx et al. 2009).

Evolutionary history—The paraphyletic status of Thismiaceae suggests that a mycoheterotrophic mode of life has evolved independently in *Afrothismia* and in the common ancestor of the remaining Thismiaceae (Merckx et al. 2009). Thismiaceae are absent from the fossil record but according to molecular clock estimates both lineages originated during the Cretaceous (Merckx et al. 2010a).

Ecology—Thismiaceae are poorly known ecologically. The mycorrhizal fungi of several species of *Afrothismia* and a single species of *Thismia* have been identified as arbuscular mycorrhizal fungi belonging to the *Glomus* Group A clade (Franke et al. 2006; Merckx and Bidartondo 2008; Merckx et al. 2012). Pollination has not been studied in detail, but the colorful, variously shaped flowers of most Thismiaceae, and the presence of glandular tissue in the flowers of some *Thismia* species indicate insect pollination (Vogel 1962; Stone 1980; Maas et al. 1986). The particular floral morphology and odor of *Tiputinia* points to sapromyophily (Woodward et al. 2007). The close proximity of the anthers and the stigma in some *Thismia* species suggests self-pollination. The seeds may be dispersed by wind or water (Stone 1980; Maas et al. 1986).

2.5.3.1 *Afrothismia* (Figs. 2.5h, 2.7f, 4.2, 4.3, and 4.4)

Afrothismia Schltr., Bot. Jahrb. Syst. 38: 138 (1906).

Herbs up to 10 cm tall. Rhizome cylindric with clusters of root tubercles, each ending in a terminal rootlet. Stems usually unbranched. Inflorescence a few-flowered cincinnus. Flowers zygomorphic, often with red and yellow pigmentation. Flower tube urceolate to cylindric, 2-chambered and bent in the middle, with an internal flange at the middle and an annulus in the throat. Tepals 6, free, equal or unequal in size. Stamens 6, inserted in the basal part of the flower tube, reflexed; anthers with connective connivent with stigma. Ovary with 3 parietal placentas basally fused into a sterile central column; style with a funnel-shaped stigma. After flowering the perianth and ovary wall soon falling off, only the placentas with the seeds remaining on top of the lengthened sterile central column. Seeds ellipsoid.

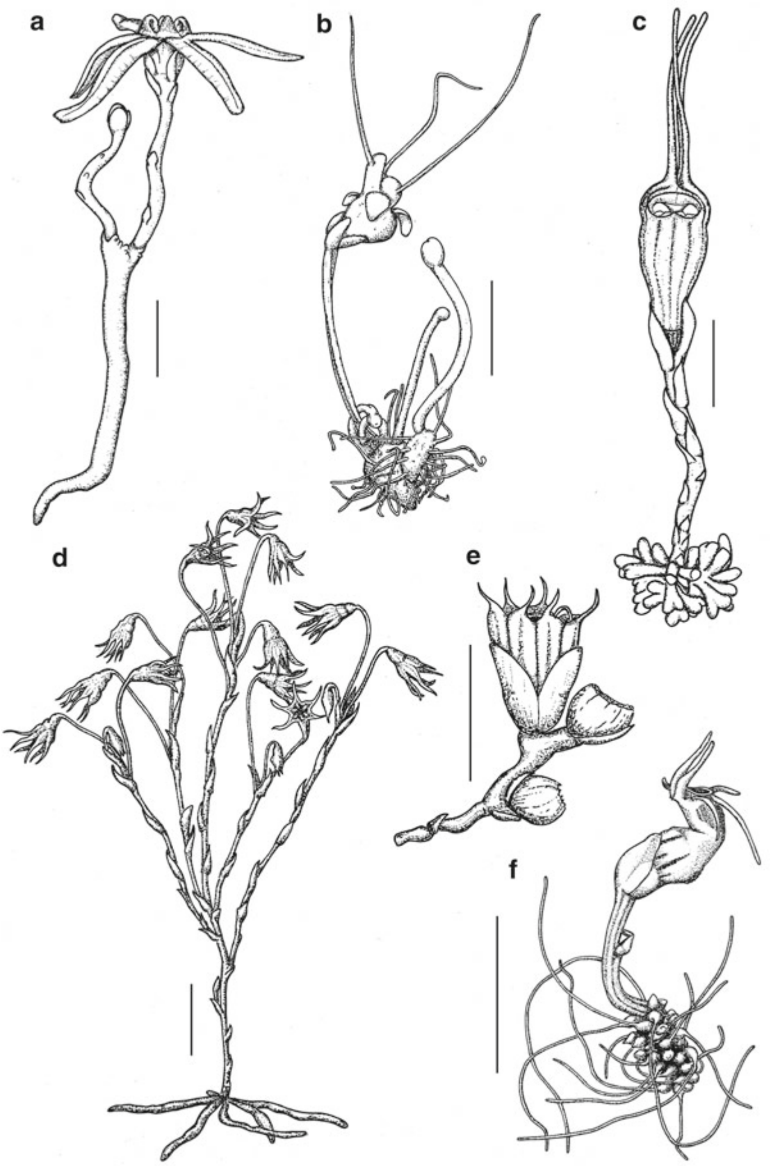

Fig. 2.7 Thismiaceae. (**a**) *Tiputinia foetida*. Redrawn from Woodward et al. (2007). (**b**) *Thismia saülensis*. Redrawn from Maas and Maas (1987). (**c**) *Thismia clavigera*. Redrawn from Chantanaorrapint and Chantanaorrapint (2009). (**d**) *Haplothismia exannulata*. Redrawn from Airy Shaw (1952). (**e**) *Oxygyne hyodoi*. Redrawn from Abe and Akasawa (1989). (**f**) *Afrothismia hydra*. Redrawn from Sainge and Franke (2005). Bar = 1 cm

Currently 12 species of *Afrothismia* are known from tropical Africa, with records from Cameroon, Gabon, Nigeria, Uganda, Malawi, Kenya, and Tanzania (Schlechter 1906; Cowley 1988; Cheek 2003a, 2007, 2009; Maas-van de Kamer 2003; Franke 2004; Franke et al. 2004; Cheek and Jannerup 2005; Sainge and Franke 2005; Sainge et al. 2005; Dauby et al. 2007). Although a few more species from West Africa are awaiting description (Sainge Moses, pers. comm.). The Guineo-Congolian rainforest in southwestern Cameroon is the main center of diversity of the genus (Franke 2007). All species grow exclusively in evergreen rainforest. Species of *Afrothismia* are often found growing with other mycoheterotrophs (Schlechter 1906; Cheek 2003b; Cheek et al. 2003; Sainge et al. 2005). Some species were collected once or are only known from a single locality. The only collection of *A. pachyantha* was made on Mount Cameroon in 1905 by Rudolf Schlechter (Schlechter 1906) and this species is possibly extinct since the type locality has been destroyed by human activity (Franke et al. 2004).

Afrothismia species form very complex mycorrhizas (Imhof 1999a, 2006) with highly specific *Glomus* Group A fungi (Franke et al. 2006; Merckx and Bidartondo 2008). The floral structure of *Afrothismia* species suggests cross-pollination by insects. But there exist only few observations of flower-visiting insects in *Afrothismia*. Engler (1905) mentioned small dipterans he found in the lower part of the perianth tube of *A. winkleri*. Cheek and Williams (1999) reported two dipterans of the same species that left the perianth tube of *A. pachyantha* after a stay of several seconds. Franke (2004) observed a drosophilid fly, which carefully inspected the tepals of an *Afrothismia* flower for several minutes. All these observations strongly suggest myophily. Dispersal agents are unknown.

2.5.3.2 *Thismia* (Figs. 2.5f, 2.7b, c, and 4.10j)

Thismia Griff., Proc. Linn. Soc. London 1: 221 (1845).
Ophiomeris Miers, Proc. Linn. Soc. London 1: 328 (1847).
Sarcosiphon Blume, Mus. Bot. 1: 65 (1850).
Tribrachys Champ. ex Thwaites, Enum. Pl. Zeyl.: 325 (1864)
Myostoma Miers, Trans. Linn. Soc. London 25: 474 (1866).
Bagnisia Becc., Malesia 1: 249 (1878).
Geomitra Becc., Malesia 1: 250 (1878).
Triscyphus Taub., Verh. Bot. Vereins Prov. Brandenburg 36: 66 (1895).
Glaziocharis Taub. ex Warm., Overs. Kongel. Danske Vidensk. Selsk. Forh. Medlemmers Arbeiter 1901: 175 (1902).
Scaphiophora Schltr., Notizbl. Bot. Gart. Berlin-Dahlem 8: 39 (1921).
Mamorea de la Sota, Darwiniana 12: 43 (1960).

Herbs up to 10 cm tall. Underground part tuberous, or creeping cylindrical roots, or a cluster of short hyaline roots. Stems unbranched with few scale-like leaves. Flowers solitary, or rarely in a few-flowered cincinnus, actinomorphic or zygomorphic, variously colored. Flower tube cylindric to urceolate, soon falling off, throat circular, surrounded by an annulus. Tepals 6, often unequal in size, in 2 distinct whorls, the inner whorl sometimes connate forming a miter. Stamens 6, inserted in the throat of the flower tube, pendent, occasionally alternating with interstaminal lobes; connective often with appendages or hairs, connate into a tube with thecae separated, or connective free and thecae united. Ovary with 3 parietal placentas or with 3 free placental columns. Style 3-branched or capitate. Fruit fleshy, cup-shaped. Seeds ellipsoid to ovoid.

Thismia comprises ca. 45 species. The majority of species is known from tropical America and Asia, but some species from Asia extend into the subtropics (southern Japan, Australia, and New Zealand; Thiele and Jordan 2002; Yang et al. 2002) and temperate zones (*T. rodwayi* in Tasmania, Roberts et al. 2003; Wapstra et al. 2005). *Thismia* species are generally known to grow in evergreen forests. A notable exception is *T. americana*. This species was discovered in August 1912 near Chicago (Illinois, USA) in a prairie (Pfeiffer 1914). The population was observed for several subsequent summers, and was probably last seen in 1916. Because the type locality has been destroyed and several intensive searches in the area have failed to rediscover the plant, it is now considered extinct (Lewis 2002). Based on morphological similarities it has been suggested that the closest relative of *T. americana* is *T. rodwayi* from Australia and New Zealand (Jonker 1938; Maas et al. 1986; but see Thiele and Jordan 2002), and thus makes it part of one of the most anomalous disjunction distributions known in flowering plants (Thorne 1972). Phylogenetic analyses based on nuclear and mitochondrial DNA data with a limited *Thismia* sampling suggests that the genus is paraphyletic, but a better sampling is required to investigate the taxonomic status of the genus (Merckx et al. 2006, 2009).

Morphological observations suggest that species of *Thismia* are growing with arbuscular mycorrhizal fungi (Groom 1895; Janse 1897; Pfeiffer 1914; McLennan 1958; Campbell 1968). Indeed, *Glomus* group A fungi were detected in roots of *Thismia rodwayi* (Merckx et al. 2012). Pollination biology was never studied in detail, but both cross-pollination and self-pollination have been hypothesized to occur in *Thismia*. Many species have strongly colored flowers, and tentacle-like tepal tips, which may show the way to enter the flower (Maas et al. 1986). The tips of the tepals, and the base of the perianth of several *Thismia* species are provided with glandular swellings, presumably functioning as osmophores (Vogel 1962). Glandular structures are also present on the anthers of some species (Thiele and Jordan 2002). The stamens of *Thismia* tend to form a funnel or even a connate tube, possibly to guide pollinators down to the stigma, and the flowers often have trap-like structures (Maas et al. 1986; Thiele and Jordan 2002). Moreover, pendent stamens opening towards the wall of the perianth make self-pollination difficult (Maas et al. 1986). *Thismia* flowers generally produce little odor, but Wapstra et al. (2005) reported an odor of rotten fish after boxing the flowers of *T. rodwayi* for a few hours. Miers (1866) reported that the flowers of *T. hyalina* never open and are therefore self-pollinating. Seed dispersal agents are not known, but it is often hypothesized that the dust-like seeds are dispersed by wind or rain-splash (Stone 1980; Maas et al. 1986). It is also possible that the fruits are eaten by birds or mammals (Maas-van de Kamer 1998; Wapstra et al. 2005).

2.5.3.3 *Tiputinia* (Fig. 2.7a)

Tiputinia P.E. Berry & C. Woodw., Taxon 56: 157 (2007).

Herbs, ca. 2 cm tall. Rhizome vertical, cylindric, sympodially branched. Stems unbranched. Flowers solitary, actinomorphic. Flower tube short, obconical. Tepals 6, free, equal in size, olive yellow. Stamens 6, inserted in the throat of the flower tube, alternating with tiny subglobose interstaminal lobes; filaments orange, thick, ascending and then recurved, forming a cage or dome over the throat, orange, with fimbriate appendages; thecae latrorsely dehiscent. Ovary with 3 parietal placentas; style with pyramidal stigma. Fruit and seeds unknown.

Monospecific genus only known from Amazonian Ecuador. Description based on a single specimen of *T. foetida* collected in April 2005 in evergreen forest at the Tiputini Biodiversity Station. Also recorded in Yasuní National Park (A. J. Perez Castañeda pers. comm.). The flowers of *T. foetida* produce a foul, rotten fish-like odor, presumably to attract pollinators (Woodward et al. 2007). Dispersal agents and mycorrhizal fungi unknown.

2.5.3.4 *Haplothismia* (Fig. 2.7d)

Haplothismia Airy Shaw, Kew Bull. 2: 277 (1952).

Herbs, 10–25 cm tall. Underground part a cluster of vermiform tuberous roots. Stems unbranched or branched. Inflorescence a panicle composed of few-flowered cincinni. Flowers nodding, pale brown. Perianth persistent. Flower tube campanulate to funnel-shaped. Tepals 6, free, equal in size. Stamens 6, inserted in the throat of the floral tube, alternating with minute interstaminal lobes; filaments adnate to the flower tube, apical part free and recurved. Ovary with 3 parietal placentas; style with 3-lobed stigma. Fruit a loculidical capsule. Seeds ellipsoid.

Haplothismia is a monospecific genus from India. *H. exannulata* was discovered by A. Abraham and K. C. Jacob in the Western Ghats in 1951 (Airy Shaw 1952). The species was rediscovered at the type locality in 1999 (Sasidharan and Sujanapal 2000). *H. exannulata* is currently known from only two populations in Parabikulam Wildlife Sanctuary, where it occurs in humus rich soil in evergreen rainforest at about 700 m altitude. Flowering and fruiting in October (Sasidharan and Sujanapal 2000). Pollination syndrome, dispersal agents, and mycorrhizal fungi unkown.

2.5.3.5 *Oxygyne* (Fig. 2.7e)

Oxygyne Schltr., Bot. Jahrb. Syst. 38: 140 (1906).
Saionia Hatus., J. Geobot. 24: 2 (1976).

Herbs up to 4 cm tall. Underground part a cluster of vermiform roots. Stems unbranched. Inflorescence a few-flowered cincinnus or reduced to a single terminal flower. Flowers actinomorphic, brown with orange or blue-green, tube funnel-shaped with a well-developed annulus in the throat, upper part of the perianth soon falling off. Tepals 6, free, equal in size. Stamens

3, recurved, inserted opposite and enclosed in the base of the inner tepals, interstaminal lobes absent. Ovary with 3 parietal placentas; style 3-branched. Fruit cup-shaped. Seeds unknown.

Oxygyne is a very rare cryptic genus with a remarkable disjunct distribution. Species of *Oxygyne* differ from other Thismiaceae species by having 3 instead of 6 stamens. The first specimen of *Oxygyne* (*O. triandra*) was discovered by Rudolf Schlechter on Mount Cameroon in September 1905 (Schlechter 1906). A second African species of *Oxygyne* was collected on Mount Etinde, but remains to be described (Cheek et al. 2006). The herbarium specimen *Tisserant 2623* (BM) collected in the Central African Republic probably belongs to *Oxygyne* as well. Other *Oxygyne* species occur in southern Japan, on the islands Shikoku, Okinawa, and Yakushima (*O. hyodoi*, *O. shinzatoi*, and *O. yamashitae*) (Hatusima 1976; Abe and Akasawa 1989; Yahara and Tsukaya 2008). A revision of this genus is required to confirm the relationship between the African and Japanese specimens.

Oxygyne triandra was collected in tropical forest growing with *Afrothismia winkleri*, *A. pachyantha* (Thismiaceae), and *Burmannia hexaptera* (Burmanniaceae) (Schlechter 1906, 1921). The type locality is almost certainly destroyed by human activity and therefore this species might be extinct (Franke et al. 2004). The Japanese species were all collected in evergreen forest and flowered in September and October (Hatusima 1976; Abe and Akasawa 1989; Yahara and Tsukaya 2008; Yokoyama et al. 2008). *O. hyodoi* was found growing together with the mycoheterotrophic plant *Burmannia liukiuensis* (now *B. nepalensis* (Burmanniaceae)) (Abe and Akasawa 1989). Ants and mites were observed visiting the flowers of *O. yamashitae* but did not transfer pollen (Yahara and Tsukaya 2008). Dispersal agents and mycorrhizal fungi unkown.

2.5.4 Triuridaceae

Triuridaceae Gardn., Proc. Linn. Soc. London 19: 160 (1843).
Lacandoniaceae E. Martínez & Ramos, Ann. Missouri Bot. Gard. 76: 128 (1989).

Mycoheterotrophic, dioecious or monoecious herbs, completely white, yellow, purple, brown, or red. Rhizome mostly well-developed, horizontally creeping to vertical, with many scale-like leaves; roots filiform, tuberous, and radiating from the base of the stem, or very rarely coral-shaped, with or without root hairs. Stems mostly unbranched, erect, or decumbent at the base. Leaves few, alternate, sessile, entire, small, and scale-like. Inflorescence a terminal, bracteate few- to many-flowered raceme or spike, in monoecious plants staminate flowers at the top and pistillate flowers at the base of the inflorescence. Flowers unisexual or rarely bisexual (*Lacandonia*, *Sciaphila*), actinomorphic or rarely bilaterally symmetrical (e.g., *Kupea*), white, yellow, purplish, red, or dark brown to black. Tepals 3–10, valvate, equal or rarely unequal, basally connate, often soon reflexed, inner side often densely papillate, apex sometimes with dense tufts of hairs (bearded) or globose knobs or appendages or caudate (with tails to 50 mm long). Bisexual flowers with 2–6 free stamens and ∞ free carpels; staminate flowers with 2–6(-8) stamens, mostly epitepalous (opposite the outer or inner tepals), free or basally connate, sometimes inserted on a central androphore (*Triuris*); anthers 4-locular or sometimes 2- or 3-locular (in *Triuris* and *Sciaphila* respectively), dithecic or rarely monothecic, sessile or filamented, anther dehiscence longitudinal to transversely extrorse or rarely introrse (*Lacandonia*, *Triuris*), staminodes sometimes present (*Seychellaria*); gynoecium rudiments rarely present (*Triuridopsis*). Pollen inaperturate with characteristic spiny-gemmate surface sculpturing. Pistillate flowers with 10-∞ free carpels inserted on the receptacle. Carpels 1-locular with 1 (or 2 in Kupeaeae) basal, anatropous ovule(s), apical part of carpel often papillate, style 1 per carpel, filiform, persistent, basal to lateral or terminal, stigmatic zone papillate, penicillate, or indistinct. Fruit consisting of indehiscent achenes or follicles dehiscent by a longitudinal slit. Seeds 1 (or 2) per carpel, globose to obovoid, small.

Numbers of genera and species—Triuridaceae comprise approximately 50 species in 11 genera and three tribes. With ca. 30 species, *Sciaphila* is the most species-rich genus, other genera include only a few species each. All species of Triuridaceae are fully mycoheterotrophic.

Distribution and habitat—Triuridaceae occur throughout the tropical parts of the Old and the New World and reach the subtropics in Japan. *Sciaphila* has a pantropical distribution, all other genera are confined to one continent. Triuridaceae generally grow in dense and humid forests, between leaf litter, at the base of large trees or along the bank of streams. Less frequently, they are found in temporarily inundated forests, forests on white sand, bamboo thickets, or on termite nests (*Sciaphila purpurea*, *S. arfakiana*). They often grow in close association with other mycoheterotrophic plants of various families (Maas and Rübsamen 1986; Maas-van de Kamer and Weustenfeld 1998).

Classification—Despite recent advances, the close affinities of Triuridaceae remain under dispute. Prior to molecular analyses, Triuridaceae were often linked with other mycoheterotrophs such as Petrosaviaceae and included in Triuridanae (Takhtajan 1997) or Triuridales (Cronquist 1981; Thorne 1992). Molecular phylogenetic analyses placed Triuridaceae with four other families (Cyclanthaceae, Pandanaceae, Stemonaceae, Velloziaceae) in a recircumscribed Pandanales (Chase et al. 2000, 2006; Davis et al. 2004), but its exact position within the order remains to be determined (e.g., Rudall and Bateman 2006). Based on morphological and embryological differences three distinct tribes within Triuridaceae are recognized: Kupeaeae, Sciaphileae, and Triurideae (Cheek 2003b).

Evolutionary history—Based on a robust morphological analysis, Rudall and Bateman (2006) postulated that the family is closely related to (perhaps embedded in) Stemonaceae (including the anomalous Sumatran genus *Pentastemona*); this hypothesis has yet to be tested in a comprehensive molecular analysis. Gandolfo et al. (1998, 2002) reported a series of fossil flowers from the Late Cretaceous (ca. 90 Ma) that show similarities with extant Triuridaceae. A cladistic analysis of 20 morphological characters placed the fossil flower genera *Mabelia* and *Nuhliantha* within Triuridaceae, with affinities to modern Triurideae. Since no vegetative parts were attached to these fossil flowers, it is impossible to determine whether the plants were mycoheterotrophic. Their affinities with extant Triuridaceae remain under debate; the fossil pollen is monosulcate with foveolate exine (Gandolfo et al. 2002), in contrast with the inaperturate spiny-gemmate pollen that characterizes all extant Triuridaceae (Furness et al. 2002; Furness and Rudall 2006; Rudall et al. 2007).

Ecology—The pollination biology of Triuridaceae remains elusive. Floral morphology strongly suggests insect pollination. The family includes protogynous plants, and unisexual flowers, flowers emitting odor and flowers with papillate tepals provided with glandular areas, hairs, or appendages (Maas-van de Kamer 1995; Maas-van de Kamer and Weustenfeld 1998; Rudall 2003, 2008). The morphology and epidermal anatomy of these filamentous structures indicate that they function as osmophores, at least in some species (Rudall 2003). Filamentous osmophores are highly characteristic of sapromyophilous mycoheterotrophs, which need to attract pollinators to otherwise inconspicuous flowers (Vogel 1990). Momose et al. (1998) reported that the flowers of *Sciaphila secundiflora* are pollinated by Calliphoridae flies. However, Márquez-Gúzman et al. (1993) described preanthetic cleistogamy in the bisexual flowers of *Lacandonia*, which are proterandrous. Seed dispersal mechanisms may include zoochory, anemochory, and hydrochory (Maas-van de Kamer 1995; Maas-van de Kamer and Weustenfeld 1998). Some seeds are reported to have a reticulate outer layer (*Lacandonia*, *Sciaphila*, *Soridium*). Root anatomical investigations show that the roots of Triuridaceae are colonized by arbuscular mycorrhizal fungi (Janse 1897; Imhof 1998, 2003, 2004; Yamato 2001). With molecular methods AM fungi were detected in the roots of *Kupea martinetugei*, *Sciaphila ledermannii*, *S. japonica*, and *S. tosaensis* (Yamato 2001; Franke et al. 2006; Merckx and Bidartondo 2008; Yamato et al. 2011a; Merckx et al. 2012).

Tribe KUPEAEAE Cheek
Plants dioecious; flowers unisexual, tepals 4, stamens 4, style terminal, fruit indehiscent, 2-seeded, bilaterally symmetrical. Two genera in tropical Africa.

2.5.4.1 *Kupea* (Figs. 2.5c, 2.8a, b, and 4.10d, e)

Kupea Cheek & S.A. Williams, Kew Bull. 58: 225 (2003).

Mycoheterotrophic, dioecious herbs, up to 10 cm tall. Rhizome horizontally creeping with 5–7 tuberous, hairy roots, radiating from the stem base. Stems usually unbranched. Leaves scale-like. Inflorescence a 20–70-flowered spike; bracts elliptic or absent. Flowers unisexual, pale yellow. Staminate flowers bilaterally symmetrical with 4 strongly unequal patent tepals, upper 3 (narrowly) elliptic, lower one much larger. Stamens 4; anthers 2-locular. Pistillate flowers radially symmetrical with 4 subequal, patent tepals and 25–60 carpels; ovary 1-locular, ovules 2, style terminal, stigmatic zone indistinct. Fruit a 2-seeded, bilaterally symmetric indehiscent achene. Seeds (1-)2 per carpel.

The genus *Kupea* consists of two species. *Kupea martinetugei* is known from several sites in Southwest Province, Cameroon (Mount Kupe and Mount Cameroon) (Cheek et al. 2003; Franke et al. 2004, 2006) and was also collected at sites in the East Province of Cameroon, near Yokadouma (Sainge 1509, 1621, 1624, YA). *Kupea jonii* is only known from the type locality in Kihansi Gorge in Tanzania, where it occurs with *Kihansia lovettii* (Triuridaceae) and *Afrothismia saingei* (Thismiaceae) in evergreen forest (Cheek 2003b; Maas and Maas-van de Kamer 2010). *Kupea martinetugei* associates with arbuscular mycorrhizal fungi from the *Glomus* Group A clade (Franke et al. 2006; Merckx and Bidartondo 2008). *Kupea* possesses two ovules per carpel, in contrast to the single ovule per locule present in all other Triuridaceae except *Kihansia* (Cheek 2003b; Rudall et al. 2007). *Kupea* is also relatively unusual in that the male flowers are zygomorphic and possess a labellum (Rudall et al. 2007). Pollination biology and seed dispersal mechanisms remain to be studied.

2.5.4.2 *Kihansia* (Fig. 2.8g, h)

Kihansia Cheek, Kew Bull. 58: 943 (2003).

Mycoheterotrophic, dioecious herbs, up to 10 cm tall. Rhizome unknown, with 7–12, tuberous, glabrous roots, radiating from the stem base. Stems usually unbranched. Leaves scale-like. Inflorescence a 2–13-flowered spike; rachis with apical sterile part; bracts dimorphic: fertile ones elliptic-rectangular; sterile ones linear. Flowers unisexual, dark brown to black. Tepals 4. Staminate flowers bilaterally symmetrical, perianth flat apart from the central androecial cavity, upper 3 lobes subequal, triangular, the lower lobe about twice as long as the others; anthers white, 2-locular. Pistillate flowers with 4 subequal, patent tepals and 80–100 carpels; ovary 1-locular, ovules 2, style terminal, stigmatic zone indistinct. Fruit a 2-seeded, bilaterally symmetrical, indehiscent achene.

Kihansia includes a single species, *K. lovettii*, known only from the type locality in the Kihansi Gorge in Tanzania. The type locality consists of evergreen tropical forest at an altitude of 720 m. Two other mycoheterotrophs, *Kupea jonii* (Triuridaceae) and *Afrothismia saingei* (Thismiaceae) were found at the same site (Cheek 2003b; Maas and Maas-van de Kamer 2010). Two collections of a presumably new, yet undescribed, *Kihansia* species have been made in southeastern Cameroon in 2005 and 2006 (Thomas and Chuyong 2006). Information about the biology of *Kihansia* is lacking.

Tribe SCIAPHILEAE Miers
Plants monoecious; flowers unisexual, rarely bisexual (*Sciaphila*); tepals 4, 6, or 8; stamens 2–4, or 6; tepals bearded, papillate or with an apical globose knob; style lateral to basal; fruit dehiscent (except *Soridium*). Five genera. Neotropics and Paleotropics.

2.5.4.3 *Seychellaria* (Figs. 2.8c and 4.10a)

Seychellaria Hemsl., Ann. Bot. (London) 21: 74 (1907).

Mycoheterotrophic, monoecious herbs, up to 20 cm tall. Rhizomes horizontally creeping with filiform, hairy roots. Stems unbranched. Leaves

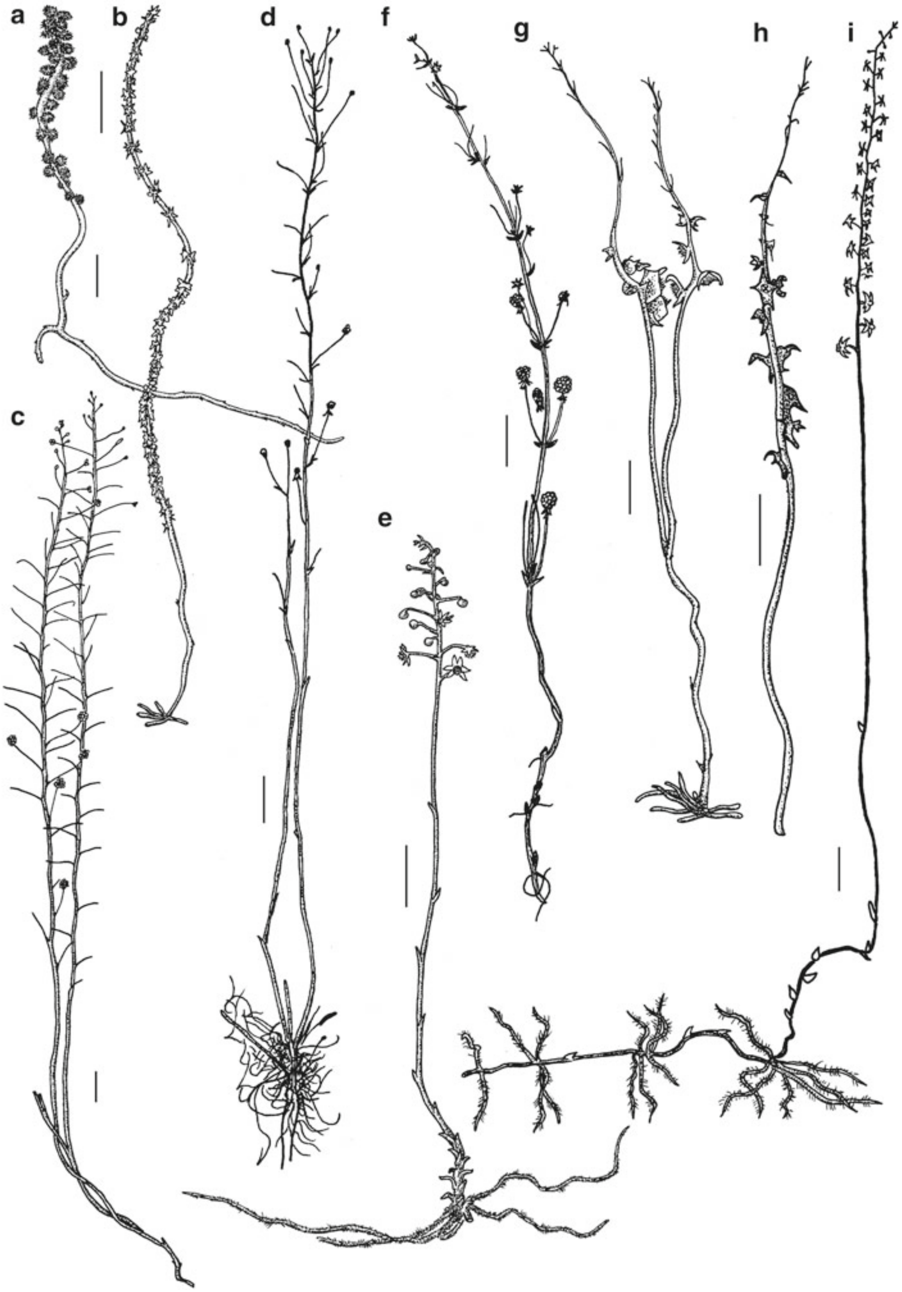

Fig. 2.8 Triuridaceae; Kupeae and Sciaphileae. *Kupea martinetugei*: (**a**) female plant, (**b**) male plant. Redrawn from Cheek et al. (2003). (**c**) *Seychellaria africana*. Redrawn from Vollesen (1982). (**d**) *Andruris australasica*. Redrawn from Giesen (1938). (**e**) *Sciaphila albescens*. Redrawn from Maas and Rübsamen (1986). (**f**) *Hyalisma janthina*. Redrawn from Giesen (1938). *Kihansia lovettii*: (**g**) female plant, (**h**) male inflorescence. Redrawn from Cheek (2003a, b). (**i**) *Soridium spruceanum*. Redrawn from Maas and Rübsamen (1986). Bar = 1 cm

scale-like. Inflorescence an up to 50-flowered raceme, sometimes with 2 flowers per node. Flowers unisexual, whitish, or reddish. Tepals 6, unequal. Staminate flowers with 3 stamens opposite the 3 larger tepals, alternating with 3 staminodes, sometimes connective provided with a long appendage; anthers 4-locular. Pistillate flowers with ∞ carpels; ovary 1-locular, ovule 1, style lateral, stigmatic zone indistinct. Fruit a dehiscent follicle.

Three species of *Seychellaria* are known: *S. madagascariensis* (Madagascar and the Comores) (including *S. perrieri*), *S. thomassettii* (the Seychelles), and *S. africana* (Iringa region in Tanzania). All species occur in rainforest. *Seychellaria* differs from *Sciaphila* mainly by the presence of staminodes in the staminate flowers (Giesen 1938; Perrier de la Bathie 1946; Vollesen 1982), and both genera are probably closely related (Rudall and Bateman 2006). Data on pollination biology, seed dispersal, and mycorrhizae are lacking.

2.5.4.4 *Sciaphila* (Figs. 2.8e, 4.8i, and 4.9a–c)

Sciaphila Blume, Bijdr. Fl. Ned. Ind. 514 (1825).
Aphyleia Champ., Calcutta J. Nat. Hist. 7: 468 (1847).
Lilicella Rich. ex Baill., Bull. Mens. Soc. Linn. Paris 2: 1188 (1895).

Mycoheterotrophic, monoecious herbs, up to 30, very rarely to 150 cm tall (*S. purpurea*). Rhizomes mostly horizontally creeping, with filiform or rarely coral-shaped, hairy to glabrous roots. Stems unbranched or sometimes branched. Leaves scale-like. Inflorescence a 7–55-flowered raceme, sometimes basally branched. Flowers unisexual, sometimes bisexual, whitish, pink, purplish, or red. Tepals (4-)6–8(-10), equal or unequal, inner side papillate, apex sometimes bearded. Staminate flowers with 2–3 or 6 stamens; anthers 3–4-locular. Pistillate flowers with ∞ carpels; carpels 1-locular, ovule 1, style (sub) basal to lateral, stigmatic zone papillate or penicillate or indistinct. Fruit a dehiscent follicle.

Sciaphila comprises ca. 29 species. Seven species occur in the Neotropics, two species are known from tropical West Africa, and 19 species occur in tropical Asia (including Japan, New Caledonia, Fiji, India and Sri Lanka) (van de Meerendonk 1984; Maas and Rübsamen 1986; Cheek 2006). The fungal associates of *S. japonica*, *S. ledermannii*, and *S. tosaensis* have been identified as glomeromycetes belonging to *Glomus* Group A and Acaulosporaceae (Yamato 2001; Franke et al. 2006; Merckx and Bidartondo 2008; Yamato et al. 2011a; Merckx et al. 2012). There is only a single report on the pollination biology of *Sciaphila*, which states that the flowers of *Sciaphila secundiflora* are pollinated by Calliphoridae flies (Momose et al. 1998). Seed dispersal mechanisms in *Sciaphila* remain unstudied.

2.5.4.5 *Hyalisma* (2.8f)

Hyalisma Champ., Calcutta J. Nat. Hist. 7: 466 (1847).

Mycoheterotrophic, monoecious herbs, up to 20 cm tall. Rhizomes unknown, roots filiform radiating from the base of the stem mostly horizontally creeping, with filiform, hairy to glabrous roots. Stems unbranched or sometimes branched. Leaves scale-like. Inflorescence an up to 20-flowered raceme, sometimes basally branched, with several flowers per node. Flowers unisexual, purplish. Tepals 8, equal. Staminate flowers with 4 stamens; anthers 4-locular. Pistillate flowers with ∞ carpels; ovary 1-locular, ovule 1, style (sub)basal to lateral, stigmatic zone indistinct. Fruit a dehiscent follicle.

Hyalisma comprises a single species, *H. janthina*, from south India and Sri Lanka. Mycorrhiza, pollination, and seed dispersal mechanisms remain unstudied (Maas-van de Kamer and Weustenfeld 1998).

2.5.4.6 *Andruris* (Fig. 2.8d)

Andruris Schltr., Bot. Jahrb. Syst. 49: 71 (1912).
Parexuris Nakai & F. Maek., Iconogr. Pl. Asiae Orient. 1: 23 (1936), partly.

Mycoheterotrophic, monoecious herbs, up to 25 cm tall. Rhizomes mostly horizontally creeping, with filiform, hairy to glabrous roots. Stems unbranched or sometimes branched. Leaves scale-like. Inflorescence a 5–50-flowered raceme, sometimes basally branched. Flowers unisexual, whitish, pink, purplish, or red. Tepals (4-)6, unequal, apex sometimes with terminal knobs. Staminate flowers with 3 stamens opposite the larger tepals; anthers 4-locular, connectives with a long subulate appendage. Pistillate flowers with ∞ carpels; ovary 1-locular, ovule 1, style (sub) basal to lateral, stigmatic zone indistinct. Fruit a dehiscent follicle.

Andruris comprises five species from Malesia, Polynesia, Micronesia, eastern India, southern Japan and northeastern Australia. Mycorrhiza, pollination, and seed dispersal mechanisms in *Andruris* remain unstudied (Maas-van de Kamer and Weustenfeld 1998).

2.5.4.7 *Soridium* (Fig. 2.8i)

Soridium Miers, Proc. Linn. Soc. London 2: 74 (1850).

Mycoheterotrophic, monoecious herbs, up to 30 cm tall. Rhizomes horizontally creeping, with filiform, hairy roots. Stems unbranched. Leaves scale-like. Inflorescence a 10–50-flowered raceme. Flowers unisexual, white. Tepals 4, inner side papillate. Staminate flowers with 2(-3) stamens; anthers 2-locular. Pistillate flowers with 25–40 carpels; carpels 1-locular, ovule 1, style lateral, stigmatic zone penicillate. Fruit an indehiscent achene.

Soridium consists of a single species, *S. spruceanum*. The genus is confined to Central America and northern South America (Maas and Rübsamen 1986). Observations about the mycorrhizal fungi, pollination biology, and seed dispersal are lacking.

TRIURIDEAE Miers
Plants dioecious, flowers unisexual, rarely bisexual (*Lacandonia*); tepals 3 or 6; stamens 3 or 6; tepals caudate or appendaged (*Triuridopsis*); style (sub)terminal or lateral (*Peltophyllum*); fruit indehiscent. Four genera in the Neotropics.

2.5.4.8 *Peltophyllum* (Fig. 2.9a, b)

Peltophyllum Gardn., Proc. Linn. Soc. London 1: 176 (1843).
Hexuris Miers, Proc. Linn. Soc. London 2: 72 (1850).

Mycoheterotrophic, dioecious herbs, up to 10 cm tall. Rhizomes vertical with filiform, glabrous roots. Stems unbranched. Leaves scale-like. Inflorescence a 6–16-flowered raceme. Flowers unisexual, yellowish white. Tepals (3-)6(-8), horizontally patent, apex caudate. Staminate flowers with 3 stamens; anthers 4-locular. Pistillate flowers with ∞ carpels; carpels 1-locular, ovule 1, style lateral, stigmatic zone indistinct. Fruit an indehiscent achene.

Peltophyllum consists of two species: *P. luteum* and *P. caudatum*. The former occurs in southeastern Brazil, northern Argentina, and southern Paraguay, but also in Guyana, in evergreen forests. The latter species is known from a single collection from Alto Macahé, Rio de Janeiro, Brazil, where it was found in the shade of large trees near a river, growing in leaf mold (Maas and Rübsamen 1986). Mycorrhizal associates, pollination syndrome, and seed dispersal of *Peltophyllum* remain to be studied.

2.5.4.9 *Lacandonia* (Fig. 2.9g)

Lacandonia E. Martínez & Ramos, Ann. Missouri Bot. Gard. 76: 128 (1989).

Mycoheterotrophic dioecious herbs, up to 10 cm tall. Rhizome horizontally creeping, with filiform, hairy roots. Stems unbranched. Leaves scale-like. Inflorescence a 3–7(-13)-flowered raceme. Flowers bisexual, sometimes unisexual, whitish. Tepals (4-)6, inner side papillate, apex caudate. Stamens (2-)3(-4); anthers 2(-3) locular. Gynoecium composed of ∞ carpels surrounding the stamens; carpels 1-locular, ovule 1, style subterminal, stigmatic zone indistinct. Fruit an indehiscent achene.

Lacandonia includes two species. *Lacandonia schismatica* occurs in scattered populations in the Lacandon rainforest in Mexico at an elevation of about 200 m (Vergara-Silva et al. 2003). Recently, a second species of *Lacandonia*, *L. brasiliana*, was described from material collected in the Atlantic rainforest in Brazil (Melo and Alves 2012). Bisexual flowers of *Lacandonia* have stamens borne inside the carpels, a characteristic unique in angiosperms (Ambrose et al. 2006; Rudall 2008). Based on this feature the genus was originally placed in its own family, Lacandoniaceae (Martínez and Ramos 1989). The flowers of *L. schismatica* are cleistogamous (Márquez-Gúzman et al. 1993). Mycorrhiza, pollination, and seed dispersal remain unstudied.

Fig. 2.9 Triuridaceae; Triurideae. *Peltophyllum luteum*: (**a**) male plant, (**b**) female plant. Redrawn from Maas and Rübsamen (1986). *Triuridopsis intermedia*: (**c**) male plant, (**d**) female plant. Redrawn from Franke et al. (2000). *Triuris hyalina*: (**e**) male plant, (**f**) female plant. Redrawn from Maas and Rübsamen (1986). (**g**) *Lacandonia schismatica*. Redrawn from Martínez and Ramos (1989). Bar = 1 cm

2.5.4.10 *Triuridopsis* (Fig. 2.9c, d)

Triuridopsis H. Maas & Maas, Pl. Syst. Evol. 192: 257 (1994).

Mycoheterotrophic, dioecious herbs, up to 12 cm tall. Rhizomes horizontally creeping, each node provided with 2 filiform, glabrous roots. Stems unbranched. Leaves scale-like. Inflorescence a 1–12-flowered raceme. Flowers unisexual, white. Tepals 3(–4), with a subapical reflexed appendage. Staminate flowers with 3 stamens with bithecal, 4-locular anthers or 6 stamens with monothecal, 2-locular anthers; center of the (staminate) flowers provided with a subulate projection. Pistillate flowers with reflexed tepals and ∞ carpels; carpels 1-locular, ovule 1, style terminal, stigmatic zone indistinct. Fruit an indehiscent achene.

Triuridopsis consists of two species: *T. peruviana* from Iquitos, Loreto, Peru, and *T. intermedia* from La Paz, Bolivia (Maas-van de Kamer and Maas 1994; Franke et al. 2000). The genus is probably closely related to *Triuris* (Maas-van de Kamer and Maas 1994). Mycorrhizal associates, pollination syndrome, and seed dispersal of *Triuridopsis* remain to be studied.

2.5.4.11 *Triuris* (Figs. 2.9e, f, and 4.8b)

Triuris Miers, Proc. Linn. Soc. London 1: 96 (1841).

Mycoheterotrophic, dioecious herbs, up to 20 cm tall. Rhizomes vertical, with filiform, glabrous to hairy roots. Stems unbranched. Leaves scale-like. Inflorescence a 1–4-flowered raceme. Flowers unisexual, white to brown. Tepals 3, soon reflexed, apex long-caudate, the tails in bud rolled inwards like a watch spring. Staminate flowers with 3 stamens with 4-locular anthers alternating with the tepals or with 6 stamens with 2-locular anthers, androphore large, fleshy, conical to deltoid, the stamens inserted at its base. Pistillate flowers with ∞ carpels; ovary 1-locular, ovule 1, style terminal, stigmatic zone indistinct. Fruit an indehiscent achene.

Three species are known. *Triuris hyalina* is widespread from Central America (Guatemala) in the North to southeastern Brazil in the South. *Triuris hexophthalma* and *T. alata* Brade are only known from the type locality in the Pakaraima Mountains, Guyana, and in Itatiaia, Rio de Janeiro, Brazil, respectively (Brade 1943; Maas et al. 1986). Mycorrhizal associates, pollination syndrome, and seed dispersal of *Triuris* remain to be studied.

2.5.5 Corsiaceae

Corsiaceae Becc., Malesia 1: 238 (1878) as "1877."

Mycoheterotrophic herbs, up to 30 cm tall. Underground part a rhizome or a cluster of tuberous roots. Stems simple, erect. Leaves reduced to a few amplexicaul sheaths. Flowers terminal, solitary, bisexual or unisexual, zygomorphic. Tepals 6, in 2 whorls, outer median tepal ("labellum") much larger than the other ones, covering the reproductive parts of the flower, sometimes with a large, glandular, basal callus; other 5 tepals filiform. Stamens 6, in 2 whorls, filaments short, anthers 2-celled, dorsifixed, extrorsely dehiscing by longitudinal slits. Ovary inferior, 1-locular with 3 parietal placentas or 3-locular with 3 axile placentas, ovules numerous; style absent, stigmas 3, sessile and connate, or style(s) present and short, either 1 with a 3-lobed stigma or 3 each with a stigma; septal nectaries absent. Fruit a capsule, dehiscing by 3 valves. Seeds numerous, very small, winged, pendent.

Number of genera and species—Corsiaceae comprise three genera and 27 species. All species are fully mycoheterotrophic. The largest genus is *Corsia* (25 species).

Distribution and habitat—Corsiaceae have a remarkable disjunct distribution, occurring in tropical and subantarctic South America (*Arachnitis*), China (*Corsiopsis*), and tropical Australasia (*Corsia*).

Classification—Corsiaceae were formerly linked to or included in Burmanniaceae (Beccari 1878; Bentham 1883; Engler 1888; Hutchinson 1959; Dahlgren et al. 1985). Based on mitochondrial *atpA* sequence data *Arachnitis* is tentatively included in Liliales (Davis et al. 2004; Fay et al. 2006), a relationship that is supported by nuclear 18S rDNA data analysis (Chase et al. 2006). Neyland and Hennigan (2003), using partial sequences for 26S rDNA alone, suggested that Corsiaceae may be polyphyletic. In their analysis, *Corsia* was placed within Liliales, whereas *Arachnitis* was related to *Thismia* (Thismiaceae). Floral anatomy and pollen morphology suggest that *Corsia* is related to Campynemataceae (Liliales) or *Thismia* (Rudall and Eastman 2002).

Evolutionary history—Due to the uncertain systematic relationships the evolutionary history of Corsiaceae remains unclear.

Fig. 2.10 Corsiaceae. *Corsia pyramidata*: (**a**) habit, (**b**) flower. Redrawn from Cribb (1985). (**c**) *Corsiopsis chinensis*. Redrawn from Zhang et al. (1999). (**c**) *Arachnitis uniflora*. Redrawn from Dimitri (1972). Bar = 1 cm

Ecology—Specimens of *Arachinitis* form arbuscular mycorrhizas and are associated with a narrow lineage within the *Glomus* group A clade (Bidartondo et al. 2002). The mycorrhizal fungi of *Corsia* and *Corsiopsis* are not known, but these genera are probably associated with arbuscualar mycorrhizal fungi as well. Pollination syndrome and dispersal agents remain poorly studied. Rudall and Eastman (2002) noted that the flowers of *Corsia* are protandrous. Moreover, during anthesis the flowers of *Arachnitis* grow considerably and show great morphological plasticity (Minoletti 1986; Ibisch et al. 1996). These observations suggest cross-pollination in Corsiaceae.

2.5.5.1 *Arachnitis* (Figs. 2.10 and 4.11a)

Arachnitis Phil., Bot. Zeitung (Berlin) 22: 217 (1864).

Mycoheterotrophic herbs, up to 30 cm tall. Underground part a cluster of tuberous roots. Stems reddish. Flowers bisexual or unisexual.

Tepals whitish yellow to violet or dark red, the 3 inner and 2 outer lateral ones filiform and spreading, the median outer tepal narrowly ovate, basally concave and covering the reproductive parts of the flower, apical part pendent. Stamens free, soon falling off. Ovary 1-locular, styles 3, each with a stigma. Fruit globose, pendent when ripe, dehiscing at the top by 3 horizontally splitting valves. Seeds ovoid.

Arachnitis comprises a single species with a remarkably wide distribution. *A. uniflora* is known from humid subantarctic *Nothofagus* forests in Argentina and Chile, and subhumid and humid tropical Andean forests in Bolivia (Ibisch et al. 1996; Neinhuis and Ibisch 1998). *Arachnitis* is also found on the treeless Falkland Islands, growing "in sand amongst rocks" (Cribb et al. 1995), occurring between sea level and 1,000 m. Some authors recognize a second species, *A. quetrihuensis*, based on differences in flower proportions (Dimitri 1972; Neinhuis and Ibisch 1998), but given the substantial morphological variability of *Arachnitis* over its wide distribution, we consider *A. quetrihuensis* conspecific to *A. uniflora* (see also Ibisch et al. 1996).

Bidartondo et al. (2002) sequenced the fungal symbionts of eight individuals of *A. uniflora* from three populations in subantarctic forests in Argentina and found that the plants form arbuscular mycorrhizae and are specialized to a narrow lineage within the *Glomus* group A clade. The pollination biology of *Arachnitis* has not been studied in the field, but Vogel (1978) suggests that *Arachnitis* may be pollinated by fungus gnats.

2.5.5.2 *Corsia* (Fig. 2.10a, b)

Corsia Becc., Malesia 1: 238 (1878) as "1877."

Mycoheterotrophic herbs, up to 30 cm tall. Rhizome cylindric, more or less horizontal; roots filiform. Stems often purplish or reddish brown. Flowers bisexual, nodding at anthesis. Tepals reddish, the 3 inner and 2 outer lateral ones filiform, spreading to pendent, the median outer tepal ovate and often cordate, with a large, glandular, basal callus, covering the reproductive parts of the flower as an umbrella-like structure. Stamens connate at the base with each other and the base of the style. Ovary 1- or 3-locular, style 1, with 3 thick, short stigmas; septal nectaries absent. Fruit fusiform, longitudinally dehiscing by 3 valves, the valves curving downwards exposing the 3 erect placentas carrying the seeds. Seeds fusiform, pendent.

Corsia contains approximately 25 species. Most species are endemic to New Guinea, but at least two are found on the Solomon Islands and one species occurs in northern Australia (Van Royen 1972; Jones and Gray 2008). *Corsia* grows in the upper parts of lowland forests and in montane forests between 900 and 2,300 m (Rübsamen 1986). The species typically grow in damp places and are often found growing together with *Sciaphila* spp. (Triuridaceae) and *Burmannia* spp. (Burmanniaceae) (Van Royen 1972). Flowers of *Corsia* are protandrous according to Smith (1909) and produce nectar (Beccari 1878), suggesting pollination is mediated by insects. Seed dispersal mechanisms and identity of mycorrhizal fungi remain unknown.

2.5.5.3 *Corsiopsis* (Fig. 2.10c)

Corsiopsis D.X. Zhang, R.M.K. Saunders and C.M. Hu, Syst. Bot. 24: 313 (1999).

Mycoheterotrophic herbs, up to 6 cm tall. Rhizome vertical, ellipsoid-obovoid. Stems white. Flowers unisexual. Tepals white, the 3 inner and 2 outer lateral ones filiform, pendent, the median outer tepal broadly ovate, erect, inflated into a bowl-shaped structure, covering the reproductive parts of the flower. Stamens free, each with an obtuse, apical extension of the connective. Ovary of female flowers narrowly ellipsoid, 1-locular, stigmas 3, sessile, connate. Fruit and seeds unknown.

Corsiopsis comprises a single species, *C. chinensis*, which is only known from a single collection from Guangdong Province, China made in 1974 (Zhang et al. 1999). Data on pollination syndrome, dispersal agents, and the identity of mycorrhizal fungi are lacking.

2.5.6 Orchidaceae

Orchidaceae Juss., Gen. Pl. 64–65 (1789).

Epiphytic, terrestrial, lithophytic, or rarely aquatic or subterranean herbs, usually green and photosynthetic, some without chlorophyll and putatively fully mycoheterotrophic. Roots subterranean or aerial, thickened, when epiphytic provided with a multilayered epidermal velamen, sometimes with tubers. Stems elongate to shortened, rarely vining (as in *Vanilla*), thickened in many species, in which case either forming a one- to several-nodal pseudobulb or subterranean corm, predominantly exhibiting sympodial growth although monopodial in some groups. Leaves membranous to thickened or terete, plicate to conduplicate, sometimes reduced to sheaths, absent in fully mycoheterotrophic species. Inflorescences elongate to condensed racemes, spikes or panicles, terminal or lateral, numerous-flowered to solitary. Flowers usually zygomorphic, frequently resupinate via a twisting of the pedicellate ovary. Sepals free, sometimes variously connate, often colored like the petals. Uppermost petal (lowermost in resupinate species) usually modified and enlarged relative to the lateral petals. Functional anthers 1–3, most frequently one, filaments and styles united to form a gynostemium (column). Column short to elongate, occasionally prolonged at base and united with sepals to form a foot, sometimes also forming a spur or mentum. Pollen usually aggregated into masses (pollinia), sometimes forming hard, bony masses, sometimes with stalks that affix the pollinia to insects, pollinia 2–8. Stigma borne on the adaxial side of the column, often below a sticky mass (viscidium) that aids in attachment of pollinia to insects. Ovary inferior, usually unilocular with parietal placentation, but trilocular and axile in some. Ovules small, up to a million or more per flower in some species. Fruits capsular except in some *Vanilla* where an indehiscent structure may be produced. Seeds minute, without differentiated embryo or endosperm.

Number of genera and species—Orchidaceae are usually considered to be the largest family of flowering plants with ca. 22,000 species in about 880 genera (Stevens 2001). Circa 235 species in 43 genera are leafless and are putative full or nearly full mycoheterotrophs. The largest genera of full mycoheterotrophs are the Old World *Aphyllorchis* (33 species) and *Gastrodia* (22 species). Partial mycoheterotrophy has been detected in many green-leaved species (e.g., *Cephalanthera* spp., *Cheirostylis montana*, *Cymbidium* spp., *Epipactis* spp., *Ophrys insectifera*, *Platanthera bifolia*) and may be relatively common in terrestrial orchids (e.g., Gebauer and Meyer 2003; Bidartondo et al. 2004; Julou et al. 2005; Tedersoo et al. 2007; Cameron et al. 2009; Roy et al. 2009a; Liebel et al. 2010; Motomura et al. 2010; Preiss et al. 2010; Girlanda et al. 2011). Occasionally achlorophyllous “albino” individuals are found in some otherwise partially mycoheterotrophic species, notably in *Epipactis* and *Cephalanthera* (Salmia 1989; Selosse et al. 2004; Abadie et al. 2006). Some terrestrial orchid species have separate vegetative and leafless flowering stages, and have been misinterpreted as mycoheterotrophs (Chen and Luo 2002).

Distribution and habitat—Orchidaceae have a worldwide distribution, occurring in almost every habitat on the planet and absent only from the polar regions and the driest of deserts (Chase 2005). The great majority are to be found in the tropics, mostly in Southeast Asia and in the Neotropics, and their diversity peaks in montane tropical regions where abundant rainfall allows for the maximum growth of epiphytes. Most fully mycoheterotrophic orchids are found in the tropics, but their diversity has a highly uneven distribution. The vast majority of tropical mycoheterotrophic orchids occur in Southeast Asia and adjacent Australasia. In contrast, the floras of tropical Africa and particularly the Neotropics are surprisingly poor in fully mycoheterotrophic Orchidaceae. A majority of orchids are perennial epiphytes, which grow anchored to trees or shrubs in the tropics and subtropics. Other species are terrestrial or lithophytes, growing on rocks or very rocky soil. Nearly all temperate orchids are terrestrial. All mycoheterotrophic orchids are terrestrial, although some species, such as

Erythrorchis cassythoides, are climbers (Dearnaley 2006).

Classification—Recent phylogenetic analyses suggest that the Orchidaceae are sister to the remainder of the Asparagales (Givnish et al. 2006; Graham et al. 2006; Pires et al. 2006). Traditionally, classification of Orchidaceae has been based on the construction of the fused gynoecium and androecium ("column" or "gynostemium"), which is, in its details, unique to the family. The number of anthers has been the primary trait emphasized, which has resulted in the family being split into three main groups, often recognized as subfamilies. Five subfamilies are currently recognized. *Apostasia* and *Neuwiedia*, two Southeast Asian genera that comprise Apostasioideae, have been sometimes viewed as orchid relatives and placed in a separate family, Apostasiaceae, believed to be more closely related to other families such as Hypoxidaceae (Hutchinson 1959) than to Orchidaceae. Vanilloideae is the most recently recognized subfamily, having been resolved by molecular data and thereby clarifying a long-standing uncertainty in the relationships of its species based on their unusual combination of primitive and advanced morphological features. The remainder of the family comprises Cypripedioideae with their distinctive slipper-shaped labellum, Orchidoideae, which contains most of the temperate species, and Epidendroideae, which contains the great majority of the family and is primarily tropical and epiphytic.

Evolutionary history—The family's placement as sister to the remainder of the Asparagales suggests a relatively ancient origin for Orchidaceae; Chase (2001) suggested that the family might date from approximately 110 Ma by relating its phylogenetic placement to other groups. Orchid fossils are rare and usually consist of pollinaria. A 15–20 Ma fossil pollinarium was recently used to date the family at 76–84 Ma (Ramirez et al. 2007). The family was undoubtedly primitively terrestrial, with multiple derivations of epiphytism, primarily in the large subfamily Epidendroideae. Containing ca. 80% of the family's diversity, Epidendroideae comprise most of the epiphytes and exhibits the most advanced pollinarium morphologies related to specialized pollination strategies. The majority of mycoheterotrophs are members of Epidendroideae. The diversity of leafless species in the family represents an estimated minimum of 30 independent shifts to heterotrophy (Freudenstein and Barrett 2010).

Ecology—Orchids are well-known for their pollination specializations, ranging from the perfume-collecting euglossine bee syndrome found in many neotropical species to the pseudocopulatory syndrome of genera such as *Ophrys* and *Chiloglottis*. Most orchids outside of Apostasioideae and Cypripedioideae disperse their pollen in masses (pollinia). Small seeds without endosperm, reliance on fungi for germination, and pollen aggregated into pollinia together form a highly specialized strategy for orchids, in which in order to produce the large numbers of highly mobile seeds required to ensure that some may find a suitable fungus, large numbers of pollen grains are also necessary. Although it might be possible to achieve this with granular pollen, pollen masses provide an "all-or-nothing" strategy in which large numbers of ovules are fertilized or none at all.

As far as is known, all orchids depend on a mycoheterotrophic interaction with a symbiotic fungus for germination (initial mycoheterotrophy) (Leake 1994). In most orchids, particularly epiphytic species, this dependence appears to be required only during early seedling development prior to photosynthesis. Leafless epiphytes, such as *Dendrophylax*, photosynthesize with their roots and thus are not mycoheterotrophic. At least some terrestrial orchids that photosynthesize also obtain carbohydrates from fungi, and so are partially mycoheterotrophic (Rasmussen 1995). In others, the initial completely fungally-dependent phase has been prolonged throughout the plant's life (the fully mycoheterotrophic species). Both roots and rhizomes may be used to interact with fungi. Coralloid rhizomes, which characterize some full mycoheterotrophs, may be viewed as a paedomorphic extension of the protocorm stage that facilitates fungal interaction in the mature plant (Rasmussen 1995). Two distinct types of orchid mycorrhiza are recognized (Burgeff 1932). In the most common *tolypophagous* type, hyphae infect the rhizome or root, form coils (pelotons) in cortical cells, and are digested. In the infrequent *ptyophagous* type, hyphae that have entered a root experience lysis at the tips and cell contents are released. The latter type is little known and may be confined essentially to the tropics.

Subfamily VANILLOIDEAE Szlachetko

2.5.6.1 *Cyrtosia*

Cyrtosia Blume, Bijdr.: 396 (1825).
Conchoglossum Breda, Gen. Sp. Orchid. Asclep. 4: t. 17 (1830).

Cyrtosia contains seven species, all of which are achlorophyllous and thus putative mycoheterotrophs (Cameron 2003). They are widespread in tropical and subtropical Southeast Asia. *Cyrtosia septentrionalis* has been reported to grow with wood-decaying *Armillaria* fungi (Hamada 1939; Cha and Igarashi 1996; Rasmussen 2002).

2.5.6.2 *Erythrorchis*

Erythrorchis Blume, Rumphia 1: 200 (1837).
Haematorchis Blume, Rumphia 4: t. 200 B (1849).
Ledgeria F. Muell., Fragm. 1: 238 (1859).

Erythrorchis comprises three species, which are full mycoheterotrophs. *Erythrorchis altissima* ranges from Indonesia to the Philippines, *Erythrorchis ochobiensis* from Japan through Taiwan to Vietnam, Cambodia, Laos, and Thailand. *Erythrorchis cassythoides* occurs in eastern Australia. *Erythrorchis ochobiensis* is reported to form mycorrhizas with a wide range of wood-rotting and ectomycorrhizal fungi (Umata 1995, 1997a, b, 1998a, b), and the roots of *E. cassythoides* are also colonized by both ectomycorrhizal and saprotrophic fungi (Dearnaley 2006).

2.5.6.3 *Galeola*

Galeola Lour., Fl. Cochinch. 2: 520 (1790).
Pogochilus Falc., J. Bot. (Hooker) 4: 73 (1842).

Galeola includes six fully mycoheterotrophic species. The genus has a remarkably widespread distribution with *G. humblotii* occurring in Madagascar and the Comores and all other species growing in tropical and subtropical Southeast Asia. *Galeola septentrionalis* is associated with species of *Armillaria* fungi (Terashita 1996).

2.5.6.4 *Lecanorchis*

Lecanorchis Blume, Mus. Bot. Lugd. Bat. 2: 188 (1856).

Lecanorchis includes approximately 20 species. All species are fully mycoheterotrophic. The genus is quite diverse in Japan, but extends widely in tropical and subtropical Southeast Asia (Hashimoto 1990).

2.5.6.5 *Pseudovanilla*

Pseudovanilla Garay, Bot. Mus. Leafl. 30: 234 (1986).

Pseudovanilla includes about eight species from Malesia and the Pacific islands. All species have reduced leaves and stems that are orange to yellow when young but are green when mature. Their (partial) mycoheterotrophic status remains to be investigated in detail.

Subfamily ORCHIDOIDEAE Lindley

2.5.6.6 *Arthrochilus*

Arthrochilus F. Muell., Fragm. 1: 42 (1858).
Drakaea Lindl. Sect. *Akaedra* Schltr., Bot. Jahrb. Syst. 45: 383 (1911).

Limited to eastern Australia (including Tasmania) and southern Papua New Guinea, this genus of ten species contains a single leafless species, *A. huntianum*, which has the typical tubers of the genus reduced to protocorm-like structures.

2.5.6.7 *Brachycorythis*

Brachycorythis Lindl., Gen. Sp. Orchid. Pl.: 363 (1838).
Schwartzkopffia Kraenzl., Bot. Jahrb. Syst. 28: 177 (1900).
Phyllomphax Schltr., Repert. Spec. Nov. Regni Veg. Beih. 4: 118 (1919).
Diplacorchis Schltr., Beih. Bot. Centralbl. 38(2): 127 (1921).

Gyaladenia Schltr., Beih. Bot. Centralbl. 38(2): 124 (1921).
Afrorchis Szlach., Richardiana 6: 82 (2006).

Brachycorythis includes ca. 35 species and is distributed from tropical and southern Africa to Madagascar and Southeast Asia. Most species are autotrophic with green leaves, except for *B. pumilio* from tropical West Africa and *B. lastii* from tropical East Africa, which are both achlorophyllous (Summerhayes 1955).

2.5.6.8 *Burnettia*

Burnettia Lindl., Gen. Sp. Orchid. Pl.: 517 (1840).

A monospecific genus comprising the mycoheterotrophic *B. cuneata*, from southeast Australia and Tasmania.

2.5.6.9 *Chamaegastrodia*

Chamaegastrodia Makino & Maek., Bot. Mag. (Tokyo) 49: 596 (1935).

Chamaegastrodia comprises three species (Govaerts et al. 2011), which are distributed from Assam to Japan. All species lack chlorophyll and are therefore considered to be fully mycoheterotrophic. *C. shikokiana* has been demonstrated to grow with ectomycorrhizal Ceratobasidiaceae fungi (Yagame et al. 2008).

2.5.6.10 *Corybas*

Corybas Salisb., Parad. Lond.: t. 83 (1807).

Corybas has a widespread distribution that ranges over temperate Asia, Southeast Asia, Australasia, temperate Australia and New Zealand, and the Pacific Islands. The genus comprises ca. 50 species. *C. cryptanthus* from the North Island of New Zealand is leafless and lacks chlorophyll and is therefore a putative full mycoheterotroph (Moore and Edgar 1970). Specimens of *C. cheesemanii* are sometimes achlorophyllous as well.

2.5.6.11 *Cryptostylis*

Cryptostylis R.Brown, Prodr. Fl. Nov. Holl.: 317 (1810).
Chlorosa Blume, Bijdr. 8: 420 (1825).
Zosterostylis Blume, Bijdr. 8: 418 (1825).

A genus of 25 species from tropical and subtropical Asia and the Southwest Pacific. One species from southeast Australia, *C. hunteriana*, is leafless but the stems are green.

2.5.6.12 *Cystorchis* (Fig. 2.11e)

Cystorchis Blume, Fl. Javae ser. 2. 1: 73. t. 24 (1858).

Cystorchis from Southeast Asia and the Pacific islands comprises ca. 20 species, three of which are achlorophyllous: *C. aphylla* from Southeast Asia, *C. saprophytica* from Borneo, and *C. peliocaulos* from New Guinea.

2.5.6.13 *Danhatchia*

Danhatchia Garay & Christenson, Orchadian 11: 469 (1995).

Previously placed in *Yoania* (Epidendroideae), *Danhatchia* was recognized as distinct based on floral structure. The single fully mycoheterotrophic species, *D. australis*, occurs in New Zealand but has recently been discovered in New South Wales, Australia as well.

2.5.6.14 *Degranvillea*

Degranvillea Determann, Amer. Orchid Soc. Bull. 54: 174 (1985).

The rare *Degranvillea dermaptera* is the sole species in this genus and is only known from French Guiana. It bears a coralloid rhizome.

2.5.6.15 *Odontochilus*

Odontochilus Blume, Fl. Javae, n.s., 1: 69 (1858).
Evrardia Gagnep., Bull. Mus. Natl. Hist. Nat., II, 4: 596 (1932).
Evrardianthe Rauschert, Feddes Repert. 94: 433 (1983).
Evrardiana Aver., Bot. Zhurn. (Moscow & Leningrad) 73: 432 (1988).

Four of 40 *Odontochilus* species are putative full mycoheterotrophs—*O. saprophyticus* from Hainan and S Vietnam, *O. poilanei* from China, Myanmar, Thailand, Vietnam, and Japan, *O. asraoa* from Assam and Nepal, and *O. guangdongensis* from southern China.

Fig. 2.11 A few examples of fully mycoheterotrophic Orchidaceae. (**a**) *Gastrodia grandilabris*. (**b**) *Cephalanthera exigua*. (**c**) *Tropidia saprophytica*. (**d**) *Epipogium roseum*. (**e**) *Cystorchis aphylla*. (**f**) *Platanthera saprophytica*. Redrawn from Wood et al. (2011), except for (**b**) redrawn from Pedersen et al. (2009). Bar = 1 cm

2.5.6.16 *Platanthera* (Fig. 2.11f)

Platanthera Rich., De Orchid. Eur.: 26 (1817).
Lysias Salisb., Trans. Hort. Soc. London 1: 288 (1812).
Sieberia Spreng., Anleit. Kenntn. Gew., ed. 2, 2(1): 282 (1817).
Mecosa Blume, Bijdr.: 403 (1825).
Diplanthera Raf., Herb. Raf.: 73 (1833).
Tulotis Raf., Herb. Raf.: 70 (1833).
Perularia Lindl., Edwards's Bot. Reg. 20: t. 1701 (1835).
Blephariglottis Raf., Fl. Tellur. 2: 38 (1837).
Conopsidium Wallr., Linnaea 14: 147 (1840).
Diphylax Hook.f., Hooker's Icon. Pl. 19: t. 1865 (1889).
Limnorchis Rydb., Mem. New York Bot. Gard. 1: 104 (1900).
Lysiella Rydb., Mem. New York Bot. Gard. 1: 104 (1900).
Gymnadeniopsis Rydb. in N.L.Britton, Man. Fl. N. States: 293 (1901).
Piperia Rydb., Bull. Torrey Bot. Club 28: 269 (1901).

Dithrix (Hook.f.) Schltr., Notizbl. Bot. Gart. Berlin-Dahlem 9: 583 (1926).
Pseudodiphryllum Nevski in V.L.Komarov (ed.), Fl. URSS 4: 752 (1935).
Tsaiorchis Tang & F.T.Wang, Bull. Fan Mem. Inst. Biol. 7: 131 (1936).
Fimbriella Farw. ex Butzin, Willdenowia 11: 323 (1981).
× *Platanthopsis* P.M.Br., N. Amer. Native Orchid J. 8: 37 (2002).
× *Blepharopsis* Efimov, Novosti Sist. Vyssh. Rast. 40:48 (2008 publ. 2009).

Broadly distributed from North America through Eurasia, including Southeast Asia, this genus of ca. 200 species includes a single fully mycoheterotrophic species, *P. saprophytica* from Borneo. This species is entirely whitish in color, except for a purple margin to the lip (Wood et al. 2011).

2.5.6.17 *Platythelys*

Platythelys Garay, Bradea 2: 196 (1977).

A New World genus of about ten species distributed from southeastern USA to Brazil and Argentina. One species, *P. pedicellata*, has leaves reduced to bracts and may be mycoheterotrophic.

2.5.6.18 *Rhizanthella*

Rhizanthella R.S.Rogers, J. Roy. Soc. Western Australia 15: 1 (1928).
Cryptanthemis Rupp, Proc. Linn. Soc. New South Wales 57: 58 (1932).

Rhizanthella is a genus of extremely rare, fully subterranean mycoheterotrophic orchids that are endemic to Australia. The genus comprises three species: *R. gardneri* from western Australia, and *R. omissa* and *R. slateri* from southeastern Australia. Fungal associates of *R. gardneri* and *R. slateri* have been identified as *Rhizoctonia*-type fungi that most likely belong to the Ceratobasidiales (Basidiomycota) (Bougoure et al. 2009). *R. gardneri* is only found growing adjacent to individual shrubs of species in the *Melaleuca uncinata s.l.* complex (Myrtaceae) in its native habitats (Bougoure et al. 2008). Fungi isolated from *R. gardneri* demonstrated the ability to form ectomycorrhizas with the roots of *Melaleuca uncinata s.l.* individuals (Warcup 1985, 1991; Bougoure et al. 2009), suggesting that *R. gardneri* obtains carbon from *Melaleuca* plants (Bougoure et al. 2009). Carbon transfer between *R. gardneri* and *Melaleuca uncinata* through common ectomycorrhizal fungi has been confirmed by microcosm experiments (Bougoure et al. 2010). Dixon (2003) suggested that seed dispersal of *R. slateri* is carried out by animals.

Subfamily EPIDENDROIDEAE Lindley

2.5.6.19 *Aphyllorchis*

Aphyllorchis Blume, Tab. Pl. Jav. Orchid.: t. 16, f. 77 (1825).
Sinorchis S.C.Chen, Acta Phytotax. Sin. 16: 82 (1978).

Aphyllorchis includes 33 fully mycoheterotrophic species. The genus is widespread in tropical and subtropical Asia. *A. montana* and *A. caudata* are able to associate with a wide range of ectomycorrhizal fungi (Roy et al. 2009a).

2.5.6.20 *Auxopus*

Auxopus Schltr., Westafr. Kautschuk.-Exped. 275 (1900).

The fully mycoheterotrophic *Auxopus* comprises three species—*Auxopus kamerunensis* and *A. macranthus* from tropical West and Central Africa and *A. madagascariensis* from tropical Madagascar.

2.5.6.21 *Cephalanthera* (Figs. 2.5g and 2.11b)

Cephalanthera Rich., Mém. Mus. Hist. Nat. 4: 51 (1818).
Callithronum Ehrh., Beitr. Naturk. 4: 148 (1789).
Lonchophyllum Ehrh., Beitr. Naturk. 4: 148 (1789).
Dorycheile Rchb., Deut. Bot. Herb.-Buch: 56 (1841).
Xiphophyllum Ehrh., Beitr. Naturk. 4: 148 (1789).
Eburophyton A.Heller, Muhlenbergia 1: 48 (1904).
Tangtsinia S.C.Chen, Acta Phytotax. Sin. 10: 194 (1965).

Cephalanthera includes ca. 18 species. Six species lack chlorophyll and are putative full mycoheterotrophs. Stable isotope data suggest that chlorophyllous species are partial mycoheterotrophs (Julou et al. 2005; Abadie et al. 2006; Preiss et al. 2010; Stöckel et al. 2011).

Albino forms of some green species are known: e.g., *C. damasonium*, *C. longifolia* (Julou et al. 2005; Abadie et al. 2006). *Cephalanthera* is widespread in temperate Eurasia, northern Africa, North America, and Southeast Asia. One achlorophyllous species, *C. austinae*, occurs in western North America. The remaining achlorophyllous species grow in Southeast Asia (*C. calcarata*, *C. ericiflora*, *C. exigua*, *C. gracilis*, *C. pusilla*) (Pedersen et al. 2009). *C. austinae* and *C. exigua* have been found to associate with ectomycorrhizal Thelephoraceae fungi (Basidiomycota) (Taylor and Bruns 1997; Roy et al. 2009a).

2.5.6.22 *Corallorhiza* (Figs. 4.12a and 6.2)

Corallorhiza Gagnebin, Acta Helv. Phys.-Math. 2: 61 (1755).
Rhizocorallon Gagnebin, Acta Helv. Phys.-Math. 2: 61 (1755).
Corallorhiza Châtel., Spec. Inaug. Corallorhiza: 5 (1760).
Cladorhiza Raf., Amer. Monthly Mag. & Crit. Rev. 1: 429 (1817).

Corallorhiza, commonly known as “coralroot orchids,” includes 12 species (Freudenstein 1997; Barrett and Freudenstein 2011). All species are achlorophyllous except for *C. trifida*, which has green stems and capsules. However, recent research has shown that *C. trifida* derives most of its carbon from ectomycorrhizal Telophoraceae fungi (McKendrick et al. 2000; Cameron et al. 2009). *Corallorhiza trifida* is extremely widespread in the temperate and subarctic Northern hemisphere. The distribution of the remaining species of *Corallorhiza* is limited to North and Central America. *Corallorhiza striata* and *C. bentleyi* are apparently associated with nonoverlapping clades of ectomycorrhizal *Tomentella* fungi (Thelephoraceae; Basidiomycota) (Barrett et al. 2010), while *C. maculata* and the closely related species *C. mertensiana* have been found to associate with nonoverlapping Russulaceae fungi (Basidiomycota) (Taylor and Bruns 1997, 1999; Taylor et al. 2004). *Corallorhiza odontorhiza* and *C. wisteriana* are sister species that occur in Mexico and northward; *C. wisteriana* is distributed across the USA, while *C. odontorhiza* occurs only in the east of the USA. *Corallorhiza odontorhiza* utilizes Thelephoraceae; populations of *C. wisteriana* in the western portion of the distribution utilize Thelephoraceae, while eastern populations utilize Russulaceae. Some polymorphic populations exist in which plants use either fungus (Freudenstein and Barrett, unpubl.).

2.5.6.23 *Cremastra*

Cremastra Lindl., Gen. Sp. Orch. Pl.: 172 (1883).

A genus of three species extending from Nepal and Sikkim through China, Korea, Japan, and Sakhalin. It contains one full mycoheterotroph, *C. aphylla* from Japan (Yukawa 1999).

2.5.6.24 *Cymbidium*

Cymbidium Sw., Nova Acta Regiae Soc. Sci. Upsal. 6: 70 (1799).
Jensoa Raf., Fl. Tellur. 4: 38 (1838) “1836.”
Cyperorchis Blume, Rumphia 4: 47 (1849).
Iridorchis Blume, Coll. Orchid.: 90 (1859).
Arethusantha Finet, Bull. Soc. Bot. France 44: 179 (1897).
Pachyrhizanthe (Schltr.) Nakai, Bot. Mag. (Tokyo) 45: 109 (1931).
× *Cyperocymbidium* A.D.Hawkes, Orchid Rev. 72: 420 (1964).
Liuguishania Z.J.Liu & J.N.Zhang, J. S. China Agric. Univ. 19(1): 73 (1998).
Wutongshania Z.J.Liu & J.N.Zhang, J. S. China Agric. Univ. 19(1): 74 (1998).
Cymbidiopsis H.J.Chowdhery, Indian J. Forest. 32: 154 (2009).

Cymbidium includes ca. 52 species (Du Puy and Cribb 2007). One species, *C. macrorhizon*, lacks foliage leaves but has green stems and capsules. Stable isotope data indicate that this species is fully mycoheterotrophic. Related species with green leaves are partial mycoheterotrophs (Motomura et al. 2010). The chlorophyllous species *C. lancifolium* and *C. goeringii* both associate simultaneously with saprotrophic Tulasnellaceae and ectomycorrhizal fungi, whereas *C. macrorhizon* establishes symbiosis exclusively with ectomycorrhizal fungi (Motomura et al. 2010).

2.5.6.25 *Didymoplexiella*

Didymoplexiella Garay, Arch. Jard. Bot. Rio de Janeiro 13: 33 (1954).
Leucolena Ridl., J. Linn. Soc., Bot. 28: 340 (1891).

Didymoplexiella comprises seven fully mycoheterotrophic species that are restricted to Southeast Asia.

2.5.6.26 *Didymoplexis*

Didymoplexis Griff., Calcutta J. Nat. Hist. 4: 383 (1843).
Leucorchis Blume, Mus. Bot. 1: 31 (1849).
Apetalon Wight, Icon. Pl. Ind. Orient. 5: 22 (1851).
Epiphanes Rchb.f. in B.Seemann, Fl. Vit.: 295 (1868).

Didymoplexis includes about 12 species, all of which are full mycoheterotrophs. The genus has a remarkably wide distribution and occurs in tropical Africa (*D. africana*) and from Afghanistan to India, Southeast Asia, northern Australia, New Guinea, and Vanuatu. *Didymoplexis* is probably absent from Madagascar (Cribb et al. 2010). Morphological observations suggest that *D. minor* is associated with saprotrophic *Marasmius* fungi (Burgeff 1932).

2.5.6.27 *Dipodium*

Dipodium R.Br., Prodr. Fl. Nov. Holl.: 330 (1810).
Leopardanthus Blume, Rumphia 4: 47 (1849).
Wailesia Lindl., J. Hort. Soc. London 4: 261 (1849).
Hydranthus Kuhl & Hasselt ex Rchb.f., Xenia Orchid. 2: 20 (1862).
Trichochilus Ames, J. Arnold Arbor. 13: 142 (1932).

Dipodium ("hyacinth orchids") contains ca. 21 species from Southeast Asia, Australia, and the Pacific Islands. While some species are green and leaf-bearing, at last nine species (e.g., *D. variegatum*, *D. roseum*, *D. hamiltonianum*) have green stems but lack foliage leaves and are likely partial mycoheterotrophs. Several studies report that *Dipodium* species associate with ectomycorrhizal Russulaceae fungi (Bougoure and Dearnaley 2005; Dearnaley and Le Brocque 2006).

2.5.6.28 *Epipogium* (Fig. 2.11d)

Epipogium S.G. Gmel. ex Ehrh., Beitr. Naturk. 4: 149 (1789).
Galera Blume, Bijdr.: 415 (1825).
Ceratopsis Lindl., Gen. Sp. Orchid. Pl.: 383 (1840).
Podanthera Wight, Icon. Pl. Ind. Orient. 5: 22 (1851).
Epipogon S. G. Gmel., Fl. Sibirica 1: 11 (1747).
Epipogion St.-Lag., Ann. Soc. Bot. Lyon 7: 144 (1880).

Epipogium comprises 2–3 fully mycoheterotrophic species: *E. aphyllum* ("Ghost Orchid") from temperate Eurasia, the questionably distinct *E. japonicum* from Japan, Taiwan, and S China, and *E. roseum* from tropical Africa, Southeast Asia, New Guinea, Australia, and the Pacific Islands. *Epipogium aphyllum* associates with ectomycorrhizal fungi (Roy et al. 2009b), while populations of *E. roseum* from Japan were found to grow with saprotrophic Coprinaceae fungi (Yamato et al. 2005; Yagame et al. 2007). *E. aphyllum* was shown to obtain carbon and nitrogen through its ectomycorrhizal association (Liebel and Gebauer 2011).

2.5.6.29 *Eulophia*

Eulophia R.Br. ex Lindl., ("*Eulophus*") Bot. Reg. 7: t. 573 (1821).
Wolfia Dennst., Schlüssel Hortus Malab.: 38 (1818).
Lissochilus R.Br., Bot. Reg. 7: t. 573 (1821).
Cyrtopera Lindl., Gen. Sp. Orchid. Pl.: 189 (1833).
Thysanochilus Falc., Proc. Linn. Soc. London 1: 14 (1839).
Hypodematium A.Rich., Tent. Fl. Abyss. 2: 286 (1850).
Orthochilus A.Rich., Tent. Fl. Abyss. 2: 284 (1850).
Pteroglossaspis Rchb.f., Otia Bot. Hamburg.: 67 (1878).
Platypus Small & Nash in J.K.Small, Fl. S.E. U.S.: 329 (1903).
Triorchos Small & Nash in J.K.Small, Fl. S.E. U.S.: 329 (1903).
Smallia Nieuwl., Amer. Midl. Naturalist 3: 158 (1913).
Donacopsis Gagnep., Bull. Mus. Natl. Hist. Nat., II, 4: 593 (1932).
Semiphajus Gagnep., Bull. Mus. Natl. Hist. Nat., II, 4: 598 (1932).

The pantropical *Eulophia* contains ca. 230 species (only two of which are neotropical). Most species are terrestrial, but a few are epiphytes or lithophytes. At least 17 species are leafless or nearly so and probably mycoheterotrophic, including *E. epiphanoides* (southwest Tanzania), *E. galeioides* (tropical Africa), *E. gastrodioides* (Mozambique and Zambia), *E. macrantha* (Malawi and Zimbabwe), *E. richardsiae* (northern

Zambia), and *E. zollingeri* (widespread in tropical and subtropical Asia and Australia). Despite its wide distribution, *E. zollingeri* was found to associate with a narrow lineage of wood-rooting fungi within Coprinaceae (Ogura-Tsujita and Yukawa 2008).

2.5.6.30 *Gastrodia* (Fig. 2.11a)

Gastrodia R.Br., Prodr. Fl. Nov. Holl.: 330 (1810).
Epiphanes Blume, Bijdr.: 421 (1825).
Gamoplexis Falc. ex Lindl., Gard. Chron. 1847: 103 (1847).
Neoclemensia Carr, Gard. Bull. Straits Settlem. 8: 180 (1935).
Demorchis D.L.Jones & M.A.Clem., Orchadian 14(8: Sci. Suppl.): xiii (2004).

Gastrodia comprises ca. 22 achlorophyllous mycoheterotrophic species (Cribb et al. 2010). The center of diversity of the genus is situated in Southeast Asia, and the genus extends to Japan, Siberia, tropical Australia, New Zealand, New Caledonia, the Pacific Islands, Madagascar, the Mascarene Islands, and tropical Africa (Cribb et al. 2010). Dearnaley and Bougoure (2010) identified a number of fungi in the roots of *G. sesamoides*; the most common were saprotrophic members of Marasmiaceae. In addition, stable isotope analysis suggests that *G. sesamoides* obtains most of its carbon from these wood-rotting fungi (Dearnaley and Bougoure 2010). *Gastrodia elata* associates with saprotrophic and parasitic *Armillaria* and *Mycena* fungi (Kusano 1911; Lan et al. 1994; Xu and Fan 2001). *Gastrodia confusa* also associates with saprotrophic *Mycena* fungi (Ogura-Tsujita et al. 2009). *Gastrodia similis* was found to grow mainly with wood-decaying *Resinicium* species (Martos et al. 2009).

2.5.6.31 *Hexalectris* (Fig. 6.1)

Hexalectris Raf., Neogenyton: 4 (1825).

Hexalectris is a New World genus of about eight fully mycoheterotrophic species, occurring throughout most of the southern U.S.A. and Mexico, with concentrations of diversity in the mountainous regions of southwest U.S.A. and northeastern and western Mexico. They often inhabit inhospitable habitats, such as desert canyons, cedar thickets, and tropical dry forests (Kennedy and Watson 2010). *Hexalectris* species are specialized toward different clades of fungi, mainly in Sebacinaceae. These fungi are presumably ectomycorrhizal with surrounding trees (Taylor et al. 2003; Kennedy et al. 2011).

2.5.6.32 *Kalimantanorchis*

Kalimantanorchis Tsukaya, M. Nakajima & H. Okada, Syst. Bot. 36: 52 (2011).

Kalimantanorchis comprises a single species, the achlorophyllous *K. nagamasui* from Borneo (Tsukaya et al. 2011), which is questionably distinct from *Tropidia*.

2.5.6.33 *Limodorum*

Limodorum Boehm., Defin. Gen. Pl.: 358 (1760).
Centrosis Sw., Adnot. Bot.: 52 (1829), nom. illeg.
Jonorchis Beck, Fl. Nieder-Österreich 1: 215 (1890).
Lequeetia Bubani, Fl. Pyren. 4: 57 (1901).

Limodorum comprises three mycoheterotrophic species: *L. arbortivum* from Europe, North Africa, and the Caucasus, *L. rubriflorum* from Turkey, and *L. trabutianum* from the Mediterranean. The plants have small scale-like leaves and a violet stem. Despite the presence of chlorophyll in *L. arbortivum* (Blumenfeld 1935), CO_2 fixation is insufficient to compensate for respiration in adult plants suggesting that *L. arbortivum* is at least partially mycoheterotrophic (Girlanda et al. 2006). C and N stable isotope signatures also support the mycoheterotrophic status of *L. arbortivum* and *L. trabutianum* (Liebel et al. 2010). Both species associate predominantly with fungal symbionts of the genus *Russula*. The associated fungi were found to be ectomycorrhizal with surrounding trees (Girlanda et al. 2006). Paduano et al. (2011) detected differences in cellular response to Russulaceae and *Ceratobasidium* fungi in *Limodorum abortivum*.

2.5.6.34 *Malaxis*

Malaxis Sol. ex Sw., Nov. Gen Sp. Prodr. 8 (1788).
Limnas Ehrh., Beitr. Naturk. 4: 146 (1789).
Achroanthes Raf., Med. Repos. N. York 5: 352 (1808).
Microstylis (Nutt.) Eaton Man. Bot. ed. 3, 115 (1822).

Cheiropterocephalus Barb. Rodr. Gen Sp. Orch. 1: 28 (1877).
Tamayorkis Szlach., Fragm. Phyt. Geobot. Suppl. 3: 121 (1995).

A widespread genus of ca. 300 species, occurring in tropical and temperate regions on all continents except Antarctica. Two species are putative full mycoheterotrophs: *M. aphylla* and *M. saprophyta*.

2.5.6.35 *Neottia*

Neottia Guett., Hist. Acad. Roy. Sci. Mém. Math. Phys. (Paris, 4to) 1750: 374 (1754).
Ophris Mill., Gard. Dict. Abr. ed. 4 (1754).
Nidus Rivinus, Icon. Pl. Fl. Irreg. Hexapet. T. 7. (1764).
Nidus-avis Ortega, Tab. Bot.: 24 (1773).
Cardiophyllum Ehrh., Beitr. Naturk. 4: 148 (1789).
Epipactis Persoon, Syn. Pl. 2: 513 (1807).
Diphryllum Raf., Med. Repos. Ser. 2, 5: 357 (1808).
Listera R.Br. in W.T.Aiton, Hortus Kew. 5: 201 (1813).
Neottidium Schltdl., Fl. Berol. 1: 454 (1823).
Distomaea Spenn., Fl. Friburg. 1: 245 (1825).
Pollinirhiza Dulac, Fl. Hautes-Pyrénées: 120 (1867).
Bifolium Nieuwl., Amer. Midl. Naturalist 3: 128 (1913).
Holopogon Kom. & Nevski in V.L.Komarov (ed.), Fl. URSS 4: 750 (1935).
Diplandrorchis S.C.Chen, Acta Phytotax. Sin. 17(1): 2 (1979).
Archineottia S.C.Chen, Acta Phytotax. Sin. 17(2): 12 (1979).

Neottia is a genus of ca. 60 species with a distribution ranging through the temperate and subarctic Northern Hemisphere. It now contains the leafy species previously placed in *Listera*. Fourteen species are achlorophyllous and presumably fully mycoheterotrophic. These include *N. acuminata*, *N. brevilabris*, *N. camtschatea*, *N. gaudissartii*, *N. listeroides*, *N. megalochila*, *N. microglottis*, *N. nidus-avis*, *N. pantlingii*, *N. papilligera*, *N. smithiana*, *N. taibaishanensis*, *N. tenii*, and *N. ussuriensis* (Govaerts et al. 2011). Natural abundance ^{15}N and ^{13}C data confirms the mycoheterotrophic nature of *N. nidus-avis* (Gebauer and Meyer 2003). *N. nidus-avis* has been found to associate with *Sebacina* fungi that are ectomycorrhizal with surrounding trees, including *Fagus sylvatica* and *Corylus* sp. (McKendrick et al. 2002; Selosse et al. 2002).

2.5.6.36 *Pogoniopsis*

Pogoniopsis Rchb.f., Otia Bot. Hamburg.: 82 (1881).

A rare genus with two mycoheterotrophic species from eastern Brazil (*P. nidus-avis* and *P. schenkii*). Previously placed in Vanilloideae, it appears to fall among the epidendroids (Cameron 2003; pers. comm.).

2.5.6.37 *Risleya*

Risleya King & Pantl., Ann. Roy. Bot. Gard. Calcutta 8: 246 (1898).

Risleya contains a single species, *R. atropurpurea*. This full mycoheterotroph has been recorded from the eastern Himalayas and China (southeastern Sichuan and northwestern Yunnan) (Govaerts et al. 2011).

2.5.6.38 *Silvorchis*

Silvorchis J.J.Sm., Bull. Dép. Agric. Indes Néerl. 13: 2 (1907).

The fully mycoheterotrophic *Silvorchis colorata* is the sole species of the genus. The species is known only from the type specimen, which was collected in Java.

2.5.6.39 *Stereosandra*

Stereosandra Blume, Mus. Bot. Lugd. Bat. 2: 176 (1856).

Stereosandra javanica, a full mycoheterotroph and the sole species of the genus, has a wide distribution in Southeast Asia, having been recorded from the eastern Himalayas, southern China, the Ryukyu Islands, Taiwan, Vietnam, Borneo, Java, Malaysia, Sumatra, the Philippines, New Guinea, the Solomon Islands, and Samoa.

2.5.6.40 *Tropidia* (Fig. 2.11c)

Tropidia Lindl., Edwards's Bot. Reg. 19: t. 1618 (1833).

Decaisnea Lindl. ex Wall., Numer. List: 7388 (1832), nom. inval.
Cnemidia Lindl., Edwards's Bot. Reg. 19: t. 1618 (1833).
Chloidia Lindl., Gen. Sp. Orchid. Pl.: 484 (1840).
Ptychochilus Schauer, Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19(Suppl. 1): 431 (1843).
Govindooia Wight, Icon. Pl. Ind. Orient. 6: 34 (1853).
Schoenomorphus Thorel ex Gagnep., Bull. Soc. Bot. France 80: 351 (1933).
Muluorchis J.J.Wood, Kew Bull. 39: 73 (1984).

A genus with ca. 20 species from tropical and subtropical Asia and the Pacific, with one neotropical species. *T. saprophytica* and *T. connata* from Borneo are full mycoheterotrophs.

2.5.6.41 *Uleiorchis*

Uleiorchis Hoehne, Arq. Bot. Estado São Paulo, n.s., f.m., 1: 129 (1944).

Uleiorchis comprises two fully mycoheterotrophic species from tropical South America. *Uleiorchis liesneri* is known from Venezuela and *U. ulei* has been recorded in Central and tropical South America (Costa Rica, Honduras, Panama, French Guiana, Guyana, Venezuela, Colombia, Ecuador, Peru, and Brazil (Born et al. 1999)).

2.5.6.42 *Wullschlaegelia*

Wullschlaegelia Rchb.f., Bot. Zeitung (Berlin) 21: 131 (1863).

Wullschlaegelia comprises two fully mycoheterotrophic species, *W. aphylla* and *W. calcarata* (Born et al. 1999). Both species are widespread in tropical South and Central America and are present in the West Indies. *Wullschlaegelia aphylla* associates with both litter-decaying *Gymnopus* and *Mycena* species (Martos et al. 2009).

2.5.6.43 *Yoania*

Yoania Maxim., Bull. Acad. Imp. Sci. Saint-Pétersbourg, III, 18: 68 (1872).

Yoania comprises four species, all fully mycoheterotrophic: *Y. amagiensis* (Japan), *Y. flava* (Japan), *Y. japonica* (Assam, China, Taiwan, Japan), and *Y. prainii* (eastern India to northern Vietnam).

2.5.7 Iridaceae

Iridaceae Juss., Gen. Pl.: 57 (1789).
Geosiridaceae Jonker, Recueil Trav. Bot. Néerl. 36: 477 (1939).

Herbs, perennial, rarely annual, evergreen, or seasonal. Underground parts a rhizome, bulb, or corm. Stems simple or branched, terete or variously compressed, angled or winged. Leaves basal and cauline, distichous; proximal 2–3 sometimes membranous, not reaching much above ground; others with open or closed sheaths, usually unifacial. Inflorescences umbellate, monochasial cymes (rhipidia), spikes, or solitary flowers; rhipidia enclosed in 2, opposed, usually large, leafy to dry bracts (spathes). Flowers usually pedicellate actinomorphic or zygomorphic, petaloid, with 2 equal or unequal whorls of 3 tepals each. Tepals usually large, showy, free or connate in tube. Stamens (2-)3, inserted at base of outer tepals or in tube, symmetrically arranged or unilateral; filaments free or partly connate; anthers with 2 pollen sacs, extrorse, usually dehiscing longitudinally. Ovary inferior, (1-)3-locular; placentation axile; ovules 2–few, anatropous; style 1, filiform at least proximally, usually 3-branched or 3-lobed. Fruits a capsule, loculicidal, rarely indehiscent, firm to cartilaginous, occasionally woody. Seeds globose to angular or discoid, sometimes broadly winged; seed coat usually dry.

Number of genera and species—Iridaceae contain over 2,000 species in 66 genera (Goldblatt et al. 2008). The family includes two fully mycoheterotrophic species, *Geosiris aphylla* and *G. albiflora* (Goldblatt and Manning 2008, 2010).

Distribution and habitat—Iridaceae have a cosmopolitan distribution, with a main center of diversity in southern Africa. They are particularly species-rich in the Cape region (Davies et al. 2005). Iridaceae are mainly found in open, seasonable habitats, but also occur in forests, savannas, and semi-arid habitats. They grow on a variety of different soil types.

Classification—Iridaceae are part of the monocot order Asparagales (Chase et al. 2000, 2006; Fay et al. 2000; APG 2009). The family consists of seven subfamilies of which the Iridoideae and Crocoideae contain the majority of the species (Goldblatt et al. 2008). Baillon who described the species *Geosiris aphylla* in 1894, already placed it in Iridaceae (Baillon 1894). However, Engler (1897) transferred *Geosiris* to Burmanniaceae without seeing a specimen. Jonker (1939) concluded that *Geosiris* was not a member of Burmanniaceae and erected a new family, Geosiridaceae, to accommodate the species. Jonker considered Geosiridaceae and Iridaceae closely related. Molecular data confirmed the placement of *Geosiris* in Iridaceae, although it is placed in its own subfamily, Geosiridoideae (Goldblatt et al. 2008).

Evolutionary history—Reliable fossils of Iridaceae date back to the Miocene (23–5 Ma), but molecular clock analyses estimated the origin of Iridaceae at 82 Ma (Wikström et al. 2001) and Ma (Janssen and Bremer 2004), respectively. The start of the divergence of the extant crown group is estimated at 61 (Goldblatt et al. 2008) or 96 Ma (Janssen and Bremer 2004). According to most recent phylogenetic hypotheses *Geosiris* is an early diverging lineage within the family (Goldblatt et al. 2008).

Ecology—The variously shaped and colored flowers of Iridaceae are pollinated by various insects (bees, beetles, flies, wasps, moths, and butterflies) and birds (hummingbirds and sunbirds). Many Iridaceae are highly specialized in their pollinator relationships. Various seed dispersal mechanisms are observed in Iridaceae. These include dispersal by wind, water, ants, and birds (Goldblatt and Manning 2008). The mycorrhizas of only few species of Iridaceae have been examined. From these observations it seems that Iridaceae are mainly associated with AM fungi (Wang and Qiu 2006).

2.5.7.1 *Geosiris* (Figs. 2.5e, 2.12, and 4.10h)

Geosiris Baillon, Bull. Mens. Soc. Linn. Paris 2:1149 (1894).

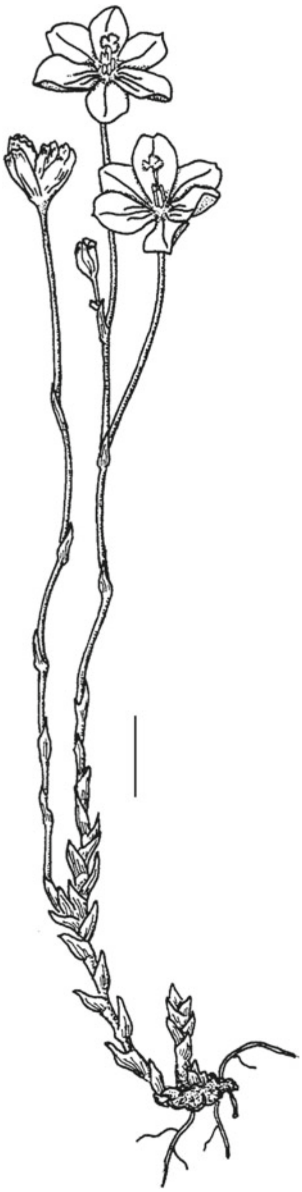

Fig. 2.12 *Geosiris aphylla*. Redrawn from Goldblatt and Manning (2008). Bar = 1 cm

Mycoheterotrophic herbs, up to 12 cm tall. Rhizome short and thick. Roots filiform. Leaves reduced to scales. Inflorescence a binate rhipidium, distorted by crowding of numerous flowers, binate rhipidia few to several. Flowers actinomorphic, without nectaries, lasting a single day. Tepals purple to white, connate at base, spreading. Stamens with free filaments; anthers loculicidal, extrorse. Ovary inferior; style slender, dividing into 3-fringed lobes or apically 3-fid. Fruit a capsule, more or less woody. Seeds minute, dust-like (Goldblatt et al. 2008; Goldblatt and Manning 2008).

Geosiris includes *G. aphylla*, known from evergreen forests in Madagascar. A second species, *G. albiflora*, is endemic to Mayotte (the Comores) (Goldblatt and Manning 2010). A third species has been discovered in Madagascar but remains to be described (Goldblatt and Manning 2010). The identity of the mycorrhizal fungi remains unknown, but like other Iridaceae *Geosiris* is presumably associated with arbuscular mycorrhizal fungi. Pollination syndrome and seed dispersal agents are unknown.

2.5.8 Polygalaceae

Polygalaceae Hoffmans. & Link, Fl. Portug. 1: 62 (1809).

Trees, lianas, shrubs, or perennial as well as annual, rarely mycoheterotrophic herbs. Leaves usually alternate, simple, entire, with pinnate venation. Inflorescence spicate, racemose, or paniculate, sometimes reduced to a single flower, terminal or axillary, bracteate. Flowers bisexual, zygomorphic to actinomorphic. Sepals usually 5, free to more or less connate, lateral sepals often large and petaloid ("wings"). Petals 3 (2 upper ones and 1 lower one) or sometimes 5, imbricate, free, but often all adnate to the staminal tube, the lower petal often boat-shaped and keeled. Stamens (2-)5–8(-10); filaments free or connate into a tube adnate to the petals; anthers basifixed, (2-)4-sporangiate, opening by pores or longitudinal slits. Ovary superior, 2–8-locular, with axile placentation, ovules mostly 1 per carpel, epitropous; style 1, bilobed with 1 stigmatic branch and 1 sterile branch, or stigma capitate. Fruit a loculicidal capsule or a samara, drupe, berry, or nut. Seeds often with stiff hairs.

Number of genera and species—Polygalaceae comprise approximately 21 genera and 1,000 species (Stevens 2001). All species of *Epirixanthes* are fully mycoheterotrophic.

Distribution and habitat—The family of Polygalaceae is cosmopolitan, with its center of diversity in tropical and subtropical areas (Eriksen and Persson 2007).

Classification—Polygalaceae were often considered to be related to Malpighiaceae or Krameriaceae, because of their common bilaterally symmetrical flowers (Cronquist 1981). Analyses of plastid DNA sequences, however, place the family in Fabales (Chase et al. 1993), as the sister group of Surianaceae (Forest et al. 2007; Stevens 2001). Within Polygalaceae four monophyletic tribes are recognized (Xanthophylleae, Polygaleae, Carpolobieae, and Moutabeae) (Eriksen and Persson 2007; Forest et al. 2007). Based on morphology *Epirixanthes* is placed in Polygaleae, but its exact phylogenetic position remains unknown.

Evolutionary history—Molecular clock analyses date the origin of the Polygalaceae to the Late Cretaceous with diversification beginning in the Paleocene (Wikström et al. 2001; Bello et al. 2009).

Ecology—The showy flowers of many Polygalaceae attract various bees and wasps, but self-pollination is also well known. In *Polygala* a pollination mechanism with a movable lower boat-shaped petal is recorded. Species with samaras are dispersed by wind, fleshy-fruited species are vertebrate-dispersed. The loculicidal capsules of *Polygala* release seeds with lobed, aril-like structures that are dispersed over short distances by ants (Judd et al. 1999; Eriksen and Persson 2007). *Polygala* and *Epirixanthes* species associate with arbuscular mycorrhizas (Wang and Qiu 2006; Imhof 2007). Species in other genera are probably arbuscular mycorrhizal as well.

2.5.8.1 *Epirixanthes* (Figs. 2.13a, b, 2.15b, and 4.13c)

Epirixanthes Blume, Catalogus 25 (1823).
Salomonia Loureiro, Fl. Cochinch. 14 (1790).

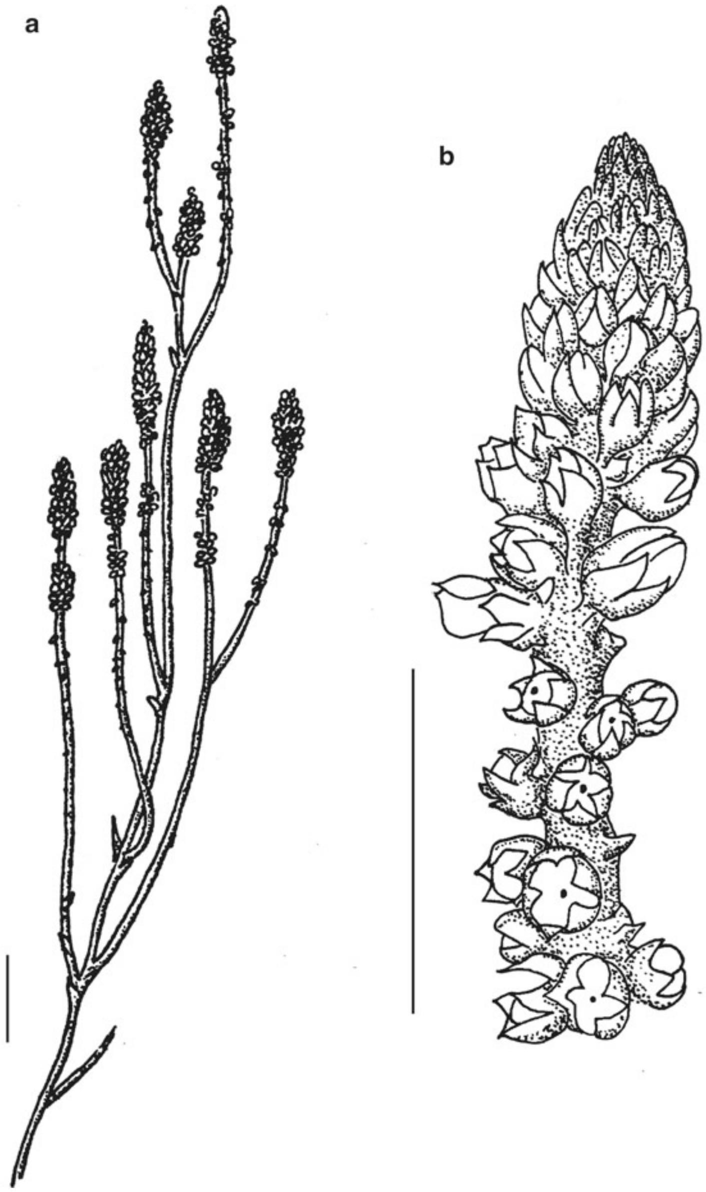

Fig. 2.13 Polygalaceae. *Epirixanthes elongata*: (**a**) habit, (**b**) inflorescence. Redrawn from Hsieh et al. (1995). Bar = 1 cm

Mycoheterotrophic herbs, up to 25 cm tall. Rhizome short. Roots filiform. Stems erect, simple or sparsely branched. Leaves sessile, reduced to scales. Inflorescence spicate, terminal. Flowers very small. Sepals 5, unequal, free or basally connate. Petals 3. Stamens 2–5; filaments united or partly free; anthers introrsely dehiscent by a slit. Ovary 2-locular, compressed; style short and bifurcate toward apex. Fruit indehiscent, with a fleshy pericarp. Seeds ellipsoid, glabrous, nearly without endosperm, with thickened tissue at micropylar end.

Epirixanthes belongs to the tribe Polygaleae. The genus comprises six species (Pendry 2010). It is widely distributed in tropical Asia, including India, Indonesia, Malaysia, Myanmar, Thailand, Vietnam, China, and the Solomon Islands. *Epirixanthes* occurs in the leaf litter of evergreen forest and bamboo groves (Hsieh et al. 1995; Shukun et al. 2008). Root anatomical observations of *Epirixanthes papuana* and *E. elongata* have shown that species of *Epirixanthes* associate with arbuscular mycorrhizas (Imhof 2007). Autogamy has been suggested for *Epirixanthes* (Wirz 1910). Observations on seed dispersal mechanisms are lacking.

2.5.9 Ericaceae

Ericaceae Juss., Gen. Pl.: 159 (1789).

Trees, shrubs, lianas, sometimes epiphytic, occasionally nearly herbaceous, associated with mycorrhizal fungi, some mycoheterotrophic. Leaves simple, alternate, opposite or whorled, margin entire to serrate, occasionally revolute, without stipules. Inflorescence usually a bracteate raceme, flowers sometimes solitary, either terminal or axillary. Flowers usually bisexual, sometimes unisexual in which case the plants are dioecious, actinomorphic to slightly zygomorphic. Sepals 4–5, free to slightly connate. Petals usually 4–5 and connate but sometimes free, often campanulate-urceolate, sometimes funnelform, often pendulous. Stamens 8–10, filaments free or adnate to corolla, sometimes connate, sometimes spurred near junction with anther; anthers becoming inverted, often opening by 2 apical pores, sometimes by slits, in some cases awned or apex narrowed to form a tubule, pollen shed in tetrads, rarely in monads, usually tricolporate, sometimes with viscin threads. Carpels 2–10, usually 5 or 4, ovary superior to inferior, usually with axile or deeply intruded parietal placentation. Style 1, hollow, with fluted cavity, stigma capitate to strongly lobed; ovules 1 to numerous per locule, unitegmic, tenuinucellar. Intrastaminal nectary disc usually present at base of superior ovary or at top of inferior ovary. Fruit a septicidal or loculicidal capsule, berry, or 1-several pitted drupe. Seeds small to minute, embryo developed to undeveloped.

Number of genera and species—Ericaceae comprise approximately 126 genera and 3,995 species (Stevens 2001). Eleven largely monospecific genera comprise fully mycoheterotrophic species. One genus, *Pyrola*, has a single mycoheterotrophic taxon.

Distribution—Cosmopolitan, but uncommon in many lowland tropical and desert regions. The mycoheterotrophic species are primarily temperate and when found in tropical regions are in montane habitats.

Classification—Ericaceae are part of Ericales, which also include Actinidiaceae, Balsaminaceae, Cyrillaceae, Clethraceae, Diapensiaceae, Ebenaceae, Fouquieriaceae, Lecythidaceae, Marcgraviaceae, Mitrastemonaceae, Pentaphylacaceae, Polemoniaceae, Primulaceae, Roridulaceae, Sapotaceae, Sarraceniaceae, Sladeniaceae, Styracaceae, Symplocaceae, Tetrameristaceae, and Theaceae (APG 2009). Ericaceae is the only family among these with mycohetrotrophic species. *Pyrola* has often been placed with three to four other small genera in its own family, Pyrolaceae, and the remaining mycoheterotrophic genera have been segregated as Monotropaceae. Recent phylogenetic analyses (summarized in Kron et al. 2002) have shown these groups to fall within, but near the base of, Ericaceae. Relationships among these basal lineages are still somewhat unclear, but the pyroloids and monotropoids do not appear to form a monophyletic group (Freudenstein and Broe, unpubl.)

Evolutionary history—Ericaceae fall clearly into Ericales, a lower Asterid group that is defined by both molecular and morphological characters (Anderberg 1992; Anderberg et al. 2002). The closest relatives of the family appear to be Clethraceae and Cyrillaceae. Fossils of Ericaceae comprise largely leaf impressions, but seeds and fruits are also known. They are from Tertiary to late Cretaceous, with perhaps the oldest being a charcoalified flower from the Turonian of New Jersey (Nixon and Crepet 1993). The crown node date for Ericales proposed by Bremer et al. (2004) based on molecular dating is ca. 114 Ma, putting Ericaceae somewhat younger than that.

Ecology—Many genera of the family are characterized by urceolate flowers, while others (e.g., *Rhododendron*), have much more open flowers. Anthers that dehisce poricidally are common, bees engaging in vibratory stimulation to release pollen. Bird pollination is also known in some

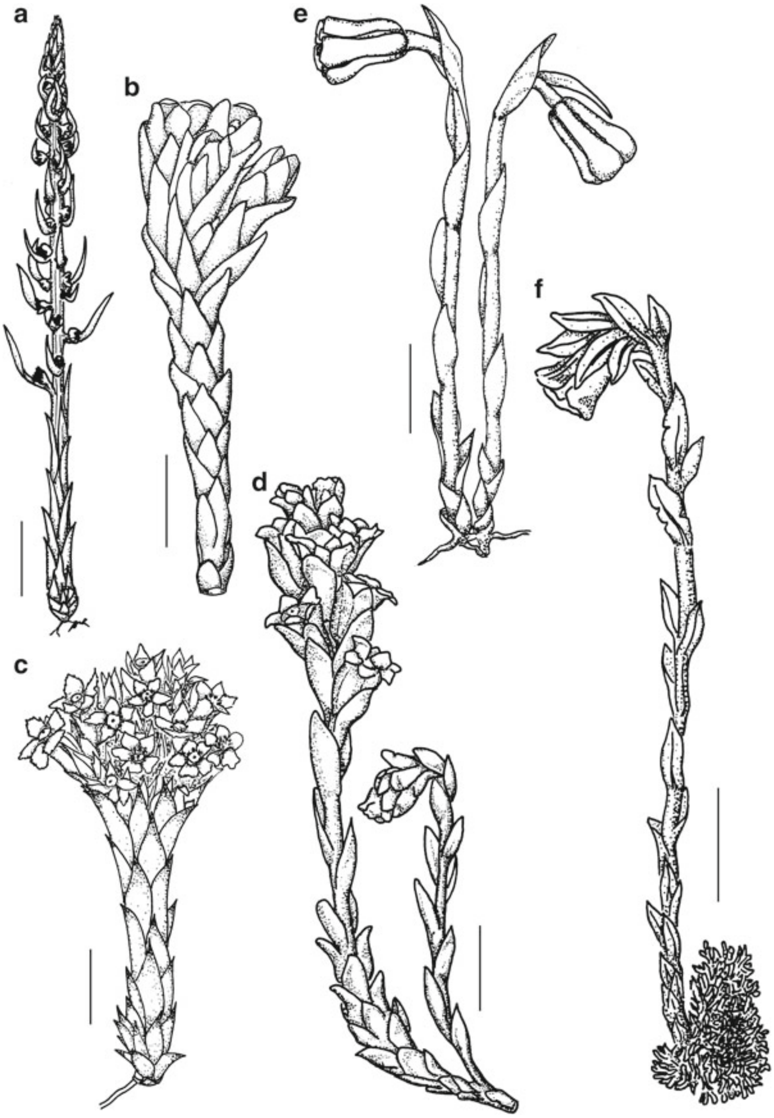

Fig. 2.14 Fully mycoheterotrophic Ericaceae (part 1). (**a**) *Allotropa virgata*. (**b**) *Cheilotheca malayana*. (**c**) *Hemitomes congestum*. (**d**) *Hypopitys monotropa*. (**e**) *Monotropa uniflora*. (**f**) *Monotropastrum humile*. Redrawn from Flora of North America Editorial Committee (2009), except (**b**) redrawn from Hooker (1886), (**d**) redrawn from Fitch (1924), and (**f**) redrawn from Yang et al. (1999). Bar = 3 cm

tropical groups. Often associated with acidic soils, most members of the family are terrestrial, but tropical epiphytes also occur. Members of the family can predominate in acidic bogs and are frequent in arctic regions. Given their frequent occurrence in areas of low nutrient availability, the family is well-known for its mycorrhizal associations. They exhibit three of the fundamental mycorrizal types listed by Smith and Read (2008)—ericoid, arbutoid, and monotropoid. Imhof (2009) examined those types in detail and characterized additional subtypes. Full mycoheterotrophy appears to have arisen twice in the family—once in the monotropoids and a second time in *Pyrola aphylla* in the pyroloids (Freudenstein and Broe, unpubl.). Bidartondo and Bruns (2001, 2002) enumerated the fungal groups with which the monotropoids associate.

2.5.9.1 *Allotropa* (Figs. 2.14a, 2.15d, and 4.16a)

Allotropa Torr. & A. Gray, Pacific Railr. Rep. 6: 81 (1858).

Racemes to 50 cm tall, fleshy, the white axis typically striped longitudinally with red, with

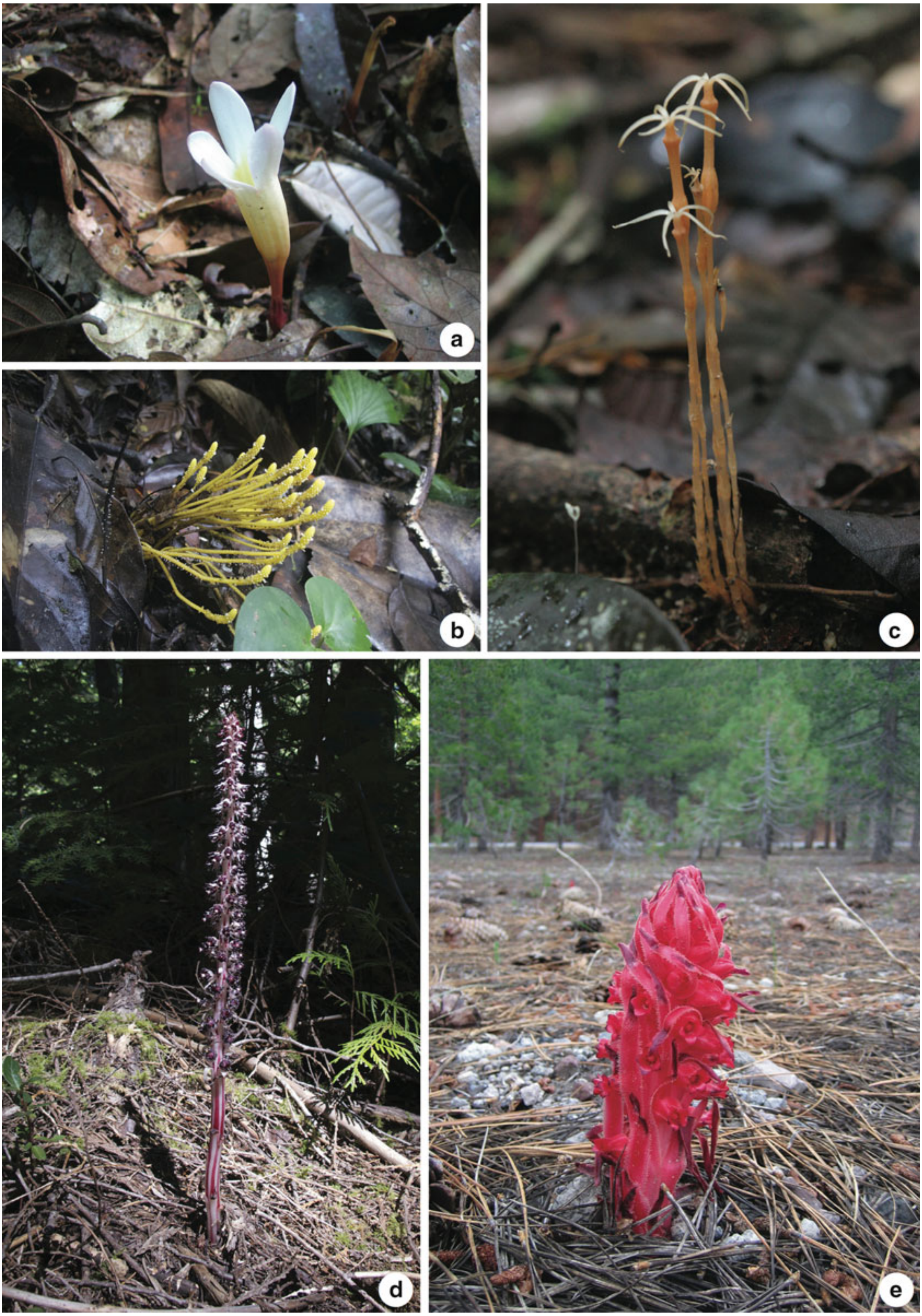

Fig. 2.15 Fully mycoheterotrophic species in eudicots: (**a**) *Voyria clavata* (Gentianaceae). (**b**) A large clump of *Epirixathes* plants (Polygalaceae) from Malaysian Borneo. (**c**) Voyria tenuiflora (Gentianaceae) photographed in French Guiana by Heiko Hentrich. (**d**) *Allotropa virgata* (Ericaceae) in Umqua Forest, Oregon, USA. (**e**) *Sarcodes sanguinea* (Ericaceae) at Lassen Volcanic National Park in California, USA

occasional white bracts that are at first appressed to axis, becoming recurved and eventually purplish with age. Root mass comprising slender brittle roots with occasional shoots, frequently several racemes produced from each mass. Flowers produced on upper half of axis, each subtended by a narrow white bract that is longer than the perianth, and borne on a short pedicel, protogynous, glabrous. Sepals rarely present, but if so reduced to two or more narrowly lanceolate or filiform segments. Petals 5, free, elliptic with rounded to acute apices, margins irregular to erose, white, forming a campanulate corolla. Stamens 10, incurved over ovary and slightly shorter than pistil, filaments white, terete except at base where they are flattened, glabrous; anthers dark red, basifixed, dehiscing by two pore-like slits. Ovary spheroid-slightly ellipsoidal, 5-locular, with axile placentation, glabrous, abruptly narrowed to a short style whose base may be sunken slightly into ovary; stigma discoid, obscurely five-lobed, red; nectary represented by 10 lobes between stamen bases. Fruit a loculicidal capsule. Seeds linear, ca. 1 mm, numerous.

One species, *A. virgata* (“Sugar Stick”), in western North America from the Sierra Nevada in California in the south to southern British Colombia in Canada in the north. Infrequent but sometimes locally abundant, in mixed or evergreen forests, generally flowering from June to August. Flowers may be selfing, although bumblebees have been observed visiting the flowers of *Allotropa* (Wallace 1975). Seeds are presumably dispersed by wind. Clonal reproduction has been reported as well (Lichthardt and Mancuso 1991). Copeland (1938) studied the morphology. Bidartondo and Bruns (2001, 2002) sequenced the ITS region of the fungal symbionts of a number of *Allotropa* plants from California and Oregon and found that all investigated specimens were associated with a narrow clade within the basidiomycete fungal genus *Tricholoma*.

2.5.9.2 *Cheilotheca* (Fig. 2.14b)

Cheilotheca J. D. Hooker in Bentham et J. D. Hooker, Gen. 2: 605, 607 (1876).
Chilotheca T.E. von Post & C.E.O. Kuntze (1903), orth. var.
Wirtgenia H. Andres, Verh. Bot. Vereins Prov. Brandenburg 56: 61 (1914).
Andresia H. Sleumer, Fl. Males., Ser. 1 6: 669 (1967).

Racemes to 10 cm tall, inconspicuous, white to reddish or purplish, stout, fleshy, and densely covered with imbricate bracts. Racemes with 1–few flowers. Root mass shallow, loosely organized, of highly branched, slender, brittle roots, probably perennial like those of all other members of the subfamily. Floral axes emerging from soil erect rather than nodding as in *Monotropa*, with usually a few inflorescences per root mass. Inflorescences with a single flower each are not uncommonly mixed in with racemes. Flowers erect at anthesis on short, stout pedicels, each subtended by a broad-based bract. Bracts broader and generally larger than perianth segments, overlapping with acute thickened apices. Calyx polysepalous; sepals 2–4, sometimes difficult to discern from nearby bracts except for their position on the pedicels, arranged in a lateral pair and a dorsiventral pair; usually the dorsiventral pair will be lacking if there are fwer than 4 sepals; sepals may lack the conspicuously constricted acute apices found on bracts. Corolla polypetalous; petals 3, distinctive, oblong, imbricate over stigma in bud; apices of petals broad, deeply concave and quite thick compared to the lower portions of petals which taper little from a point just below apex. Stamens 6, in 2 series of alternating lengths; filaments flattened, straight, finely pubescent. Anthers in *Cheilotheca khasiana* basifixed linear, dehiscing by longitudinal slits; in *C. malayana* anthers hippocrepiform, dehiscing by a single, somewhat introrse, terminal slit over the connate sacs. Pistil narrow ampulliform with imperceptible external transition area between style and ovary; stigma with 6 low lobes, capitate and slightly umbilicate; style straight, tapering, and stout; ovary slightly pubescent, unilocular; placentation parietal; placentas 6; nectaries represented (not clear in *C. khasiana*) by short lobes projecting downwardly between staminal bases. Seeds numerous, embedded in viscous material within fruit (Reproduced with small changes from Wallace 1975).

Cheilotheca comprises three species, *C. khasiana*, *C. malayana*, and *C. sleumeriana*, which are achlorophyllous and putative full mycoheterotrophs. They are all very poorly known. *Cheilotheca khasiana* is only known from the type locality in western Assam, India. *C. malayana* is restriced to the state of Perak in Malaysia, where it has been found in upper montane dipterocarp and oak-laurel forests (Keng 1974; Wallace 1975). *C. sleumeriana* is based on a single collection from Sumatra (Keng 1974). Keng (1974) merged *Cheilotheca* and *Monotropastrum*, creating a heterogeneous group. Observations on pollination, seed dispersal, and mycorrhiza for these rare species are lacking.

2.5.9.3 *Hemitomes* (Fig. 2.14c)

Hemitomes A. Gray, Pacific Railr. Rep. 6: 80 (1858).
Newberrya Torr., Ann. Lyceum Nat. Hist. New York 8: 55 (1864).

Root mass comprising short brittle roots from which emerge one or more inflorescences. Inflorescence axis covered with imbricate bracts. Racemes congested, to 10 cm tall, variable in form, from a simple structure compressed into a capitate inflorescence at the soil surface to a compound structure with cymulose branches to occasionally a solitary flower. Flowers and inflorescence axis reddish to pink to white or slightly yellowish, each flower subtended by a ciliate-margined bract that is longer than the perianth. Flowers 4–5-merous, protogynous. Pedicels stout, erect. Sepals free, appressed to corolla, glabrous on abaxial surface, with scattered trichomes on adaxial surface, when four of two unequal pairs, with lateral pair keeled, longer than dorsiventral pair, which are flattened. Petals connate, apical lobes narrowly ovate, glabrous abaxially but densely hairy adaxially, slightly saccate at base. Stamens usually 8, in two series with alternating lengths, filaments slender, terete, pubescent; anthers basifixed, without awns or appendages, dehiscing by two elongate slits; adaxial anther sacs smaller and shorter, becoming joined to adaxial sacs at dehiscence, obscured at maturity. Pistil narrowly ampulliform, style pubescent, merging imperceptibly with ovary. Stigma discoid, smooth, unlobed, subtended by a ring of hairs, with a depression in the center, yellow; ovary unilocular, with parietal placentation. Nectaries present as 8 paired lobes projected between staminal bases. Fruit a globose berry with a sticky mass of numerous minute seeds inside. Seeds subovoid, endosperm present.

One species, *Hemitomes congestum* ("Gnome Plant"), in mixed or coniferous forests in western North America. Self-pollination may occur, although bumblebees have been collected visiting the flowers (Wallace 1975). Seed dispersal has not been studied, but the sticky seeds are presumably dispersed by animals. Morphology and anatomy were studied by Copeland (1934, 1941). Populations of *Hemitomes congestum* from Oregon were found to associate with a narrow range of *Hydnellum* fungi (Basidiomycota) (Bidartondo and Bruns 2001).

2.5.9.4 *Hypopitys* (Fig. 2.14d)

Hypopitys J. Hill, Brit. Herbal 221 (1756).
Hypopithys G.A. Scopoli, Fl. Carniol., ed. 2. 1: 285 (1771).
Hypopithis Rafinesque, Med. Repos. ser. 3. 1: 297 (1810).

Racemes slender, to 30 cm tall, fleshy, arising from a mass of brittle roots, 1-several flowered, secund, nodding at anthesis, erect in fruit, cream-colored to tawny brown to reddish, with occasional bracts. Flowers subtended by single pubescent bracts that are elliptic to ovate to narrowly ovate, erose-lacerate. Pedicels slender, finely pubescent. Sepals usually 4–5, oblanceolate, pubescent adaxially or on both surfaces, margin ciliate. Petals rectangular to slightly spatulate, pubescent on adaxial only or on both surfaces, slightly deflexed at apex, narrowed at base by infolding of margins to form a distinct saccate structure, pubescent on one or both surfaces, erose to coarsely toothed. Stamens included, about equaling the length of the pistil, filaments pubescent, somewhat flattened, arranged in two series of alternating lengths. Anthers hippocrepiform, shortened, opening by a terminal slit across the anther sacs. Ovary spheroidal, lobed, pubescent, narrowed abruptly to a cylindrical style that broadens toward apex, bearing a funnelform stigma with undulating inward lobes, with a distinct zone of coarse hairs just below stigma. Nectaries represented by 8–10 paired lobes projecting downward between stamen bases. Fruit a loculicidal capsule. Seeds minute, scobiform.

Hypopitys monotropa has the broadest continuous distribution range of any Monotropoideae, and any mycoheterotrophic plant in general (but it may consist of multiple separate species). In the New World *H. monotropa* occurs from Alaska and British Colombia in the north, throughout northwestern and eastern USA, and into Mexico and Central America in the south. In the Old World, it is found throughout most of Europe and into Central Asia, and east through Afghanistan and along the Himalayas in India and Nepal into China and Japan. *Hypopitys* associates with *Tricholoma* fungi (Bidartondo and Bruns 2001). Bumblebees (*Bombus* spp.) serve as cross-pollination agents in *Hypopitys* (Klooster and Culley 2009).

Although *H. monotropa* and *Monotropa uniflora* have often been placed together in *Monotropa*, molecular phylogenetic studies have demonstrated the paraphyletic nature of *Monotropa* and suggest the presence of cryptic species within *M. hypopithys* (Cullings 2000; Bidartondo and Bruns 2001, 2002; Tsukaya et al. 2008; Freudenstein and Broe, unpubl.).

2.5.9.5 *Monotropa* (Figs. 2.14e and 4.14a)

Monotropa L., Sp. Pl. 1: 387 (1753).
Monotropion Saint-Lager, Ann. Soc. Bot. Lyon vii: 130 (1880).

Inflorescence 1-flowered, slender, often clustered, to 30 cm tall, wholly white to red, arising from a dense mass of highly branched brittle roots, nodding as it emerges from the soil and at anthesis, but erect in fruit, with occasional bracts on the axis. Bracts subtending flowers narrowly elliptic to lanceolate with a lacerate to erose margin. Sepals apparently absent. Petals 5–8, quincuncial, spatulate, apex truncate to rounded, pubescent adaxially, prominently saccate at base. Stamens 8–14, filaments terete above, flattened below, sparsely pubescent. Anthers short, appearing somewhat peltate because of a horizontal orientation at maturity, without awns or appendages, opening by slits that are oriented laterally. Ovary ovoid, appearing as if covered by plates corresponding to the 5–6 locules that will eventually form the capsular valves, glabrous, placentation axile. Style distinct, stout, gradually expanding to a broadened stigma that is lobed-undulating with a prominent central cavity. Nectary present as prominent pairs of fingerlike lobes surrounding bases of alternate stamens. Capsule loculicidal, containing numerous minute scobiform seeds with endosperm.

Monotropa uniflora is widespread in North America, and its distribution extends into Central America and even Colombia. The species is absent from Europe and Central Asia, but occurs in southern China, Japan, northern India, Nepal, and Bhutan. Copeland (1941) studied its morphology and anatomy. *Monotropa uniflora* roots are colonized by a narrow range of Russulaceae fungi (*Russula* or *Lactarius*) (Bidartondo and Bruns 2001, 2002; Bidartondo 2005). Bumblebees (*Bombus* spp.) serve as cross-pollination agents in *Monotropa* (Klooster and Culley 2009).

2.5.9.6 *Monotropastrum* (Fig. 2.14f)

Monotropastrum Andres, in Hand.-Mazz., Symb. Sin. 7: 766 (1936).
Monotropa D. Don, Prodr. Fl. Nepal 151 (1825).
Monotropanthum H. Andres, Feddes Repert. Spec. Nov. Regni Veg. 64: 87 (1961).

Inflorescences arising from masses of congested brittle roots, often several per root mass. Inflorescences scapose or racemose, to 15 cm tall, elongate, fleshy, white, with sterile bracts, emerging from soil with the flowers nodding and nodding at anthesis, but erect in fruit. Flower 3–4 (-5)-merous, white, but reported to be occasionally yellowish or reddish. Sepals free, usually 3, elliptic-ovate, glabrous, appressed to corolla, with entire to lacerate margins, rounded to obtuse to acute at apex. Petals free, 3–4, oblong-obovate, pubescent adaxially, glabrous abaxially, saccate at base, convex, margins entire, apices rounded to truncate. Stamens 6–10, twice as many as petals, in two series of alternating lengths. Filaments pubescent to glabrous. Anthers basifixed, horizontally reniform, with a nearly horizontal dehiscence suture. Ovary globose to ovoid, lacking grooves or plates on sides, finely pubescent, unilocular, placentation parietal. Style arising from the narrowed ovary, short, stout, terminating in a broad funnelform stigma, which may be bluish-black or yellow. Nectaries present as slender projections in pairs around bases of alternating stamens or as a lobed circular structure. Fruit a globose to ovoid berry bearing many minute ovoid seeds.

This genus contains two to three species: *Monotropastrum humile* and its occasional segregate *M. humile var. glaberrima*, and *M. sciaphilum*. *Monotropastrum humile* is known from montane mixed and deciduous forests in temperate and subtropical Asia (Bhutan, Burma, southern China, India, Japan, Laos, Nepal, Russia, South Korea, Thailand, and Vietnam). *Monotropastrum sciaphilum* is known only from the type collection (as *Eremotropa sciaphila*) from Yunnan, China (Wallace 1987). *Monotropastrum humile* is pollinated by bumblebees (Tanaka 1978) and seeds are dispersed by insects (Ushimaru and Imamura 2002). Populations of *Monotropastrum humile* var. *humile* from Japan and Taiwan were found to associate with basidiomycete fungi within the genus *Russula* (Bidartondo and Bruns 2001; Bidartondo 2005; Yokoyama et al. 2005), while plants referable to *M. humile* var. *glaberrima* were asscoiated with Thelephoraceae (Yokoyama et al. 2005)

2.5.9.7 *Monotropsis* (Figs. 2.16a and 7.3a, b)

Monotropsis Schweinitz ex S. Elliott, Sketch Bot. S. Carolina 1: 478 (1817).
Schweinitzia S. Elliott ex T. Nuttall, Gen. 2: Add. (1817).
Cryptophila W. Wolf, Amer. Midl. Naturalist 8: 115 (1922).

Inflorescences in clusters or solitary, arising from a diffuse mass of roots. Racemes emerging from soil in a somewhat nodding position, secund, with more or less crowded flowers. Axes purplish-pinkish, to 13 cm tall, with elongate, acute, scarious bracts becoming brown at or after anthesis. Flowers subtended by a single membranous bract and often 2–3 smaller bracteoles. Flowers tyically 5-merous, purplish to maroon to white, borne on short pedicels. Sepals free, narrowly lanceolate to ovate, closely appressed to corolla and in *M. odorata* somewhat obscuring it, glabrous, brown-scarious at maturity. Petals connate, lobes free for about 1/3 their length, either purplish-violet with or without white tips, or entirely white, glabrous, slightly saccate at base. Stamens 10, occuring in two series of alternating lengths; filaments slender, flattened, glabrous. Anthers dorsifixed, without awns or appendages, the sacs of equal size, dehiscing with a common slit for each pair of ad- and abaxial sacs. Pistil flask-shaped and glabrous with a subglobose ovary from which a style narrows, capped by a thickened discoid stigma, obscurely lobed and with a central depression. Overy unilocular with parietal placentation. Nectaries comprising 10 downward-pointing pairs of lobes between bases of the short series of stamens. Fruit a globose berry with a sticky mass containing the numerous minute seeds that contain endosperm.

Monotropsis consists of two mycoheterotrophic species, *M. odorata* (“Sweet Pinesap”), which occurs in the Appalachian Mountains of southeastern North America and *M. reynoldsiae*, restricted to northern Florida. *Monotropsis odorata* is found almost exclusively growing in upland, mixed oak–pine forests where it flowers in spring (Jones 2005), while *M. reynoldsiae* occurs in scrub oak hammocks and flowers in December-January. *Monotropsis odorata*, which is relatively rare and easily overlooked, is known for its highly fragrant flowers (Wallace 1975). Copeland (1939) studied the morphology of *M. odorata*. Cross-pollination of *M. odorata* is carried out by bumblebees (*Bombus* spp.) and the seeds are animal dispersed (Klooster and Culley 2009). *Monotropsis odorata* was found to associate with a narrow clade of fungi of the genus *Hydnellum* (Basidiomycota) (Bidartondo and Bruns 2001; Bidartondo 2005). *Monotropsis reynoldsiae* is even more rare and has not always been recognized as distinct from *M. odorata*.

2.5.9.8 *Pityopus* (Figs. 2.16b and 4.17a)

Pityopus Small, N. Amer. Fl. 29: 16 (1914).
Monotropa Eastwood, Bull. Torrey Bot. Club 29: 75, pl. 7 (1902).
Hypopitys A. Heller, Muhlenbergia 9: 68 (1913).

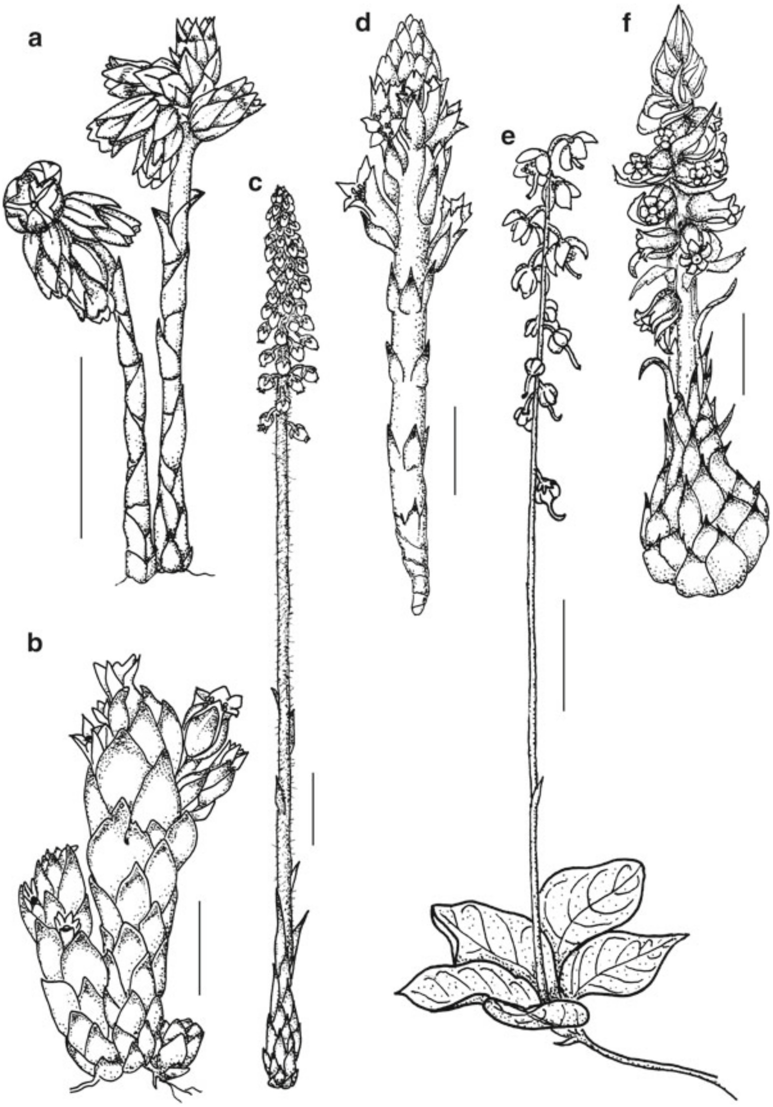

Fig. 2.16 Fully mycoheterotrophic Ericaceae (part 2). (**a**) *Monotropsis odorata*. (**b**) *Pityopus californica*. (**c**) *Pterospora andromedea*. (**d**) *Pleuricospora fimbriolata*. (**e**) *Pyrola picta*. (**f**) *Sarcodes sanguinea*. Redrawn from Flora of North America Editorial Committee (2009). Bar = 3 cm

Root mass comprising a network of slender, brittle, branched roots. Racemes compact, to ca. 10 cm tall, up to several per root mass, sometimes branched below soil level resulting in a congested mass of racemes, usually several-flowered but sometimes reduced to a single flower, often appearing only slightly above soil level, white to yellowish. Flowers subtended by single concave bracts that are longer than perianth segments, erect, 4-merous, terminal flower sometimes 5-merous. Sepals free, narrowly ovate to oblanceovate, appressed to corolla, glabrous; margins ciliate to erose, lateral pair longer than dorsiventral pair. Petals free, 4(-5), rounded and erose at apex, somewhat saccate at base, glabrous abaxially, densely hirsute adaxially. Stamens twice as many as petals, in two series alternating in length, filaments slender, dorsiventrally somewhat flattened, glabrous or somewhat pubescent basally. Anthers hippocrepiform, opening by a single slit curving over the anther apex. Pistil ampulliform. Stigma yellow, slightly lobed, subtended by a ring of dense hairs, style indistinct, gradually tapering from ovary. Ovary unilocular, pubescent, with parietal placentation. Nectaries comprising lobes that project downward between stamen bases. Fruit a globose berry containing a sticky mass with numerous small seeds.

This genus contains a single species, *P. californicus* ("California pinefoot"), growing in moist conferious or mixed forests in California, Oregon, and Washington. It flowers from May to July, but is very difficult to spot and is among the rarest of all North American Monotropoideae. Its morphology was studied by Copeland (1935). Pollination syndrome and dispersal agents have not been studied in detail, athough there is some information that bumblebees may act as cross-pollination agents (Wallace 1975). *Pityopus californicus* associates with several species groups of *Tricholoma* fungi (Basidiomycota) (Bidartondo and Bruns 2002).

2.5.9.9 *Pleuricospora* (Fig. 2.16d)

Pleuricospora A. Gray, Proc. Amer. Acad. Arts 7: 369 (1868).

Racemes one or several from a slender, brittle, diffuse root system, erect, to 15 cm tall, often forming clumps, usually multiflowered but can be reduced to a single flower, cream to yellowish. Bracts imbricate, extending from base of plant to apex, upper subtending individual flowers, entire to erose, becoming brownish with age. Flowers usually 4-merous, protogynous, erect on stout pedicels. Sepals free, glabrous, narrowly ovate, erose. Petals free, narrowly ovate, erose-fimbriate, glabrous, apices acute to rounded, spreading at maturity. Stamens 8, glabrous, filaments flattened with a prominent connective between the slender anther sacs. Anther sacs elongate, dehiscing by 2 long slits, without appendages or awns. Pistil ampulliform, style indistinct, narrowed gradually from the ellipsoid, unilocular ovary and capped by five prominent lobes that form the stigma. Nectaries obscure, represented by 8 low ridges. Fruit a globose whitish berry, fleshy with numerous minute, ovoid seeds.

Pleuricospora consists of a single, fully mycoheterotrophic species, *P. fimbriolata* ("Fringed Pinesap"). *Pleuricospora fimbriolata* grows in mixed or coniferous forests in western North America (California, Oregon, Washington), but there are also doubtful records from Mexico (Wallace 1975). *Pleuricospora* flowers mainly in July and August. Observations on pollination syndrome and seed dispersal mechanism are lacking for this species, but its morphology was studied by Copeland (1937). *Pleuricospora fimbriolata* associates with a narrow lineage of fungi within the basidiomycete genus *Gautieria* (Bidartondo and Bruns 2002).

2.5.9.10 *Pterospora* (Figs. 2.16c and 4.15a)

Pterospora Nuttall, Gen. N. Amer. Pl. 1: 269 (1818).

Racemes to 200 cm, slender, many-flowered, reddish-pink to tawny brown, with a narrow glandular to pubescent bracteate axis arising from a tight mass of heavily branching brittle roots. Flowers urceolate, protogynous, pendent on slender pedicels, each subtended by a narrow, lanceolate, glandular-pubescent bract with ciliate margins that extends as long or longer than the flower. Sepals 5, free, glandular-pubescent, lanceolate, appressed to corolla, reddish-pink to brownish. Petals connate, cream-colored, apices free, reflexed, rounded to blunt, glabrous, margins minutely erose. Stamens 10, in two series of alternating lengths; filaments slender, laterally flattened and thickened, glabrous. Anthers basifixed and essentially horizontal at maturity, with prominent awns extending from the lower portion of proximal anther sacs, dehiscing by lateral slits. Ovary spheroidal, 5-locular, glabrous, from which ascends a stout, straight, glabrous style, ending in a flat, shallowly 5-lobed stigma, placentation axile. Nectaries present as 10 shallow lobes projecting between staminal bases. Fruit an oblate spheroidal loculicidal capsule, brownish at maturity, pendent. Seeds small, each with a thin membranous wing.

Pterospora consists of a single species, *P. andromedea* ("Pinedrops"), which has a widespread distribution in North America. It is most common in western USA and now rare in the east, and its distribution extends to central Mexico. Copeland (1941) studied its morphology. Pollinators are not known. The winged seeds are presumably dispersed by wind. *Pterospora andromedea* relies on a narrow range of mycorrhizal fungi of the basidiomycete genus *Rhizopogon* (Cullings et al. 1996; Bidartondo and Bruns 2001, 2002; Dowie et al. 2011; Hazard et al. 2011). Fungal specialization exceeds the species level: different genotypes of *Pterospora* were found to grow with different fungal lineages, even when growing in sympatry (Bidartondo and Bruns 2002).

2.5.9.11 *Pyrola* (Fig. 2.16e)

Pyrola L., Sp. Pl. 1: 396 (1753).
Braxilia Rafinesque, Aut. Bot. 102 (1840).
Amelia Alefeld, Linnaea 28: 8, 25 (1856).
Thelaia Alefeld, Linnaea 28: 8, 33 (1856).
Erxlebenia Opiz ex Rydberg, N. Amer. Fl. 29: 28 (1914).

Subshrubs to ca. 40 cm in height. Rhizomes slender, creeping, with sparse roots. Racemes arising from a lax basal rosette of leaves. Leaves subtended by single lanceolate bracts, petioles typically longer than blades, base of lamina often decurrent along petiole, ovate-orbicular-reniform-obovate-elliptical, membraneous to coriaceous, glabrous, sometimes reduced or absent. Flowers subtended by single bracts, pedicels distinct, slender. Flowers pendulous, usually somewhat zygomorphic (although essentially actinomorphic in *P. minor*), with style, stamens, and lower petals downcurved. Sepals usually free or united slightly at base, triangular-lanceolate, margins entire to erose, greenish. Petals free or just slightly united at base, usually obovate, apex broadly rounded, concave. Stamens 10, free, filaments slender, broadened toward base, glabrous, anthers inverting late in development, with two prominent to indistinct horns at base, each with a pore or slit. Ovary spherical-oblate, into which is inserted a narrow style, terminated by a capitate-lobed stigma. Style elongate and downcurved in all but *P. minor*, where it is short and straight. Nectaries absent. Fruits loculicial capsules, pendent, valves connected by slender tissue threads when dehisced. Seeds minute, scobiform, with undifferentiated embryo and loose cellular-reticulate testa.

Pyrola comprises ca. 35 species of small, loosely rosette-forming, nearly herbaceous plants that are found circumboreally and south in the New World to Guatemala and in the Old World to Sumatra in montane habitats. Some species, such as *P. chlorantha*, are occasionally almost leafless. Many species are difficult to separate, especially from preserved material. In the western USA, leafless forms can be relatively common. They have sometimes been treated as a form of *P. picta* (Camp 1940); more recent molecular studies by Jolles (2007) suggest that they may warrant the species status, as *P. aphylla*, that they have often been given. Stable isotope analysis showed that *P. aphylla* was highly enriched in ^{13}C, exhibiting a pattern seen in mycoheterotrophs that associate with ectomycorrhizal fungi, while *P. picta* and other green pyroloids were not enriched for ^{13}C compared to autotrophs (Zimmer et al. 2007; Hynson et al. 2009). However, all examined pyroloids, and especially *P. aphylla*, were enriched for ^{15}N, indicating incorporation of nitrogen from fungi. Both *P. aphylla* and *P. picta* were found to associate with a diversity of fungi, mainly ectomycorrhizal (Hynson and Bruns 2009). Morphological and molecular data support a clade comprising *P. chlorantha* and *P. picta* (including *P. aphylla*) (Freudenstein 1999; Liu et al. 2010). Species of *Pyrola* are cross-pollinated by insects, most commonly flies. Seeds are very small ("dust seeds") and presumably dispersed by wind.

2.5.9.12 *Sarcodes* (Figs. 2.15e and 2.16f)

Sarcodes Torrey, Proc. Amer. Assoc. Advancem. Sci. 4: 193 (1851).
Pterosporopsis A. Kellogg, Pacific (San Francisco) 3: 122 (1854).

Racemes arising from a large mass of brittle roots, with a thick axis and large flowers, to 50 cm tall, strikingly red, solitary or clumped, stout, glandular-pubescent. Flowers horizontal to somewhat downfacing, borne on stout pedicels, subtended by lanceolate, ciliate bracts that are longer than the flowers. Flowers red, protogynous, urceolate, with 5 free sepals that are glandular-pubescent, narrowly ovate, and appressed to the corolla. Petals connate, apices free and spreading, glabrous. Stamens 10, included, glabrous, with slender filaments that are flattened near their bases. Anthers dorsifixed, elongate, opening by large terminal slits. Ovary oblate spheroidal, 5-locular, glabrous, with axile placentation, into which is inserted a stout glabrous style. Stigma subcapitate with 5 shallow lobes and a slight central depression. Nectaries present as 10 low lobes between staminal filament bases. Fruit an irregularly dehiscent capsule. Seeds small, within membranous wings.

The bright red species *Sarcodes sanguinea* ("Snow Plant") is the only member of this genus. It grows in mixed or coniferous forests in western North America (California, Nevada, and Oregon) and Mexico (Baja California). Both bumblebees and hummingbirds have been reported visiting the flowers, but self-pollination has been demonstrated as well (Wallace 1975). The seed dispersal mechanism remains unknown, and the species may reproduce by vegetative reproduction as well (Oliver 1890). *Sarcodes sanguinea* plants rely on a relatively narrow range of mycorrhizal fungi of the basidiomycete fungal genus *Rhizopogon* (Kretzer et al. 2000; Bidartondo and Bruns 2001, 2002; Dowie et al. 2011).

2.5.10 Gentianaceae

Gentianaceae Juss., Gen. Pl.: 141 (1789).

Annual, biennial or perennial, glabrous herbs, shrubs, trees, or rarely lianas; autotrophic, a few achlorophyllous and mycoheterotrophic. Stems erect, decumbent, rarely trailing; rhizomes sometimes present. Leaves generally opposite-deccussate, sometimes in a basal rosette, rarely whorled or alternate, simple and entire, sessile to petiolate; stipules generally absent. Sometimes presence of colleters (multicellular glands) in leaf axils. Inflorescence terminal or axillary (dichasial or monochasial cymes, thyrses, verticillasters or having a solitary terminal flower only); flowers actinomorphic, sometimes slighty zygomorphic, usually monomorphic, rarely imperfect; andromonoecious, gynodioecious or dioecious, iso- or heterostylous. Sepals fused, but free in a few genera, usually green, persistent or rarely absent, often keeled or winged. Petals fused, lobes contorted (twisted) to the right while in bud. Stamens isomerous and alternate with petals; anthers basifixed or dorsifixed, free, rarely connate, two thecae dehiscing longitudinally, rarely with terminal pores. Ovary superior, unilocular or bilocular, rarely pseudotetralocular, placentation parietal or axile; ovules few to many/numerous; style present or absent, straight or deflexed to one side; stigma filiform or two-parted (rarely decurrent along carpel sutures), often capitate, funnelform or 2-lobed. Fruit a capsule, occasionally a berry. Seeds usually small, non-arillate.

In spite of the indubitable monophyly of the Gentianaceae in their current definition (Struwe et al. 1994, 2002; Thiv et al. 2002; Yuan et al. 2003), there is no synapomorphic diagnostic feature confined to the entire family (Struwe and Albert 2002) except the presence of a combination of specific secondary metabolites (xanthone and secoiridoids) (Mandal et al. 1992; Rodriguez et al. 1998; Jensen and Schripsema 2002).

Number of genera and species—Gentianaceae comprise 92 commonly accepted genera and over 1,650 species (Struwe and Albert 2002, updated here). Twenty-five species are achlorophyllous and putative full mycoheterotrophs. These species are part of four genera: *Voyria*, *Voyriella*, *Exacum*, and *Exochaenium*. Species of the North American genera *Bartonia* (four spp.) and *Obolaria* (one sp.) are partial mycoheterotrophs (Cameron and Bolin 2010). Partial mycoheterotrophy is suggested to occur in *Curtia tenuifolia* and species of *Neurotheca* as well (Struwe et al. 2002; Molina and Struwe 2009).

Distribution and habitat—Gentianaceae are a cosmopolitan family, absent only from Antarctica. The majority of the species occurs in temperate zones but the mycoheterotrophic species are restricted to rain forests in the Neotropics and Paleotropics. However, some species of *Voyria* also occur in savannas and extend into subtropical Central America.

Classification—Gentianaceae are part of the order Gentianales, which also includes Rubiaceae, Apocynaceae, Gelsemiaceae, and Loganiaceae (APG 2009). The relationships between these families remain largely unclear (Stevens 2001). Gentianaceae comprise six tribes: Saccifolieae, Exaceae, Chironieae, Helieae, Potalieae, and Gentianeae (Struwe and Albert 2002). Several molecular evidences support the following classification: Saccifolieae is sister to the rest of the family, followed by Exaceae, Chironieae, Potalieae, and finally Helieae and Gentianeae (Struwe et al. 2002; Yuan et al. 2003; Kissling et al. 2009).

Evolutionary history—Fossil records for Gentianaceae are scarce (Struwe and Albert 2002; Yuan et al. 2005) and a minimum age of ca. 50 Ma for the family has been estimated with molecular clock analyses (Yuan et al. 2003). Full mycoheterotrophy has evolved at least four times independently in the family: once in Saccifolieae (*Voyriella*), twice in Exaceae (*Exacum* and *Exochaenium*), and a fourth time in the ancestor of *Voyria* (unplaced, but supposedly not closely related to any of the other fully mycoheterotrophic Gentianaceae lineages).

Ecology—Gentianaceae flowers are pollinated by various vectors, including bees, beetles, hummingbirds, moths, and bats (Struwe and Albert 2002). Fruits and seeds are dispersed by animals (including mammals, bats, and birds) or wind or rain (cf. seed dispersal of *Voyria*). Most species of Gentianaceae are probably arbuscular mycorrhizal but non-mycorrhizal Gentianaceae have been reported as well (Wang and Qiu 2006).

2.5.10.1 *Voyria* (Figs. 2.15a, c, 2.17a, 4.18, 4.19, 4.20, and 7.4)

Voyria Aubl., Hist. Pl. Guiane 1:208 (1775).
Humboldtia de Necker, Elem. Bot. 2: 16 (1790).
Lita Schreb., Gen. Pl. 2: 795 (1791).
Leiphaimos Schltdl. & Cham., Linnaea 6: 387 (1831).
Leianthostemon (Griseb.) Miq., Stirp. Surinam. Select. 147 (1851).
Pneumonanthopsis (Griseb.) Miq., Stirp. Surinam. Select. 150 (1851).
Disadena Miq., Stirp. Surinam. Select. 150 (1851).
Biglandularia H. Karst., Linnaea 28: 416 (1857).

Erect, mycoheterotrophic herbs, up to 30 cm tall. Root system star-like with unbranched roots, or small and coral-like or large with repeatedly branched roots. Stems usually simple, less often brancherd, terete, solitary, or a few together. Leaves opposite, somewhat connate at the base, small, scale-like, the lower ones sometimes alternate. Inflorescence a terminal few- to 30- flowered dichasial/bifurcate cyme or the plant having a solitary, terminal flower only. Flowers erect, rarely nodding, (4-)5(-7)-merous, short- or long-pedicellate, actinomorophic. Calyx tubular to campanulate, (4-)5(-7)-lobed, persistent, sometimes provided with discoid scales at the inner base. Corolla salverform to infundibular, variously colored, far exceeding the calyx, marcescent, apical part often papillate inside, tube elongate, lobes (4-)5(-7), contorted, spreading to recurved, rarely erect. Stamens (4-)5(-7), included in the corolla tube, rarely somewhat exceeding the corolla tube, inserted at various levels in the corolla tube, filaments conspicuous or virtually absent, anthers free or often coherent just below the stigma. Ovary 2-carpellate, 1-locular, sometimes borne on a short gynophore, the parietal placentae protruding, the base of the ovary often provided with two opposite glandular marks or ellipsoid glands, sometimes with two distinctly stalked glands, or eglandular; style filiform, gradually widened towards the ovary; stigma infundibular, rotate, or capitate, with undulate margin, or weakly 2-lobed, appendages sometimes present, ovules anatropous. Fruit a capsule, fusiform to globose, septicidally dehiscent, dehiscing entirely or in the middle only, often indehiscent. Seeds numerous, globose to filiform, in some species with two hair-like projections, embryo few-celled, endosperm present (Maas and Ruyters 1986; Franke 2002).

Voyria has a disjunct distribution with 18 species in tropical and subtropical America and one species with a widespread distribution in tropical

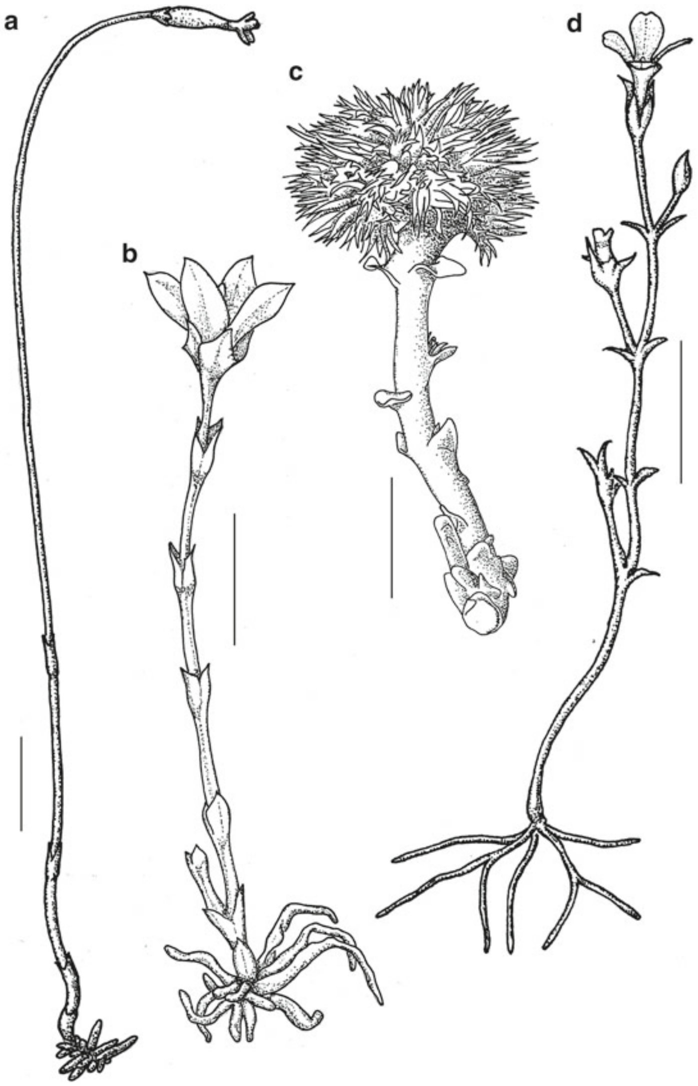

Fig. 2.17 Fully mycoheterotrophic Gentianaceae. (**a**) *Voyria aphylla*. Redrawn from Maas and Ruyters (1986). (**b**) *Exacum tenue*. Redrawn from Struwe and Albert (2002). (**c**) *Voyriella parviflora*. Redrawn from Maas and Ruyters (1986). (**d**) *Exochaenium oliganthum* (drawn after Merckx et al. 103, LV). Bar = 1 cm

West Africa (records from Liberia, Ivory Coast, Ghana, Nigeria, Cameroon, Gabon, and DR Congo) (Raynal-Roques 1967a; Maas and Ruyters 1986; Albert and Struwe 1997). Many neotropical species are widely distributed as well. *Voyria* species occur in various forest types, including lowland rainforest creek forest, swamp forest, montane rainforest hammock forest, and Amazonian caatinga forest. A few species prefer drier vegetation types and grow in white sand savannas and savanna forests. All species are terrestrial, but are sometimes found on dead, decaying logs (Maas and Ruyters 1986). Remarkably, two species have been found growing as epiphytes up to 30 m high on trees (Groenendijk et al. 1997).

Currently DNA data of *Voyria* are lacking, and therefore the phylogenetic relationships of this genus remain to be determined. Certain characteristics (opposite leaves, hypogynous flowers, no latex, no stipules) point to a position close to or in Gentianaceae (Struwe and Albert 2002).

Preliminary analyses based on nuclear and mitochondrial DNA sequences suggest that *Voyria* is an early diverging lineage within Gentianaceae (V. Merckx unpublished results).

Most species of *Voyria* possess brightly colored flowers that emit scent and offer nectar. Consequently, they are generally considered to be cross-pollinated (Maas and Ruyters 1986). Indeed, cross-pollination by butterflies and bees has been observed, although some species may rely on a mixed pollination strategy (individual reproduces both by self-fertilization and out crossing with genetically different individuals) to ensure seed production when pollen transfer by visitors fails (Hentrich et al. 2010). Seed dispersal vectors are poorly studied, but may include water and various animals (Maas and Ruyters 1986; Hentrich et al. 2010). Species of *Voyria* are associated with arbuscular mycorrhizal fungi (Leake 1994; Imhof 1997, 1999b; Imhof and Weber 1997; Franke 2002). Molecular sequencing detected *Glomus* Group A and Diversisporales fungi in the roots of neotropical *Voyria* species (Bidartondo et al. 2002; Merckx et al. 2010b; Courty et al. 2011).

2.5.10.2 *Voyriella* (Fig. 2.17c)

Voyriella Miq., Stirp. Surinam. Select.:146 (1851).
Voyria Aubl. Sect. *Voyriella* Miq., Tijdschr. Wis.-Natuurk. Wetensch. Eerste Kl. Kon. Ned. Inst. Wetensch. 2: 122 (1849).

Erect, mycoheterotrophic herbs, completely white, up to 15 cm tall. Roots filiform. Stems branched or unbranched, fleshy, quadrangular to slightly winged. Leaves opposite, scale-like, small. Inflorescence a terminal or rarely axillary, more or less contracted, 1- to many-flowered bifurcate cyme. Flowers erect, (4-)5(-6)-merous, shortly pedicellate. Sepals almost free, narrowly triangular, persistent, provided with discoid scales at the inner base. Corolla actinomorphic, salverform to tubular, hardly exceeding the calyx, soon falling off, papillate within, lobes small. Stamens (4-)5(-6), included, inserted at various levels in the corolla tube; filaments long or short, anthers free or coherent, introrse, basifixed; connective prolonged beyond the thecae or not, rounded at the base and apex. Ovary bicarpellate, bilocular at the base, unilocular in the upper part, eglandular; placentae parietal. Style filiform, stigma 2-lobed, papillate, ovules numerous, strictly orthotropous. Fruit a capsule, globose to ovoid, indehiscent, provided with a persistent, bifid style. Seeds subglobose, pitted, embryo few-celled, endosperm present.

The genus *Voyriella* consists of one fully mycoheterotrophic species: *Voyriella parviflora* (Maas and Ruyters 1986; Maguire and Boom 1989). Nuclear and chloroplast data suggest that *Voyriella* is a member of the tribe Saccifolieae (Struwe and Albert 2002). *Voyriella parviflora* occurs in lowland forests of northern South America and adjacent Panama. Its main center of distribution is in the Guianas (Maas and Ruyters 1986). *Voyriella parviflora* is autogamous (Oehler 1927). Seed dispersal mechanisms are unknown. *Voyriella parviflora* has been found to associate with *Glomus* Group A fungi (Bidartondo et al. 2002).

2.5.10.3 *Exacum* (Fig. 2.17b)

Exacum L., Sp. Pl. 112 (1753).
Cotylanthera Blume, Bijdr. Fl. Ned. Ind. 707 (1826).

Erect annual herbs to perennial subshrubs, 2 cm to 1 m tall. Stems terete to quandrangular, often with four wings or lines/ribs. Leaves opposite-decussate, rarely verticillate or rosulate, almost leafless in achlorophyllous species. Inflorescence a monochasial or dichasial cyme, sometimes umbel-shaped. Flowers 4- or 5-merous, actinomorphic to often zygomorphic by having the anthers forming a cone above a bent style (enantiostyly). Calyx persistent, each lobe furnished with a keel or a wing that might enlarge in fruit, rarely zygomorphic by having two well-developed wings and three reduced ones. Corolla white to violet, up to 7 cm long, tube short and lobes usually spreading, rarely persistent in fruit. Stamens protruding from the corolla tube, anthers usually connivent around or above the style forming a cone, dehiscent by 1 (in the achlorophyllous species) or 2 apical pores, usually furnished by small papillae on their dorsal sides. Ovary 2-carpellate, 2-locular, placentation axile; style filiform, straight, or curved; stigma small, entire to slightly 2-lobed.

Fruit a capsule, septicidally dehiscent. Seeds numerous, angular, rarely cup-shaped. Testa cells star-shaped or isodiametric. For a detailed description and taxonomy of *Exacum*, see Klackenberg (1985, 2002, 2006)

The genus *Exacum* comprises 68 species (Klackenberg 1985, 2006; Thulin 2001) and shows a typical paleotropical distribution (Klackenberg 1985, 2002; Thulin 2001). *Exacum* has two main centers of diversity, namely Madagascar and the area including Southern India and Sri Lanka. Only a few species occur in Socotra (and the Arabian peninsula), in the Himalayas, Southeast Asia, New Guinea, and in extreme northern Australia. *Exacum* species have a wide spectrum of habitat preferences. Taxa are found from sea level up to the highest mountain tops in Madagascar (ca. 2,800 m elevation), and up to ca. 2,000 m in the Himalayas, South India, and New Guinea. Most species occur in lowland and montane rainforest areas, although they usually grow in full sun (Klackenberg 1985, 1990, 2002). *Exacum* originated in Madagascar and has experienced multiple out-of-Madagascar dispersals (Yuan et al. 2005). The most important is the long-distance dispersal to Sri-Lanka/South-India, which resulted in the extensive radiation of the Socotra-Arabia and other Asian lineages in the northern India Ocean basin regions (Yuan et al. 2005). More recent out-of-Madagascar dispersals include single dispersal of *E. oldenlandioides* to the African mainland, or several dispersals to other islands around Madagascar including the Comores (*E. stenopterum*), or the volcanic island of Mauritius (*E. quinquenervium*) (Klackenberg 1985). The four mycoheterotrophic *Exacum* species occur only in Asia and presumably diversified from an Asian descendant (Klackenberg 2006).

Most *Exacum* species have bright colored enantiostylous flowers suggesting pollination by bees, however no thorough pollination studies have been yet performed on *Exacum*.

Exacum contains four achlorophyllous species (*E. loheri*, *E. nanum*, *E. paucisquamum*, and *E. tenue*) previously placed in the genus *Cotylanthera*. They are distributed from the Himalayas throughout Southeast Asia to New Guinea (Klackenberg 2006). Based on morphological evidences they belong to a small clade of *Exacum* comprising four other tiny chlorophyllous species (Klackenberg 2006) and share the same distribution. The evolution of mycoheterotrophy inside a predominantly chlorophyllous genus has occurred twice within the tribe Exaceae: in *Exacum* in Asia and in *Exochaenium* in Africa. However, yet, few studies have focused on the biology or the evolution of mycoheterotrophy in *Exacum*. Figdor (1897) studied mainly the morphology and anatomy of *E. tenue*, while Oehler (1927) studied its cytology.

2.5.10.4 *Exochaenium* (Fig. 2.17d)

Exochaenium Griseb., DC. Prod. 9: 55 (1845).

Annual, erect or dwarf herbs, rarely achlorophyllous. Stems simple or branched, usually tetragonal, more or less 4-ridged or 4-winged. Leaves well-developed or reduced and scale-like, sessile, opposite, linear-lanceolate to suborbicular. Inflorescence a terminal 1- to many-flowered bifurcate or dichasial cyme. Flowers 5-merous, pedicellate, corolla white, sometimes yellow or salmon, often pendent or inclined, generally with a stylar polymorphism (short- and long-styled flowers). Sepals almost free or forming a short tube, lobes linear-lanceolate to ovate or obovate, dorsally keeled or winged. Corolla tube cylindrical or infundibuliform, the lower portion enlarged in fruit, lobes oblong-obovate, obtuse at the apex or acuminate; filaments filiform, inserted at mid-length of the corolla tube. Stamens included; anthers oblong, basifixed, free or coherent, with a conspicuous apical stipitate gland, with or without two basal minute glands. Ovary ovoid to globose, bilocular, placentation axile, ovules numerous. Style filiform, included in the corolla tube; stigma filiform or clavate, entire or very slightly bilobed, rarely bifid, papillate. Capsule ovoid or obovoid, membranous or coriaceous, septicidally dehiscing by 2 valves. Seeds cubical, black; testa cells star-shaped.

Exochaenium comprises 22 species, all endemic to Africa (Kissling 2012). Most of the species occur on the Katanga plateau (Angola, DR Congo, and Zambia), many extending their distribution to the Sudano-Zambesian domain sensu White (1986). *E. oliganthum*, the single mycoheterotrophic species of the genus, has a remarkable widespread distribution in tropical Africa and has been recorded from Ethiopia, Sudan, Uganda, DR Congo, Equatorial Guinea, Gabon, Central African Republic, Cameroon, Nigeria, Ivory Coast, Guinea-Bissau, Zambia, and Tanzania (Raynal-Roques 1967b; Cheek 2006; Kissling 2012).

The ecology and particular morphology of *E. oliganthum* was described by Raynal-Roques (1967b) and its mycoheterotrophic status has been confirmed. However several individuals determined as *E. oliganthum* have been found to "parasitize" roots of other plant species (mainly Cyperaceae or Poaceae; Nemomissa 2002), but additional research is needed to investigate this claim. Also, within a Zambezi population (*Dessein et al. 499*, NEU) both achlorophyllous and chlorophyllous individuals of this species have been found (Kissling 2012). Fully mycoheterotrophic specimens of *E. oliganthum* associate with arbuscular mycorrhizal fungi from the *Glomus* Group A clade (Franke et al. 2006).

Exochaenium oliganthum is reported to have both underground cleistogamous flowers and aerial chasmogamous flowers (Raynal-Roques 1967b). Heterostyly has consistently been reported for this species (only in the chasmogamous flowers). Its pollination biology has not been studied, but the presence of heterostyly strongly suggests a high outcrossing rate for the chasmogamous flowers, while the morphology of the cleistogamous flowers (i.e., the anthers being compressed on the stigma) suggest selfing. Thus a mixed pollination strategy seems to occur in this mycoheterotrophic species.

Currently no complete phylogeny of the genus exists, however it has been found that *E. oliganthum* is nested deeply inside the genus (Kissling et al. 2009).

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