Chapter 2
History and Natural History of Plants and Their Associates

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Keywords Terrestrialization • Tracheophyte • Mycorrhiza • Origin of pollination • Angiosperm diversification • Bee • Seed dispersal • Bird • Mammal • Cultivation mutualism

2.1 Origin of Land Plants

Life on Earth originated in the sea; thus, land is a frontier for aquatic organisms. Although colonization of land by plants occurred in the Ordovician about 450 million years ago (ma; Field et al. 2015), aquatic microorganisms colonized land as early as 3500 mya (Beraldi-Campesi 2013). When aquatic microorganisms (including cyanobacteria) headed to land, they encountered adverse terrestrial conditions such as drought, extreme diurnal and seasonal temperature changes, low nutrient supply, and strong sunlight. These microorganisms are considered to have achieved terrestrialization by developing a tough, pigmented cell wall, an agglutinated colony structure, and a symbiotic lifestyle. Although modern lichens are associations of internal algae with external advanced fungi belonging to Ascomycetes and Basidiomycetes, colonylike associations of microorganisms, including basal algae and fungi, are thought to have colonized land before the Phanerozoic. Colonization of terrestrial habitats by photosynthesizing multicellular organisms occurred in a clade of green plants containing chlorophyll a and b (Delaux et al. 2012). The order Charales in the division Charophyte adapted to life in ephemeral freshwater pools, which frequently dry up. The body of the Charales is a monoploid gametophyte and comprises a main axis and lateral branchlets occurring in whorls on each node of the axis (Fig. 2.1). The reproductive organs consist of the nucleus (i.e., archegonia-producing ova) and globules (i.e., antheridia-producing flagellate sperm; Fig. 2.2). The sperm swim to the archegonium and fertilize the ovum. The zygote develops into an oospore, which is protected by its tough cell wall containing an unusually stable polymer, sporopollenin. The oospore can resist

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M. Kato, A. Kawakita (eds.), *Obligate Pollination Mutualism*, Ecological Research Monographs, DOI 10.1007/978-4-431-56532-1_2

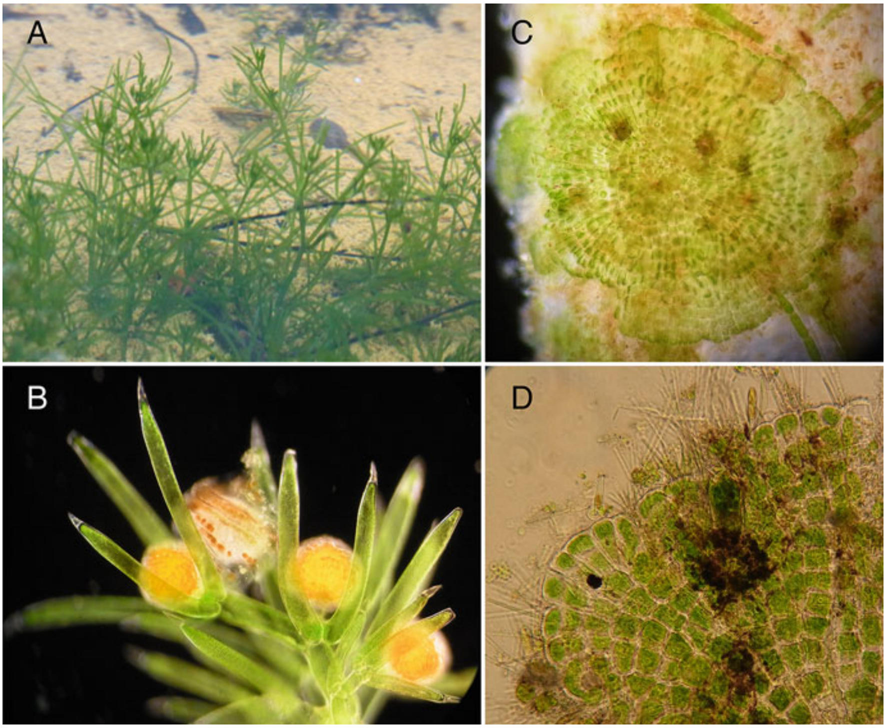

Fig. 2.1 Two derived orders of Charophyta: Charales (**a**–**b**) and Coleochaetales (**c**–**d**). (**a**) *Chara australis*; (**b**) *Nitella flexilis*; (**c**, **d**) *Coleochaete* sp. growing on reed shoots in a pond near Biwa Lake, Japan

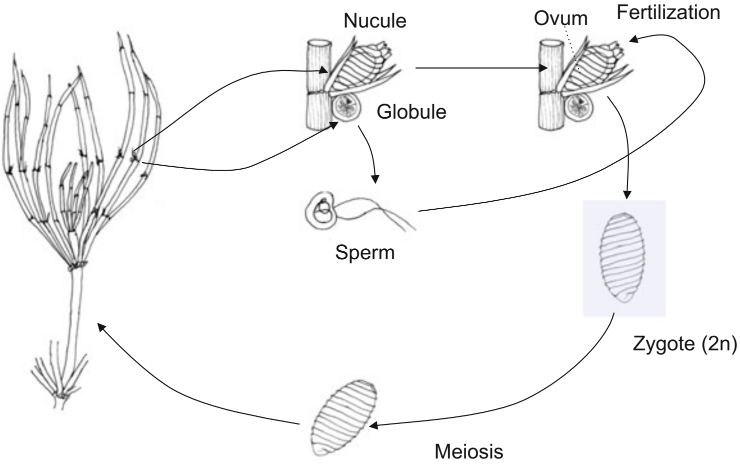

Fig. 2.2 Life cycle of a charophyete, *Chara braunii*

desiccation by remaining in a dormant state, and undergoes meiosis before germination of protonema. Another charophyte order, Coleochaetales, is a parenchymatous disclike alga that grows on substrata in waterfront habitats (Fig. 2.1). In the *Coleochaete*, plural meiospores are produced from a zygote, suggesting that embryos are protected and nourished in maternal tissue (Graham and Wilcox 2000).

The earliest plant that accomplished terrestrialization was the bryophyte (Fig. 2.3), which has acquired a thin extracellular waxy cuticle. Bryophytes possess a precursor of lignan, but lack actual lignin (Weng and Chapple 2010). Sexual reproduction of bryophytes only occurs in wet habitats on rainy days because flagellate sperm released from the antheridium must reach the archegonia by swimming within the water film (Fig. 2.4). The most important adaptation to terrestrial life in bryophytes is protection of zygotes from desiccation and shortage of assimilates. For this purpose, zygotes are protected in maternal gametophyte tissue as embryos, and growth of the sporophyte embryo is facilitated by nutrients provided by the host gametophyte. The parasitic sporophytes finally bear spores, which are coated with a sporopollenin-coated cell wall and are generally dispersed by the wind. Biotic spore dispersal, however, occurs in arctic mosses of the family Splachnaceae. These mosses grow on the dung of herbivorous mammals, and the colored sporophytes emit stinking volatiles to attract flies, which disperse the spores to other dung deposits (Koponen 1990). Bryophytes comprise three distinct clades: Hepaticae (liverwort), Musci (moss), and Anthocerotophyta (hornwort; Fig. 2.5); however, the phylogenetic relationships among these groups are unclear (Cox et al. 2014). Liverworts are thalloid or foliose, mosses are foliose, and hornworts are thalloid. In contrast to mosses and hornworts, liverworts have intracellular oil bodies, which contain various terpenoids and lipophilic aromatic compounds and might contribute to antiherbivore defense. Similar to vascular plants, sporophytes of mosses and hornworts have stomates, which cannot be closed.

2.2 Plants Standing Up from the Land

In the Silurian, a lineage of plants stood up from the land by acquiring upright or clambering shoots with vascular bundles and ramified roots. The former contributed to efficient transportation of water within the plant, and the latter contributed to anchoring and supporting the plant and absorbing water and nutrients from the soil. These vascular land plants are known as tracheophytes, and comprise three extant monophyletic groups: lycophytes (division Lycophyta), ferns (division Polypodiopsida including Sphenophyta), and seed plants (division Spermatophyta; Fig. 2.6). The phylogeny of the three groups is Lycophyta, Polypodiopsida, and Spermatophyta, whereas lycophytes and ferns have been treated as pteridophytes. Vascular bundles are complex structures comprising two organic monomers, cellulose and lignin. Cellulose is a linear chain of β-linked D-glucose, and lignin is synthesized via lignan from phenylpropanoid, which is synthesized from the amino

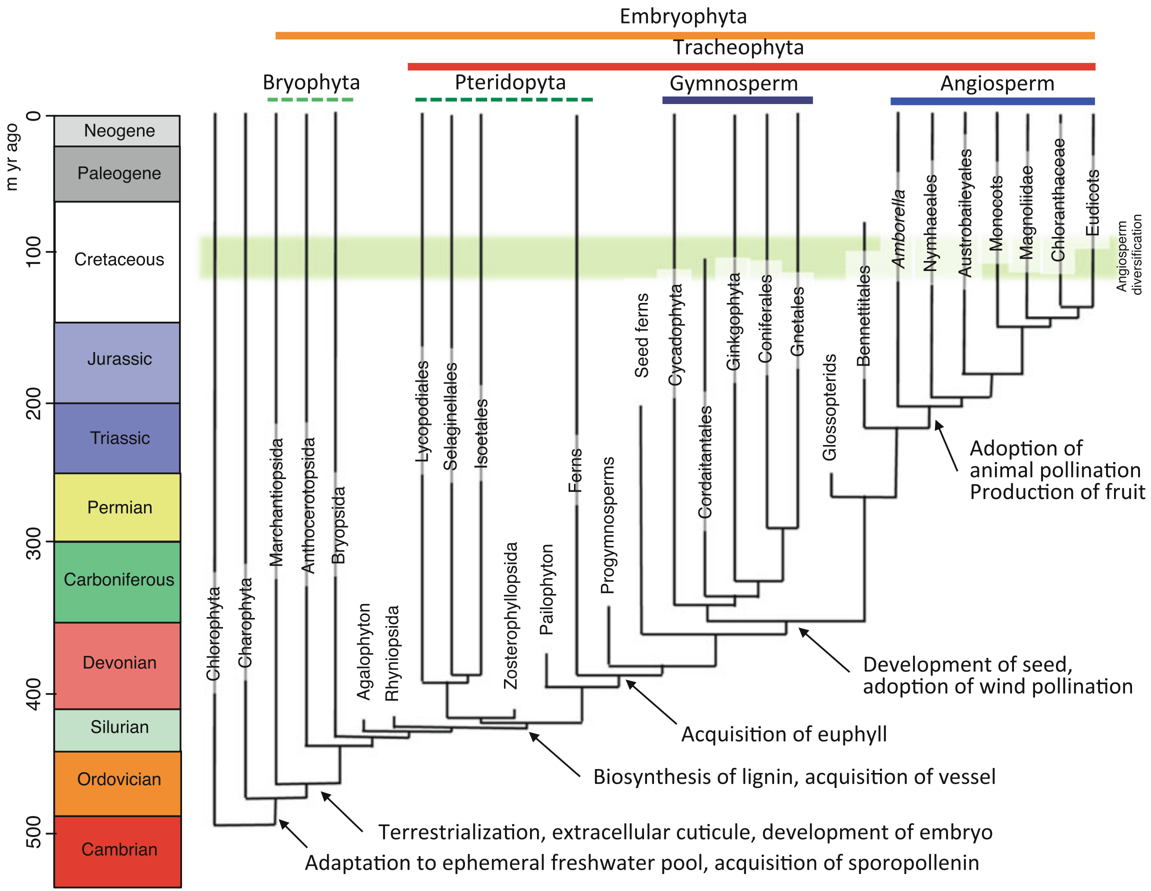

Fig. 2.3 History of diversification of the land plants. The groups shown in broken lines are not monophyletic. Phylogeny and divergence times are based on Kenrick and Crane (1997), McCourt et al. (2004), and Zeng et al. (2014)

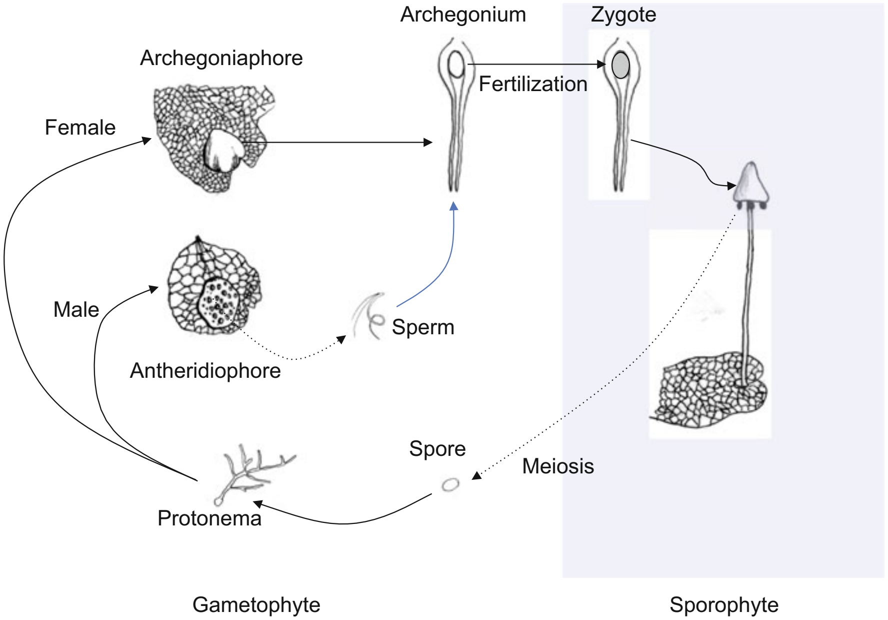

Fig. 2.4 Life cycle of a bryophyte, *Conocephalum conicum*. In bryophytes, small sporophytes parasitize gametophytes. Broken lines show airborne transportation and a *blue* line shows migration in water film

acid phenylalanine. Acquisition of tough vascular bundles enabled tracheophytes to rise up from the land and overpower bryophytes through competition for light. Cellulose and lignin accumulated in the lateral meristem in shoots and formed the cambium, which contributed to secondary growth of shoots and formation of woody shoots and trunks. In pteridophytes, gametophytes (i.e., prothallium) in a monoploid generation and sporophytes in a diploid generation grow separately and independently, although gametophytes are small and lack vascular bundles (Fig. 2.7). Gametophytes are dioecious or monoecious, and have an antheridium and archegonium. As in bryophytes, flagellate sperm released from the antheridium must reach archegonia by swimming within a water film, suggesting that pteridophytes cannot live outside damp habitats. Fertilization occurs in the archegonia, and growth of the zygotes is nourished by the gametophytes. The diploid sporophytes bear spores in the sporangium on fronds (Fig. 2.6). Spores of modern ferns are frequently infested by various insects such as stathmopodid and tineid moths and mirid bugs (Sawamura et al. 2009). Spores released from sporangia are dispersed by the wind, and germinate to form prothallia. Spore dispersal mutualism has not been reported in pteridophytes. The first shrublike forest on Earth formed in damp habitats during the Devonian. The woody plants became greater in height and in trunk diameter, and forests in the Carboniferous were composed of large pteridophyte trees (e.g., *Lepidodendron*, *Sigillaria* [Lycophyta], and *Calamites* [Pteridophyta]). Although arboreal lycophytes became extinct during the Paleozoic,

Fig. 2.5 Three clades of bryophytes: liverworts (**a**–**c**), moss (**d**–**e**) and hornworts (**f**). (**a**–**c**) *Conocephalum conicum*. (**d**) *Polytrichum commune*. (**e**) *Pogonatum minflexum*. (**f**) *Megaceros flagellaris*. On gametophytes, antheridia (**a**), archegonia (**b**, **d**), and sporophytes (**c**, **e**, **f**) are observed

herbaceous lycophytes have survived to the present (Fig. 2.6). The woody trunks of these Paleozoic arboreal plants were embedded underground and turned to coal without decomposing, in part because these forests were formed in swamps where submerged woody deposits tend not to decompose, and because efficient wood-decomposing fungi had not emerged.

2.3 Formation of Mycorrhiza

The roots of tracheophytes are multicellular organs ramifying in the soil. Each root is covered by monocellular root hairs, which mediate absorption of water and nutrients. The root hairs are morphologically and ecologically similar to rhizoids of bryophytes. The absorption function of tracheophyte roots, however, is often mediated by symbiotic mycorrhizal fungi. Cooperative associations between algae and fungi have been widespread since the early stages of terrestrialization (Field et al. 2015) because they could compensate for their functional defects through symbiosis (i.e., algal photosynthesis and fungal absorption of water and nutrients).

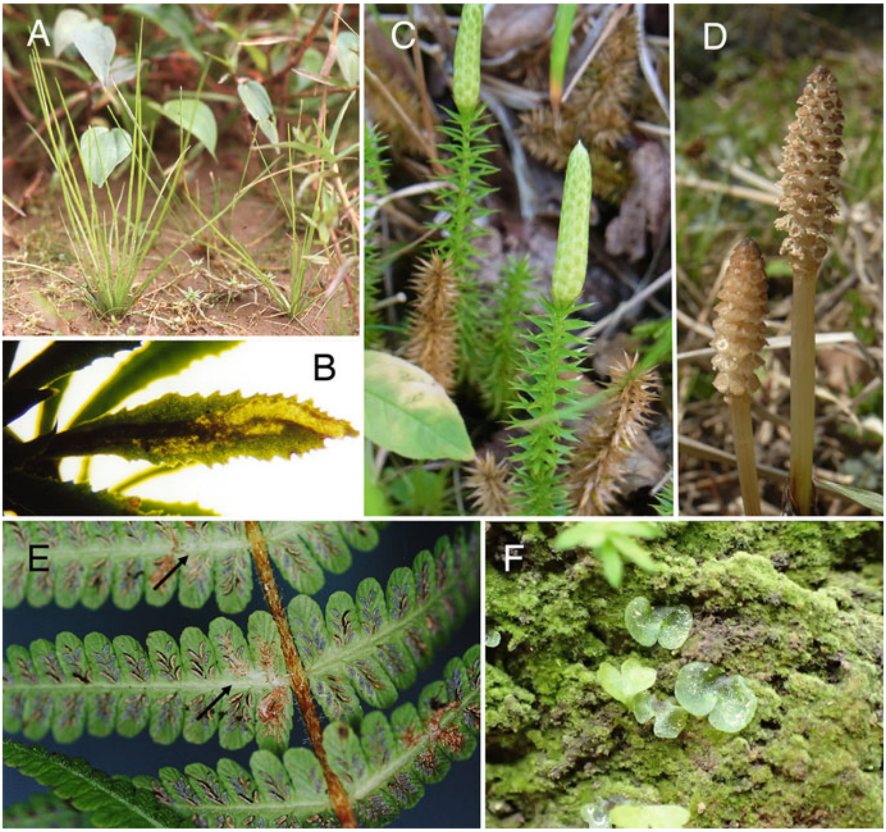

Fig. 2.6 Growing habits of Lycopodiophyta (**a**–**c**) and Pteridophyta (**d**–**f**): Isoetopsida (**a**) Lycopsida (**b**–**c**) Sphenopsida (**d**) and Polypodiopsida (**e**–**f**). (**a**) *Isoetes japonica*. (**b**) *Lycopodium serratum* the leaf of which is mined by a pallopterid fly larva. (**c**) *Lycopodium annotinum* with strobili. (**d**) *Equisetum arvense* with strobili. (**e**) Sori of *Stegnogramma pozoi* with sori, which are infested by stathmopodid moth larvae (shown by *arrows*). (**f**) Prothallia of *Stegnogramma pozoi*

The origin of mycorrhizal symbiosis may be traced back to the Precambrian symbiosis between algae and fungi. The most widespread mycorrhizal symbiosis in the present era is arbuscular mycorrhizal symbiosis. In this symbiosis, the minute hyphae of the basal fungi of the phylum Glomeromycota invade a root cell of land plants and form a highly ramified structure (i.e., an arbuscule; Fig. 2.8), where exchange of assimilates and nutrients between the plant cell and the fungi occurs. Although there is the potential for conflicts of interest between the plants and their mycorrhizal fungi, mycorrhizal mutualism is maintained by the sanction of the plant and fungus against noncooperative behavior by their partners (Kiers et al. 2011). In arbuscular mycorrhiza, the hyphae extending from host roots produce minute underground sporangia, which release spores in the soil. Mycorrhizal symbiosis is believed to be ancient (Simon et al. 1993) because Glomeromycota

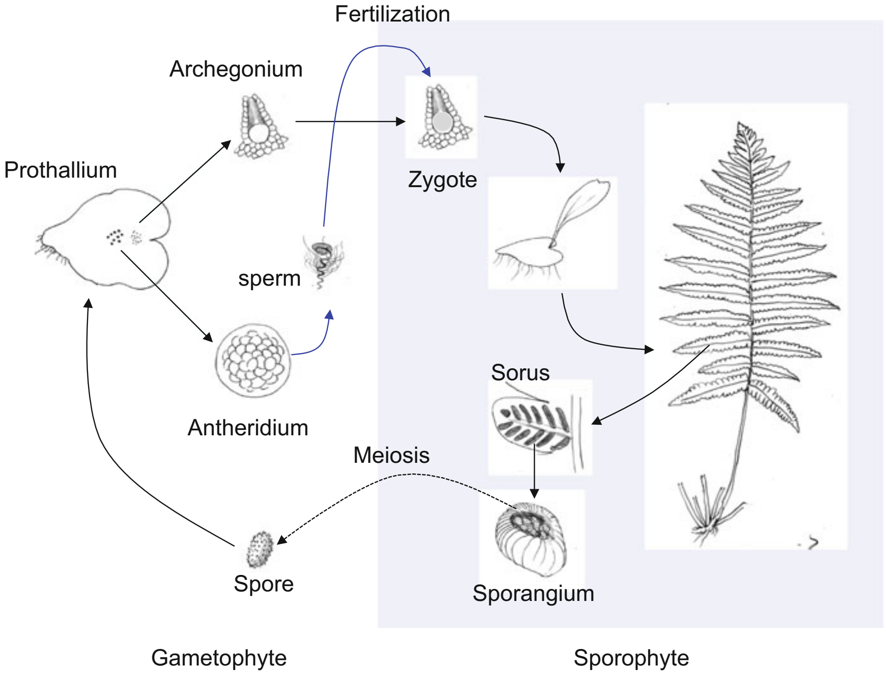

Fig. 2.7 Life cycle of a pteridophyte, *Stegnogramma pozoi*. In pteridophytes, gametophytes and sporophytes grow separately and independently. A broken line shows airborne transportation and *blue* lines show migration in water film

is a basal lineage in the fungal phylogenetic tree, because almost all land plants (including bryophytes) engage in the symbiosis, and because fossilized hyphae of Glomeromycota are found from the Ordovician when only bryophytes grew on land (Redecker et al. 2000). Symbiosis with Glomeromycota is known even in liverworts, which do not have roots. In basal thalloid liverworts, hyphae of the mycorrhizal fungi invade cells of the thallus, and enhance plant fitness by promoting phosphorus and nitrogen uptake from soil (Humphreys et al. 2010). These facts suggest that the initial colonization of land by liverworts was assisted by these arbuscular mycorrhizal fungi. Liverworts and hornworts are symbiotic with arbuscular mycorrhizal fungi of the Glomeromycota and Mucoromycotina, whereas most mosses with multicellular rhizoids are free from mycorrhizal fungi (Bidartondo et al. 2011; Desirò et al. 2013). The sporophytes and gametophytes of Pteridophytes are symbiotic with arbuscular mycorrhizal fungi (Zubek et al. 2010; Ogura-Tsujita et al. 2016). Furthermore, the roots of almost all seed plants, with the exception of several plant families (e.g., Brassicaceae) and aquatic plants, are also symbiotic with Glomeromycota (Table 2.1; Heijden et al. 2015).

The most diverse fungal lineage is the subkingdom Dikarya, which is well-adapted to terrestrial life by losing flagella, acquiring tolerance to desiccation, and developing aerial spore dispersal (James et al. 2006). Dikarya are characterized by a

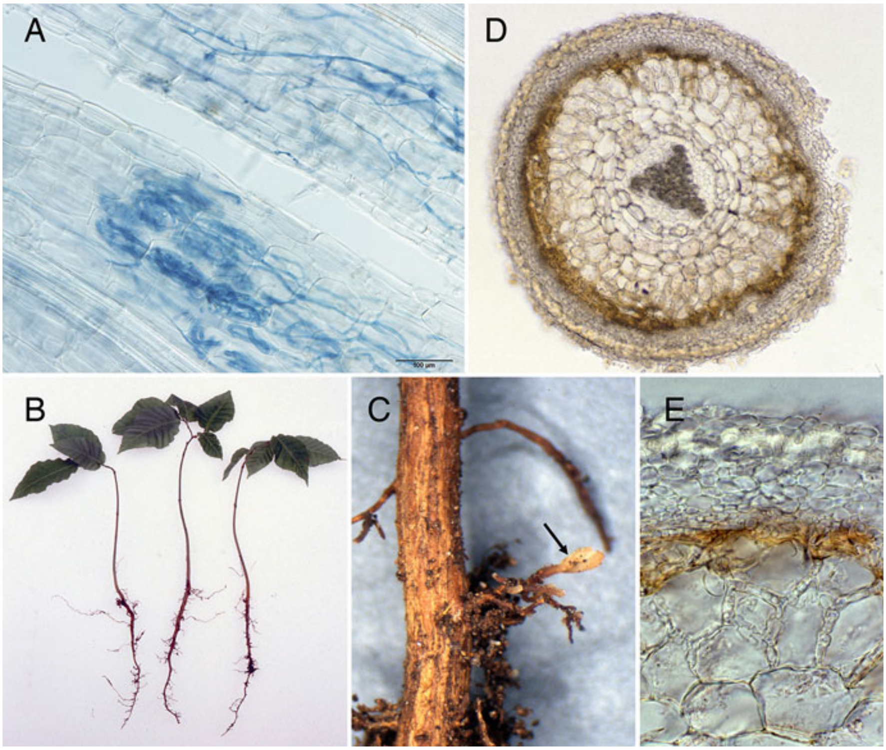

Fig. 2.8 Arbuscular mycorrhiza of *Dioscorea japonica* (**a**) and ectomycorrhiza of *Fagus crenata* (**b**–**e**). (**a**) Roots invaded by hyphae of Glomeromycotal fungi. (**b**) Seedlings. (**c**) A root system with nonmycorrhizal and mycorrhizal (shown by an *arrow*) roots. (**d**) A cross-section of the mycorrhizal root. (**e**) External fungal layer and fungal hyphae invading interspace of root cells

dikaryon (i.e., each cell contains two unfused nuclei) and comprises two phyla, Ascomycota and Basidiomycota. Dikarya grow in a filamentous (as hyphae) or unicellular (as yeasts) manner and have diverse habits including consumption of organic materials and fluids, decomposition of plant litter or wood, and parasitization of various organisms and mycorrhizal symbionts. Dikarya typically form ectomycorrhiza, in which a root is thickly enveloped by a hyphal sheath and its highly branched hyphae penetrate deep into the intercellular space of inner root cells but not into the root cells (Fig. 2.8). Ectomycorrhiza are formed on the roots of a few plant families (e.g., Pinaceae, Fagaceae, Betulaceae, Salicaceae, Myrtaceae, and Dipterocarpaceae). Ectomycorrhizal fungi produce large fruit bodies (i.e., mushrooms) from the ground in forests comprising pines, larches, firs, hemlocks, oaks, beeches, birches, poplars, myrtles, and dipterocarps. The diversity and abundance of mushrooms of these mycorrhizal fungi in these forests contribute to the diversity and abundance of mycophagous insects and fungivorous vertebrates. Photosynthetic organisms relinquish their surplus carbohydrate assimilates in various ways. Aquatic algae secrete surplus polysaccharides on the surface of their

Table 2.1 Mycorrhizal types

Mycorrhizal type	Fungi	Plants	Morphology of Mycorrhiza	Host specificity
Arbuscular mycorrhiza	Mucoromycotina	Basal liverworts	Hypha invades thallus cells and occupies mucilage filled space	Low
Arbuscular mycorrhiza	Glomeromycota	Liverworts and hornworts	Hypha invades thallus cells and forms arbuscules in the cells	Low
Arbuscular mycorrhiza	Glomeromycota	Vascular plants except aquatic plants, Brassicaceae, Crassulaceae, Orobanchaceae, and Proteaceae	Hypha invades plant's root cell and forms arbuscules in the cells	low
Ectomycorrhiza	Basidiomycota (Agaricales, Boletales, Russulales) and Ascomycota	Pinaceae, Fagaceae, Betulaceae, Salicaceae, Dipterocarpaceae; a part of Myrtaceae, Rosaceae, and Fabaceae	Hypha surrounds roots and penetrates in interspace of root cells	High
Ericoid mycorrhiza	Ascomycota (Helotiales) and some Basidiomycota (Sebacinales)	Ericaceae	Hypha surrounding fine hair root invades epidermal cells and forms intracellular coil	High?
Orchid mycorrhiza	Basidiomycota (*Ceratobasidium, Sebacina, Tulasnell*a and *Russula*)	Orchids	Hypha invades root cells and forms coils (peloton), which are digested by the orchid cell	High

Heijden et al. (2015)

algal bodies to prevent fouling by organisms such as macrophytes, and to deter predation by zooplankton. In contrast, land plants provide large quantities of assimilates to symbiotic mycorrhizal fungi, which in turn contribute to translocation of water and inorganic nutrients from soil to plant roots and to protection of roots against soil pathogenic fungi and bacteria. Moreover, the mycorrhizal system is parasitized by diverse mycoheterotrophic plants such as Orchidaceae, Triuridaceae, and Burmanniaceae (Bidartondo 2005). The intricate underground network of mutual and antagonistic plants and fungi makes the interactions and dynamics complex. In addition to roots, the internal tissues of aerial parts of plants are also inhabited by diverse fungi, bacteria, and other microorganisms (Table 2.1; Hardoim et al. 2015). These microbial endophytes are either pathogenic or beneficial to plants, either obligate or opportunistic, and are transmitted either vertically or horizontally. The most common obligate mutual endophytic fungi are ascomycetes of the genera *Balansia*, *Epichloe*, and *Neotyphodium* (Clavicipitaceae), which promote plant growth and protect the host plant against biotic and abiotic stresses by producing antibiotics or other secondary metabolites, stimulating plant growth, or activating the expression of particular host genes. Plant roots are also inhabited by unique endophytes, which have dark septate hyphae (Mandyam and Jumpponen 2005). Infection by dark septate endophytes (DSEs) can have beneficial or pathogenic effects on plants depending upon the environmental factors and interactions with root mycorrhizal fungi. Because mutualistic endophytes may be pathogenic, interactions between plants and endophytes must be evolutionarily dynamic. It is beneficial to a plant to host an endophyte with low pathogenicity at a cost, because the endophyte may protect against invasion by more virulent pathogens. Thus, the high infection rate and high diversity of obligate mutualistic endophytes in plants suggest the prevalence of protection mutualism involving plant pathogens.

2.4 Appearance of Insects

Following the terrestrialization of green plants, arthropods also colonized land. The subphylum Hexapoda of the phylum Arthropoda is a genuinely terrestrial clade, but its phylogenetic linkages are unknown. Recent molecular phylogenetic analysis suggested that the sister group of Hexapoda is Remipedia (Regier et al. 2010), which is a group of small swimming crustaceans with numerous pairs of swimming appendages that live in brackish groundwater in anchialine caves. Hexapoda and Remipedia are morphologically distinct: Remipadea have up to 42 pairs of swimming appendages, in contrast to three pairs of legs in Hexapoda. However, an autosynapomorphy between Hexapoda and Remipedia has been found (i.e., the presence of a mandibular venom gland; Regier et al. 2010), which suggests that the route of terrestrialization of the hexapod class Entognatha (the most basal wingless hexapods, exemplified by springtails) was through coastal aquifers. Having colonized land, a Hexapoda lineage developed an external mouthpart structure in the Silurian, which is the origin of insects (i.e., the class Insecta; Fig. 2.9). The most important innovation of insects was the acquisition of wings. Wings are thought to have originated in aquatic insects because the most basal winged insect is Ephemeroptera, whose larvae live in aquatic habitats, and because the morphological and developmental characteristics of ephemeropteran gills resemble those of wings. Insects with wings (i.e., Pterygota) appeared in the Devonian and underwent adaptive radiation in diverse niches, such as herbivores, grazers, fungivores, detritivores, predators, scavengers, parasitoids, and parasites, in aquatic and terrestrial ecosystems (Fig. 2.9). The great diversity of insects is considered to have resulted from adoption of herbivory, because the five orders that feed on seed plants (i.e., Hemiptera, Coleoptera, Diptera, Hymenoptera, and Lepidoptera) achieved megadiversity. The great diversity of herbivorous insects is closely related to their high host specificity (Ehrlich and Raven 1964).

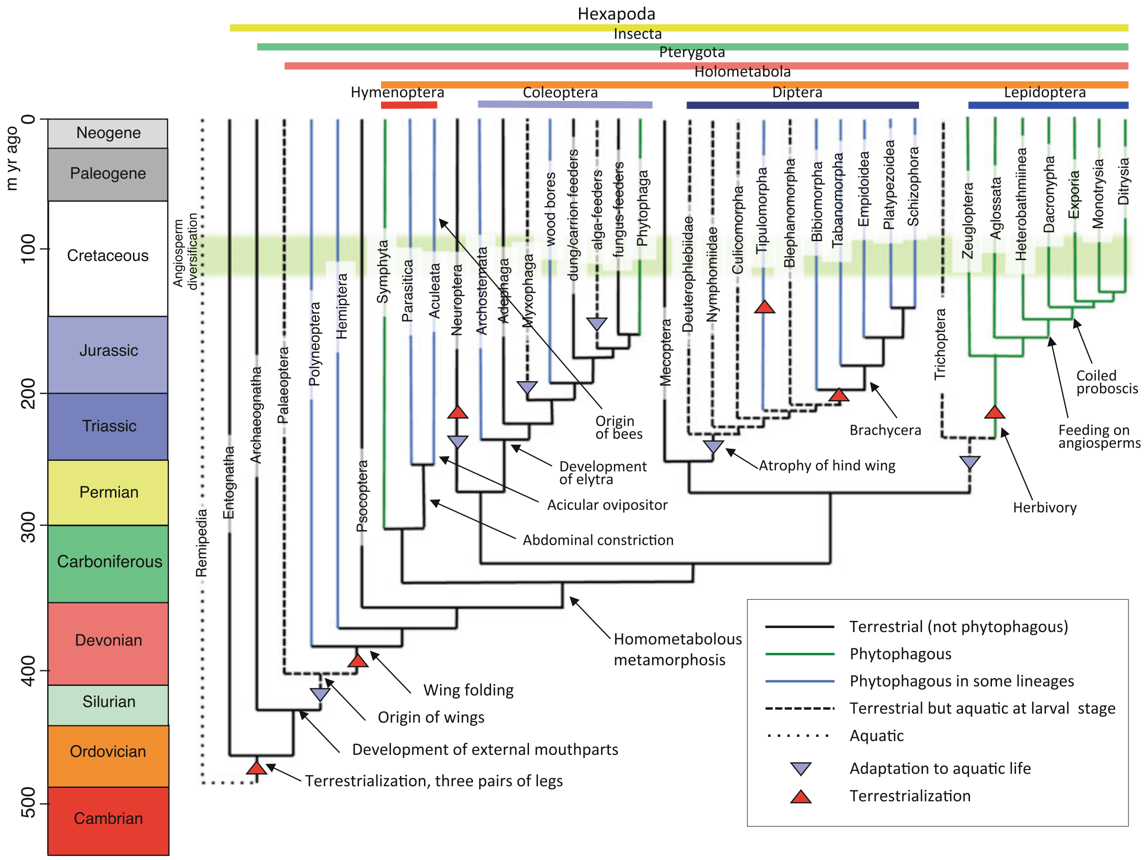

Fig. 2.9 History of diversification of insects focusing on crossing the border between terrestrial and aquatic ecosystems and adoption of herbivorous life. Dominant pollinators evolved from the herbivorous lineages. Phylogeny and divergence times are based on Wiegmann et al. (2011), Imada et al. (2011), Ronquist et al. (2012), Misof et al. (2014), and Regier et al. (2015)

In general, plants defend against herbivore predation by producing toxic secondary metabolites, and herbivorous insects have evolved mechanisms to detoxify or tolerate these agents. Accordingly, coevolutionary arms races between plants and herbivorous insects have reinforced the host specificity of herbivorous insects. Herbivory originated at least several times in various insect orders from algal grazers, detritus feeders, and fungal feeders, whereas the origins of herbivory are unclear. Bryophytes are infested by limited groups of insects, such as bugs (Peroidae and Tingidae), crane flies (Cylindrotomidae), flies (Rhagionidae and Agromyzidae), and moths (e.g., Micropterigidae, Pyralidae). Ferns are infested by various insect herbivores, including leaf miners (agromyzid and anthomyiid flies, stathmopodid moths, and chrysomelid beetles) and defoliators (diverse lepidopterans, hemipterans, and sawflies). The diversity of fern-feeding insects is considerably lower than that of angiosperm-feeding insects, likely due to the low morphological complexity of ferns (Hendrix 1980). Herbivores of lyophytes are only known in lepidopterans and pallopterid flies (Fig. 2.10; Kato 2002). Seed plants (particularly angiosperms) are infested by exceedingly diverse lineages of the above-mentioned five orders of insects, the diversity of which accounts for one-quarter of global biodiversity.

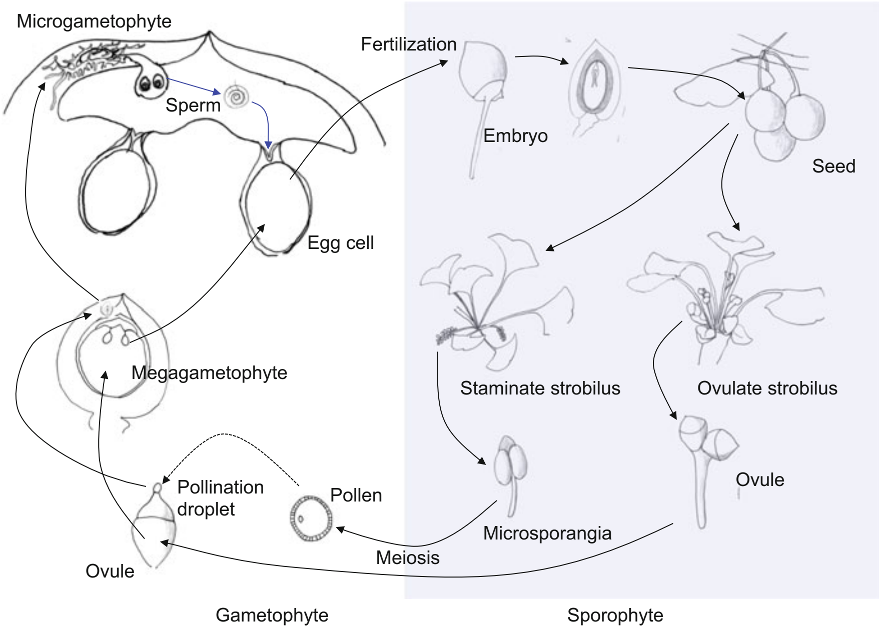

Fig. 2.10 Life cycle of a gymnosperm, *Ginkgo biloba*. In seed plants including gymnosperms, male and female gametophytes are parasitic to sporophytes. In *Ginkgo*, male gametophytes growing in an ovule produce sperm, which fertilize egg cells of female gametophytes. A broken line shows airborne transportation, and *blue* lines show migration in fluid

2.5 Origin of Pollination and Invention of Seeds

Evolution from pteridophytes to seed plants occurred through radical morphological and life history modification. In the first step, spores of a tracheophyte lineage become dimorphic (i.e., megaspores and microspores). Next, the megaspores and microspores germinate without being released and, respectively, become megagametophytes and microgametophytes on maternal plants. The megagametophyte is parasitic to maternal sporophytes (the ovule harbors megagametophytes on megasprorophylls) and produces archegonia. Using nutrients supplied by sporophytes, the archegonia produce egg cells that are fertilized and grow as seeds on the sporophyte. The microgametophytes become enclosed in a tough coat with a sporopollenin shell (pollen harbors microgametophytes on microsporophylls) and then are released and transported to megagametophytes by the wind (Fig. 2.11). Thus, in contrast to free-sporing pteridophytes, in seed plants, the whole microgametophyte rather than sperm moves to the archegonia by the wind rather than by swimming in a water film. This new process of pollen transfer to ovules is pollination.

Fig. 2.11 Extant conifers. (**a**) *Araucaria humboldtensis* (Araucariaceae). (**b**, **c**) *Parasitaxus usta*, parasitic to root of another conifer, *Falcatifolium taxoides* (both host and parasite are Podocarpaceae). (**d**) *Sciadopitys verticillata* (a monotypic family Sciadopityaceae endemic to Japan). (**e**) *Chamaecyparis obtuse* (Cupressaceae) with male cones. (**f**) *Cephalotaxus harringtonia* with female flowers secreting pollination droplets from ovules. (**g**) *Pinus thunbergii* (Pinaceae) with male and female cones. (**a**–**c**) Endemic to New Caledonia; (**d**–**f**) endemic to Japan

The successfully transported microgametophyte produces antheridia. In ginkgo, the antheridia release flagellate sperms in the ovule and the sperm fertilizes an egg in an archegonium. In conifers, however, the successfully transported microgametophyte produces an unflagellated sperm cell, which is guided to the archegonia via a pollen tube. The zygote is nourished by the maternal sporophyte, develops within ovules, and matures as a seed. This modification of life history liberated the seed plants from dependence on aquatic habitats for reproduction. Based on the protective structure of ovules, seed plants are classified into gymnosperms and angiosperms, and the gymnosperms are paraphyletic. The extant members of gymnosperms are the cycads (Cycadophyta), ginkgo (Ginkgophyta), conifers (Pinophyta), and gnetophytes (Gnetophyta; Fig. 2.11). The oldest gymnosperm fossil is from the Carboniferous, and there are many extinct gymnosperm groups such as Bennetiales, Caytoniales, and Glossopteridales.

In most gymnosperms, pollen is dispersed by wind and caught by pollination droplets secreted from ovules. However, some cycads and gnetophytes are pollinated by insects. In *Gnetum gnemon* var. *tenerum* in tropical regions of Southeast Asia, both the megasporophyll and microsporophyll emit an unpleasant odor after sunset, secrete pollination droplets from ovules of the megasporophyll and residual ovules of the microsporophyll, and are visited by nocturnal nectar-seeking moths (Fig. 2.12). The pollination droplet contains sugar and is harvested by moths as a reward for

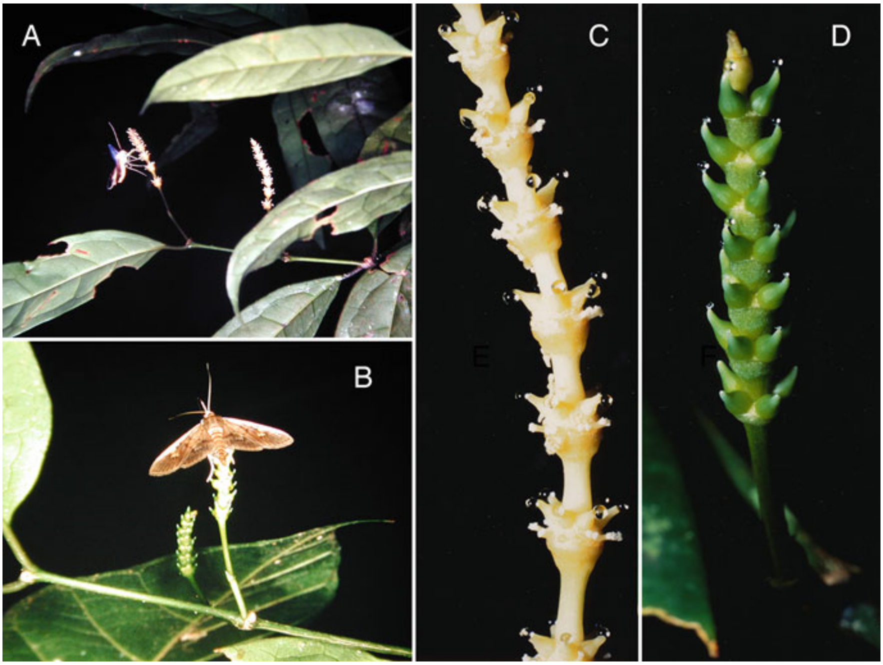

Fig. 2.12 Entomophily of a gnetophyte, *Gnetum gnemon tenellum*. (**a**) Male strobili visited by a pyralid moth. (**b**) Female strobili visited by a pyralid moth. (**c**, **d**) Male and female strobili secreting pollination droplets

pollination (Kato and Inoue 1994). The insect pollination system of this *Gnetum* is different from that of zoophilous angiosperms in that pollinators are attracted by an odor emitted from the sporophyll and the pollen is received by pollination droplets secreted from ovules. Recent fossil evidence indicates that insect feeding on pollen, pollination droplets, and reproductive tissues of extinct gymnosperm lineages date back to the Permian (Labandeira 2010). The Mesozoic anthophilous insects comprise mandibulate insects (e.g., Coleoptera and Hymenoptera), which feed on pollen and pollination drops, and long proboscid insects (e.g., Neuroptera, Mecoptera, and Diptera), which utilize fluid secreted from plants such as pollination droplets (Ren et al. 2009). Whereas some of these insects are considered to contribute to pollination of extinct gymnosperms, these associations were extinguished by the late Cretaceous and were succeeded by new types of associations with angiosperms.

In addition to adoption of pollination, seed plants developed a novel system to disperse their offspring. A seed contains an embryo and is covered by the seed coat, which consists of the inner tegmen and outer testa. Thus, the embryo is protected from environmental stresses such as desiccation and can be dispersed from mother plants by wind or other agents. Although the seeds of gymnosperms are naked, in some gymnosperm genera, such as *Ephedra* (Gnetales) and *Taxus* (Coniferes), inner cone scales are modified to enclose the seed and become red and fleshy (Fig. 2.13). Consequently, the cone has an appearance similar to a red fruit and is

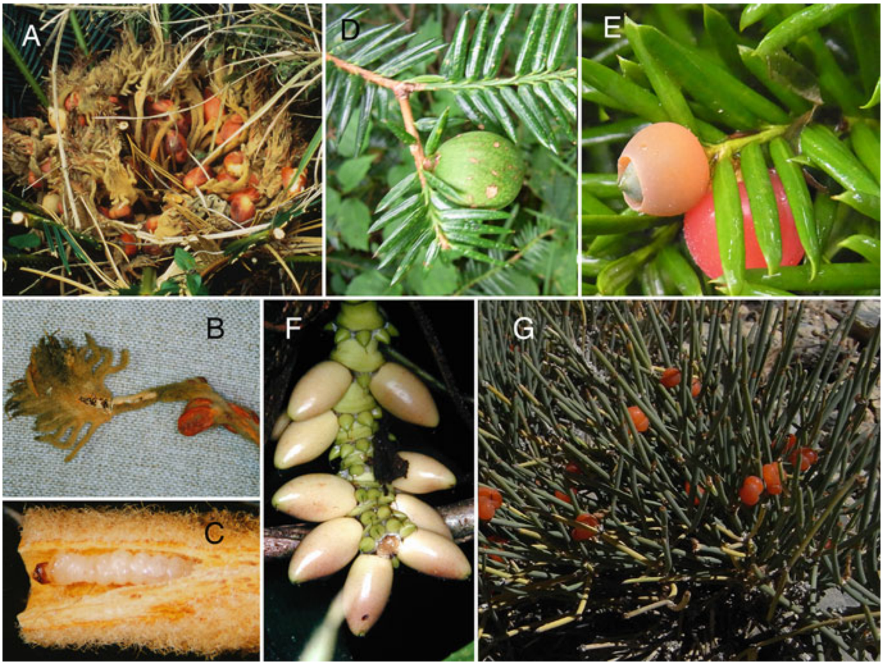

Fig. 2.13 Reproductive organs of gymnosperms. (**a**–**c**) *Cycas revoluta*. (**d**) *Torreya nucifera*. (**e**) *Taxus cuspidata*. (**f**) *Gnetum cuspidatum*. (**g**) *Ephedra gerardiana*. (**a**, **d**–**g**) seeds. (**b**–**c**) megasporophyll mined by a cerambycid beetle larva. In the seeds of *Taxus* and *Ephedra*, a red fleshy aril is developed

dispersed by birds. All of the extant gymnosperms are woody plants, including an archaic tree of the monotypic genus *Sciadopitys* (Sciadopityaceae) that is found only in Japan, and a plant-parasitic achlorophyllous treelet, *Parasitaxus usta* (Podocarpaceae), which is endemic to New Caledonia (Fig. 2.11). Most gymnosperms have arbuscular mycorrhiza symbiotic with fungi of Glomerales. In contrast, the conifer family Pinaceae is unique in being symbiotic with ectomycorrhizal fungi of the basidiomycetes. Gymnosperms are infested by various insect herbivores such as leaf miners (gelechid, gracillariid, coleophorid, and tortricid lepidopterans), defoliators (various families of lepidopterans, and sawflies), and wood bores (siricid sawflies, buprestid, cerambycid, curculionid, scolytid, and platypodid beetles). Because gymnosperms flourished in the Mesozoic, relict plant–herbivore associations have remained; seeds of a basal conifer *Agathis* (Araucaliaceae) are infested by a basal lepidopteran, *Agathiphaga* (Agathiphagidae), buds of *Abies* fir are bored by xyelid sawflies, microsporophylls of pines are infested by xyelid sawflies, and the rotten wood of pines is infested by basal cupedidid beetles (suborder Archostemata).

2.6 Invention of Flowers and Fruits

Megagametophytes and microgametophytes of a lineage of gymnosperms became reduced and protected in multilayered, delicately enfolded structures of the megasporophyll and microsporophyll. The structure harboring the compactly assembled reproductive organs is called the flower, and was invented by the angiosperm clade (Fig. 2.14). The megasporophyll and the microsporophyll in gymnosperms, respectively, became the pistil and stamen in angiosperms. The pistils and stamens are subtended by tepals. When the inner and outer tepals differentiate, they are termed petals and sepals, respectively. The flower structure is considered to have evolved to protect gametophytes against biotic and abiotic environmental stresses (e.g., attack by herbivores and pathogens, rain, and desiccation), and so that tepals could contribute to attracting pollinators. The pistil comprises the basal ovary, intermediate style, and apical stigma; these parts function to house ovules, support/project stigma, and receive pollen, respectively. Pollen attached to the stigma germinates and extends as a pollen tube in the style, and passes into the ovule. Thus, the long style facilitates pollen tube elongation. Microgametophytes in angiosperms became reduced in size and cell number (i.e., a pollen tube is a single multinuclear cell with one pollen tube nucleus and two sperm nuclei). The reduction of pollen size reduced time from pollination to fertilization. Full-grown megagametophytes (i.e., embryo sac) only have seven cells with eight nuclei (i.e., an egg cell, two synergids, three antipodals, and two polar nuclei). The reduction in megagametophyte size also reduced the time from fertilization to seed set. In contrast to the long time from pollination to seed set (~1 year in conifers), the rapid fertilization and seed set in angiosperms contributed to adaptation to an annual herbaceous life cycle. After entering ovules, the pollen tubes fertilize the egg and the polar nuclei,

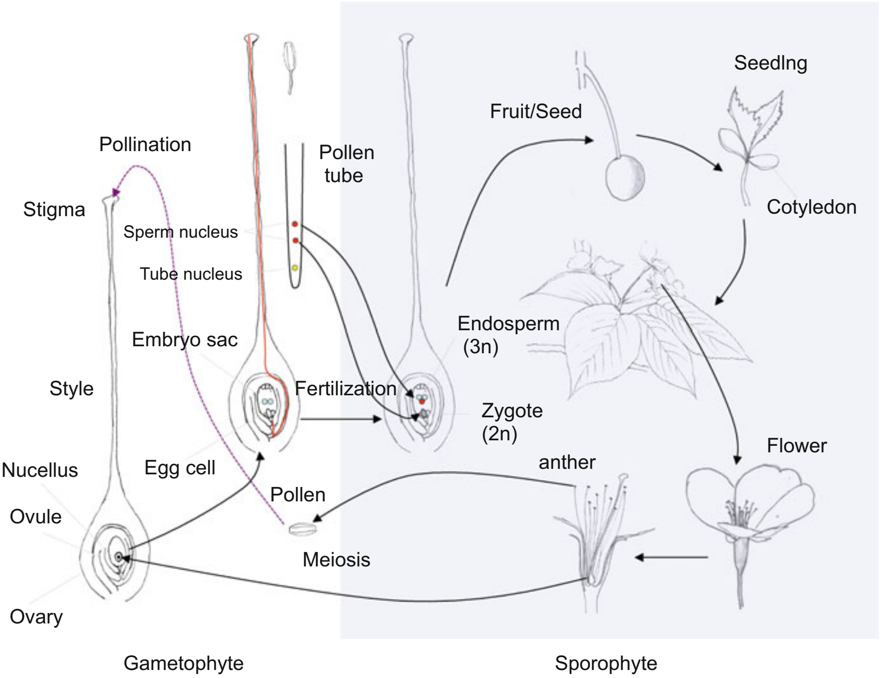

Fig. 2.14 Life cycle of an angiosperm, *Prunus speciosa*. A purple *broken* line shows transportation by animals. A pollen tube extends in the tissue of the pistil and reaches an egg cell of an embryo sac through a micropyle

which develop into the seed embryo and endosperm, respectively. This double fertilization is unique to angiosperms.

The earliest known angiosperm fossil is the aquatic herbaceous plant *Archaefructus liaoningensis* in the early Cretaceous (Sun et al. 2002), whereas angiosperms are thought to date back to the Jurassic. The pollen fossil data suggest that angiosperms became dominant over gymnosperms in the middle Cretaceous. Compared to leaves and shoots, pollen and spores are small but are protein-rich resources for herbivores, and accordingly, some herbivorous insects became specific feeders on pollen or spores. Although their nutritional quality is similar, pollen and spores evolved differently. A pollen-feeding insect transporting pollen from a flower to another conspecific flower facilitates pollination by accident, whereas a spore-feeding insect cannot serve a fern. Thus, the appearance of pollen-feeding insects enabled the innovative evolution of seed plants. Because pollen is costly, nectar became a popular reward for pollinators. Unlike the naked ovule in gymnosperms, the ovule of angiosperms is enveloped by several fused carpels; this structure is the ovary, which develops into the fruit. The fruit morphology is remarkably diverse among angiosperm species, and adapted for protection against abiotic and biotic stresses and for seed dispersal (Table 2.2). In general, dehiscent fruits release seeds, which are the dispersal units, but seed-containing indehiscent

Table 2.2 Seed dispersal syndromes

Syndrome	Agent of seed dispersal	Reward	Plant's adaptation	Plant examples
Nonbiotic				
Anemochory	Wind	Absent	Dust seed	Orchidaceae
	Wind	Absent	Seed or fruit with developed wings	Pinaceae, Ulmaceae, Dioscoreaceae, Aceraceae, Dipterocarpacea, Oleaceae, *Alsomitra* (Cucurbitaceae)
	Wind	Absent	Seed or fruit with developed plumes	Salicaceae, Aceraceae, *Clematis, Pulsatilla* (Ranunculaceae), Ascrepiadaceae, Asteraceae
	Wind	Absent	Air bladderlike fruit	*Cardiospermum* (Sapindaceae), *Physalis* (Solanaceae)
Hydrochory	Water	Absent	Floating fruit with developed cork layer or spongy tissue	*Cocos* (Arecaceae), *Barringtonia* (Lecythidaceae), Rhizophoraceae, *Terminalia* (Combretaceae), *Paliurus* (Rhamnaceae), Ipomoea (Convolvulaceae), Trapaceae, Scaevola (Goodeniaceae)
Autochory	Spring-operation	Absent	Fruit with ballistics	*Impatiens* (Balsaminaceae), *Geranium* (Geraniaceae), *Oxalis* (Oxalidaceae)
Barochory	Gravity	Absent	Heavy seed?	
Biotic, but not mutual				
Epizoochory	Migratory animals with fur and feathers	Absent	Fruit with hooked spines	Herbacious plants such as *Geum* (Rosaceae), *Achyranthes* (Amaranthaceae), *Xanthium, Bidens* (Asteraceae)
	Migratory animals with fur and feathers	Absent	Adhesive appendages on fruit	Herbacious plants such as *Oplismenus* (Poaceae), *Desmodium* (Fabaceae), *Torilis* (Apiaceae), *Adenocaulon* (Asteraceae)

(continued)

Table 2.2 (continued)

Syndrome	Agent of seed dispersal	Reward	Plant's adaptation	Plant examples
Biotic and mutual				
Endozoochory (Ornithochory)	Frugivorous bird (e.g., passeriformes)	Juicy pulp or other tissue of fruit/seed	Red/black fleshy fruit with hard seed coat	Zingiberaceae, Myricaceae, *Malus, Rosa, Rubus, Prunus, Pyrus* (Rosaceae), *Ribes* (Grossulariaceae), *Viscum* (Santalaceae), Ficus (Moraceae), Ericaceae, Symplocaceae, Vitaceae, *Breynia, Glochidion* (Phyllanthaceae), *Viburnum* (Adoxaceae), *Lonicera* (Caprifoliaceae), Rubiaceae etc.
Endozoochory (Chiropterochory)	Frugivorous bat	Sweet pulp or other tissue of fruit	Aromatic fleshy fruit with hard seed coat	Musaceae, *Ficus* (Moraceae)
Endozoochory	Frugivorous nonflying mammal	Sweet pulp or other tissue of fruit	Aromatic fleshy fruit with hard seed coat	Myricaceae, Actinidiaceae, *Durio* (Malvaceae)*, Nephelium, Dimocarpus* (Sapindaceae), *Diospyrus* (Ebenaceae)*, Mangifera* (Anacardiaceae), *Lansium* (Meliaceae), *Garcinia* (Clusiaceae), *Ficus, Artocarpus* (Moraceae)
Endozoochory (Piscichory)	Omnivorous fish	Creamy pulp or other tissue of fruit	Fleshy fruit with hard seed coat	trees in flood plain in Amasonia, Annonaceae, *Virola* (Myristicaceae), *Lucuma, Pouteri*a (Sapotaceae), Elaeocarpaceae, *Ficus* (Moraceae) etc.
Synzoochory	Scatter-hoarding mammal (e.g., rodent)	Seed itself	Nut (fruit with hard shell) or hard shelled seed	*Quercus, Litocarpus, Castanopsis* (Fagaceae)*, Corylus* (Betulaceae), Juglandaceae

(continued)

Table 2.2 (continued)

Syndrome	Agent of seed dispersal	Reward	Plant's adaptation	Plant examples
	Scatter-hoarding bird (e.g., raven, nutcracker, jay)	Seed itself	Nut (fruit with hard shell) or hard shelled seed	*Pinus, Picea* (Pinaceae), *Quercus* (Fagaceae), *Corylus* (Betulaceae)
Myrmecochory	Ant	Elaiosome	Seed with elaiosome	*Anemone, Corydalys, Hepatica* (Ranunculaceae), Primulaceae, Violaceae, *Erythronium* (Liliaceae), *Asarum* (Aristolochiaceae)

Howe and Smallwood (1982), Sorensen (1986), and van Oudtshoornand and van Rooyen (2013)

fruits are themselves dispersed. Although fruits are larger and heavier than spores and pollen, the fruits of some plants can be dispersed by wind if they have developed wings or plumes (anemochory). In addition, although most fruits are heavier than water, the fruits of some riparian plants have developed corky or spongy tissues to enable them to float and thus be dispersed by water (hydrochory). Some herbaceous plants developed automatic seed dispersal mechanisms, in which seeds are flicked off by the spring function of dehiscent fruits (autochory). Some herbaceous plants developed fruits with an attachment apparatus (e.g., hooked spines and adhesive mucilage), which attach to the fur of mammals and are dispersed by them (epizoochory). The predominant means of seed dispersal in extant angiosperms, however, is mutualistic zoochory, in which plants delegate seed dispersal to specific migrant animals by offering them rewards.

2.7 Diversification of Angiosperms

The estimated number of angiosperm species is 352,000, which outnumbers that of gymnosperms (1000), pteridophytes (13,000), and bryophytes (20,000; The Plant List 2013). The exceeding diversity of angiosperms is closely related to zoophily for many reasons: first, zoophilous plants can achieve pollination even on the forest floor where wind is rarely available; second, because even small, rare, isolated plants can achieve pollination if reliable pollinators move among the same species; and third, because the pollinators evolve floral fidelity to maximize foraging efficiency and the pollinator's behavior canalizes gene flow, which contributed to speciation and diversification. Zoophilous plants are estimated to account for 87.5% of the total number of angiosperm species (Ollerton et al. 2011). Molecular phylogenetic studies (Angiosperm Phylogeny Group 2003) have revealed the

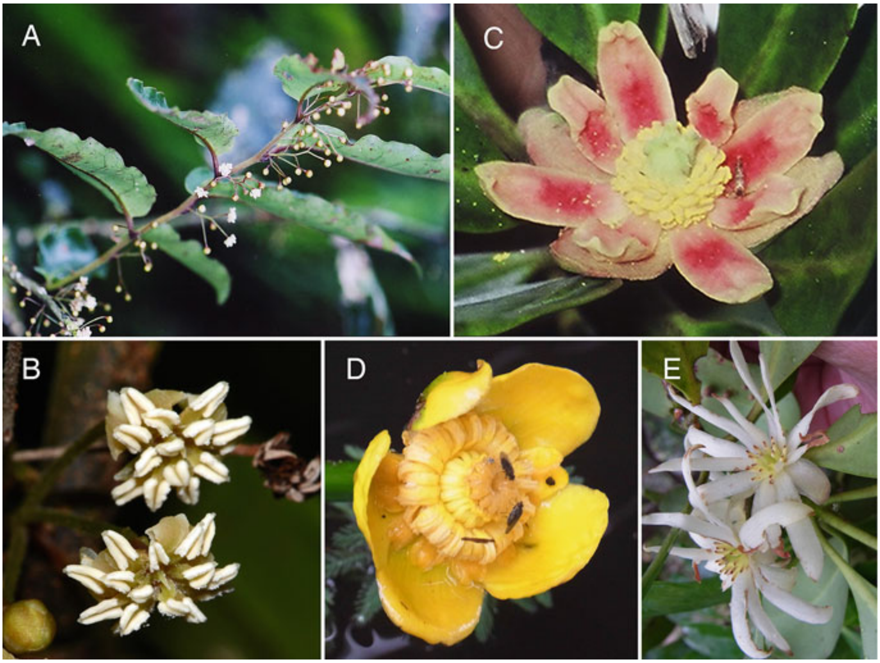

Fig. 2.15 Flowers of basal angiosperms. (**a**, **b**) Male flowers of *Amborella trichopod*a (Amborellaceae). (**c**) A flower of *Zygogynum baillonii* (Winteraceae) visited by a micropterigid moth. (**d**) A flower of *Nuphar japonicum* (Nymphaeaceae) visited by ephydrid flies. (**e**) Flowers of *Illicium anisatum* (Schisandraceae)

phylogeny of angiosperms: (Amborellaceae (Nymphaeace (Austrobaileyales (Chloranthaceae (Magnoliid (monocots (Ceratophyllales, Eudicots))))))). This shows that the most basal extant angiosperm is *Amborella* (the monotypic family Amborellaceae, endemic to New Caledonia). *Amborella* is a dioecious evergreen shrub. Its female flower has 7–8 white tepals, several staminodes, and a spiral of several free carpels; in contrast, the male flower has 6–15 white tepals and 10–21 spirally arranged stamens (Fig. 2.15). Pollen is readily released from anthers by wind, whereas various unspecialized insects visit and pollinate male and female flowers, suggesting ambophily (adoption of zoophily and anemophily simultaneously; Thien et al. 2003). The *Amborella* pollination system suggests that the earliest angiosperm adopted insect pollination by developing attractive petals in addition to anemophily.

Petals of zoophilous flowers likely played an important role in angiosperm diversification, because most pollinators are diurnal sight-sensed animals that are attracted by the nongreen color of petals (Table 2.3). Absorption of extraviolet light by a part of the petal can contribute to guiding pollinators to the nectary. Floral odor is also important for attracting pollinators, particularly in nocturnally opening flowers. Most zoophilous flowers secrete nectar, the sugar concentration of which

Table 2.3 Pollination syndrome of diverse seed plants

Pollination type	Floral property								
Pollination agent	Color[1]	Symmetry[2]	Shape[3]	Anthesis[4]	Reward[5]	Odor[6]	Distribution[7]	Characteristics of pollination system	Plant exampls
Wind pollination									
Wind	g	n	a	d	–	–	W	Enormous number of light pollen grains are shed	Diverse seed plants
Water pollination									
Water current	g	n	a	d	–	–	W	Thread like pollen istransported by water	Aquatic monocots
Water current and wind	g	n	a	d	–	–	TR	buoyant anthur is also blown by wind	*Enhalus*
Ambophily									
Insect and wind	w	n	o	d	p	–	NC	Pollinated by wind and unspecialized insect	*Amborella*
Bee pollination									
Bumblebee	w, y, p	z, a	b, c, o, s, t	d	n, p	+	HA, SA	Homeothermic bees with high floral constancy	Diverse angiosperms
Honeybee	w, y, p	z, a	b, c, o, s, t	d	n, p	+	PA, AF, OR	Scout–recruit foraging using letter 8 dance	Diverse angiosperms
Stingless bee	w, y, p	z, a	b, c, o, s, t	d	n, p	+	TR	Scout–recruit foraging using pheromone	Diverse angiosperms
Euglossine bee (female)	w, y, p, r	z, a	c, s, t	d	n, p	+	SA	Long-proboscid bees trapline scattered flowers	Diverse angiosperms
Euglossine bee (male)	y	z	c	d	fr	+	SA	Floral fragrace is harvested and reused	*Coryanthes*
Small solitary bee	w, y, p	z, a	b, c, o, s, t	d	n, p	+	W	Flowers often having nectar guids	Diverse angiosperms

(continued)

Table 2.3 (continued)

Pollination type	Floral property								
Pollination agent	Color[1]	Symmetry[2]	Shape[3]	Anthesis[4]	Reward[5]	Odor[6]	Distribution[7]	Characteristics of pollination system	Plant exampls
Anthophorine bee	w, y, p, r	z, a	c, s, t	d	n, p	+	W	Long-proboscid bees trapline scattered flowers	Diverse angiosperms
Leafcutter bee	w, y, p, r	z, a	c, s, t	d	n, p	+	W	Middle-sized bees adopting buzz-pollination	Fabaceae etc.
Carpenter bee	w, y, p	z, a	b, c, o, s, t	d	n, p	+	W	Large-sized bese adopting buzz-pollination	Fabaceae etc.
Oil-collecting bee	w, y, p	z, a	c, t	d	o, p	+	W	Bees collect and use oil in sterad of nectar	Several families
Wasp pollination									
Hunting wasp	w, y	a	o	d	n	+	W	Nectar accessible to wasps	Diverse angiosperms
Social wasp	g	a	o	d	–	+	AU	Green-leaf volatiles attract prey-seeking wasps	*Epipactis*
Sphecid wasp	bl	z	c	d	–	+	AU	Deceptive pollination with pseudocopulation	*Cryptostylis*
Ant	g	a	o	d	n	+	W	Subaerial small flowers accesible by ants	Subaerial plants
Fig wasp	g	n	a	d	s	+	TR	Obligate mutualism	*Ficus*
Lepidopteran pollination									
Butterfly	w, y, p, r	a	b, c, o, s, t	d	n	+	W	Style and pistils protruded from corolla	Diverse angiosperms
Hawkmoth	w	a	s, t	n, d	n	+	W	Long-distance transportation of pollen	Diverse angiosperms
Nocturnal moth	w	a	b, o, s, t	n	n	+	W	Flowers emit odor in night	Diverse angiosperms

Nocturnal moth	g	a	a	n	d	+	W	Pollination drop is harvested by moths	*Gnetum*
Yucca moth	w	a	o	n	s	+	NA	Obligate mutualism	Diverse angiosperms
Leafflower moth	g	a	a	n	s	+	TR	Obligate mutualism	Diverse angiosperms
Dipteran pollination									
Hoverfly	w, y	a	b, c, o	d	o, p	+	W	Hoverflies harvest nectar and pollen	Diverse angiosperms
Blow fly	br	a	o	d	–	+	W	Deceptive pollination, flowers mimic rotting Flesh	*Rafflesia*
Drosophilid fly	w	a	a, o	d	n	+	TR	Brood-site pollination	*Colocasia*
Fungus gnat	g	a	o	d	n	+	HA	Highly specific mutualism	*Mitella*
Fungus gnat	bl, g	a	o	d	–	+	HA	Deceptive pollination	*Arisaema*
Phorid fly	g	n	a	d	fl	+	W	Brood-site pollination	*Aristolochia*
Mosquito	w, p	a	o	d	n	+	W	Utilizing nectar instead of blood	*Persicaria* etc.
Gall midge	g	n	a	d	fl	+	OR	Brood-site pollination	*Artocarpus*
Coleopteran pollination									
Scarabaeid beetle	w	a	a, o	d	p	+	TR	Flowers emit strong odor	Diverse angiosperms
Carrion beetle	w, bl	n	a	n	c	+	TR	Flowers emit strong aminoid odor	*Amorphophallus* etc.
Dung beetle	bl	z	o	n	–	+	OR	Deceptive pollination via floral fetid odor	*Orchidantha*
Cerambycid beetle	w	a	b, o	d	p	+	W	Pollen is main reward	Diverse angiosperms
Small beetle	w	a	b, o	d	p	+	W	Pollen is main reward	Diverse angiosperms

(continued)

Table 2.3 (continued)

Pollination type	Floral property								
Pollination agent	Color[1]	Symmetry[2]	Shape[3]	Anthesis[4]	Reward[5]	Odor[6]	Distribution[7]	Characteristics of pollination system	Plant exampls
Hemipteran pollination									
Mirid bug	w	a	o	d, n	fl	+	OR	Brood-site pollination	*Macaranga*
Thrips pollination									
Thrips	w, g	a	o	d, n	p, fl	+	W	Brood-site pollination	*Dioscorea* etc.
Amphipod pollination									
Amphipod	bl	a	c	d, n	p	+	OR	Cryptic ground flower visited by soil organisms	*Aspidistra*
Bird pollination									
Hummingbird	r, y	a, z	c, t	d	n	–	NA, SA	Deep flowers secrete ample nectar	Diverse angiosperms
Sunbird	r, y	a, z	c, t	d	n	–	AU, OR, AF	Deep flowers secrete ample nectar	Diverse angiosperms
Spiderhunter	r, y	a, z	c, t	d	n	–	OR	Deepest flowers secrete ample nectar	Diverse angiosperms
Honeycreeper	r, y	a, z	c, t	d	n	–	SA	Deep flowers secrete ample nectar	Diverse angiosperms
Honeyeater	r, y	a, z	c, t	d	n	–	AU, PC	Deep flowers secrete ample nectar	Diverse angiosperms
White-eye	r	a, z	c, t	d	n	–	AF, OR, AU	Deep flowers secrete ample nectar	Diverse angiosperms
Bulbul	r	a, z	c, t	d	n	–	AF, OR	Deep flowers secrete ample nectar	Diverse angiosperms

Mammal pollination									
Echo-locating bat	w	a	b, c, t	n	n	–	SA	Echo-acoustic signals to lure flying bats	Diverse angiosperms
Flying fox (megabat)	w	a	b, c, t	n	n	+	TR	Flowers emit strong odor in night	Diverse angiosperms
Arboreal mammals	w	a	c, o	n	n	+	TR	Large flowers secrete large amount of nectar	Diverse angiosperms
Terrestrial mammals	w	a	b,o	n	n	+	AU, AF	Strong musty odor and large amount of nectar	*Protea* etc.
Monkey	p	a	o	d	n	–	TR	Red-colored, abundant nectar	Fabaceae

[1] *bl* black, *br* brown, *g* green, *p* pink, *r* red, *w* white, *y* yellow

[2] *a* actinomorphic, *n* nonsymmetric, *z* zeigomorphic

[3] *a* apetalous, *b* brush, *c* campanulate, *o* open, *s* long-spurred, *t* tubular

[4] *d* diurnal, *n* nocturnal

[5] *c* copulation site, *fl* floral tissue, *fr* fragrance, *n* nectar, *o* oil, *p* pollen, *s* seed

[6] + present, − absent

[7] *AF* Africa, *AU* Australian, *HA* Holoarctic, *NA* North America, *NC* New Caledonia, *OR* Oriental, *PA* Palaearctic, *PC* Pacific, *SA* South America, *TR* Pan-tropics, *W* worldwide

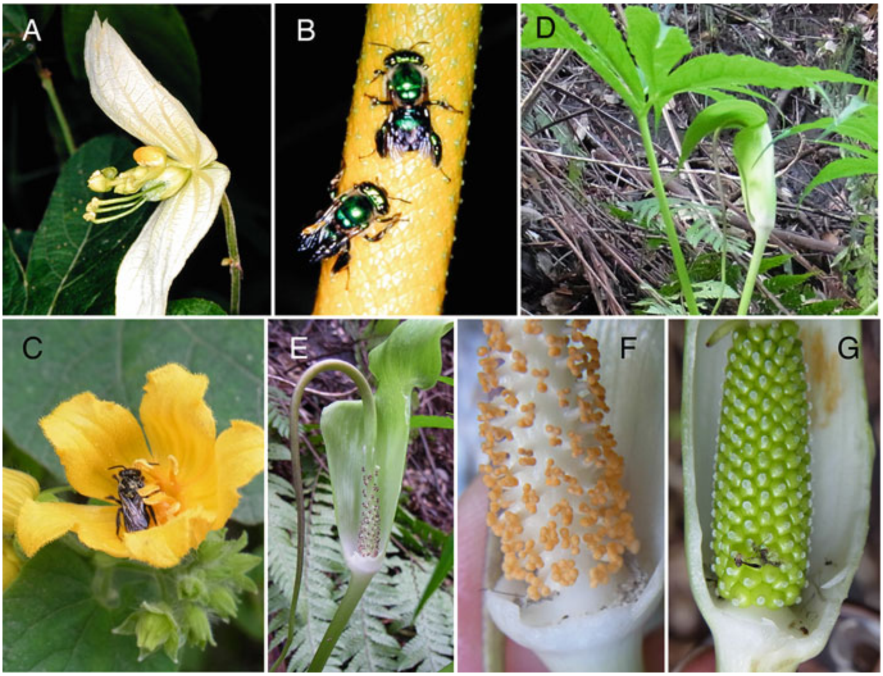

Fig. 2.16 Diversity of floral rewards of angiosperms. (**a**) A flower of *Dalechampia tiliifolia* (Euphorbiaceae) secreting resin for euglossine bees. (**b**) Female inflorescence of *Anthurium* sp. (Araceae) attracting male euglossine bees by floral odor. (**c**) A flower of *Thladiantha nudiflora* (Cucurbitaceae) secreting floral oil and visited by an apid bee, *Ctenoplectra cornuta*. (**d**–**g**) Inflorescence and flowers of *Arisaema negishii* lacking floral reward (Araceae). (**d**) Male spathe. (**e**) Cross-section of a spathe. (**f**) Male spadix. (**g**) Female spadix. In a female spathe, there are dead fungus gnats attracted by the floral odor

is 10–50%, which is lower in bird- and moth-pollinated flowers. The association between flowers and pollinators is generally mutual because pollinators offer flowers pollination services, and in turn, flowers provide pollinators with rewards such as nectar and pollen. More rare floral rewards include floral oil (several genera in Orchidaceae, Primulaceae, Malpighiaceae, Cucurbitaceae, and Scrophulariaceae) for oil-collecting bees (Fig. 2.16), floral resin (*Dalechampia* in Euphorbiaceae) for euglossine bees (Fig. 2.16), and a part of ovules or seeds (Agavaceae, Ranunculaceae, Saxifragaceae, Cactaceae, Moraceae, and Phyllanthaceae), which are detailed below. In contrast to mutual relationships, some plants achieve pollination by deception without offering a reward. For example, flowers of jack-in-the-pulpit (*Arisaema* spp., Araceae; Fig. 2.16) attract fungus gnats (Mycetophilidae) by emitting a mushroomlike odor (Barriault et al. 2010). The perennial monocot is dioecious and has an erect inflorescence known as a spadix, which is covered by a spathe. Male and female spathes are similar, although male spathes have an aperture at the basal seam, whereas female spathes do not. Both male and female spadices attract fungus gnats by emitting a floral odor, and the fungus gnats attracted to a male spadix escape from the spathe aperture with their bodies dusted with pollen. Orchids, which exhibit a diverse floral morphology, use various deceptive pollination mechanisms, including generalized food deception, food-deceptive floral mimicry, brood-site imitation, pseudoantagonism, and sexual deception (Jersáková et al. 2006). For example, flowers of some orchid genera attract nectar-seeking bees by visually mimicking other nectariferous plants. In contrast, some orchids attract mate-seeking males of sphecid wasps or sciarid fungus gnats by chemically mimicking the sexual pheromone of pollinator females, and are pollinated by the male pollinators during pseudocopulation (Schiestl et al. 1999, Blanco and Barboza 2005, Gaskett 2011). The insect pollinators of basal angiosperms in the early to mid-Cretaceous are considered to have been Mesozoic insects such as beetles, mecopterans, dipterans, sawflies, and micropterigid moths (Fig. 2.9). A relic plant–pollinator interaction remains evident in New Caledonia, where *Zygogynum*, a genus of the basal plant family Winteraceae, is pollinated by micropterigid moths (Fig. 2.15; Thien et al. 1985). However, the principal pollinators of modern diverse angiosperms are mammals (particularly bats and nonflying arboreal mammals), birds, and insects belonging to four of the five above-mentioned megadiverse orders: Coleoptera (particularly Staphylidae, Nitidulidae, Scarabaeidae, Cerambycidae, Chrysomelidae, and Curculionidae), Diptera (particularly Syrphidae, Bombyliidae, Drosophilidae, and Calliphoridae), Hymenoptera (particularly bee families; i.e., Apoidea), and Lepidoptera (particularly various families of long-tongued moths and butterflies). All of these diverged simultaneously with angiosperms after the late Cretaceous.

2.8 Evolutionary History of Hymenopterans

Bees have played the most prominent role as pollinators of angiosperms. Before focusing on their role, we review the prehistory of bees. Hymenoptera is an order of insects with hyaline wings, and comprises two suborders, Symphyta and Apocrita. Symphyta, although nonmonophyletic, are the sawflies, characterized by lack of a body constriction between the thorax and abdomen. Larvae of most sawflies are external or internal herbivores (Fig. 2.17). The most basal clade of Symphyta, Xyelidae, appeared in the Triassic, and the larvae of extant xyelids are bud borers of firs, male cone borers of pines, and defoliators of walnut leaves. In contrast to Symphyta, Apocrita comprises parasitic or hunting wasps (the ant is one of the hunting wasp clades) and is characterized by a body constriction between the thorax and abdomen; specifically, the constriction exists between the first and second segments of the abdomen. This body constriction is thought to have evolved to handle their ovipositors efficiently and powerfully (Iwata 1971). In parasitic wasps (Parasitica), ovipositors are utilized to insert eggs into the insect hosts (in parasitoid wasp superfamilies, e.g., Chalchidoidea, Ichneumonoidea, and Proctotrupoidea) or rarely into plants (in several genera in Chalchidoidea and Ichneumonoidea, and the gall wasp superfamily, Cynipoidea; Fig. 2.17). A great number of parasitoid wasp

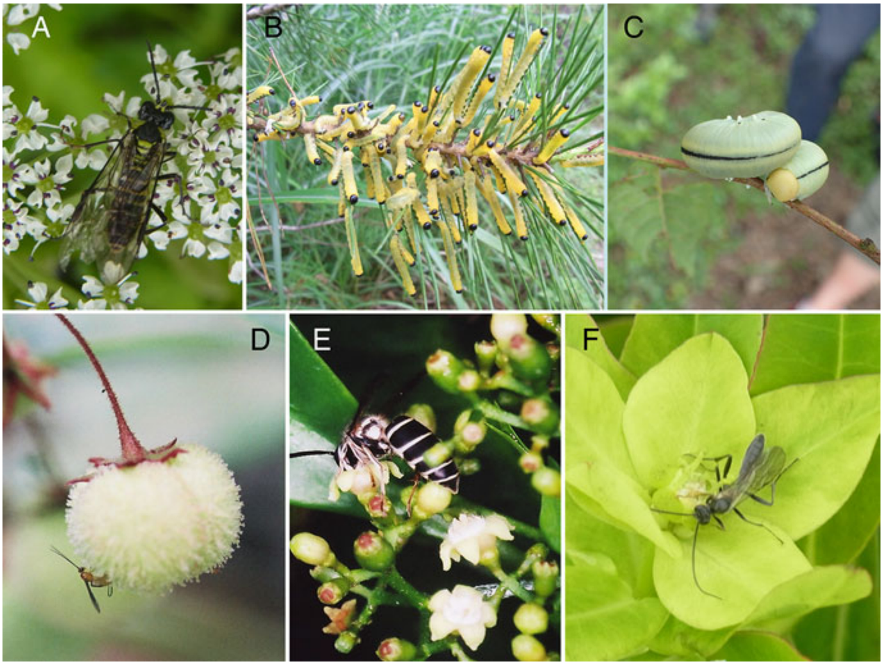

Fig. 2.17 Diverse hymenopterans associated with plants: (**a**–**c**) Suborder Symphyta; (**d**–**f**) Suborder Apocrita. (**a**) A sawfly *Tenthredo nigropicta* (Tenthrenididae) visiting flowers of *Angelica polymorpha* (Apiaceae). (**b**) Aggregation of larvae of a sawfly, *Diprion nipponicus* (Diprionidae) on pine tree *Pinus densiflora*. (**c**) A larva of a sawfly *Cimbex conatus* (Cimbicidae) on Japanese alder *Alnus japonica*, mimicking a land snail *Euhadra amaliae*. (**d**) A braconid wasp inserting her ovipositor into a fruit of *Phyllanthus pulcher* in Laos. (**e**) A vespid wasp *Vespula shidai amamiana* visiting flowers of *Psychotria rubra* (Rubiaceae). (**f**) A sphecid wasp visiting flowers of *Euphorbia jolkinii* (Euphorbiaceae)

species are associated with eggs, larvae, pupae, and even adults of various insects in diverse habitats and constitute important natural enemies particularly of phytophagous insects. The parasitoid community is diverse, particularly in endophytic insects such as leaf miners (Askew 1980), which contributes to regulation of host population dynamics (Kato 1996a). In parasitic wasps, Parasitica, a shift from insect-parasitic life to plant-parasitic life has occurred in a few clades (e.g., Braconidae, Torymidae, and Agaonidae). The last family is unique because all of the members are parasites of fig seeds or parasitize fig wasps (Fig. 2.27). Fig wasps are obligate, exclusive pollinators of *Ficus* (Moraceae), and are estimated to have originated in the late Cretaceous (Machado et al. 2001). Hunting wasps (Aculeata) evolved from parasitic wasps by developing a series of behaviors (e.g., hunting prey, constructing nests, transporting prey to their nests, laying eggs in the host, and sometimes resupplying prey). During this evolutionary process, ovipositors lost their ability to insert eggs and were only utilized to inject paralyzing venom into insect prey (Iwata 1971). The nesting habit likely evolved to escape from attack by predators and parasitoid wasps and from inclement weather conditions. To maintain a clean nest interior, hunting wasps developed sophisticated behavior such as grooming eggs, applying antimicrobial substances to their nest, and exterminating parasites. Aculeata comprises two superfamilies, Vespoidea and Apoidea. The former includes spider wasps (Pompilidae), potter wasps and hornets (Vespidae), and ants (Formicidae). The hunting wasps of Vespoidea are important predators of herbivorous insects, and contribute to regulation of herbivore populations. In Vespoidea, eusociality has evolved twice in Vespidae and Formicidae, and a shift from carnivory to pollenivory has occurred once in Masarinae in Vespidae.

Ants are apterous eusocial wasps and flourish in various ecosystems, particularly in the canopy of tropical rainforests (Hölldobler and Wilson 1990). Because numerous workers forage for insects by walking away from the nest, herbivorous insects around the nest are heavily predated. Thus, some plants have evolved to attract ants by providing extrafloral nectar or domatia for nest sites. Extrafloral nectaries are located on leaf laminae, petioles, rachids, bracts, stipules, pedicels, fruits, and so forth of the following families: Rosaceae, Fabaceae, Passifloraceae, Euphorbiaceae, Malvaceae, and Bignoniaceae (Bentley 1977). The myrmecophytic plants that offer ants cavities for nesting are known as “ant plants.” Most ant plants have hollows as domatia in their shoots, trunks, or rhizomes (Table 2.4; Beattie and Hughes 2002). The high diversity of ant plant taxa in tropical regions suggests that protection mutualism with ants has been a successful strategy against herbivory. Borneo is renowned for its high diversity of the ant tree genus *Macaranga*, and most *Macaranga* species are associated with ants, which nest in shoot cavities of the host tree (Fig. 2.18). The association is highly host-specific and obligatory, because only the seedlings colonized by the ant colony can grow thereafter (Itioka 2005). If the symbiotic ant colony is artificially killed, the host tree would blast due to heavy damage by herbivores. The aggressiveness of symbiotic ants (i.e., the intensity of the antiherbivore defense) is negatively correlated with the chemical defense capacity of the host plant (Itioka et al. 2000).

The epiphytic myrmecophytic ferns, *Lecanopteris* and *Platycerium* (Fig. 2.19), are also inhabited by symbiotic ants, which not only patrol the fern and host tree to hunt herbivores but also kill other epiphytes and lianas climbing the host tree (Tanaka and Itioka 2011). Accordingly, dipterocarp trees harboring epiphytic ant ferns are almost free of other epiphytes and climbing lianas. Ants are generally not efficient pollinators, because apterous ants cannot transport pollen directly between arboreal flowers and because antimicrobial substances secreted from the ant integument are detrimental to pollen viability (Beattie et al. 1984). Weedy short plants, however, sometimes depend on ants for pollination, as described in subsequent chapters. Some ants have shifted their food from insects to seeds or seed appendages, and seed-harvesting ants sometimes contribute to seed dispersal (Fig. 2.20). Seeds of some angiosperm species have fleshy appendages (i.e., elaiosomes) that contain lipid and protein (Beattie and Hughes 2002). Because the elaiosome is firmly attached to the seed, ants cannot free themselves. Seeds with elaiosomes are

Table 2.4 Protection mutualism between plants and its guards

Mutualism type	Guard	Plants	Plant's reward	Guard service	Host specificity	Colonization/ transmission	Region
Extrafloral nectar-involved mutualism	Ant	Bignoniaceae, Euphorbiaceae, Fabaceae, Malvaceae, Passifloraceae, Rosaceae etc.	Extrafloral nectar	Attack on herbivores around nectaries	Low	Migration	Worldwide
Rhizome domatia-involved mutualism	Ant	epiphytic plants such as *Lecanopteris, Platycerium* (Polypodiaceae), Myrmecodia, Hydnophytum (Rubiaceae)	Domatia in rhizome hollow	Attack on herbivores and on other epiphyte and climbers	High	Colonization by a queen	Southeast asia
Stem domatia-involved mutualism	Ant	*Korthalsia* (Arecaceae), *Piper* (Piperaceae), *Dischidia* (Asclepiadaceae), *Macaranga* (Euphorbiaceae), *Medinilla* (Melastomataceae), *Crypteronia* (Crypteroniaceae), *Myrmecorandia* (Rubiaceae)	Domatia in stem hollow sometimes with food body	Attack on herbivores on host plants	High	Colonization by a queen	Southeast asia
Stem domatia-involved mutualism	Ant	*Cecropia* (Cecropiaceae), *Clidemia* (Melastomataceae), *Hirtella* (Chrysobalanaceae), *Cordia* (Boraginaceae), *Duroia* (Rubiaceae)	Domatia in stem hollow sometimes with food body	Attack on herbivores on host plants	High	Colonization by a queen	Neotropics
Stem domatia-involved mutualism	Ant	*Leonardoxa* (Fabaceae), *Cola* (Sterculiaceae), *Canthium* (Rubiaceae)	Domatia in stem hollow sometimes with food body	Attack on herbivores on host plants	High	Colonization by a queen	Africa
Stem domatia-involved mutualism	Ant	*Acasia* (Fabaceae)	Domatia in stem hollow sometimes with food body	Attack on herbivores on host plants	High	Colonization by a queen	Australia

Leaf domatia-involved mutualism	Predatory and fungivory mites	*Annona* (Annonaceae), *Cinnamomum* (Lauraceae), *Cupania* (Sapindaceae), *Terminalia* (Combretaceae), *Vitis* (Vitaceae), *Elaeocarpus* (Elaeocarpacea), *Viburnum* (Adoxaceae), *Coffea* (Rubiaceae), *Tabebuia* (Bignoniaceae)	Leaf domatia in vein axil	Attack on herbivorous mites on leaf	Medium	Migration	Worldwide
Fungal endophyte-involved mutualism	*Colletotrichum Curvularia* (Ascomycetes)	diverse plants	Habitat and assimilate	Protect the host from biotic and abiotic stresses	High	Vertically or horisontary transmitted	Worldwide
Fungal endophyte-involved mutualism	*Epichloë, Neotyphodium* (Ascomycetes)	Poaceae, Cyperaceae	Habitat and assimilate	Protect the host from biotic and abiotic stresses	High	Vertically transmitted	Temperate zone
Bacterial endophyte-involved mutualism	Bacteria	Diverse plants	Habitat and assimilate	Protect the host from biotic and abiotic stresses	High	Vertically or horisontary transmitted	Worldwide

Bentley (1977), Tsai et al. (1994), and Romero and Benson (2005))

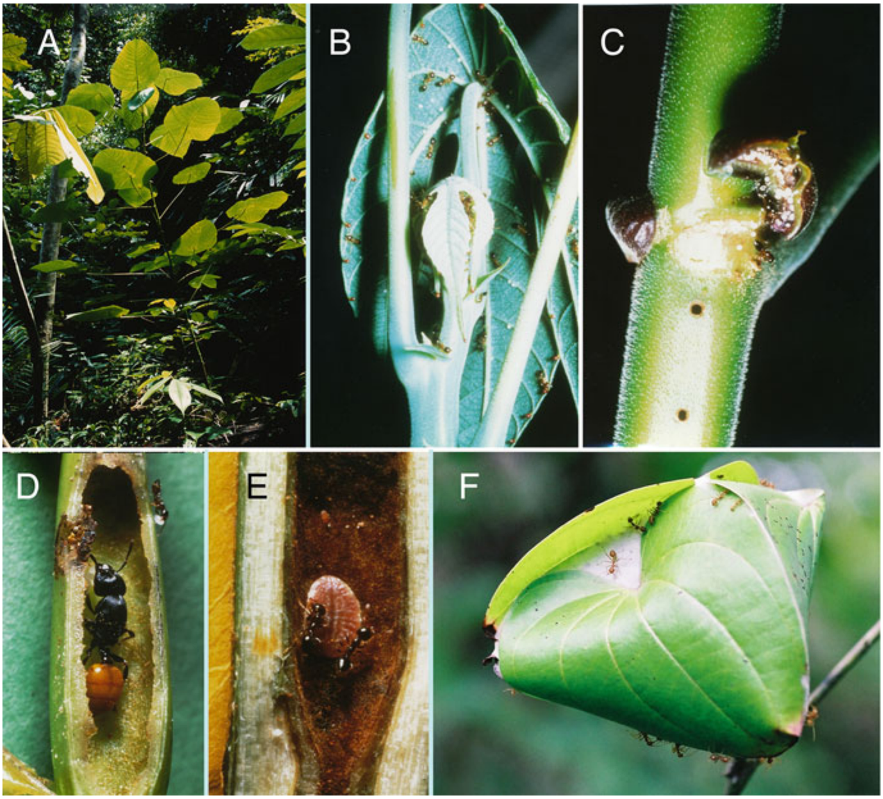

Fig. 2.18 Protection mutualism in Southeast Asia. (**a**–**e**) Obligate mutualism between a myrmecophyte *Macaranga bancana* and an ant *Crematogaster* sp.: (**a**) A fast-growing juvenile tree in a forest gap. (**b**) Young leaves patrolled by many ants. (**c**) Exit holes of the ant's nest on a shoot with food bodies around stipules. (**d**, **a**) Founder queen ants living in a hollow of a seedling. (**e**, **a**) Scale insects kept inside the ant's nest. (**f**) Facultative mutualism of an ant *Oecophylla smaragdina* with a facultative host plant *Strychnos nux-blanda* in Laos. The ant's nest is spun on a branch with a few leaves tied together

harvested by the ants, transported to their nest, and fed to the larvae. Infestation of the seed by adult and larval ants is prohibited by its hardness. Accordingly, the undamaged seed is removed from the nest and is discarded in a waste disposal area, where it germinates. Although the seed is not transported a great distance, the newly colonized site is rich in nutrients, and root pathogens are removed from the seed by antimicrobial substances secreted by the ants. Myrmecochory has evolved independently in at least 11,000 plant species in 77 families, and the elaiosomes derived from various seed or fruit tissues have undergone convergent evolution (Lengyela et al. 2010).

Fig. 2.19 Epiphytic ferns *Platycerium* sp. (**a**) and *Lecanopteris crustacea* (**b**) growing on canopy branches of dipterocarp trees. In the litter within basal fronds of the former fern, myrmecophytic ants and specialized cockroaches live. In the cavity of the hollow rhizomes of the latter fern, myrmecophytic ants nest. These ants are very aggressive and attack almost all herbivores and gnaw off all shoots of climbing liana and epiphytes (**c**) thus the canopy around the fern is free from lianas and epiphytes (Photo by T. Itioka)

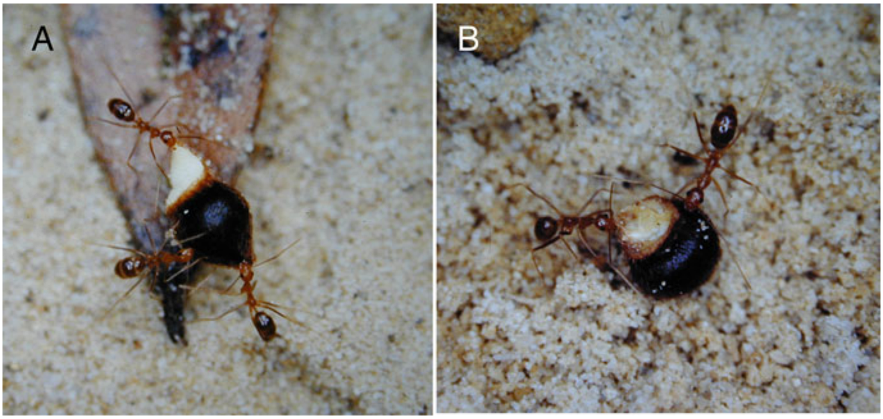

Fig. 2.20 Seed dispersal of *Aquilaria* sp. (Thymelaeaceae) by ants in a tropical rain forest in Borneo. A seed with elaiosome is transported by ants to their nest (**a**), and afterward the seed without elaiosome is transported to their waste site (**b**) and discarded

2.9 Diversification of Bees

Bees are members of the superfamily Apoidea, and are derived from their sister family, Sphecidae sensu lato. Sphecids are solitary hymenopterans, which dig burrows belowground using their mandibles and legs and rear their larval offspring in the nest by feeding them hunted insects. When bees changed their larval food from hunted prey to pollen and nectar, wasps became bees (Iwata 1971). Although the basic morphology of bees is similar to that of sphecid wasps, bees have developed novel derived characteristics (i.e., delicately branched hair on their body for collection of pollen and an extended proboscis for collection of nectar; Fig. 2.21). Nectar and pollen are sources of carbohydrate and protein, respectively, for bee larvae. Because bees are dependent on flowers for food for themselves and their offspring, they are the most frequent visitors to angiosperms. To collect nectar

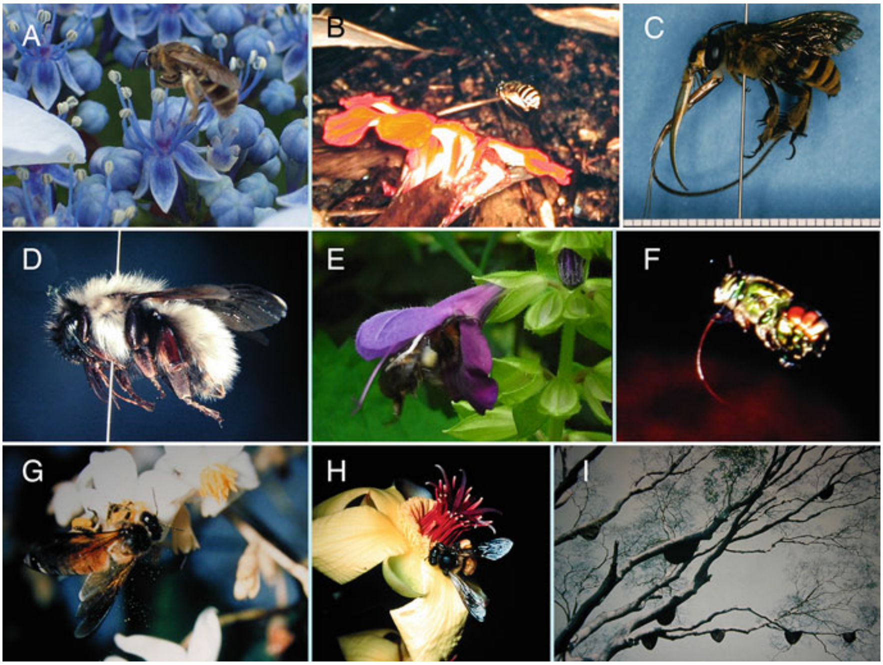

Fig. 2.21 Diverse morphology and behavior of bees: (**a**) A female of *Lasioglossum sibiriacum* (Halictidae) visiting flowers of *Hydrangea macrophylla* (Hydrangeaceae). (**b**–**c**) Exceedingly long-tongued bees *Amegilla elephas* (Apidae) visiting an exceedingly long-tubed flower of *Etlingia* sp. (Zingiberaceae) in Sumatra. (**d**) A queen of *Bombus senex* (Apidae) endemic to mountain forests in Sumatra. (**e**) *Bombus diversus* visiting a zygomorphic flower of *Salvia glabrescens* (Lamiaceae). (**f**) A hovering female of *Euglossa tridentata* (Apidae) in Panama. (**g**, **h**) Workers of the giant honeybee *Apis dorsata* visiting flowers of *Dryobalanops lanceolata* (Dipterocarpaceae) and *Dillenia suffruticosa* (Dilleniaceae). (**i**) Nests of *Apis dorsata* hung below the boughs of an emergent tree in a tropical rain forest in Lambir Hills National Park in Borneo during a mass-flowering event in 1996 (**g**–**i**, Photo by Tamiji Inoue)

and pollen efficiently, bees visit limited types of flowers. Their frequent and selective visits to flowers and thick coats of branched hair have made them the most important pollinators of diverse angiosperms (Table 2.1). The total number of bee species is estimated to exceed 20,000, most of which are solitary species nesting below ground or in plant cavities (Michener 2007). In contrast to many other insects, the center of bee diversity is located not in tropical rain forests but in scrub land in Mediterranean climate regions, which harbor diverse rare oligolectic (depending on a few flower species) solitary bees. Oceanic islands are unique in that the bee faunae are only composed of solitary bees nesting in plant cavities, suggesting that colonization of oceanic islands occurred by drifting of nests in wood. The small size and scanty hair of solitary bees residing on oceanic islands (e.g., *Hylaeus* in Colletidae, which transport pollen not on their bodies but in their gastric contents) are thought to have enhanced the geitonogamy of the insular woody plants, which increases the risk of inbreeding and accordingly the evolution of dioecy by these insular plants (Kato and Nagamasu 1995). As a result of coevolution with bees, melittophilous (bee-pollinated) flowers became white or yellow, fragrant, nectariferous, and often zygomorphic. The proboscises of some bee species (particularly Anthophorini and Euglossini in Apidae) are strongly extended as a result of the arms race with nectariferous plants, which have tubular corollas or spurs. These long-tongued bees forage scattered deep flowers by following defined routes over long distances. This behavior is known as traplining, and has been observed in *Amegilla* (Anthophorini) in tropical regions of Asia (Fig. 2.21; Kato 1996b) and in *Euglossa* (Euglossini) in the Neotropics (Fig. 2.21; Janzen 1971). Euglossine bees are termed orchid bees, because males are attracted to specific orchids and aroids by the floral odor (Fig. 2.16).

In contrast to nectariferous flowers, another type of coevolution occurred in oil-secreting flowers, which offered oil instead of nectar to bee pollinators as a reward. The forelegs of some oil-collecting bees (*Redivia*, Melittidae) in South Africa are remarkably extended as a result of an arms race with plants that have two oil-secreting floral spurs (Scrophulariaceae; Buchmann 1987). The principal reward for pollinators is not nectar but pollen in some plants such as *Caesalpinia* (Fabaceae), *Diospyros* (Ebenaceae), *Melastoma* (Melastomataceae), *Pyrola* (Ericaceae), *Solanum* (Solanaceae), and *Vaccinium* (Ericaceae). On these flowers, leaf-cutter bees (Megachilidae), carpenter bees (Xylopopini, Apidae), and bumblebees (Bombini, Apidae) grasp and vibrate anthers and efficiently collect the dislodged pollen (Knudsen and Olesen 1993). The pollination system involving this technique is known as buzz pollination. To reduce pollen removal, some plants have evolved a dimorphy of anthers. For example, in *Melastoma*, pollen of yellow anthers is harvested by bees as a reward, but pollen of purple anthers contributes to actual pollination without being harvested (Luo et al. 2008). As with hornets (vespid wasps) and ants, eusociality has evolved in at least five clades of bees: *Lasioglossum* (Halictidae), *Ceratina* (Xylocopinae, Apidae), bumblebee (Bombinae, Apidae), honeybee (Apinnae, Apidae), and stingless bee (Meliponinae, Apidae; Sakagami and Maeta 1989, Michener 2007). Retention of workers specialized in foraging nectar and pollen made eusocial bees more competitive and efficient pollinators. The morphological differentiation between queen and worker is weak in *Lasioglossum* and *Ceratina*, but is prominent in highly eusocial bees: bumblebees, stingless bees, and honeybees.

Bumblebees are densely furry bees (Fig. 2.21) that were originally distributed in the Northern Hemisphere and South America. Most bumblebee species are adapted to temperate and boreal climates, however, there are a few tropical species in South America. Bumblebees nest in underground cavities such as abandoned vole nests. A queen bumblebee can found a nest by herself. Bumblebees have coats of long hairs to which pollen readily attaches, and they can maintain their body temperature at about 30–38 °C, even in cold weather. Bumblebee workers exhibit characteristic foraging behavior, in that each individual specializes in a single plant species and continues to visit only flowers of this species (Heinrich 1979). This results in flower constancy by bumblebees. Thus, the bumblebee is a reliable pollinator for plants, because each bumblebee worker transports ample pollen to other flowers of the same plant species. Because bumblebee larvae are brooded in a mass of pollen and nectar, not in separate cells, worker size varies greatly. Workers with different body sizes visit flowers of different sizes, because morphological matching between flower and bee is a critical determinant of their foraging efficiency. A bee colony can utilize diverse flower species because it contains workers of various sizes. In addition, to enhance foraging efficiency, bumblebee workers avoid visiting flowers that have recently been visited by other conspecifics (Kato 1988). The floral cues perceived by the bumblebees involve a repellent scent that they deposit (Stout et al. 1998) and floral electric fields that they charge (Clark et al. 2013).

In contrast to bumblebees, honeybees are only distributed in Eurasia and Africa and their center of diversity is in the tropical region of Southeast Asia, where five honeybee species coexist. Giant honeybees construct large uncovered nests below branches of emergent trees (the giant honeybee *Apis dorsata*; Fig. 2.21) or on cliffs (the Himalayan giant honeybee *Apis laboriosa*), whereas Asian and European honeybees nest in hollows of tree trunks. Honeybees reproduce by swarming of a queen and her workers, because a queen cannot found a nest herself. Because larvae are brooded in separate standardized cells, workers are similar in size. Honeybees forage using a scout–recruit strategy. Scouting workers that have completed scouting of a floral resource return to the nest and transmit information on the location of a promising flowering patch to colony members via figure-eight dances. The workers rush to the flowers and collect the concentrated floral resource. Due to the high efficiency of the scout–recruit foraging strategy, honeybees have a competitive advantage over other solitary bees, particularly in landscapes where flowers are distributed in clumps, as in tropical rain forests. The predominance of social bees (particularly honeybees and stingless bees) explains the inferiority of solitary bees and the low diversity of bee species in tropical forests. In tropical rainforests in Borneo, five species of honeybee are the predominant pollinators, and giant honeybees are important pollinators of canopy trees, including Dipterocarpaceae, Anacardiaceae, and Fabaceae (Momose et al. 1998). The canopy trees mass-flower for about 3 months at an interval of 4–6 years, and the mass flowering is triggered by drought and/or low temperature for several weeks (Sakai et al. 2006). During the nonflowering period, there are no giant honeybees in the forest. When mass flowering begins, the giant honeybees appear from somewhere (possibly nearby swamp forests), and the number of colonies hanging below branches of emergent trees increases rapidly. Because giant honeybees can fly at least several kilometers, they can pollinate flowers of distant, isolated, rare canopy trees. In the Neotropics, where honeybees are not distributed, eusocial stingless bees were the dominant pollinators before the introduction of European honeybees and the subsequent expansion of Africanized honeybees (Roubik 1992). Extensive observations of flower visitors and pollen attachment to the visitors assist determination of the pollination systems of plant species. By compiling these data, plant pollination systems in different climatic zones can be compared. In five types of forest in Asia, bee pollination (melittophily) is predominant, whereas the main pollinator bee groups vary among climatic zones. In temperate regions in Japan, bumblebees and solitary bees are the most important pollinators, whereas long-tongued bees (*Amegilla*), carpenter bees (*Xylocopa*), and leaf-cutting bees (Megachilidae) are also important pollinators in subtropical and tropical monsoon forests (Fig. 2.22; Kato et al. 2008). For more than a century, European honeybees have been introduced for apiculture to regions in which they were absent (e.g., the New World, Australia, and oceanic islands). The native bee faunae of oceanic islands, which were originally dominated by cavity-nesting solitary bees, were affected by artificial introduction of the honeybee, particularly the Ogasawara Islands in Japan (Kato et al. 1999), Mauritius (Hansen et al. 2002), New Caledonia (Kato and Kawakita 2004), and the Canary Islands (Dupont et al. 2004).

2.10 Lepidopterans as Herbivores and Pollinators

Although bees are indeed important pollinators in most regions of the world, butterflies may be more eye-catching on flowers. Lepidoptera, to which butterflies belong, is the only order that has preadapted to herbivory, and almost all of the members have evolved as herbivores. Trichoptera is the sister group of Lepidoptera, whose larvae are aquatic detritivores or algal grazers. Both orders have the ability to spin silk, although their wings are covered by different structures: scales in Lepidoptera and hairs in Trichoptera. The earliest clade of lepidopterans known is Micropterigidae, which originated in the Jurassic. Micropterigid moths have functional mandibles but lack a tubular proboscis and their larvae are grazers of liverworts (Fig. 2.23). In the Japanese Archipelago, there are 25 species of micropterigid moths of which 22 are specialists of the liverwort species of the genus *Conocephalum*. In micropterigid moths with weak flight activity, vicariant speciation without host plant shift has occurred in the Japanese Archipelago (Imada et al. 2011). Other basal moths with functional mandibles include the agathiphagids, whose larvae are seed parasites of the basal conifer *Agathis* (Araucariaceae); and heterobathmiids, whose larvae are leaf miners of the relict angiosperm *Nothofagus* (Nothofagaceae; Fig. 2.23; Kristensen 1984). Other

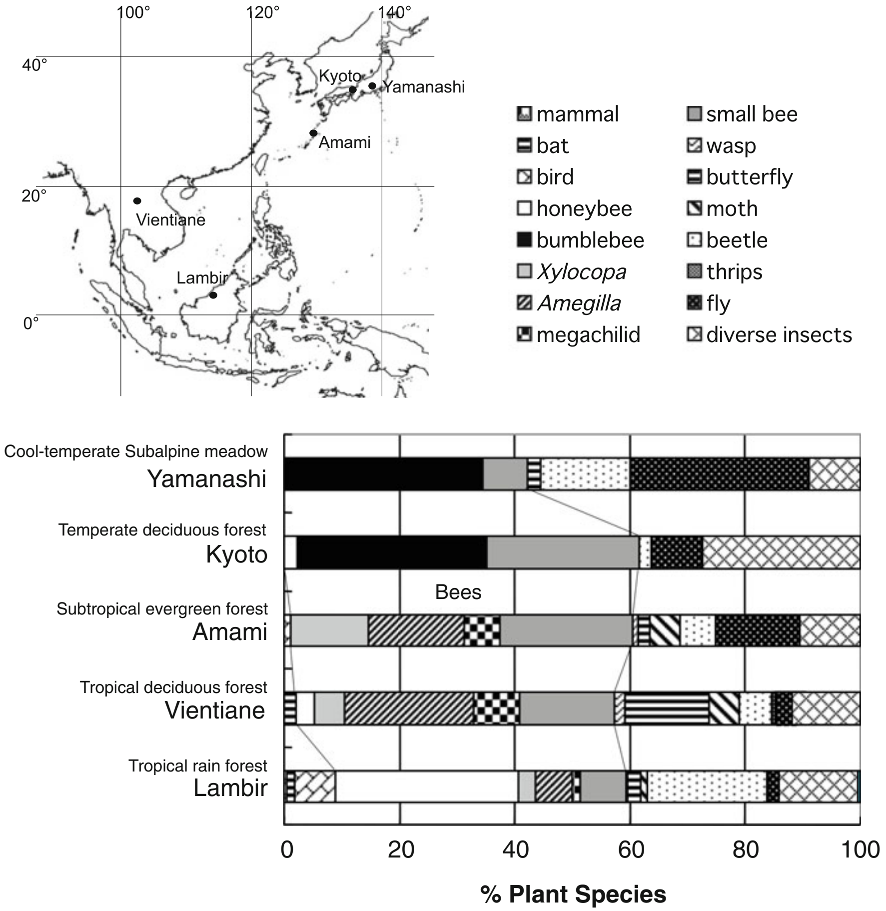

Fig. 2.22 Community-level comparison of pollination systems of plants among various types of forests in Asia: subalpine coniferous forest and meadow in Mt. Kushigata, Yamanashi, cool temperate deciduous forest in Ashiu, Kyoto, subtropical evergreen forest in Amami, tropical monsoon forest in Laos, tropical rainforest in Lambir, Malaysia (Modified from Kato et al. 2008)

members of Lepidoptera have tubular proboscises (suborder Glossata), which suggests that these long-tongued moths evolved after the appearance of nectariferous angiosperm flowers. Although lepidopterans are frequent visitors to flowers, their contribution to pollination is less prominent than that of bees, probably because lepidopterans with exceedingly long proboscises can imbibe nectar without touching stamens and pistils. However, some plants have evolved pollination by lepidopterans. For example, nocturnal flowers with exceedingly long floral tubes or spurs (e.g., Orchidaceae, Caryophyllaceae, Onagraceae, Thymelaeaceae, Rubiaceae, Solanaceae, Campanulaceae, and Apocynaceae) are pollinated by nocturnal long-tongued moths belonging to Pyralidae, Geometridae, Noctuidae, and Sphingidae (Fig. 2.24). Diurnal long-tubed flowers in Liliaceae,

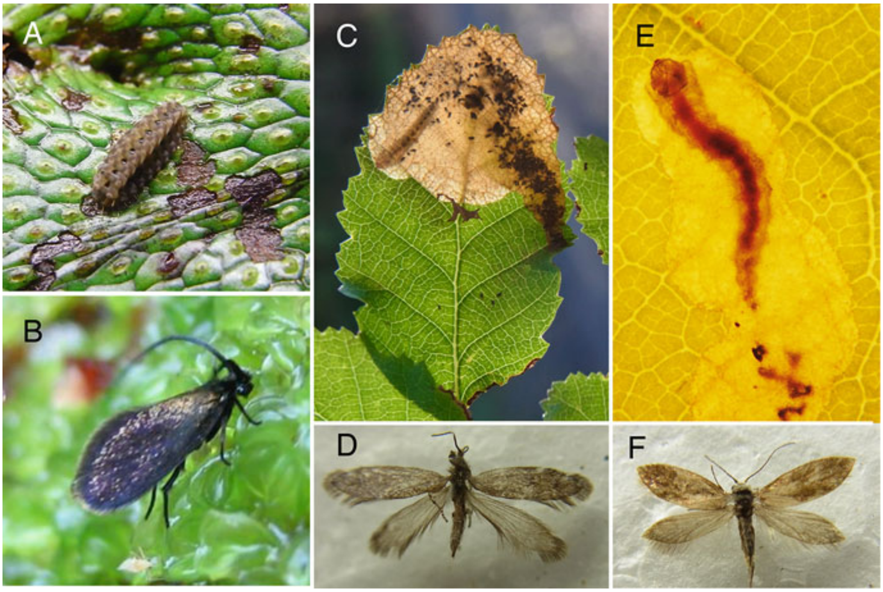

Fig. 2.23 Basal lineages of Lepidoptera. (**a**–**b**) *Neomicropteryx nipponensis* (Micropterigidae). (**c**–**d**) *Heterobathmia pseuderiocrania* (Heterobathmiidae). (**e**–**f**) *Issikiocrania japonicella* (Eriocraniidae). Host plants are a liverwort *Conocephalum conicum* (Conocephalaceae) (**a**), *Nothofagus glauca* (Nothofagaceae) (**c**), and *Fagus crenata* (Fagaceae) (**e**)

Ericaceae, and Lamiaceae are mainly pollinated by butterflies and diurnal hawkmoths. Microlepidopterans have rarely been reported to be pollinators, with the exception of the yucca moth family Prodoxidae, which participates in obligate pollination mutualism with Agavaceae and Saxifragaceae, as detailed below (Pellmyr and Thompson 1992; Pellmyr et al. 1996a, b).

Most members of the proboscid lepidopteran clade, Glossata, are herbivores of angiosperms, whereas some are associated with conifers, pteridophytes, and rarely, with bryophytes. The basal clades of Glossata are small internal herbivores such as leaf miners (Eriocranidae, Nepticulidae, Opostegidae, Heliozeidae, Incurvariidae, Gracillariidae, Tischeridae, Elachistidae, and Cosmopterigidae), leaf gallers (a part of Gracillariidae), shoot borers (Pyralidae and Cossidae), cambium miners (Opostegidae), seed borers (a part of Gracillariidae and Pyralidae), fruit borers (Carposinidae), case bearers (Adelidae, Incurvariidae, Tineidae, Psychidae, and Coleophoridae), leaf rollers (Pyralidae and Tortricidae), and leaf tiers (Gelechidae, Oecophoridae, Pyralidae, and Tortricidae; Fig. 2.25). To break away from the internal life style, the lepidopteran larvae had to adopt novel habits such as draping nettling hair, developing an aposematic or cryptic coloration, mimicking poisonous models, or only being active during the night. By shedding their shelters in this way, lepidopteran larvae could become larger. The scaling-up of lepidopteran size must have made a considerable impact on host plants, and thus had greater selective pressure on plant antiherbivore mechanisms. Thus, the plant–herbivore chemical

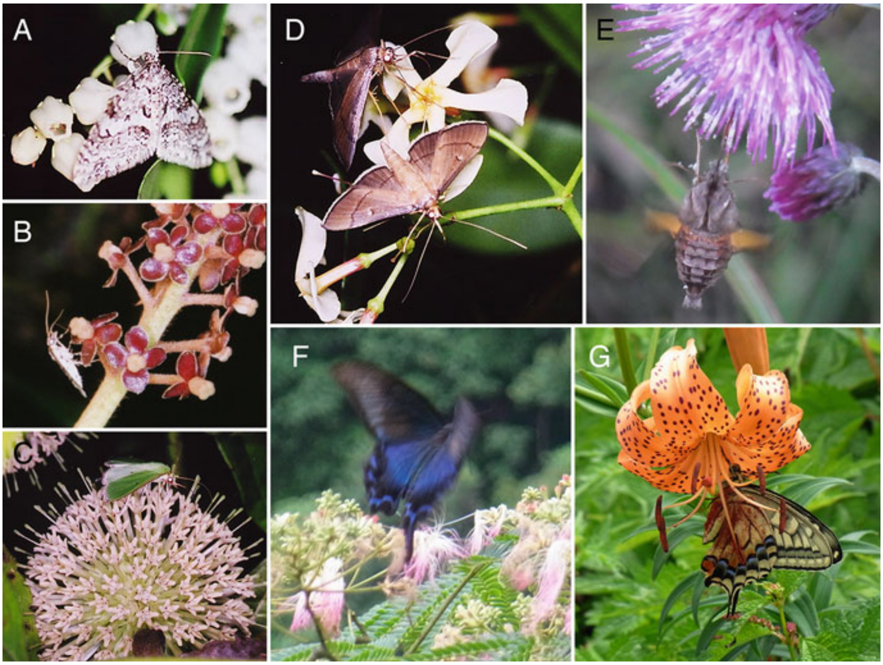

Fig. 2.24 Lepidopterans visiting angiosperm flowers for floral nectar: (**a**) A noctuid moth visiting flowers of *Pieris japonica* (Ericaceae). (**b**) A pyralid moth visiting flowers of a pitcher plant *Nepenthes vieillardii* (Nepenthaceae) in New Caledonia. (**c**) A pyralid moth visiting flowers of *Uncaria rhynchophyll*a (Rubiaceae) in Laos. (**d**) Pyralid moths *Bradina trigonalis* visiting flowers of *Trachelospermum asiaticum* (Apocynaceae). (**e**) A sphingid moth *Neogurelca himachala* visiting a flower head of *Cirsium sieboldii* (Asteraceae). (**f**) A papilionid butterfly *Papilio bianor* visiting flowers of *Albizia julibrissin* (Fabaceae). (**g**) A papilionid butterfly *Papilio machaon* visiting a flower of *Lilium lancifolium* (Liliaceae)

arms race resulted in the high host specificity of lepidopterans, and the rarity of a shift in their host plant is hypothesized to have facilitated their diversification (Ehrlich and Raven 1964; Fordyce 2010).

2.11 Dipterans also Pollinate Flowers

Diptera is a two-winged insect order with great diversity, several members of which are notorious for their bite, pest damage, dirtiness, nuisance, and insanitation. The most basal clades of extant Dipterans (Deuterophlebiidae, Nymphomyiidae, and Blephariceridae) are aquatic alga-grazers or detritus-feeders, and there are several basal clades of aquatic dipterans, such as Culicomorpha (Brian et al. 2011), suggesting that dipterans originated in an aquatic habitat (Fig. 2.9). Larvae of terrestrial dipterans lack legs and are adapted to mining media rich in organic

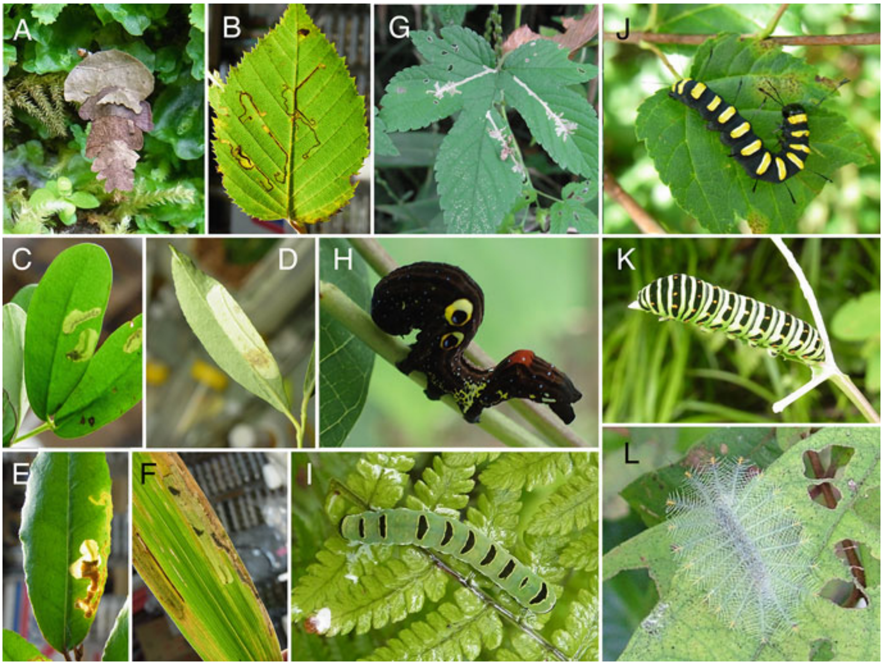

Fig. 2.25 Diversity of morphology and feeding habits in lepidopteran larvae: (**a**) A case-bearing larva of *Adela* sp. feeding on fallen leaves (Adelidae). (**b**) Linear mines of *Stigmella betulicola* (Nepticulidae) on a leaf of *Betula grossa* (Betulaceae). (**c**) Larvae of *Cuphodes* sp. (Gracillariidae) mining a leaflet of *Caesalpinia decapetala* (Fabaceae). (**d**) Blotch mine of *Phyllonorycter* sp. (Gracillariidae) on a leaf of *Salix subfragilis* (Salicaceae). (**e**) A larva of *Apatetris elaeagnella* (Gelechidae) mining a leaf of *Elaeagnus pungens* (Elaeagnaceae). (**f**) A larva of *Elachista canis* (Elachistidae) mining a leaf of a dwarf bamboo *Sasa nipponica* (Poaceae). (**g**) Leaf mines of *Cosmopterix zieglerella* (Cosmopterigidae) on a leaf of *Humulus japonicas* (Cannabaceae). (**h**) A larva of *Eudocima tyrannus* (Noctuidae). (**i**) A larva of *Callopistria* sp. (Noctuidae) on a fern *Stegnogramma pozoi* (Thelypteridaceae). (**j**) A larva of *Jocheaera alni* (Noctuidae) on *Acer ginnala* (Sapindaceae). (**k**) A larva of *Papilio machaon* (Papilionidae) feeding on leaves of *Angelica pubescens* (Apiaceae). (**l**) A thorn-covered larva of *Euthalia* sp. (Nymphalidae) on *Cratoxylum* sp. (Hypericaceae)

matter in wet habitats. Herbivory originated in various clades of these terrestrial dipterans. The herbivorous dipterans comprise leaf miners (Sciaridae, Rhagionidae, Tephritidae, Agromyzidae, Ephydridae, and Anthomyiidae), gallers (Cecidomyiidae), shoot borers (Diopsidae and Chloropidae), fruit borers (Tephritidae and Drosophilidae), and so forth. A basal group of the snipe fly family Rhagionidae, Spaniinae is associated with liverworts and mosses, and its association with bryophytes is thought to have been maintained for more than 100 million years since the Jurassic (Imada and Kato 2016a, b). The mouthparts of dipterans are adapted not to bite solid food but to lick liquid or powdery food. Thus, many dipteran adults consume floral nectar, pollen, tree sap, and animal secretions, and some dipterans with aciform mouthparts suck the blood of vertebrates. Among

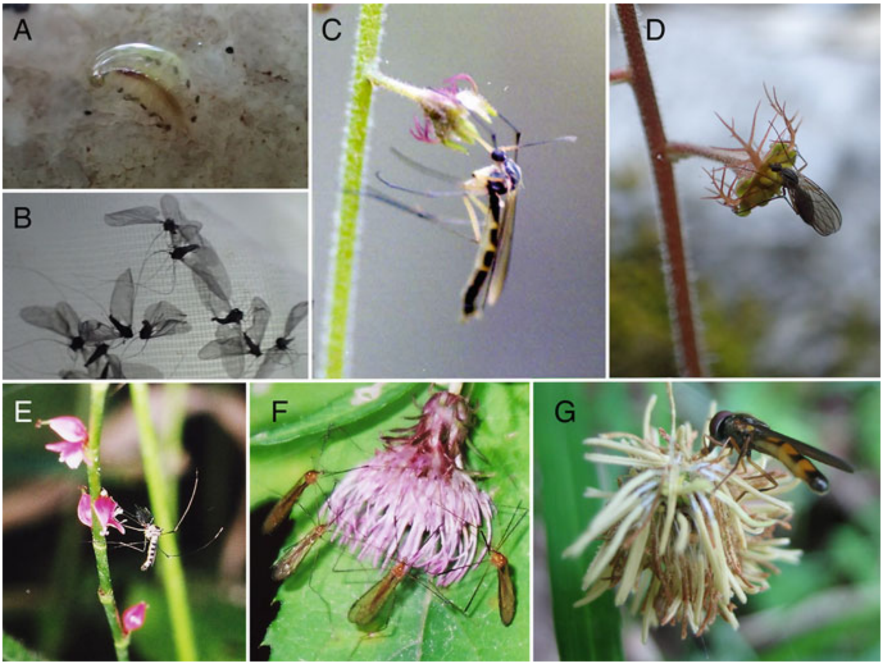

Fig. 2.26 Diversity of morphology and habits of dipterans in Japan: (**a**–**b**) An algae-grazing larva (**a**) and adults (**b**) of the basal dipteran *Deuterophlebia nipponica* (Deuterophlebiidae). (**c**) A fungus gnat *Gnoriste mikado* (Mycetophilidae) visiting a flower of *Mitella furusei* var. *subramosa* (Saxifragaceae). (**d**) A fungus gnat *Coelosia* sp. (Mycetophilidae) visiting a flower of *Mitella pauciflora*. (**e**) A male of a mosquito *Tripteroides bambusa* visiting a flower of *Persicaria filiformis* (Polygonaceae). (**f**) Tipulid flies *Elephantomyia* sp. visiting a flower head of *Cirsium nippponicum* var. *yoshinoi* (Asteraceae). (**g**) A syrphid fly *Melanostoma mellinum* visiting male flowers of *Carex foliosissima* (Cyperaceae)

these dipterans, hoverflies (Syrphidae), bee flies (Bombyliidae), blow flies (Calliphoridae), and fruit flies (Drosophilidae and Tephritidae) are frequent visitors to flowers. However, their contribution to pollination is less prominent than that of bees, because their visit frequency, floral constancy, and pollen attachment are inferior to those of bees.

Among anthophilous dipterans, fungus gnats of the family Mycetophagidae are unique exclusive pollinators of the perennial genus *Mitella* (Saxifragaceae; Fig. 2.26; Okuyama et al. 2004). The larvae of pollinator gnats feed on mosses, which grow in the same habitat as *Mitella*. The inconspicuous flowers with branched linear petals secrete species-specific blends of volatiles, and attract specific species of fungus gnats (Okamoto et al. 2015). Accordingly, loss of a floral volatile triggers a change in the pollinator, causing speciation of pollinator-mediated plants.

Some dipterans participate in brood-site pollination mutualisms, in which adult females pollinate and oviposit on flowers and the pollinator larvae develop in

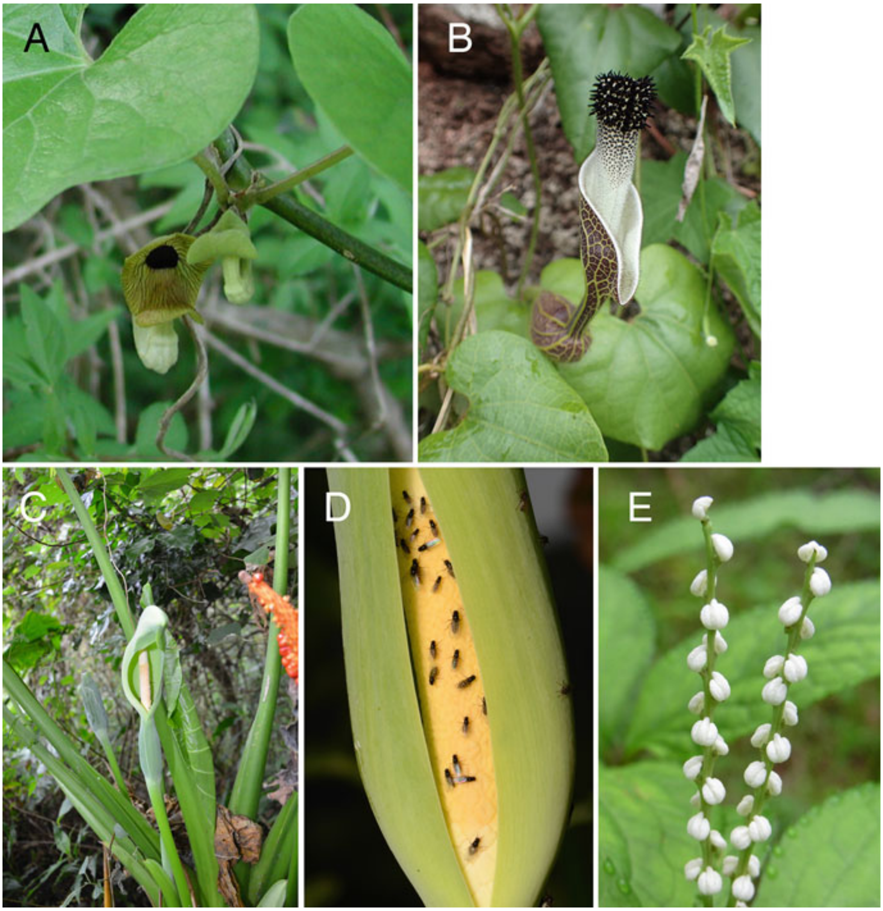

Fig. 2.27 Flowers involved in brood-site pollination by phorid flies (**a**, **b**), drosophilid flies (**c**, **d**) and thrips (**c**). (**a**) *Aristlochia kaempferi* in Japan. (**b**) *Aristlochia* sp. in Peru. (**c**, **d**) *Alocasia odora* in Taiwan. (**e**) *Chloranthus serratus* in Japan

vegetative tissue of inflorescences (Sakai 2002). In this association, host specificity of the pollinator is not high, pollinators sometimes have alternative hosts, and the plants often have copollinators. Brood-site pollination mutualism has been reported between *Alocasia* (Araceae) and drosophilid flies, between *Aristolochia* (Aristolochiaceae) and phorid flies, and between *Artocarpus* (Moraceae) and cecidomyiid flies (Fig. 2.27). In the last case, male inflorescence infected by a few species of fungi is the growth medium for the pollinator larvae (Sakai et al. 2000). The associations between these plants adopting brood-site pollination and the pollinators utilizing floral tissue are less reciprocally obligate than the associations between the plants providing seeds as rewards and the host-specific pollinators whose larvae utilize the seeds, probably because floral tissue is a perishable resource for the pollinator larvae, and because pollination service did not increase fitness of the pollinator.

2.12 Birds with Red Fruits and Red Flowers

In addition to winged insects, birds and bats are essential partners of plants. The bird (class Aves) is an offspring of the dinosaur clade (clade Dinosauria), and the bat (order Chiroptera) is a clade of the class Mammalia. Because birds originated and achieved air supremacy in the late Jurassic, bats, which appeared in the late Cretaceous were forced to become nocturnal. Another flying vertebrate, the pterosaur (clade Ornitodera), was extant in the Mesozoic, but was extinct by the end of the Cretaceous. Due to their acquisition of wings, birds in forest ecosystems have undergone adaptive radiation as insectivores and frugivores. Frugivorous birds play a pivotal role in dispersing the seeds of angiosperms. Fleshy fruits with red, yellow, purple, black, or (rarely) blue colors attract frugivorous birds (Fig. 2.28), which only consume the juicy pulp of the fruits and cast seeds with feces or pellets at

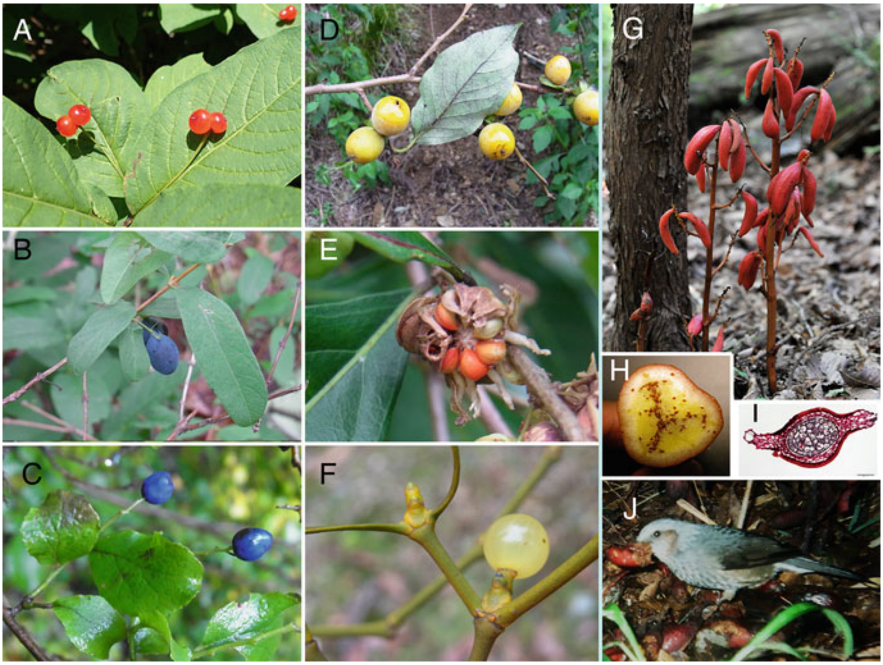

Fig. 2.28 Diverse fleshy fruits of angiosperms in Japan: (**a**) *Lonicera chamissoi* (Caprifoliaceae). (**b**) *Lonicera caerulea*. (**c**) *Symplocos sawafutagi* (Symplocaceae). (**d**) *Diospyros japonica* (Ebenaceae). (**e**) *Glochidion obovatum* (Phyllanthaceae). (**f**) *Viscum album* (Santalaceae). (**g–j**) *Cyrtosia septentrionalis* (Orchidaceae). Pericarps of fruits (**a–c**, **f**, **g**) or outer seed coat (**e**) are brightly colored for seed dispersal by birds

various sites, sometimes far from the mother plant. This directed, long-distance seed dispersal by birds likely enabled angiosperms bearing fleshy fruits to colonize new, isolated, suitable habitats, and even a desert oasis or isolated oceanic island. The fact that a great number of plant species bear fleshy fruits suggests that seed dispersal by birds favored evolution of a juicy pulp and brilliantly colored pericarp. Ornithochory (seed dispersal by birds) has also evolved in orchids, which generally bear numerous dust seeds lacking an endosperm. The red fruits of the mycoheterotrophic orchid *Cyrtosia* growing in the dark on the forest floor are ingested by thrushes, and are dispersed by being discarded in the feces (Suetsugu et al. 2015).

Some insectivorous and frugivorous birds have developed slender bills and long extensible tongues, and imbibe nectar from deep flowers, which are pollinated by the birds. The anthophilous birds comprise hummingbirds (Trochillidae), sunbirds and spiderhunters (Nectariniidae), honeyeaters (Meliphagidae), bulbuls (Picnonotidae), white-eyes (Zosteropidae), Hawaiian honeycreepers (Drepanidini of Fringillidae), and so forth (Table 2.2). Bird-pollinated (ornithophilous) flowers have red, tubular, tough corollas that secrete ample dilute nectar containing ~20% sugar (Cronk and Ojeda 2008; Fig. 2.29). In the Neotropics where hummingbirds

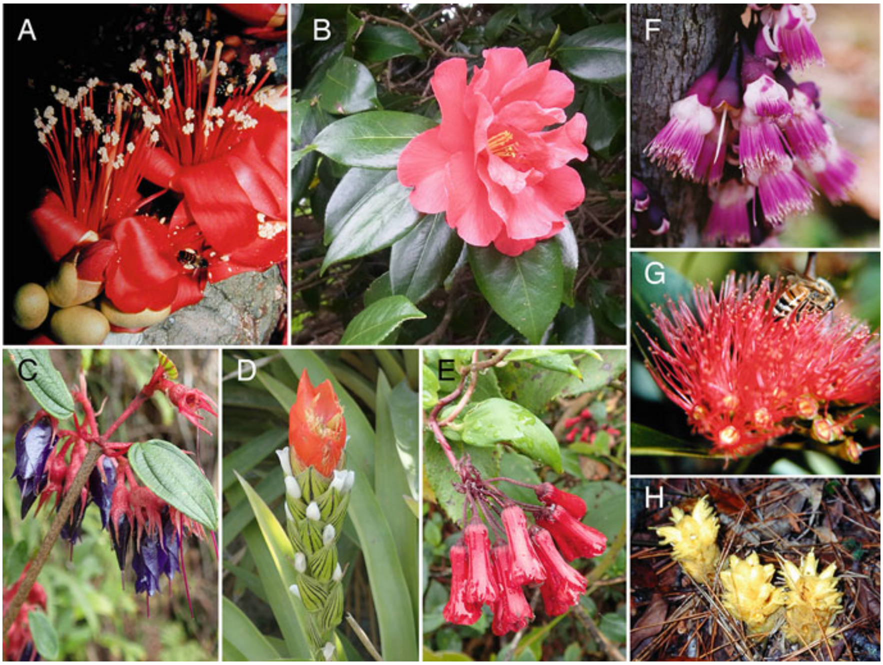

Fig. 2.29 Ornithophilous flowers in the world: (**a**), *Durio lowianus* (Malvaceae) in Borneo. (**b**) *Camellia rusticana* (Theaceae). (**c**) *Brachyotum quinquenerve* (Melastomataceae). (**d**) *Guzmania monostachia* (Bromeliaceae). (**e**) *Bomarea* sp. (Alstroemeriaceae). (**f**) *Syzygium acre* (Myrtaceae). (**g**) *Metrosideros boninensis* (Myrtaceae). (**h**) *Orobanche boninsimae* (Orobanchaceae). (**a**) Sarawak; (**b**) Japan; (**c**–**e**) Peru; (**f**) New Caledonia; (**g**–**h**) Ogasawara Islands, Japan. The putative bird pollinators of the last two plant species in the oceanic islands are now extinct

flourish, there are many ornithophilous plants in Heliconiaceae, Zingiberaceae, Bromeliaceae, Gesneriaceae, Apocynaceae, Rubiaceae, and Lamiaceae (Bawa 1990). Phylogenetic studies of monkeyflowers (*Mimulus*, Phrymaceae) suggest that hummingbird pollination in North America has evolved twice from insect pollination, and has resulted in drastic changes in the color and shape of flowers (Beardsley et al. 2003). In Southeast Asian tropical rainforests, in which sunbirds and spiderhunters reside, the ornithophilous plants include Zingiberaceae, Musaceae, Bombacaceae, Sapotaceae, and Loranthaceae (Momose et al. 1998). Sunbirds and spiderhunters must perch on nearby branches to collect floral nectar, whereas hummingbirds can imbibe nectar during hovering. In fact, in Southeast Asian tropical forests, some epiphytes of Loranthaceae have inflorescences whose axis functions as a stout perch for bird pollinators (Yumoto et al. 1997), and the red ground flowers of some tall gingers are pollinated by nectar-seeking spiderhunters on the forest floor. Bird pollination (ornithophily) is also prevalent in Australia, New Zealand, and New Caledonia, where honeyeaters (Meliphagiidae) are frequent visitors to flowers (Fig. 2.29). In Hawaii, there are diverse ornithophilous plants, the flowers of which are pollinated by several Hawaiian honeycreepers with diverse bill morphologies. A recent molecular phylogenetic analysis revealed that these honeyeater-like birds belong to the finch family (Fringillidae) and have undergone adaptive radiation on the islands in the last 5.7 million years (Lerner et al. 2011). In the Ogasawara Islands in Japan there is an endemic nectarivorous bird *Apalopteron familiare*, which was demonstrated to be a member of Zosteropidae. These necatariferous birds on oceanic islands are now threatened by artificial invasions of rats and feral cats, as well as destruction of forests (Kawakami and Higuchi 2013). In the Ogasawara Islands, three of four endemic bird species have become extinct within the last 200 years, which has hampered pollination of some putatively ornithophilous plants (Fig. 2.29). In temperate regions of the Japanese Archipelago, common nectarivorous birds are the brown-eared bulbul and Japanese white-eye, which visit flowers of *Camellia* (Camelliaceae), *Loranthus* (Loranthaceae), and *Myoporum* (Scrophulariaceae). Because the song of the Japanese white-eye has been praised by Japanese people since the Edo period, they were kept as caged birds to perform in song contests. However, they have also been introduced to various oceanic islands, such as Hawaii, where they occupy the niche of the extinct Hawaiian honeycreepers.

2.13 Associations Between Plants and Mammals

Although the megafauna of the current terrestrial ecosystem are dominated by mammals, there is a long suppressed prehistory of mammals. Egg-laying mammals originated in the Triassic, and placental and marsupial mammals have undergone adaptive radiation after the dinosaurs became extinct at the end of the Cretaceous. In the Mesozoic, diverse herbivorous dinosaurs must have depended upon pteridophytes and gymnosperms. During the Paleogene, many clades of mammals adopted herbivory and diversified as angiosperm grazers. Because mammals have fur, they are utilized by some plants as seed dispersers by means of their sticky or prickly fruits, which readily attach to mammalian fur (Table 2.2). The mammals that have adapted to arboreal life are primates and rodents, which can access the fruits on canopy trees. The seeds of these arboreal fleshy fruits are dispersed by mammals through their intestines. In the tropics, many cauliflorous trees that bear flowers directly on the trunk are extant (Fig. 2.30). These cauliflorous habits are thought to be related to seed dispersal (and/or pollination) by arboreal mammals. Southeast Asian rainforests are renowned for their abundance and diversity of native delicious fleshy fruits, such as durian (*Durio*, Malvaceae), mangosteen (*Garcinia*, Clusiaceae), rambutan (*Nephelium*, Sapindaceae), langsat (*Lansium*, Meliaceae), mango (*Mangifera*, Anacardiaceae), jackfruit (*Artocarpus*, Moraceae), starfruit (*Averrhoa*, Oxalidaceae), banana (*Musa*, Musaceae), salak (*Salacca*, Arecaceae), and so forth. These fruits likely evolved to be dispersed by arboreal mammals, particularly primates such as the orangutan, gibbon, and macaque, which have a gustatory sense similar to that of humans. Thus, these fruits are considered delicious, and are sold in local markets (Fig. 2.31).

In contrast to the fleshy fruits, nuts of Fagaceae, Betulaceae, and Juglandaceae are dry indehiscent fruits, each containing one seed. The nut is surrounded by a tough shell (equals the pericarp), and the copious starch stored in the nut guarantees rapid initial seedling growth. The large, nutrient-rich nuts are targeted by various seed-infesting (seminivorous) insects, birds, and mammals, which are thought to be seed predators. Among these seminivorous animals, some rodents (e.g., voles and squirrels) and corvid birds such as ravens and jays conceal surplus nuts in scattered caches for future consumption. The scatter hoarding of food items (i.e., caching) is underpinned by their episodic-like memory, future planning, and mental attribution (Grodzinski and Clayton 2010). A portion of the stored nuts remains intact without being utilized and then germinates at the caches. Thus, in seed dispersal by scatter-hoarding animals, the seed itself is the reward for the seed-dispersing seed

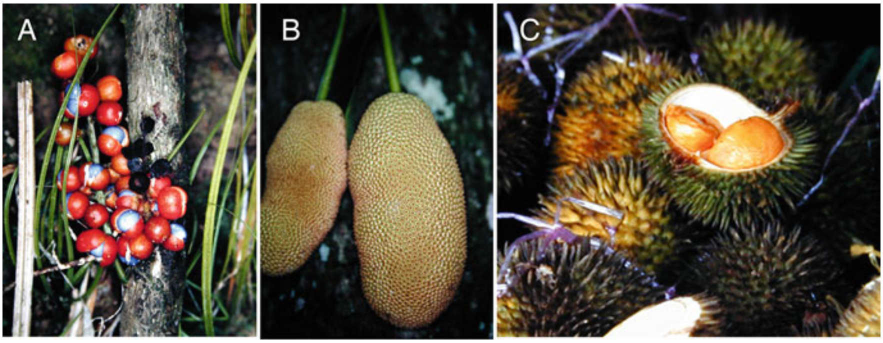

Fig. 2.30 Delicious fruits in tropical rain forests in Borneo. (**a**) *Baccaurea racemosa* (Phyllanthaceae). (**b**) *Artocarpus integer* (Moraceae). (**c**) *Durio kutejensis* (Malvaceae). Cauliflorous habits of these fruits are associated with seed dispersal by mammals

Fig. 2.31 Wild or semidomesticated, native edible seeds and fruits sold in local markets: (**a**) Traditional Asian nuts (from the top clockwise): ginkgo (raw and roasted), shii (*Castanopsis sieboldii,* Fagaceae), kaya (*Torreya nucifera,* Taxaceae), and walnut (*Juglans regia,* Juglandaceae) sold at observance of the close of winter at Yoshida-Jinja temple in Kyoto; (**b**) Native Amazonian fruits sold in a market in Tarapoto, Peru (from the top clockwise): macambo (*Theobroma bicolor*, Malvaceae), cocona (*Solanum sessiliflorum*, Solanaceae), palta (*Persea americana*, Lauraceae), umari (*Poraqueiba sericea* Icacinaceae), camucamu (*Myrciaria dubia*, Myrtaceae), cherimoya (*Annona cherimolina*, Annonaceae), papaya (*Carica papaya*, Caricaceae); (**c**–**d**) Native Malayan fruits sold in a market in Miri, Sarawak, Malaysia: (**c**) Chempedak (*Artocarpus integer,* Moraceae), rambutan (*Nephelium lappaceum,* Sapindaceae); (**d**) Salak (*Salacca zalacca,* Arecaceae), belimbing merah (*Baccaurea angulate,* Euphorbiaceae)

predators. These nuts were an important source of food for humans until the development of agriculture (Fig. 2.31). Nut-bearing trees are apt to mass flower and mast synchronously at an interval of one or a few years. The mast seeding maximizes seed escape because seed predators consume a decreasing proportion of available seeds with increasing seed production (Fletcher et al. 2010). Thus, episodic and synchronous mast seeding contributes to escape from heavy attack and efficient seed dispersal by these vertebrates in the masting year (Vander Wall 2010). In addition to fruits and seeds, flowers also provide various mammals with nectar as a reward for pollination. Particularly in tropical forests, some nocturnal flowers are visited by nectarivorous mammals such as rodents, primates, and bats, among which bats are the most important pollinators. In Southeast Asia, tubular flowers of *Musa* (Musaceae), *Mucuna* (Fabaceae), and *Fagraea* (Gentianaceae), and brushlike flowers such as *Barringtonia* (Lecythidaceae) are white in color, emit a fermentation odor, secrete copious nectar at night, and are pollinated by fruit-bats (flying foxes or megabats), which search for fragrant flowers using their olfactory sense (Momose et al. 1998). In contrast, the Neotropics harbor echolocating fruit-microbats, which are pollinators of nocturnal flowers of the following families: Agavaceae, Bromeliaceae, Cactaceae, Fabaceae, Malvaceae, Campanulaceae, Bignoniaceae, Gesneriaceae, and Solanaceae (Fleming et al. 2009). A chiropterophilous plant of the genus *Mucuna* (Fabaceae) in the Neotropics has unique petals, which resonate the ultrasonic wave emitted by echolocating microbats and guide the bats to the floral nectar (von Helversen and von Helversen 1999, Simon et al. 2011).

2.14 Cultivation Mutualism

Humans, as primates, have evolved as erect-walking omnivorous hunter–gatherer species who collect fruits and vegetables; hunt mammals, birds, and reptiles; catch insects; and fish aquatic organisms. About 4000–12,000 years ago, several human populations started to cultivate useful plants that yielded nutritious seeds, fruits, leaves, and tubers (Larson et al. 2014). The cultivated plants became domesticated through careful management of their reproduction by humans, and eventually became crops that can only grow with management and protection by humans. Thus, the interaction between human and crops is an obligate cultivation mutualism that originated from an antagonistic plant–herbivore interaction. Although various parts of diverse crop species have been utilized by humans, the most important crops are cereals (Poaceae), which yield a large quantity of nutritious and storable harvest irrespective of their minute seed size. In the process of domestication of cereal crops, nonshattering habit and larger seed size have been selected, and hybridization and polyploidization of wild plant species have also been performed. Ancient human civilizations originated in 10 regions, precisely where domestication and cultivation of crops commenced (Diamond 2002). Human–crop cultivation mutualism has swept the Earth during the past several thousand years, and maize, rice, and wheat production reached 1018, 738, and 711 million metric tons in 2013, respectively (FAOSTAT 2014).

Cultivation mutualism has only evolved between plants and humans. Although the chimpanzee has an episodic memory (Martin-Ordas et al. 2010), even rudimentary plant cultivation has not been observed. In aquatic systems, however, cultivation mutualism has evolved between algae and algivorous damselfish. The damselfish, *Stegastes nigricans*, living in a coral reef ecosystem manages algal farms by defending territory against invading grazers and by weeding of unpalatable algae (Fig. 2.32). As a result, the algal farms are dominated by one filamentous red alga species, *Polysiphonia* sp. (Hata and Kato 2006). The alga is the staple food of the fish, and the alga only grows in territories inhabited by the fish, suggesting an obligate cultivation mutualism. In coral reef ecosystems harboring many algivorous damselfish species, fish species engaged in intensive farming typically utilize

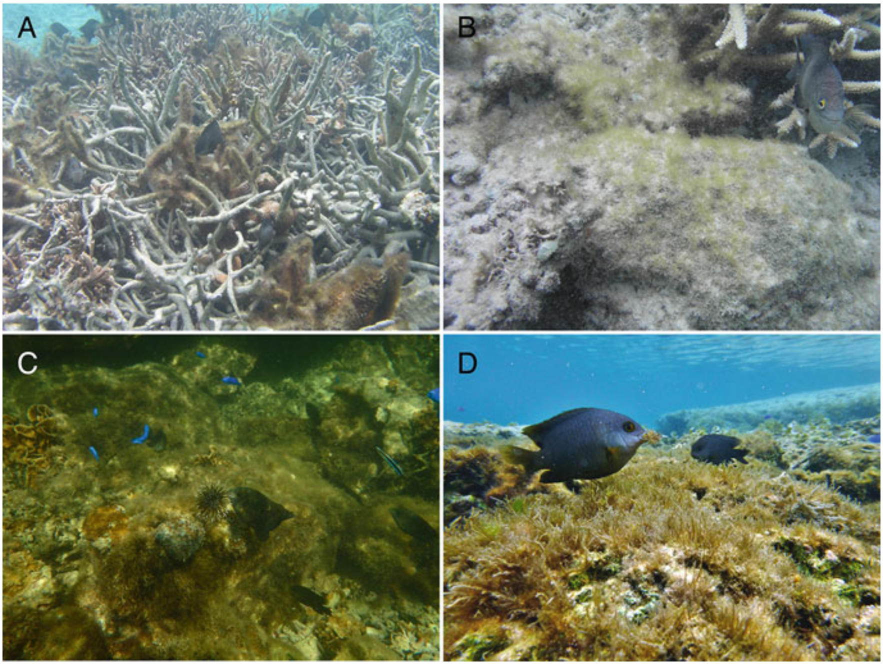

Fig. 2.32 Damselfish–alga cultivation mutualism between *Stegastes nigricans* and a rodophyte *Polysiphonia* sp. observed in a coral reef of the Ryukyu Archipelago, Japan: (**a**) Exclusively distributed algal farms, each of which is occupied by a damselfish. (**b**) A closeup of an algal mat kept by a damselfish. (**c**) A damselfish removing algivorous sea urchin *Echinometra mathaei* out of its territory. (**e**) A damselfish weeding unpalatable algae (Photos by Hiroki Hata)

monoculture, whereas fish species engaged in extensive farming tend mixed-crop farms comprising several species of algae (Hata et al. 2010). In algal cultivation, neither episodic memory nor management of algal reproduction is necessary because the algae can colonize a new patch by releasing spores, and the algal farms are generally colonized by their offspring or conspecifics.

2.15 Obligate Pollination Mutualism

As described above, some seed plants have evolved palatable seeds as a reward in seed-dispersal mutualism and cultivation mutualism. In these mutualisms, seed predators became seed-dispersers and cultivators, respectively. In addition, another mutualism that involves rewarding of seeds between plants and pollinating seed-predators has been established (i.e., obligate pollination mutualism). More than 100 years ago, two popular systems were discovered in *Ficus* (Moraceae) and *Yucca* (Agavaceae), which are pollinated by fig wasps (Agaonidae) and yucca moths (Prodoxidae), respectively (Cunningham 1888, Riley 1873). The intimate

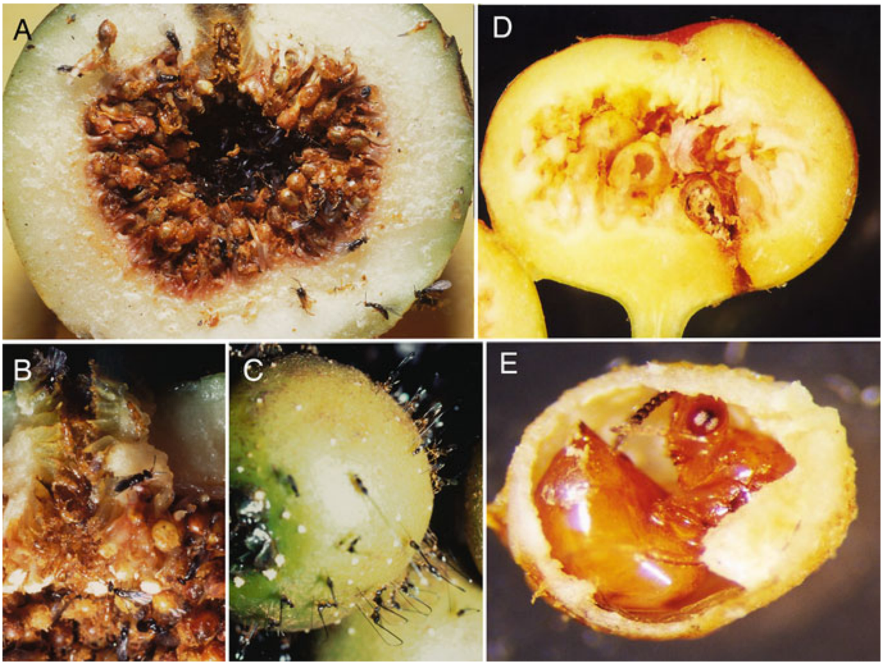

Fig. 2.33 Fig–fig wasp obligate pollination mutualism: (**a**–**c**) *Ficus* sp. in Borneo (Photo by Tamiji Inoue). (**d**–**e**) *Ficus septica* in Okinawa, Japan. (**a**) A cross-section of a syconium, showing numrous small galled ovules which produce pollinator fig-wasps. (**b**) The exit passage, through which newly emerged fig-wasps go out of the syconium after collecting pollen from the male flowers just before the exit passage. (**c**) Parasitic fig-wasps trying to insert their long ovipositors into the syconium. (**d**) A cross-section of a syconium showing infested fig seeds and the tunnel that emerged male fig-wasp bored. (**e**) Emerged female fig wasps in an infested seed

pollination mutualisms between figs and fig wasps (Fig. 2.33) and those between yuccas and yucca moths (Fig. 2.34) have long intrigued biologists because they are some of the most sophisticated examples of insect pollination. All of the species of figs and yuccas are pollinated exclusively by females of host-specific fig wasps and yucca moths, respectively, which lay eggs in the pollinated fig/yucca ovules and nourish their larvae with the resulting seeds (Janzen 1979, Powell 1992, Weiblen 2002, Pellmyr 2003, Herre et al. 2008). Some pollinating fig wasps and all of the pollinating yucca moths are morphologically and behaviorally adapted to "actively" pollinate flowers to ensure that larval food (i.e., seeds) is produced for their offspring (Pellmyr 1997, Kjellberg et al. 2001, Pellmyr and Krenn 2002, Jousselin et al. 2003). These mutualistic relationships were recognized more than a century ago; the importance of fig wasps for fig fruit maturation has been known since ancient times (Condit 1947), whereas the basic natural history of the yucca–yucca moth mutualism unfolded with Riley's observations in the late nineteenth century (Riley 1872, 1880, 1881). Detailed accounts of active pollination by fig

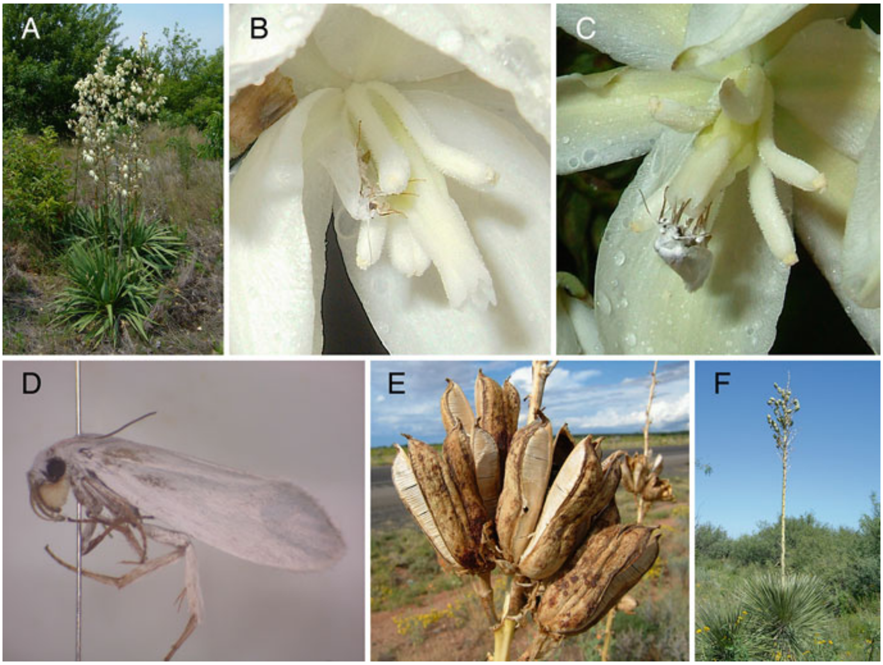

Fig. 2.34 Yucca–yucca moth obligate pollination mutualism: (**a**–**d**) *Yucca filamentosa* and its pollinator *Tegeticula yuccasella* in New York, USA. (**e**–**f**) *Yucca elata* in Arizona, USA. (**a**) Habitat of the plant; (**b**) A female yucca moth ovipositing in the ovary. (**c**) A female yucca moth actively pollinating the stigma. (**d**) A female yucca moth with a large clump of pollen on the mouthpart, gathered using specialized tentacles. (**e**) Dehisced capsule showing a feeding tunnel made by a yucca moth larva. (**f**) Fruits borne on tall stalk

wasps were provided more recently by Galil and Eisikowitch (1969) and Ramírez (1969).

Although long recognized as classic examples of obligate mutualisms, these associations have become principal models in various fields of ecology and evolutionary biology over the past few decades (Thompson 1994, 2005, Herre et al. 1999, 2008, Weiblen 2002, Cook and Rasplus 2003, Pellmyr 2003). Most prominently, these systems provide ideal models for studying the coevolutionary dynamics of species interactions and the mechanisms that maintain the stability of the mutualisms. The high degrees of species specificity in these associations allow straightforward assessments of the effects of coevolutionary selection acting on each species, and the high species richness (>750 and >40 species of figs and yuccas, respectively) allows a comparative approach for studying the outcomes of reciprocal selection. In addition, the costs and benefits of the mutualism for the plant can easily be measured by counting the number of seeds produced/destroyed, rather than by quantifying nutrients or protection, which most other mutualisms trade (Heil and McKey 2003, Mueller et al. 2005, Kiers and Denison 2008); this facilitates analyses of how mutualisms are maintained in the face of apparent destabilizing potential. In fact, major breakthroughs in our understanding of the coevolutionary process and mutualism stability were brought about by studies of these obligate pollination mutualisms (Pellmyr and Thompson 1992, Pellmyr and Huth 1994, Pellmyr et al. 1996a, b, Molbo et al. 2003). Recently, a remarkable pollination mutualism analogous to the fig–fig wasp and yucca–yucca moth mutualisms was discovered between the tree genus *Glochidion* (Phyllanthaceae, formerly Euphorbiaceae) and the moth genus *Epicephala* (Gracillariidae; Kato et al. 2003). In the long history of plants and their associates, mutualism is one of the most interesting interactions because their host specificity is exceedingly high and because they have attained remarkable codiversification. We focus on this mutualism in the following chapters.