Chapter 4
Diversity of Phyllanthaceae Plants

Atsushi Kawakita and Makoto Kato

Keywords *Breynia* • *Flueggea* • *Glochidion* • *Margaritaria* • Natural history • Phyllanthaceae • Phyllantheae • *Phyllanthus* • Phylogeny • *Sauropus*

4.1 Taxonomy of Phyllanthaceae

Euphorbiaceae, one of the major components of tropical flora worldwide, has long been considered a heterogeneous group (Webster 1994; Radcliffe-Smith 2001). Recent molecular phylogenetic analyses have clearly shown that Euphorbiaceae is nonmonophyletic, and consequently, Pandaceae, Phyllanthaceae, Picrodendraceae, Putranjivaceae, Peraceae, and Centroplacaceae have been removed from it, although these families all belong to the order Malpighiales together with the updated Euphorbiaceae (Euphorbiaceae s. str.; Angiosperm Phylogeny Group III 2009). Thus, the small unisexual flowers and trilocular capsule that characterize the plants of the former Euphorbiaceae are plesiomorphic or convergent characters. For example, Rafflesiaceae, the family with the world's largest, unisexual but unilocular flowers, is embedded in the former Euphorbiaceae (Davis et al. 2007); the clade sister to Rafflesiaceae is now Euphorbiaceae s. str., and the lineage sister to (Rafflesiaceae + Euphorbiaceae s. str.) is split as Peraceae (Fig. 4.1). Of the seven former Euphorbiaceae families, Euphorbiaceae s. str. and Phyllanthaceae are by far the largest, with the former containing about 300 genera and about 7500 species, and the latter 54 genera and about 2000 species (Table 4.1). Webster (1994) noted an important morphological feature of Phyllanthaceae that clearly distinguishes them from Euphorbiaceae s. str.; the former has two ovules per locule whereas the latter only has one ovule per locule.

A. Kawakita (✉)
Center for Ecological Research, Kyoto University, 2-509-3 Hirano, Otsu, Shiga 520-2113, Japan
e-mail: kawakita@ecology.kyoto-u.ac.jp

M. Kato
Graduate School of Human and Environmental Studies, Kyoto University, Yoshida-Nihonmatsu-cho, Sakyo, Kyoto 606-8501, Japan
e-mail: kato@zoo.zool.kyoto-u.ac.jp

M. Kato, A. Kawakita (eds.), *Obligate Pollination Mutualism*, Ecological Research Monographs, DOI 10.1007/978-4-431-56532-1_4

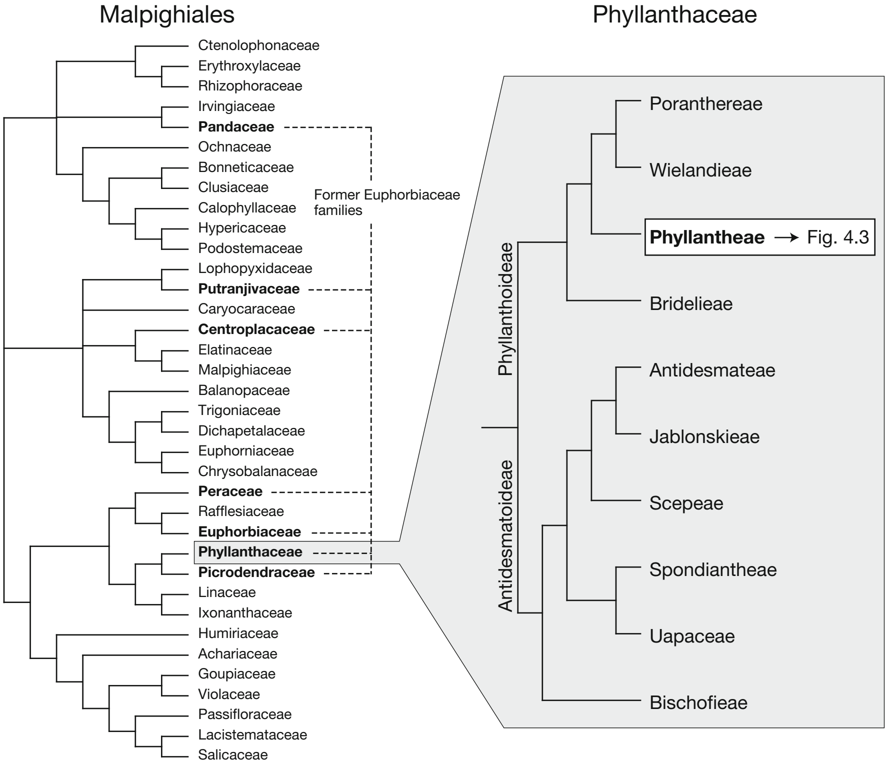

Fig. 4.1 Phylogenies of Malpighiales (*left*) and Phyllanthaceae (*right*). Former Euphorbiaceae families on the Malpighiales phylogeny are indicated in bold. Phyllanthaceae is divided into two subfamilies, Antidesmatoideae and Phyllanthoideae, the latter of which includes the tribe Phyllantheae. Phylogenetic relationships are based on Davis et al. (2005) for Malpighiales and Kathriarachchi et al. (2006) for Phyllanthaceae

Phyllanthaceae is a predominantly tropical family of shrubs and treelets and rarely of herbs and trees. Depending on the author, the family contains 54–60 genera, grouped into 2 monophyletic subfamilies and 10 well-defined, monophyletic tribes (Table 4.1). Of these, association with *Epicephala* moths is limited to Phyllantheae, which has more than half the species in the family (>1200 species) and contains *Glochidion*, *Breynia*, and *Phyllanthus*. Therefore, this chapter focuses entirely on the tribe Phyllantheae and reviews its diversity, phylogeny, and natural history. Recent molecular phylogenetic studies have greatly advanced our understanding of Phyllantheae classification, setting a cornerstone of evolutionary analysis on obligate pollination mutualism.

Table 4.1 Families traditionally classified in Euphorbiaceae and tribal classification of Phyllanthaceae

Family Subfamily Tribe	Genera	Species	Representative genera
Euphorbiaceae	300	7500	*Euphorbia*, *Croton*, *Acalypha*, *Macaranga*
Pandaceae	3	15	*Galearia*, *Microdesmis*, *Panda*
Picrodendraceae	24	80	*Picrodendron*, *Oldfieldia*, *Austrobuxus*
Putranjivaceae	4	210	*Drypetes*
Peraceae	5	135	*Clutia*, *Pera*
Centroplacaceae	2	6	*Centroplacus*, *Bhesa*
Phyllanthaceae	25	2000	
Antidesmatoideae			
Bischofieae	1	1	*Bischofia*
Uapaceae	1	60	*Uapaca*
Spondiantheae	1	1	*Spondianthus*
Scepeae	8	200	*Aporosa*, *Baccaurea*
Jablonskieae	2	2	*Jablonskia*
Antidesmateae	8	120	*Antidesma*
Phyllanthoideae			
Bridelieae	13	230	*Bridelia*, *Cleistanthus*, *Amanoa*
Wielandieae	6	25	*Wielandia*
Poranthereae	8	120	*Actephila*, *Andrachne*, *Meineckia*
Phyllantheae	9	1200	*Phyllanthus*, *Glochidion*, *Breynia*, *Sauropus*

4.2 Genera of Phyllantheae

The generic classification of Phyllantheae is still contentious (Hoffmann et al. 2006; Kathriarachchi et al. 2006; Hoffmann 2008; van Welzen et al. 2014), and the number of genera is likely to change as additional progress is made. In this book, we use the following nine genus names to refer to the plants of Phyllantheae, acknowledging the fact that some are unnatural (paraphyletic) groups and should be redefined: *Margaritaria*, *Plagiocladus*, *Lingelsheimia*, *Heterosavia* (formerly a section of *Savia*), *Flueggea* (including former *Richeriella*), *Phyllanthus* (including former *Reverchonia*), *Sauropus*, *Breynia*, and *Glochidion* (Table 4.2). Of these, the last three genera (*Sauropus*, *Breynia*, and *Glochidion*) are clearly embedded within *Phyllanthus* (Kathriarachchi et al. 2005, 2006). *Breynia* is further nested within *Sauropus* (Pruesapan et al. 2008, 2012).

Hoffmann et al. (2006) proposed inclusion of *Sauropus*, *Breynia*, and *Glochidion* in *Phyllanthus* to avoid paraphyletic construction of the latter. By including the three embedded genera, *Phyllanthus* becomes a giant genus of >1200 species. A number of taxonomic and nomenclatural changes have been made for regional flora (Chakrabarty and Balakrishnan 2009; Wagner and Lorence 2011), but many more new combinations are necessary to accommodate fully the >400 species of *Sauropus*, *Breynia*, and *Glochidion* in *Phyllanthus*. Alternatively,

Table 4.2 The genera of Phyllantheae used in this book

Genus	No. of Species	Distribution
Margaritaria	13	Widely distributed in tropics
Plagiocladus	1	Cameroon, Congo, Gabon
Lingelsheimia	7	Africa (Tanzania, Zaire, Gabon), Madagascar
Heterosavia	4	Caribbean
Flueggea	16[a]	Scattered in tropics, temperate east Asia and Europe
Phyllanthus	>800[b]	Widely distributed in tropics and subtropics
Sauropus	>80	Indo-Australian, Mascarene Islands
Breynia	35	Indo-Australian, the Pacific east to Fiji Islands
Glochidion	>300[c]	Indo-Australian, the Pacific east to Pitcairn Islands

[a] Including former *Richeriella* (Hoffmann et al. 2006)
[b] Including former *Reverchonia* (Webster 2007)
[c] Excluding seven Madagascan species transferred to *Phyllanthus* (Hoffmann and McPherson 2003)

van Welzen et al. (2014) proposed dividing *Phyllanthus* into >20 smaller genera because there is no morphological characteristic that defines the expanded *Phyllanthus*. In fact, the flowers, fruits, and growth forms of *Phyllanthus* are unusually diverse for a single genus, particularly if the genus is expanded to include *Sauropus*, *Breynia*, and *Glochidion*. Because the most recent molecular phylogenetic study of Phyllantheae only included approximately 10% of the constituent species (Kathriarachchi et al. 2006), an improved taxon sampling may group the species of *Phyllanthus* into many monophyletic, morphologically recognizable clades that can be recognized at generic rank. However, in the absence of a firm consensus at present, we adopt the traditional use of *Phyllanthus*, *Sauropus*, *Breynia*, and *Glochidion* in this book (Webster 1994; Radcliffe-Smith 2001; but see Chap. 12 for alternative names of Polynesian *Glochidion* species).

The genus *Sauropus* and the embedded *Breynia* have recently been thoroughly reviewed based on morphology and molecular data (Pruesapan et al. 2008, 2012; van Welzen et al. 2014). Based on the results of well-sampled phylogenetic analysis, van Welzen et al. (2014) expanded *Breynia* to include the Southeast Asian species of *Sauropus*, and reinstated the Australian *Synostemon*, a section of *Sauropus*, to generic rank, making each genus monophyletic and morphologically definable. However, we did not reflect these changes here due to the lack of consensus on whether to expand or divide *Phyllanthus*, as discussed above. On the other hand, the inclusion of *Richeriella* in *Flueggea* (Hoffmann et al. 2006) and of *Reverchonia* in *Phyllanthus* (Webster 2007) is generally not contradicted, so we adopted these changes in this book. The name *Phyllanthus* is derived from the Latin *phyll* (leaf) and *anthus* (flower), and its common name is leafflower. This is because the leaves on the lateral, flower-bearing branches of most *Phyllanthus* are flatly arranged on a horizontal plane, resembling the leaflets of compound leaves, and giving an overall impression that flowers are borne on (compound) leaves. Thus, *Phyllanthus* plants are relatively easy to recognize in the field compared to plants of other Phyllanthaceae genera. Phyllanthoid branching is a distinguishing morphological characteristic shared among most, but not all *Phyllanthus* species including

Fig. 4.2 Phyllanthoid (**a**) and nonphyllantoid (**b**) branching. (**a**) Vertical axis of *Breynia retusa* lacks normal leaves (*arrows*), and thus the branching is phyllanthoid. (**b**) Vertical axis of *Flueggea suffruticosa* bears normal leaves and flowers (*arrows*), retaining the ancestral nonphyllanthoid branching

Sauropus, *Breynia*, and *Glochidion* (Webster 1956; Fig. 4.2). In species with phyllanthoid branching, the leaves on the main (vertical) axes are reduced to scales (called cataphylls), and normal leaves are only developed on lateral, flower-bearing axes. This is another reason that the lateral axes of *Phyllanthus* look like compound leaves, particularly in species in which the branchlets are deciduous. Phyllanthoid branching was once gained at an early stage of *Phyllanthus* diversification, probably as an adaptation to herbaceous or shrubby habits in open forest habitats, and was independently lost in several derived lineages, some of which are arboreal. Figure 4.3 summarizes the most recent understanding of Phyllantheae phylogeny based on molecular data (Kathriarachchi et al. 2006; Kawakita and Kato 2009), incorporating the most recent subgeneric arrangements within *Phyllanthus* (Kathriarachchi et al. 2006; Ralimanana and Hoffmann 2011, 2014; Ralimanana et al. 2013). The genus *Phyllanthus* is subdivided into about 15 subgenera and numerous sections, some of which are still poorly defined and require revision. Note that there are many more species of *Phyllanthus*, the phylogenetic positions of which have not been determined; only half of the entire *Phyllanthus* diversity is represented in the figure. An important and rather unexpected finding of molecular phylogenetic analyses was the correspondence between clades and biogeographic boundaries. For example, in *Phyllanthus*, the Neotropical species are grouped into three well-supported clades (although additional clades may appear when additional species are sampled), therefore there were probably only three dispersals from the Old World to the New World and no dispersal in the reverse direction. Therefore, traditional sections or subgenera that spanned both sides of the Pacific are all artificial. The *Sauropus–Breynia* clade is divided into two subclades (corresponding to *Breynia* and *Synostemon* of van Welzen et al. 2014), each occurring exclusively in Australia and Southeast Asia (with the exception of *Sauropus macranthus* that occurs in both regions). In addition, there is a large

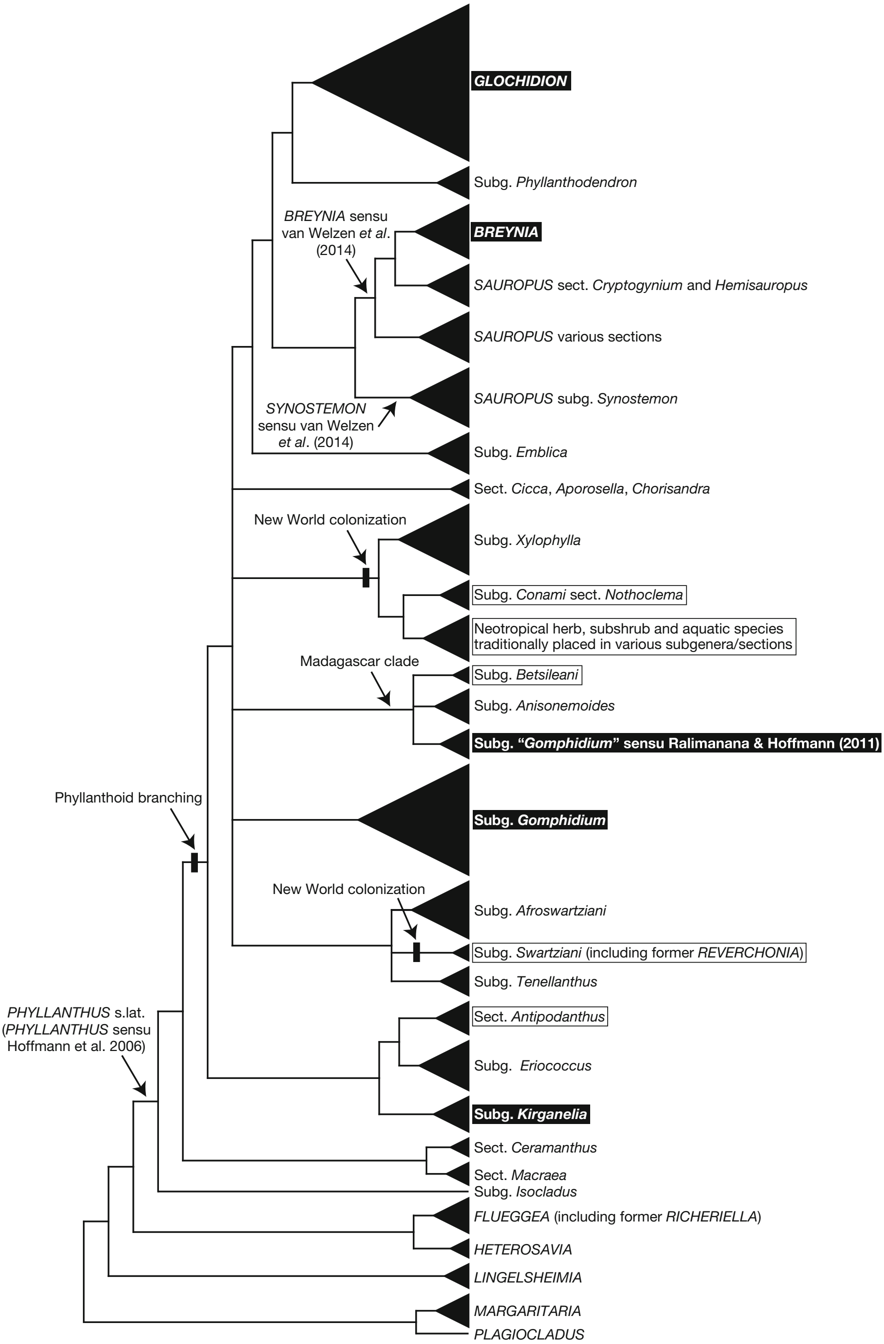

Fig. 4.3 Phylogeny of the tribe Phyllantheae. The tree is based on the most recent phylogenetic analyses of the tribe by Kathriarachchi et al. (2006) and Kawakita and Kato (2009). Species richness of each terminal clade, compiled from various sources, is provided as the area of the clade

monophyletic group of *Phyllanthus* species consisting entirely of species endemic to Madagascar. Thus, long-distance dispersals were probably much less frequent than inferred from traditional taxonomy.

4.3 Global Distribution and Diversity Patterns

The overall distribution of the five basal genera (*Margaritaria*, *Plagiocladus*, *Lingelsheimia*, *Heterosavia*, and *Flueggea*) is highly relictual. For example, *Flueggea* is widespread in the Paleotropics but also has fragmentary distributions in the Iberian Peninsula, Turkey, Caribbean, Ecuador, and northeastern Brazil (Webster 1984; Gemici 1993), which are most likely relicts (there is a single apparent dispersal to Hawaii; Hayden 1987). Similarly, *Plagiocladus*, *Lingelsheimia*, and *Heterosavia* have highly restricted distributions in West Africa, Africa and Madagascar, and the Caribbean, respectively (Table 4.2; Govaerts et al. 2000; Radcliffe-Smith 2001; Lebrun and Stork 2006; Hoffmann 2008), suggestive of range contractions from once broader distributions. On the other hand, distributions of the more derived genera (*Phyllanthus*, *Sauropus*, *Breynia*, and *Glochidion*) are likely the result of more recent dispersals. For example, *Glochidion* includes more than 300 species and ranges throughout the tropical parts of Asia, Australia, and the Pacific, with species colonizing as far east as the Pitcairn Islands (Govaerts et al. 2000). The Southeast Asian tropics have the highest diversity of Phyllantheae plants at both species and genus levels (Fig. 4.4, Table 4.2), although there are also notable diversity centers in New Caledonia (>110 spp.), Madagascar (ca. 60 spp.), Cuba (ca. 50 spp.), and Venezuela (ca. 60 spp.). *Phyllantheae* plants are less common in dense rainforests and thus have low diversity in the Amazonian basin. Much of the current Southeast Asian diversity is attributable to recent diversification of a few derived genera (*Sauropus*, *Breynia*, and *Glochidion*) rather than richness of major *Phyllantheae* lineages. The relative abundance of basal lineages (*Margaritaria*, *Plagiocladus*, *Lingelsheimia*, and *Flueggea*) in Africa, Madagascar, and South America (Table 4.2) may suggest a Gondwanan origin for the tribe as a whole.

4.4 Growth Form and Habitat

The tribe Phyllantheae has remarkable diversity of vegetative form and habitat. The plants range from very small shrubs to canopy-layer trees and a number of *Phyllanthus* lineages have become herbaceous (annual or perennial), which is

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Fig. 4.3 (continued) triangle. The five lineages containing *Epicephala* moth-pollinated plants are indicated by *black* shadows on group names. *Phyllanthus* clades that have secondarily lost phyllanthoid branching are indicated by brackets around group names

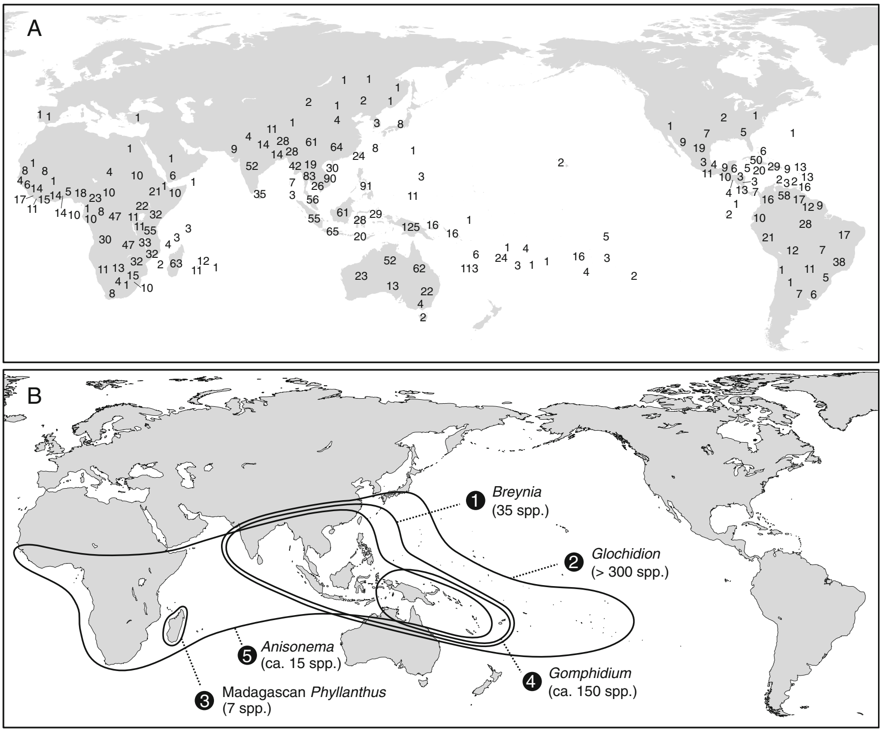

Fig. 4.4 Global distribution of Phyllantheae plants. (**a**) Number of Phyllantheae plants occurring at each geographic region, as defined by Hollis and Brummitt (1992). Data were taken from Govaerts et al. (2000). Note that the geographic regions differ in size, which affects species abundance. (**b**) Approximate distributions of the five Phyllantheae lineages with *Epicephala*-pollinated species

rare among the predominantly woody Phyllanthaceae. Herbaceous species include weeds that have become naturalized in many tropical regions of the world (e.g., *P. amarus*, *P. urinaria*, and *P. tenellus*). One Neotropical species, *P. fluitans*, is a free-floating aquatic (Macbride 1951). There are also a number of rheophytes, including *P. bourgeoisii* in New Caledonia (Schmid 1991), *P. rheophyticus* in Hainan (Li et al. 2008), and *Sauropus heteroblastus* in Indochina (van Welzen 2003). *P. microcarpus* is a scandent shrub that ascends by clinging to the surrounding vegetation (Luo et al. 2011a). *P. mirabilis* is the only succulent species (Chantaranothai 2005).

Phyllantheae plants are most frequently found in open habitats such as forest margins, roadsides, savannas, swamp edges, riverbanks, or coastal scrublands. However, some *Phyllanthus* and *Sauropus* species occur in forest understory, whereas *Margaritaria* and *Glochidion* constitute the canopy of rainforests. Large numbers of species have clear associations with limestone or serpentine vegetation (Webster 1956, 1957, 1958; Schmid 1991; Radcliffe-Smith 1996; van Welzen 2003; Thulin 2003; Gilbert and Thulin 2008; Hoffmann 2008), indicating the propensity of these plants to survive adverse soil conditions. Major radiations of *Phyllanthus* subgenera *Gomphidium* and *Xylophylla* took place in New Caledonia and Cuba, respectively (Webster 1956, 1957, 1958; Schmid 1991), where the land is abundant in serpentine substrates and is barely forested. Some *Phyllanthus* and *Sauropus* species are specialized to limestone cliffs and calcareous rock crevices (Webster 1970; Thulin 2005; Gilbert and Thulin 2008). *P. warnockii* (formerly *Reverchonia arenaria*; Webster 2007) occurs on sand dunes in arid regions of the southwestern United States (Webster and Miller 1963).

Unlike supra-annual flowering of canopy trees in Asian tropical rain forests, the shrubby/herbaceous growth form and open habitat of *Phyllanthus* plants resulted in periodical or continuous flowering, which must have been a prerequisite for the association with pollinator moth partners, because the moths must reproduce periodically and synchronously with their host plants.

4.5 Floral Biology

The flowers of Phyllantheae plants are small (usually <1 cm in diameter) and unisexual. The basal lineages (*Margaritaria*, *Plagiocladus*, *Lingelsheimia*, *and Flueggea*) primarily consist of dioecious plants (although monoecious conditions occur in *Lingelsheimia* and *Flueggea*; Webster 1984; Radcliffe-Smith 2001), whereas the derived genera (*Phyllanthus*, *Sauropus*, *Breynia*, and *Glochidion*) are almost entirely monoecious. Flowers are usually borne singly or in clusters on leaf axils but rarely on the elongate inflorescence axis (e.g., *Flueggea gracilis*, *P. acidus*). Cauliflory occurs in several *Phyllanthus*, *Sauropus*, and *Glochidion* species (Takeuchi 1999, 2003; van Welzen 2003; Thin 2007). Flowers lack petals (except in *Heterosavia*; Hoffmann 2008), as is common to many groups within the family (Webster 1994; Radcliffe-Smith 2001; Hoffmann et al. 2006). Tepals are predominantly greenish regardless of the pollination system, although some non-*Epicephala*-pollinated plants have red-purple or white tepals. Thus, Phyllantheae flowers exhibit relatively poor floral display, and although flowers of *Epicephala*-pollinated plants are hardly conspicuous, inconspicuousness itself is not necessarily their exclusive feature. Nectar production has been confirmed in many taxa (Kawakita and Kato 2004a, 2009), although many, but not all *Epicephala*-pollinated plants are nonnectariferous (Kato et al. 2003). Flowering phenology has not been well studied, but both flowering and fruiting appear to be continuous throughout the year in most species. Clear seasonality occurs in some temperate taxa (e.g., *P. flexuosus*). The most distinctive floral features associated with pollination mode are the structures of the pistils and stamens (Kawakita and Kato 2009; Kawakita 2010). The styles are usually free and bifid at the apices in non-*Epicephala*-pollinated plants, but are reduced to entire tips and are medially fused in most *Epicephala*-pollinated species (Kawakita and Kato 2009; Kawakita 2010). Similarly, filaments and anthers are usually free in non-*Epicephala*-pollinated plants, but are variously fused in species with *Epicephala* pollination. These morphological characteristics are likely associated with the pollination behavior by *Epicephala* females (Chap. 3). In the majority of species, the ovary consists of three locules, each of which has two ovules (Webster 1994; Radcliffe-Smith 2001). Thus, a single fruit contains six seeds. Exceptions include some *Glochidion* and *Phyllanthus* species that have 6, or rarely, 12–15 locules and hence twice the number of seeds. Fruits are predominantly capsules and seeds are dispersed by explosive dehiscence. Fleshy fruits (berries and drupes) occur in a number of groups, including *Flueggea*, *Breynia*, and *Phyllanthus* sections *Anisonema*, *Cicca*, and *Emblica*, which are adapted for bird dispersal. Fruits of *Margaritaria*, *Glochidion*, and some *Sauropus* and *Breynia* are tardily dehiscent, and the seeds are coated with fleshy sarcotesta, which is also consumed by birds (seeds of one New Guinean *Glochidion* are consumed by cassowaries; Takeuchi 2003).

4.6 Natural History of Each Group

To date, *Epicephala* pollination has been uncovered in five separate lineages within Phyllantheae (Kawakita and Kato 2009). In this section, we describe the natural history of each lineage of Phyllantheae along the phylogeny in Fig. 4.3, with a special focus on pollination biology and association with *Epicephala* moths. Overall, there is substantial variation among lineages in the pollination system and mode of association with *Epicephala*, which are both critically important in understanding the origin and evolutionary dynamics of obligate pollination mutualism in Phyllanthaceae.

4.6.1 Margaritaria, Plagiocladus, Lingelsheimia, *and* Heterosavia

One of the most surprising results of recent molecular phylogenetic studies of Phyllanthaceae is the inclusion of *Lingelsheimia* and *Heterosavia* in Phyllantheae. *Lingelsheimia* is a small genus of six species distributed in equatorial Africa (Gabon, Zaire, and Tanzania) and Madagascar, and was traditionally placed in Putranjivaceae (near *Drypetes*) due to its unusually large number of stamens (15–35; Webster 1994), although this placement has been questioned. *Heterosavia*, a genus of five species endemic to the Caribbean, was formerly a section of the genus *Savia*, which was shown to be polyphyletic in recent molecular phylogenetic studies (Kathriarachchi et al. 2005) and now contains only two species in the tribe Bridelieae, with the remaining species transferred to Wielandieae (Hoffmann et al. 2006). *Heterosavia* is unique among Phyllantheae with petals (Hoffmann et al. 2006). Another Phyllantheae lineage that was recently recognized at generic rank is *Plagiocladus*. This genus consists of a single central African species *Plagiocladus*

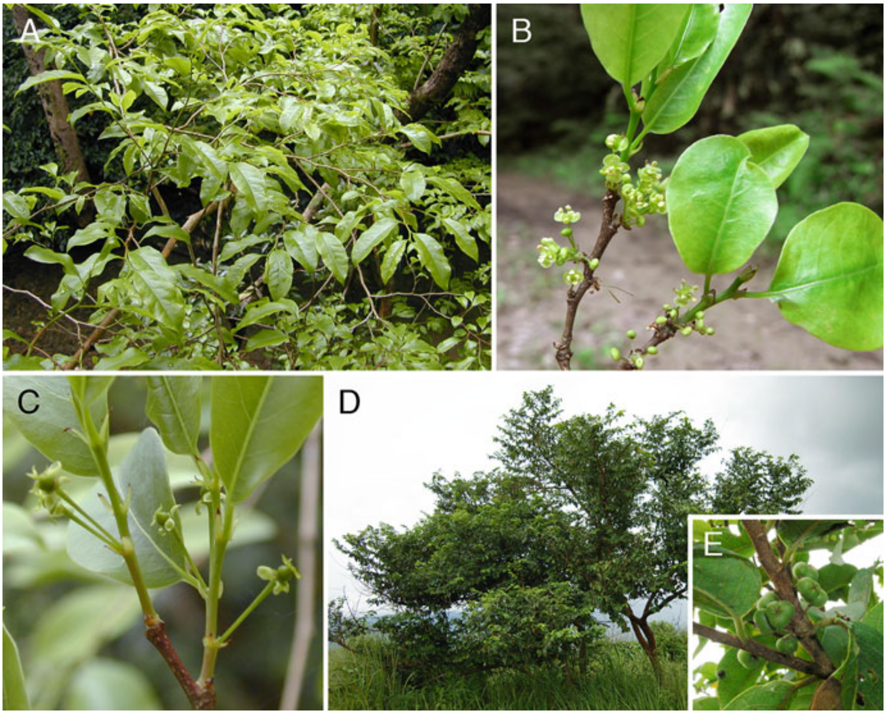

Fig. 4.5 Genus *Margaritaria*. (**a**–**c**) *M. indica*. (**d**, **e**) *M. discoidea*. (**a**) Canopy of *M. indica* in subtropical forest of Okinawa Island, Japan. (**b**) Male flowers. (**c**) Female flowers. (**d**) *M. discoidea* in a grassland habitat in Guinea. (**e**) Fruiting branch. Photos (**d**, **e**) courtesy of Ryutaro Goto

diandrus, which was formerly a *Phyllanthus*, but molecular phylogenetic studies clearly placed it as a sister to *Margaritaria* (Kathriarachchi et al. 2006). *Plagiocladus*, *Lingelsheimia*, and *Heterosavia* have never been observed in the field, thus it is still unknown how they are pollinated or whether they are associated with *Epicephala* moths.

Margaritaria (Fig. 4.5) consists of 14 species that are widely distributed in the tropics, with concentrations of species in the Caribbean (4 spp.) and Madagascar (4 spp.). The plants are usually dioecious, with flowers possessing distinct nectaries. Although studies on pollination of the genus have been limited due to their low abundance and canopy-reaching habit, observation of *Margaritaria indica* in Japan indicated that the greenish flowers are frequently visited by nectar-seeking flies (Kawakita and Kato 2009). Information on the fruit-feeding insect fauna is also limited, but gracillariid larvae were not found from fruit samples of *Margaritaria discoidea* collected in Guinea (Kawakita and Kato 2009). Further studies are clearly needed to search more broadly for gracillariid seed feeders in *Margaritaria*. The seeds of some species of *Margaritaria* have a spectacularly metallic blue-green, fleshy sarcotesta, which is likely involved in seed dispersal by birds. The cellular structure of *Margaritaria nobilis* seeds has recently inspired a new fiber material that changes color as it stretches (Kolle et al. 2013).

4.6.2 *Flueggea*

Flueggea (Fig. 4.6) is another lineage of early branching Phyllantheae. The genus consists of 16 species, and as noted earlier (Section 4.4), their distribution is highly relictual. Some of these species are confined to the Iberian Peninsula, Turkey, Indochina, South Africa, the Caribbean, Ecuador, and northeastern Brazil, indicating substantial range contraction of a once more continuous distribution. There is one very widespread species (*Flueggea virosa*) that occurs throughout the tropics of Asia, Australia, and Africa, and another species (*Flueggea suffruticosa*) that occurs widely in the temperate regions of east Asia. *F. virosa* is one of three species in the genus that possess baccate fruits and is dispersed by birds (A. Kawakita, personal observation), which is probably responsible for its wide distribution. *Flueggea neowawraea* is one of the two Phyllantheae species that reached Hawaii (the other being *P. distichus*), although it is unclear how they reached the islands because both plants have dry capsules and the seeds are dispersed by explosive dehiscence. *F. gracilis*, distributed in Southeast Asia, produces flowers in an elongated inflorescence axis, and the species was placed in another genus, *Richeriella*, based on this trait. The genus was subsumed to *Flueggea* after recent molecular phylogenetic studies (Hoffmann et al. 2006). Pollination biology and association with gracillariid moths have been well studied in the Japanese *F. suffruticosa* (Fig. 4.6). This species is dioecious as with most other species of the genus, and both male and female plants produce abundant nectar that is foraged by diurnal bees, flies, beetles, and butterflies (Kawakita and Kato 2009). Similar pollination biology was confirmed for *F. virosa* in Taiwan. Interestingly, *F. suffruticosa* is associated with a gracillariid moth, *Conopomorpha flueggella*, which visits female plants at night and lays eggs in the buds, flowers, or young fruits. The hatched larvae eat the developing seeds in the fruit, and each larva usually consumes all of the six seeds in its natal fruit to complete larval development. None of the moths collected on flowers possessed pollen on the proboscis or displayed pollination behavior on flowers, therefore they are pure seed parasites of *Flueggea*. The moth was initially identified as a species of *Epicephala* (Kawakita and Kato 2009), but subsequent taxonomic study described it under *Conopomorpha*, a genus that includes seed feeders of longan and lychee. However, the species is distantly related to the proper *Conopomorpha* (Kawakita et al. 2010) but is more closely related to *Epicephala*, thus it is best placed in a new genus (also see Chap. 5).

It is interesting to look further for gracillariid seed feeders in other species of *Flueggea*. To date, searches for larvae in *F. virosa* in Taiwan and Laos and *Flueggea jullienii* in Laos have yielded negative results, but examination of herbarium material suggests that the seeds of Ecuadorian *Flueggea elliptica* are

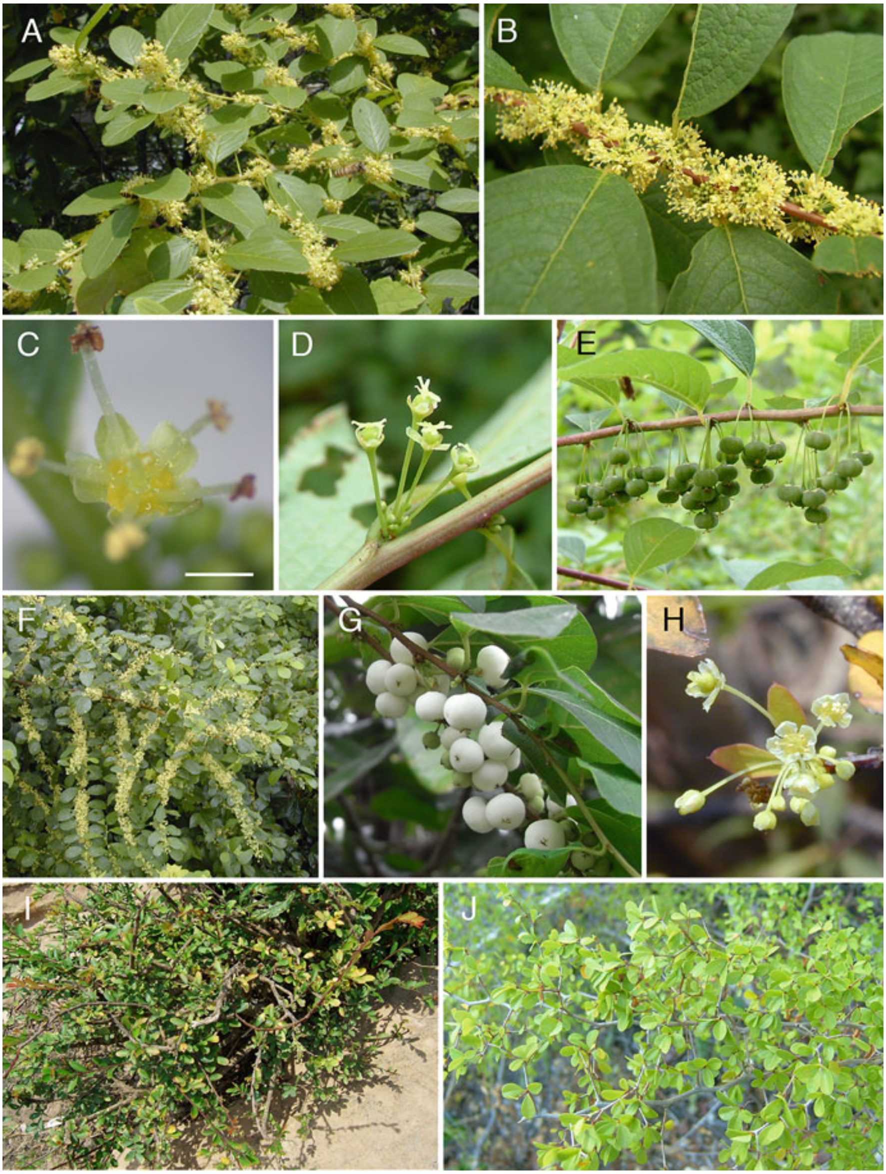

Fig. 4.6 Genus *Flueggea*. (**a**–**e**) *F. suffruticosa*: (**a**) flowering male individual in a temperate forest in Japan; (**b**) male flowers; (**c**) male flower showing nectariferous gland; (**d**) female flowers; (**e**) fruits. (**f**, **g**) *F. virosa*: (**f**) flowering male individual in tropical Taiwan; (**g**) fruiting branch. (**h**, **i**) *F. jullienii*: (**h**) male and female flowers of *F. jullienii*; (**i**) general habitat on a rocky riverbank in Laos. (**j**) *F. acidoton* in a spiny thicket developed on limestone soil in Jamaica

infested by *Epicephala*-like larvae (see also Chap. 5). Whether the Ecuadorian moth is related to the Asian *Conopomorpha flueggella*, or is alternatively a product of more recent colonization of *Flueggea* by *Epicephala* associated with Neotropical *Phyllanthus*, remains to be determined.

4.6.3 *Subgenus* Isocladus *and Sections* Macraea *and* Ceramanthus

The subgenus *Isocladus* was proposed by Webster (1956) to group all of the *Phyllanthus* species with nonphyllanthoid branching. However, as shown by recent molecular phylogenetic analysis, phyllanthoid-branching taxa are not monophyletic, and consequently, the only species placed in this subgenus is the type species, *P. maderaspatensis*, an herbaceous plant that originally occurred in India but has since been introduced to many parts of the African, Asian, and Australian tropics. Molecular phylogenetic analysis placed *P. maderaspatensis* as sister to the clade including all of the other *Phyllanthus* species (Kathriarachchi et al. 2006). Sections *Macraea* and *Ceramanthus* (Fig. 4.7) are two of the four sections that were separated from former *Isocladus*. Of these, *Macraea* is a group of weedy herbs or

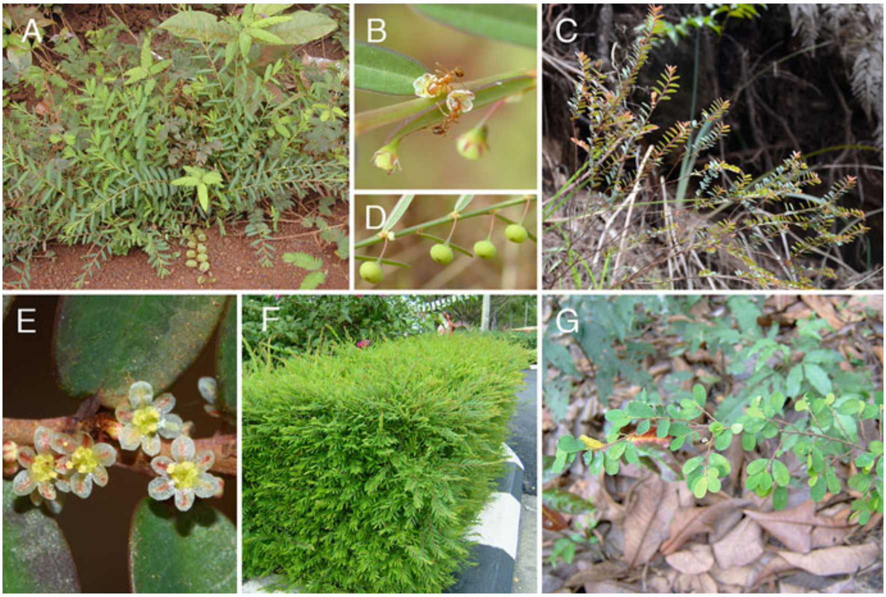

Fig. 4.7 *Phyllanthus* sections *Macraea* and *Ceramanthus*. (**a**–**c**) *P. virgatus*: (**a**) general habitat on disturbed land in Laos; (**b**) male flowers visited by the ant *Solenopsis* sp.; (**c**) mature fruits. (**d**, **e**) *P. chrysanthus*: (**d**) general habitat on forest edge of serpentine forest in New Caledonia; (**e**) male flowers. (**f**) *P. myrtifolius* used as hedge plant in Malaysia. (**g**) General habitat of *P. cochinchinensis*

subshrubs distributed in the Old World tropics, but some have colonized the Pacific islands, including *P. chrysanthus*, which is endemic to New Caledonia. *P. myrtifolius*, originally recorded from Sri Lanka, is planted as an ornamental bush in many tropical areas. The most abundant visitors to male and female flowers of *P. ussuriensis* in Japan and *P. virgatus* in Laos are ants that seek nectar in flowers and are likely the most effective pollinators (Kawakita and Kato 2009). Notably, the fruits of *P. ussuriensis* in Japan and *P. chrysanthus* in New Caledonia are infested by larvae of *Epicephala* moths. Although the behavior of adult moths has not been observed in the field, eggs are only found in developing fruits and not in pollination-stage flowers, suggesting that moths only visit young fruits to lay eggs and do not pollinate the plants. A single larva destroys all of the six seeds contained in a fruit. *Ceramanthus* is a Paleotropical section and consists of four species. The group contains *P. cochinchinensis* (Fig. 4.7), a forest understory shrub distributed in Indochina, the flowers of which are pollinated by *Deltophora* moths (Gelechiidae) that are reported to consume *Phyllanthus* pollen by chemically breaking down sporopollenin on the surface of their proboscis (Luo et al. 2011b). The larvae feed on the leaves of *P. cochinchinensis*, therefore this is another form of reciprocally dependent mutualism. A similar mutualism was reported between *P. rheophyticus* and a different species of *Deltophora*, but the phylogenetic position of *P. rheophyticus* has yet to be determined. At present, ecological information is lacking for other members of the section *Ceramanthus*.

4.6.4 Subgenus **Kirganelia**

The subgenus *Kirganelia* (Fig. 4.8) is a Paleotropical subgenus of about 15 species and is one of the five Phyllantheae lineages currently known to have mutualistic associations with *Epicephala*. The subgenus is most easily recognized by the baccate fruits, which is otherwise only known in *Breynia* within *Phyllanthus* s. lato. Pollination by host-specific *Epicephala* has been studied in *P. reticulatus* and *P. microcarpus* (both in section *Anisonema*), which have particularly wide overlapping distributions from India and Sri Lanka to throughout Southeast Asia (Luo et al. 2011a; their presence in Africa remains to be verified). A detailed natural history of the obligate pollination mutualism is given in Chap. 11. The section *Anisonema* additionally contains four species endemic to Madagascar (Ralimanana and Hoffmann 2011). Although their pollination biology has not been studied, they share the fused style morphology with *P. reticulatus* and *P. microcarpus*, and herbarium specimens of the Madagascan species contained fruits infested by *Epicephala* larvae. Thus, obligate pollination mutualism is likely widespread within the section *Anisonema*.

However, there are species in this subgenus that have conspicuously colored flowers and lack association with *Epicephala*. For example, *P. flexuosus*, which is distributed in Japan, has male flowers with red-purple tepals, and female flowers with widespread styles. Flowers emit an unpleasant odor during the daytime and are

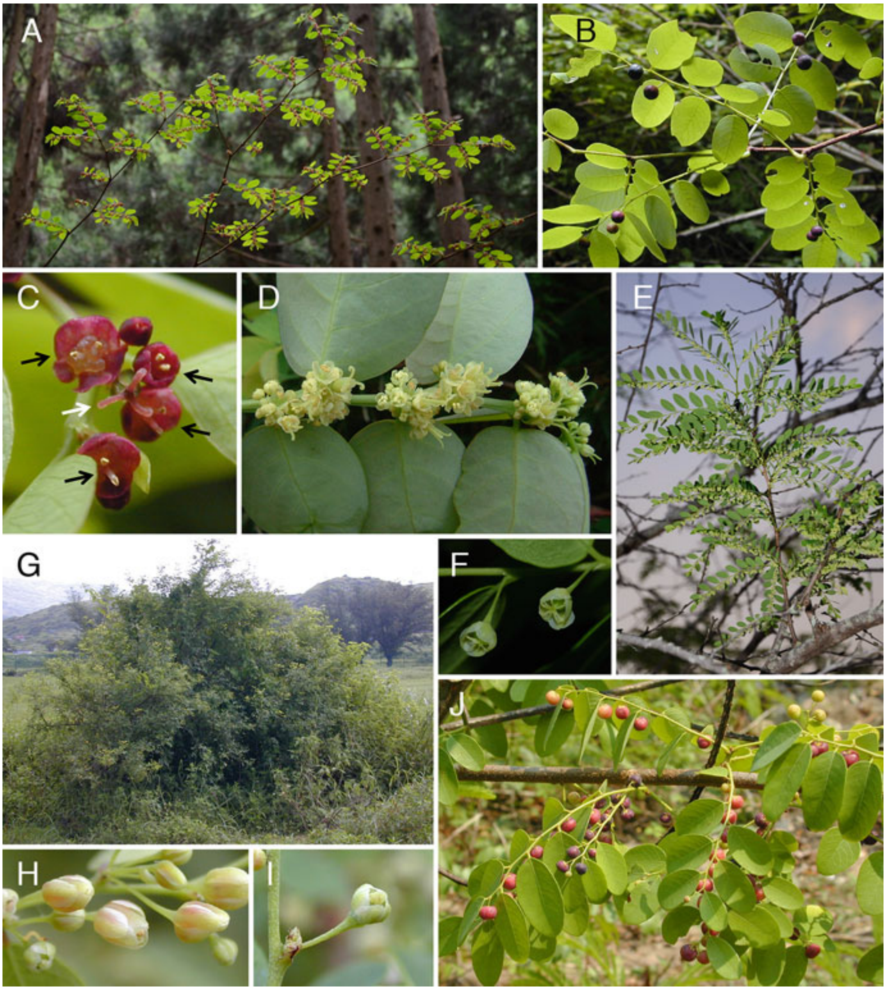

Fig. 4.8 *Phyllanthus* subgenus *Kirganelia*. (**a**–**c**) *P*. *flexuosus*: (**a**) flowering individual in the understory of *Cryptomeria* plantation in temperate Japan; (**b**) fruiting individual; (**c**) male (*black arrows*) and female (*white arrow*) flowers. (**d**) Male and female flowers of *P*. *oligospermus*. (**e**, **f**) *P*. *deplanchei*: (**e**) general habitat in a dry sclerophyllous forest in New Caledonia; (**f**) female flowers. (**g**–**i**) *P*. *reticulatus*: (**g**) general habitat in a disturbed roadside land in tropical Taiwan; (**h**) male flower; (**i**) female flower. (**j**) Fruiting individual of *P*. *microcarpus* in a forest edge in Laos

visited by dipteran and coleopteran insects (Kawakita and Kato 2009). *Epicephala* moths have not been found in any population studied to date, indicating that this species is free of *Epicephala*. *P*. *oligospermus*, which occurs in southern Japan and Taiwan, also has an overall similar ecology.

4.6.5 Subgenus **Eriococcus** *and Section* **Antipodanthus**

Eriococcus (Fig. 4.9) is a group of approximately 30 shrub species with marked diversity in the Indochina region. They are easily distinguished from other *Phyllanthus* by usually having tetramerous male flowers with only two stamens and four distinctly lacerate tepals. Tepals are also often red-purple in color as in *P. flexuous*, which may be an indication of a common pollination system. However, to date, observing flower visitors in *Eriococcus* has been difficult. In *P. liukiuensis*

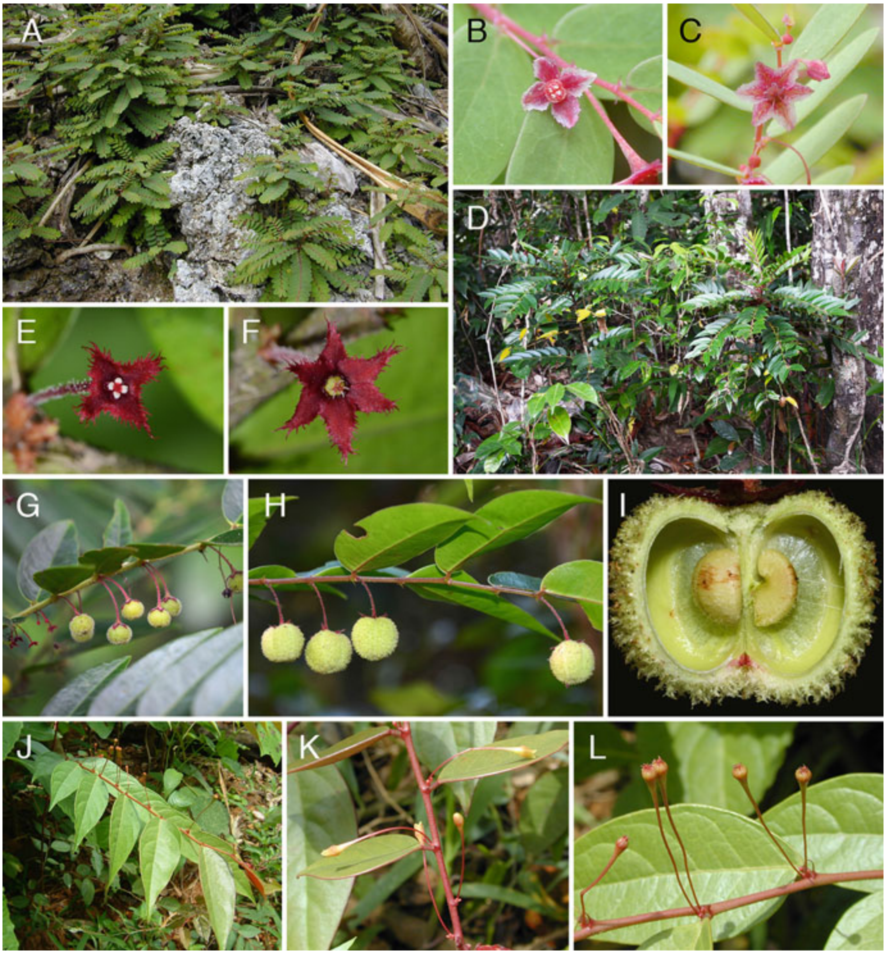

Fig. 4.9 *Phyllanthus* subgenus *Eriococcus*. (**a**–**c**) *P. liukiuensis*: (**a**) habitat on a limestone outcrop in subtropical Japan; (**b**) male flower; (**c**) female flower. (**d**–**g**) *P. pulcher*: (**d**) general habitat on a forest floor along a river in lowland Laos; (**e**) male flower; (**f**) female flower; (**g**) fruits. (**h**, **i**) *P. pulcheroides*: (**h**) fruits; (**i**) longitudinal section of fruit with fully developed seeds and large internal airspace. (**j**–**l**) *P.* sp.: (**j**) habitat on forest floor of secondary forest in Vietnam; (**k**) male flowers; (**l**) female flowers

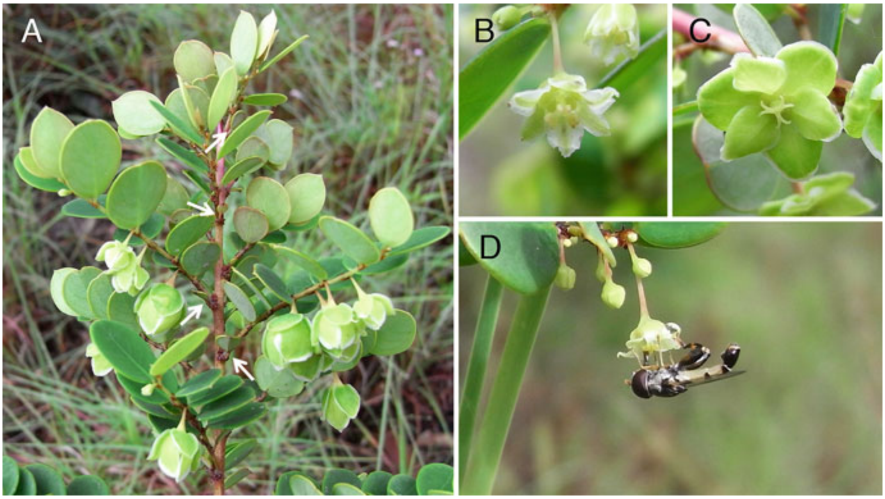

Fig. 4.10 *Phyllanthus* section *Antipodanthus*. (**a**–**d**) *P. dallachyanus*: (**a**) general habitat in understory of fire-prone forest in Queensland, Australia; (**b**) male flower; (**c**) female flower; (**d**) hoverfly nectaring on male flower

occurring in Japan, a few pollen-bearing gall midges were collected on flowers (Kawakita and Kato 2009), so dipterans may pollinate these plants. Another group of species in this subgenus has flowers with long pedicels that are remarkably erect in female flowers. In such species, the tepals of male flowers are imbricate, so they may have a pollination system that is entirely different from species with lacerate and colored tepals. Because *Epicephala* has not been recorded from any *Eriococcus* species, the plants in this subgenus likely have an unknown specialized pollination system. In addition, some *Eriococcus* species have unique, distinctly swollen fruits with a hollow space between the seeds and the endocarp. This is probably an adaptation to escape attack by seed-feeding braconid wasps because their seeds are frequently infested by braconid larvae, and because adult wasps oviposit through the fruit wall using exceptionally long ovipositors. Section *Antipodanthus* (Fig. 4.10) is an entirely Australian group of 13 species (Webster 2002). The plants are subshrubs and occur in fire-prone, open forests. They are notable for the lack of phyllanthoid branching. Both male and female flowers have clearly visible nectaries, and hoverflies were regularly observed visiting flowers to lick nectar during daytime.

4.6.6 Subgenera **Afroswartziani, Swartziani** *(Including Former* **Reverchonia***), and* **Tenellanthus**

The subgenera *Afroswartziani*, *Swartziani*, and *Tenellanthus* (Fig. 4.11) comprise a clade that traditionally contains many herbs or small shrubs placed in various

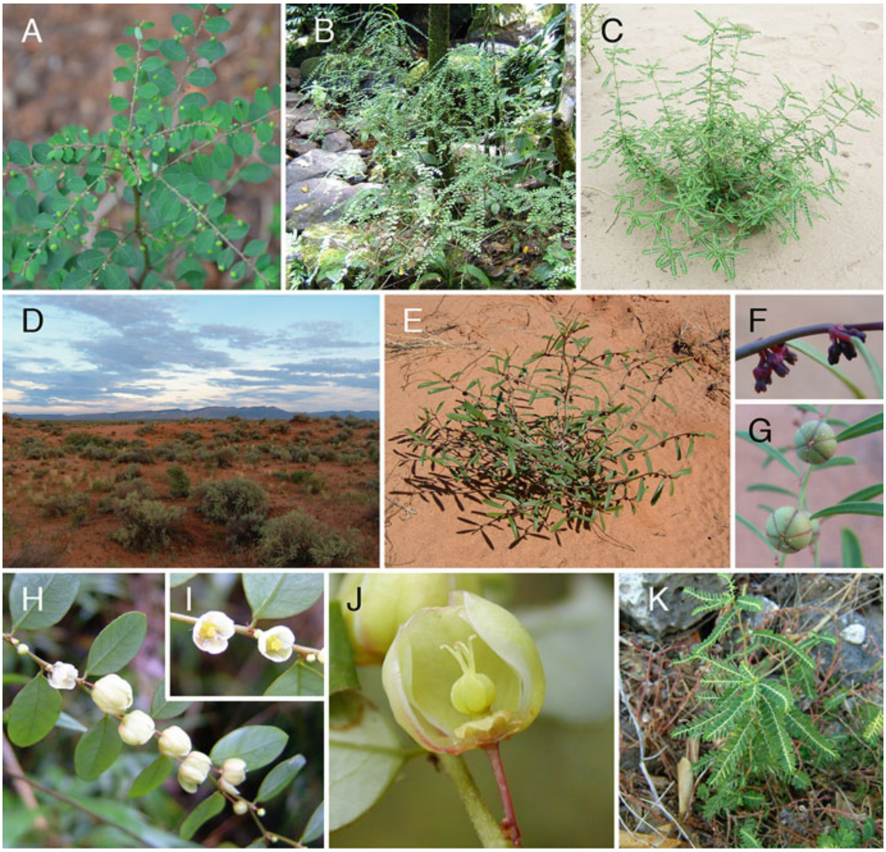

Fig. 4.11 *Phyllanthus* subgenera *Tenellanthus*, *Swartziani*, and *Afroswartziani*. (**a**) *P. tenellus* (*Tenellanthus*) on roadside in New Caledonia. (**b**) *P. nummulariifolius* (*Tenellanthus*) in rainforest understory in Madagascar. (**c**) *P. amarus* (*Swartziani*) on sandy riverbank in its introduced range in Laos. (**d**–**g**) *P. warnockii* (*Swartziani*): (**d**) habitat on sandy desert in New Mexico, USA; (**e**) general habitat on sandy dune; (**f**) flowers; (**g**) fruits. (**h**–**j**) *P. lokohensis* (*Afroswartziani*): (**h**) flowering branch; (**i**) male flowers; (**j**) section of female flower showing airspace between tepals and ovary. (**k**) *P. deblis* on roadside in its introduced range in Japan

sections and subgenera. Ralimanana and Hoffmann (2011) and Ralimanana et al. (2013) reorganized these species into the above three subgenera to reflect phylogenetic relationships. *Afroswartziani* contains shrubs, trees, and rarely herbs that mainly occur in Madagascar and Africa, but many Asian species not sampled in previous molecular phylogenetic studies may also belong to this subgenus. A Madagascan species, *P. madagascariensis*, has male and female flowers with five obovate whitish green tepals and a nectariferous disk, and are visited by nectar-seeking insects such as long-proboscid crane flies. Some Madagascan species (e.g., *P. lokohensis*) have female flowers, the tepals of which form a globe surrounding the pistil that may function to keep the ovary away from *Epicephala* oviposition because their fruits are infested by *Epicephala* larvae (probably nonpollinating species). *P. debilis*, a global weed, also belongs to this subgenus. The subgenus *Swartziani* was revised by Ralimanana et al. (2013) to only include three species native to the New World. These are *P. amarus*, *P. abnormis*, and *P. warnockii* (formerly *Reverchonia arenaria*). *P. amarus* is now a globally distributed weed, and in its introduced populations in Laos their flowers are pollinated by ants, and their fruits are parasitized by nonpollinating species of *Epicephala*. *P. abnormis*, native to the southeastern United States, is also parasitized by an *Epicephala* moth, as demonstrated by the presence of pupae in herbarium specimens. *P. warnockii* is an unusual *Phyllanthus* that grows on sand dunes of the southwestern United States. The flowers are dark red and are visited by flies and small bees in the daytime. *Tenellanthus* is a well-defined subgenus of four species occurring in Madagascar, the Comoro Islands, and Africa, with one species, *P. tenellus*, becoming a pantropical weed. To date association with *Epicephala* has not been found in this subgenus.

4.6.7 *Subgenus* Gomphidium

The subgenus *Gomphidium* is distributed in tropical Australia, New Guinea, and the Pacific Islands as far east as Tonga, with the greatest concentration of species in New Caledonia. The subgenus consists of about 150 species of shrubs or trees, of which 106 species occur in New Caledonia, all of which are endemic except *P. bourgeoisii* (Schmid 1991). New Caledonia (Fig. 4.12) is located in the Pacific Ocean about 1200 km from Australia and consists of the main island (Grande Terre) and a number of surrounding small islands, with a total area of 18,580 km^2. New Caledonia was part of the Gondwana supercontinent and was separated from Australia as early as 66 Ma, although a significant proportion of the land mass was once submerged under the sea around approximately 35 Ma and many of the plants are thought to be descendants of later colonizations (Grandcolas et al. 2008). New Caledonia is renowned for its unique flora; the islands have five endemic angiosperm families (Amborellaceae, Oncothecaceae, Paracryphiaceae, Phellinaceae, and Strasburgeriaceae) and more than 100 endemic genera with the proportion of endemic species exceeding 90%. The earliest branching angiosperm Amborellaceae is only known from New Caledonia, although its fossils are known from other parts of the world. The uniqueness of the flora is exacerbated by the prevalence of serpentine rocks, which cover roughly 40% of the total land area. Serpentine rocks are ultrabasic, and plants occurring on serpentine substrates require particular adaptation to tolerate adverse, magnesium-rich soil conditions, resulting in high endemicity. Many of the notoriously invasive plants, such as *Leucaena leucocephala*, *Aleurites fordii*, and *Psidium littorale*, do not occur on serpentine soil, although they are abundant on nonserpentine regions of New Caledonia. The New Caledonian species of *Phyllanthus* are remarkably diverse in their habitats and vegetative forms, representing one of the most spectacular adaptive radiations in the plant kingdom (Fig. 4.13). It is the largest plant genus

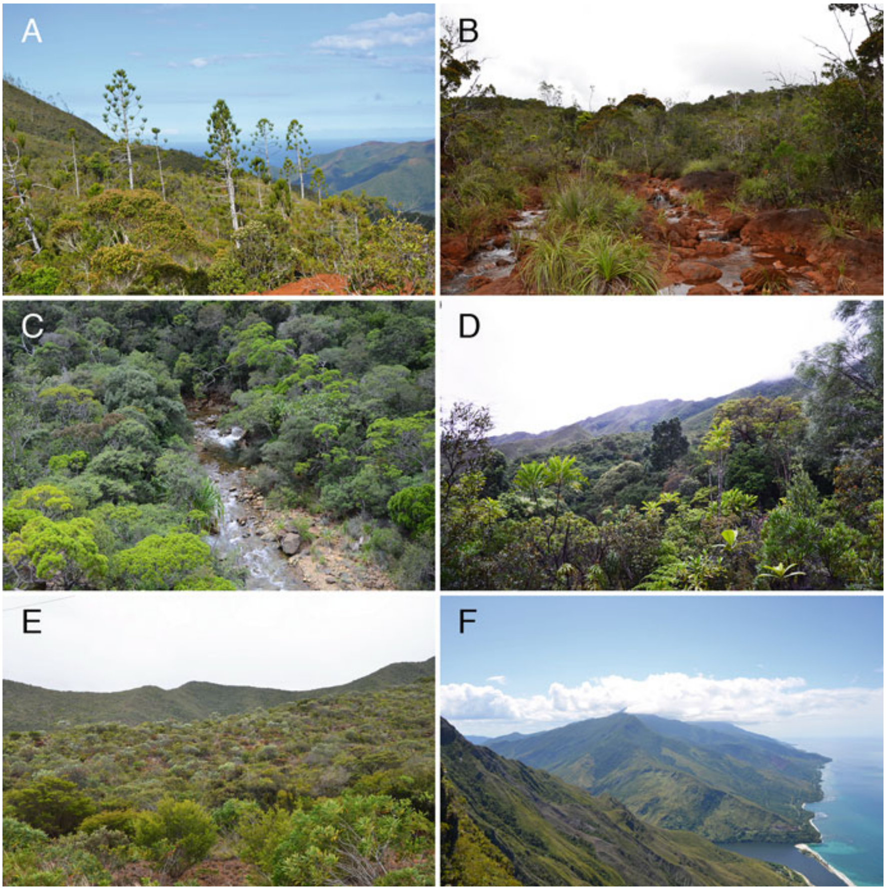

Fig. 4.12 Diverse habitats of New Caledonian *Phyllanthus*. (**a**) *Araucaria*-dominated scrubland on serpentine rock in Poro harboring *P. pancherianus* and *P. bupleuroides*. (**b**) Maquis vegetation near Prony in the southern part of Grande Terre. Note that the soil has the color of iron oxide and lacks introduced plants. (**c**) Rainforest along the valley of Troulala harboring *P. serpentinus*, *P. buxoides*, and *P. pilifer*. (**d**) Rainforest on the foot of Mt. Koghi harboring *P. koghiensis* and *P. yaouhensis*. (**e**) Maquis vegetation along the northwestern coast near Koumac harboring *P. koumacensis*, *P. poumensis*, and *P. peltatus*. (**f**) Humid rainforest of Massif du Panié on the northeastern coast harboring *P. baladensis*, *P. valeriae*, *P. gneissicus*, *P. bourgeoisii*, and *P. loranthoides*

in New Caledonia with 114 recorded species, of which 96% are endemic. The diversity is exceptional for an island that is smaller in size than the state of New Jersey (22,610 km^2) or the island of Sicily (25,710 km^2). Their habitats range from rainforest understory, dry sclerophyllous forest, calcareous forest, riverbank, and maquis (scrubland developed on serpentine soil) with the majority of species being very narrow endemics. *P. bourgeoisii*, *P. loranthoides*, and *P. dracunculoides* are rheophytes with narrow lanceolate leaves. *P. peltatus* is unique with peltate leaves.

Fig. 4.13 New Caledonian *Phyllanthus* (subgenus *Gomphidium*). (**a**) *P*. *mouensis* in montane forest of Mont Mou. (**b**) *P*. *peltatus* with peltate leaves in the understory of serpentine scrubland in Koumac. (**c**) *P*. *poumensis* on serpentine rock in Paagoumène. (**d**) *P*. *serpentinus* on the understory of serpentine scrub in Troulala. (**e**) *P*. *valeriae* on the understory of rainforest of Mont Panié. (**f**) *P*. *mangenotii* along stream in Cap Bocage. (**g**) *P*. *aeneus* on the understory of serpentine forest in Thio. (**h**) *P*. *luciliae* in coastal forest of Cap Bocage. (**i**) *P*. *bourgeoisii* on flood-prone habitat in Cascade de Bâ. (**j**) *P*. *dracunculoides* on flood-prone habitat in Tiwaka. (**k**) *P*. cf. *montrouzieri* on dry serpentinous scrubland in Kaala-Gomen. (**l**) *P*. *koghiensis* tree in rainforest habitat of Mont Koghi

Fig. 4.14 Flowers of New Caledonian *Phyllanthus* (subgenus *Gomphidium*). (**a**–**h**) Section *Adenoglochidion* (male and female flowers on upper and lower column, respectively): (**a**) *P. peltatus*; (**b**, **f**) *P. serpentinus*; (**c**) *P. umbraecola*; (**d**) *P. pronyensis*; (**e**) *P. aeneus*; (**g**) *P. baladensis* (photo courtesy of Eri Yamasaki) and (**h**) *P. dorotheae*. (**i**–**p**) Section *Gomphidium* (male and female flowers on upper and lower column, respectively): (**i**, **m**) *P. poumensis*; (**j**, **n**) *P. kouaouaensis*, (**k**, **o**) *P. pilifer*; (**l**, **p**) *P. castus*. An *Epicephala* egg is laid externally on the female flower in (**n**)

The subgenus *Gomphidium* contains two large sections, *Gomphidium* and *Adenoglochidion*, and both sections occur in New Caledonia. Male flowers have imbricate folded tepals with narrow apical openings and connate stamens in *Gomphidium*, or spread tepals and free stamens in *Adenoglochidion* (Fig. 4.14). Female flowers have nonbifid styles that are either fused in the middle or spread, although species with bifid styles are known in other parts of the Pacific (Webster 1986). *Epicephala* pollination has been confirmed in two New Caledonian species, *P. bourgeoisii* and *P. aeneus*, belonging to *Gomphidium* and *Adenoglochidion*, respectively (Chap. 3).

4.6.8 Madagascan Clade

There are seven Madagascan endemic *Phyllanthus* species that have until recently been considered members of *Glochidion* (Hoffmann and McPherson 2003; Fig. 4.15). This classification was based on their much reduced and entire styles, a characteristic most likely reflecting the shared *Epicephala* pollination syndrome. Indeed, these species are otherwise widely different from the true *Glochidion* in terms of floral and seed characters as well as growth form (Hoffmann and McPherson 2003). These plants are confined to the cloud forests in the northern part of Madagascar and are pollinated by *Epicephala* moths that feed on their seeds (Kawakita and Kato 2009).

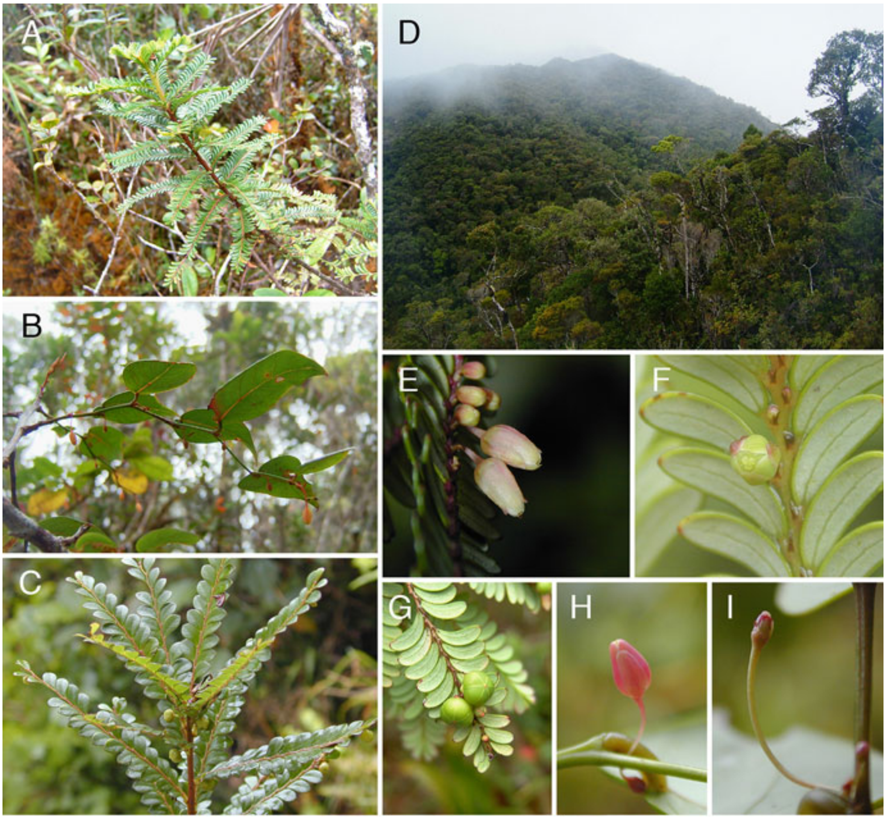

Fig. 4.15 Madagascan *Phyllanthus*. (**a**) *P. marojejiensis*. (**b**) *P. humbertii*. (**c**) *P. sambiranensis*. (**d**) Cloud forest at approximately 2500 m a.s.l. of Mt. Marojeji, Madagascar where *P. marojejiensis*, *P. humbertii*, and *P. sambiranensis* occur in the understory. (**e–g**) *P. marojejiensis*: (**e**) male flower; (**f**) female flower; (**g**) fruit. (**h**, **i**) *P. humbertii*: (**h**) male flower; (**i**) female flower

Ralimanana and Hoffmann (2011) placed the above seven species and an additional three species in the subgenus *Gomphidium*, but molecular phylogenetic analysis suggests that they are distinct from *Gomphidium* known from New Caledonia and Australasia. Thus, the imbricate tepals of male flowers and reduced styles used as the basis for their placement in *Gomphidium* is again a morphological convergence associated with *Epicephala* pollination. These Madagascan species are rather strongly united to subgenera *Betsileani* and *Anisonemoides*, both of which are also confined to Madagascar and contain 3 and 15 species, respectively. Collectively, these three lineages comprise a medium-sized clade that is entirely confined to Madagascar. Pollination biology is unknown for any of the species in *Betsileani* and *Anisonemoides*, but this information is critical to understanding the origin of *Epicephala* pollination in Madagascar. *Epicephala* pollination was studied in *P. marojejiensis* and *P. humbertii* at Mt. Marojeji in northeastern Madagascar. In both species, male flowers have imbricate tepals with either connate or free stamens, and female flowers have very short and entire styles that lean inward (Fig. 4.15). Although flower visitation by *Epicephala* has not been directly observed, pollination by *Epicephala* is suggested by the following observations: (i) fruits of the two species were both infested by species-specific *Epicephala* larvae; (ii) an *Epicephala* female bearing pollen on the proboscis was collected on *P. marojejiensis*; and (iii) there was a near exclusive association between the pollinated status of female flowers and infestation by moth eggs, suggesting that ovipositing moths are the only pollinators (Kawakita and Kato 2009). Eggs are laid internally within the ovary, and a single larva destroys all of the six seeds in each fruit.

4.6.9 The New World Clade

This large clade of entirely New World species consists of the subgenus *Xylophylla*, section *Nothoclema* of subgenus *Conami*, and various Neotropical herb, subshrub, and aquatic species traditionally placed in divergent taxonomic groups. Of these, *Xylophylla* (Fig. 4.16) is a morphologically well-characterized and species-rich group with the center of diversity in the Caribbean Islands. The largest island in the Caribbean is Cuba, which has the greatest concentration of *Xylophylla* species. Its landmass is a mosaic of soil types, including serpentine and limestone; thus, the radiation of *Phyllanthus* in Cuba is reminiscent of *Phyllanthus* diversification in New Caledonia. Many *Xylophylla* species possess flowers with fused tepals and fused styles, and their seeds are infested by *Epicephala* larvae, suggesting that at least some species are pollinated by *Epicephala* moths. However, there are species with well-developed, showy tepals and distinct nectaries (Fig. 4.16), which are probably pollinated by diurnal bees and flies. Two species in section *Cauliflori* have cauline inflorescences. Species of the section *Xylophylla* are characterized by flattened photosynthetic branches (phylloclades) and an associated reduction of leaves (Fig. 4.16). They often occupy exposed habitats on limestone or coastal cliffs

Fig. 4.16 *Phyllanthus* subgenus *Xylophylla*. (**a**) A flowering *P*. *chamaecrystoides* individual along stream in serpentine forest of Cuba. (**b–d**) *P*. *williamioides*: (**b**) flowering individual in serpentine scrubland in Cuba; (**c**) male flower; (**d**) female flower. (**e–g**) *P*. *orbicularis*: (**e**) flowering plant with brightly white flowers in serpentine scrubland in Cuba; (**f**) male flowers; (**g**) female flower. (**h**, **i**) *P*. *cauliflorus*: (**h**) cauline inflorescences in limestone forest of Jamaica; (**i**) female flower. (**j–l**) *P*. *angustifolius*: (**j**) habitat on limestone cliff in Jamaica; (**k**) individual bearing male and female flowers on phylloclades; (**l**) fruits. (**m**) *P*. *arbuscula* bearing male and female flowers on phylloclades. (**n–p**) *P*. *nutans*: (**n**) branch bearing erect male flowers; (**o**) branch with female flowers and fruits; (**p**) fruits (one on the lower right has exit hole excavated by *Epicephala* larva)

but are surprisingly robust to hurricane winds. Thus, the loss of leaves and substitution of photosynthesis by branches may be an adaptation to hurricane turbulence. *P. arbuscula*, a species with phylloclades, has bright red flowers, indicative of another unusual pollination system. *Xylophylla* is perhaps the most diverse lineage of *Phyllanthus* in terms of floral and vegetative adaptation, and further studies of the ecology of these plants are required. Section *Nothoclema* is another well-defined group of 11 tree species occurring widely from Mexico to Peru (Webster 2003). They can be easily distinguished from other *Phyllanthus* by their nonphyllanthoid branching, which is otherwise unknown in tree *Phyllanthus*. *Epicephala* moths are frequently found in the herbarium specimens of *Nothoclema* species, but the details of the association are still unknown. The clade sister to *Nothoclema* contains many herbs and subshrubs native to the New World with little known natural history. *P. fluitans* is a floating aquatic native to the Amazon but has also spread commercially as a water plant worldwide. *P. niruri* is used as a medicine to cure bladder stones. The members of the New World clade provide ample opportunity to study *Phyllanthus–Epicephala* association in the New World. The relationship likely varies from obligate pollination mutualism to pure parasitism, the latter involving nonpollinating moth species.

4.6.10 Sections Cicca, Aporosella, *and* Chorisandra

Sections *Cicca*, *Aporosella*, and *Chorisandra* each contain only one or two species and collectively form a monophyletic group of four species. Production of cauline inflorescences unites the four species morphologically. *P. acidus* (Fig. 4.17) is native to South America but is now widely cultivated in tropical parts of the world, particularly in tropical Asia. It is the most common fruit tree to be planted at home by the Lao people. The plant produces edible yellow drupes, which are eaten fresh or candied in sugar or pickled in salt. *P. acidus* produces abundant fruits under cultivation apparently in the absence of *Epicephala*, although the pollinator of the species is yet unknown. Ecological information is unavailable for species of *Aporosella* and *Chorisandra*.

4.6.11 Subgenus Emblica

The subgenus *Emblica* (Fig. 4.18) was traditionally confined to a few Asian shrub species, but Ralimanana et al. (2013) expanded the subgenus to include the herbaceous section *Urinaria*, which has clear phylogenetic affinity to the species traditionally included in *Embli*ca. One such herbaceous species is *P. lepidocarpus*, the flowers of which produce abundant nectar and are effectively pollinated by nectar-seeking ants. The plants are self-compatible and commonly attain 100% fruit even when non-ant visitors are experimentally excluded from flowers. The fruits of

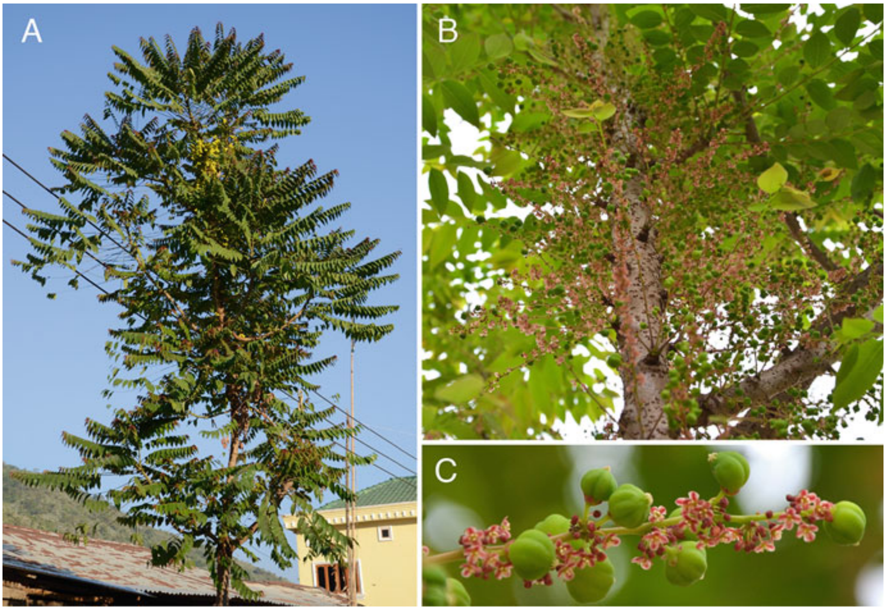

Fig. 4.17 *Phyllanthus* section *Cicca*. (**a**–**c**) *P. acidus*: (**a**) fruiting tree in a village of Laos; (**b**) cauline inflorescences; (**c**) inflorescence with male flowers and young fruits

P. lepidocarpus are infested by *Epicephala parasitica*, which lacks the pollination behavior and oviposits in young fruits (Kawakita and Kato 2016). The resulting larvae destroy all of the seeds contained in each fruit. *P. emblica*, known as Indian gooseberry, is widely distributed in Southeast Asia and is common along the edges of seasonally dry tropical forests. The plant produces numerous male flowers among which female flowers are embedded, and is visited by honey bees in its native range in China. The plants produce near- spherical drupes about 2 cm in diameter, which is an exceptionally large nondehiscent fruit otherwise unknown in *Phyllanthus*. As with *P. acidus*, the edible fruits are very sour and popularly eaten in many parts of tropical Asia, but the natural consumer of the fruit is unknown, and thus no information is available on the mechanism of seed dispersal. Other members of the subgenus *Emblica* are still poorly known. Because nectaries are well developed in flowers of *Emblica*, they are most likely pollinated by unspecialized, nectar-seeking insects as in *P. lepidocarpus* and *P. emblica*.

4.6.12 Sauropus

The genus *Sauropus* as traditionally circumscribed is clearly a paraphyletic group with respect to the embedded *Breynia* (Pruesapan et al. 2008, 2012). Within the

Fig. 4.18 *Phyllanthus* subgenus *Emblica*. (**a**–**c**) *P*. *lepidocarpus*: (**a**) weedy habitat on roadside pebbles in Japan; (**b**) flowering and fruiting branch; (**c**) male flower; (**d**) female flower; (**e**) the ant *Tetramorium* sp. nectaring on male flower. (**f**–**h**) *P*. *emblica*: (**f**) flowering branch in Guangzhou, China; (**g**) male flowers; (**h**) fruits sold at market in Vientiane, Laos. (**i**–**l**): *P*. sp.: (**i**) habitat on limestone forest in northern Laos; (**j**) flowering branch; (**k**) male flowers; (**l**) male flowers with nectar in flower

Sauropus–*Breynia* clade, the Australian species of *Sauropus* forms a monophyletic group and is the earliest branching lineage. Earlier taxonomists placed Australian *Sauropus* in a separate genus, *Synostemon*, and van Welzen et al. (2014) reinstated *Synostemon* to the generic rank to refer to this Australian clade. The remaining Southeast Asian *Sauropus* and *Breynia* were grouped by van Welzen et al. (2014) in the expanded *Breynia*. The expanded *Breynia* is divided into the subgenera *Sauropus* and *Breynia*, the latter of which is further divided into sections *Cryptogynum* and *Breynia*. However, because *Sauropus* and *Breynia* are deeply embedded in *Phyllanthus*, whether to adopt the generic changes proposed by van

Welzen et al. (2014) is tightly linked to the issue of whether to subsume *Sauropus*, *Breynia*, and *Glochidion* in an expanded *Phyllanthus*. Due to a lack of consensus at present, we followed the traditional circumscription of *Sauropus* and *Breynia*, while acknowledging that the former is a paraphyletic group. *Sauropus* (Fig. 4.19) produces flowers that are among the most unusual of all Phyllantheae.

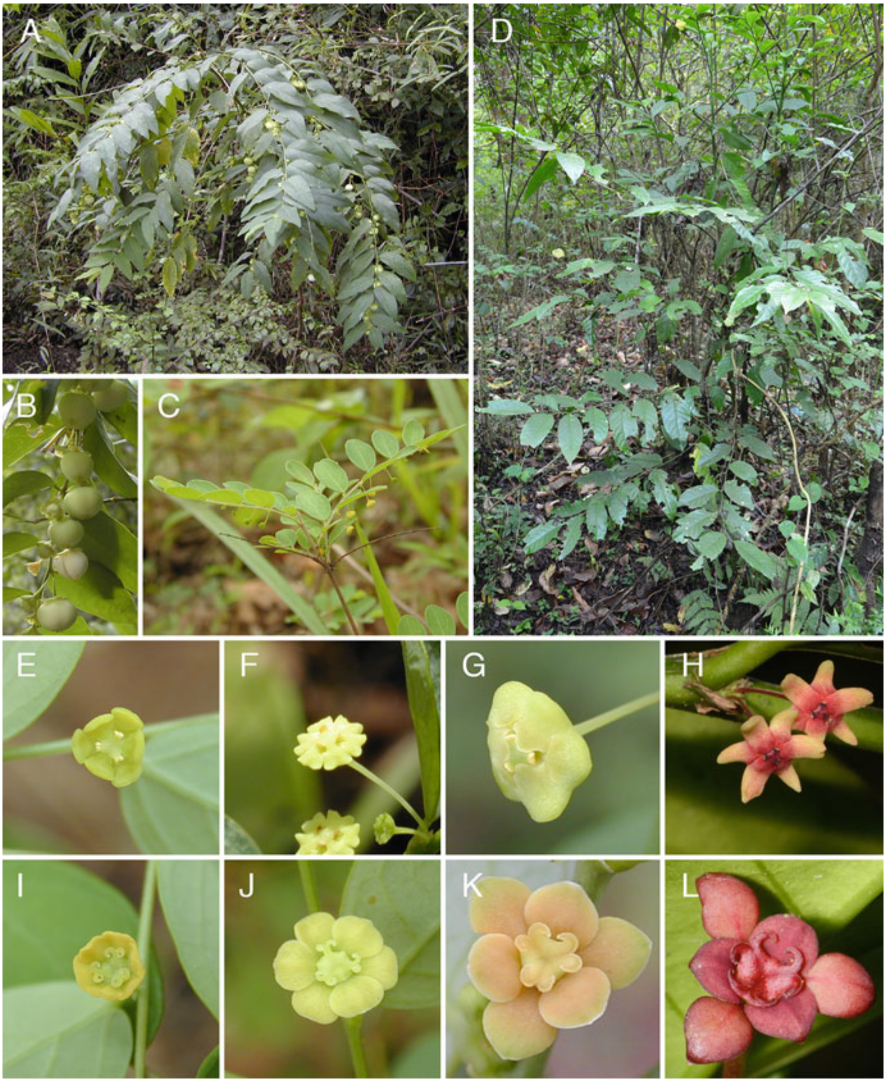

Fig. 4.19 Genus *Sauropus*. (**a**–**b**) *S. androgynus*: (**a**) general habitat at forest edge on limestone in Laos; (**b**) fruits. (**c**) *S.* cf. *quadrangularis* in the understory of seasonal dipterocarp-dominated tropical forest in Laos. (**d**) *S. macranthus* in the understory of evergreen broad-leaved forest in mountainous region of Laos. (**e**–**l**) Flowers of *Sauropus* species (male and female flowers on upper and lower column, respectively): (**e**, **l**) *S.* cf. *quadrangularis*; (**f**, **j**) *S. brevipes*; (**g**, **k**) *S. androgynus*; (**h**, **j**) *S. macranthus*. Photographs of flowers are on the same scale

In most Southeast Asian species, the tepals of both male and female flowers are spread flat on a horizontal plane, and as a result, the flowers are more or less disclike. In male flowers, the tepals are further inflexed toward the androecium, and together with the short, horizontally spread androecium, form three small cavities on the surface of the disc-shaped flower. As the anthers are held toward the cavities, pollen can only be picked up from inside these small cavities. The bifid styles of female flowers are also spread horizontally, and the stigmatic surface faces outward. Thus, as in male flowers, female flowers can only pick up pollen from flower visitors that approach or hold on to the flower in a particular manner. Several *Sauropus* species produce cauline inflorescences (e.g., *S. racemosus*) or are even geoflorous (*S. discocalyx*). Species that produce flowers in forest understory habitats tend to possess red-purple-colored tepals. Despite these interesting floral morphological characteristics, the pollination system of *Sauropus* is still unknown. None of the *Sauropus* species studied to date host *Epicephala* larvae in the fruit, therefore the moths are not involved in the pollination of *Sauropus*. Their pollination system holds the key to understanding the evolution of *Epicephala* moth pollination in *Breynia*. The ecology of Australian *Sauropus* is much less well known. Most species are rare and have very limited distributions, and new species continue to be found (Telford and Naaykens 2015). One Southeast Asian *Sauropus* species (*Sauropus androgynus*) is cultivated as a leaf vegetable in many parts of tropical Asia.

4.6.13 Breynia

Breynia (Fig. 4.20) contains 35 species distributed throughout the Australasian tropics extending far east to Fiji (Govaerts et al. 2000). Several continental species are very widely distributed, which is likely due to their bird-dispersed fruits. For example, the distribution of *Breynia vitis-idaea* extends from Pakistan in the west to Japan and the Philippines in the east (Chakrabarty and Gangopadhyay 1996). The flowers of most *Breynia* species resemble those of *B. vitis-idaea*, so *Epicephala* moth pollination is likely widespread in the genus. However, at least one species, *Breynia retusa* (Fig. 4.20), does not have an association with *Epicephala* (Kawakita and Kato 2009). The flowers of *B. retusa* are very different from those of *B. vitis-idaea*, suggesting that the plant has an alternative pollination mechanism. Fruit characteristics are also variable in the genus. Most species, including *B. vitis-idaea*, produce berries, whereas others produce dry capsules containing seeds with a fleshy sarcotesta (Fig. 4.20).

B. disticha, a native of New Caledonia, has a horticultural variety that produces strongly variegated leaves, which is known as “Snow Bush” and is popularly cultivated as an ornamental plant in tropical parts of the world.

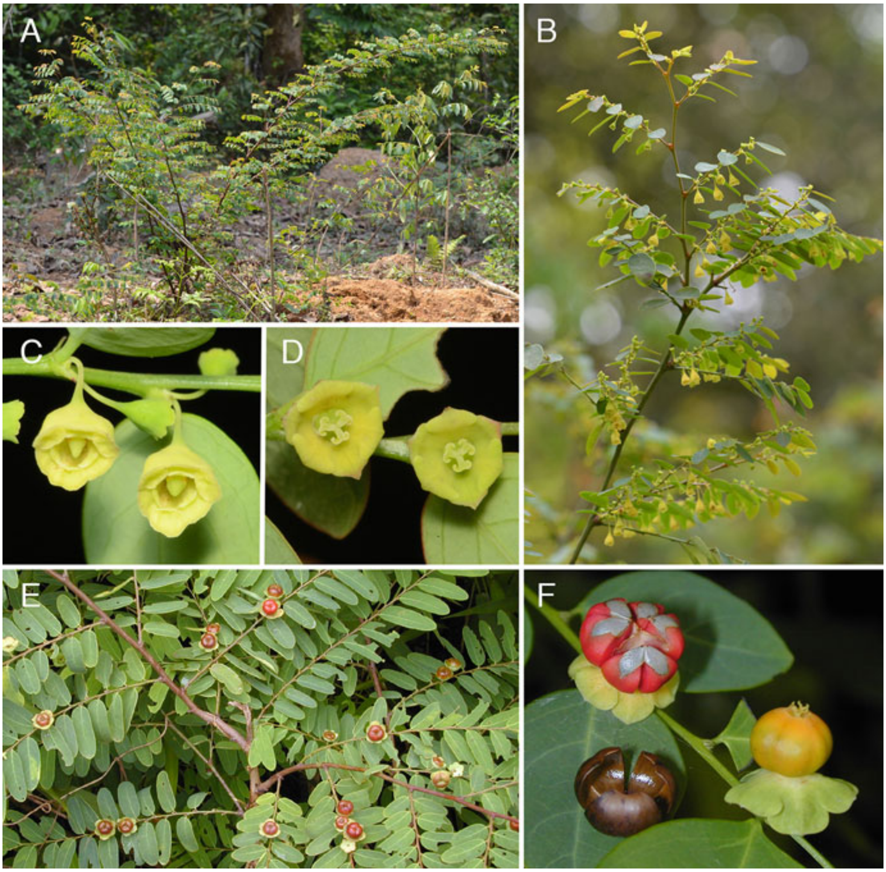

Fig. 4.20 Genus *Breynia*. (**a**–**e**) *B. retusa*: (**a**) general habitat on forest edge in Laos; (**b**) flowering branch; (**c**) male flowers; (**d**) female flowers; (**e**) fruiting individual. (**f**) Fruits and seeds of *B. fruticosa*. Note that the fruit is a capsule, and the seeds have an orange sarcotesta

4.6.14 Phyllanthodendron

Subgenus *Phyllanthodendron* (Fig. 4.21) contains approximately 10 species occurring in Southeast Asia. Species of this subgenus have characteristic bell-shaped flowers that are unlike those of any other *Phyllanthus*. In addition, their growth form and leaf traits more resemble those of *Glochidion* than those of most *Phyllanthus*. Thus, the subgenus is often treated at generic rank (Li et al. 2008), and molecular phylogenetic analysis provided support for its unusual placement; *Phyllanthodendron* is sister to *Glochidion* and distantly related to all other *Phyllanthus* (Kathriarachchi et al. 2006).

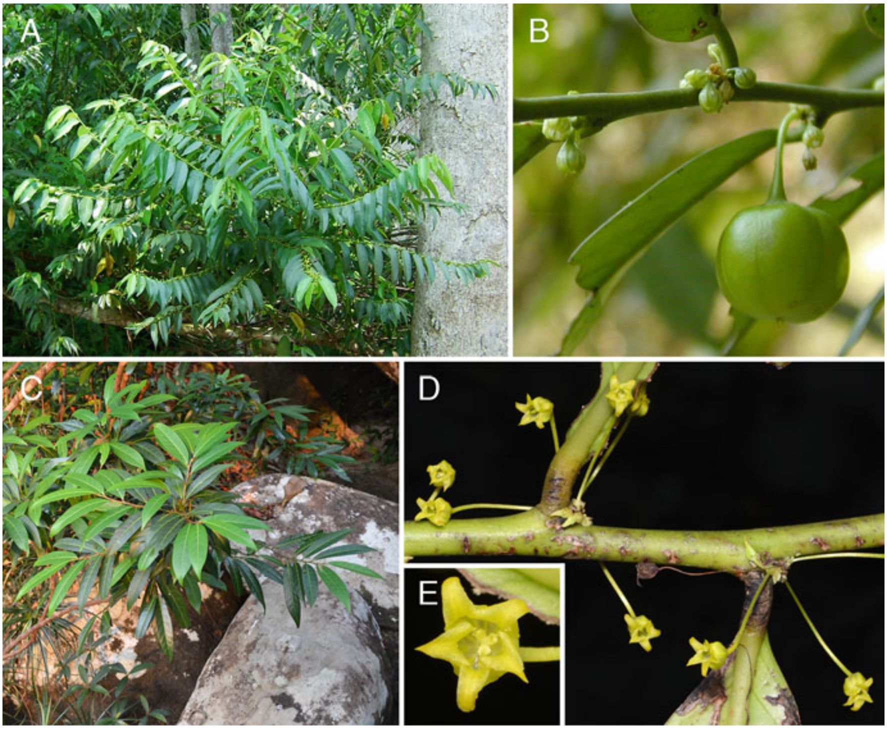

Fig. 4.21 *Phyllanthus* subgenus *Phyllanthodendron*. (**a**, **b**) *P. roseus*: (**a**) flowering individual on forest edge of seasonal tropical forest in Laos; (**b**) flowers and fruit. (**c**–**e**) *P.* cf. *caudatifolius*: (**c**) general habitat on rocky riverbank in Laos; (**d**) branch with male flowers; (**e**) close-up of male flower showing the fused anthers

Pollination occurs during the daytime by numerous flies that visit flowers for nectar in *P. roseus*. None of the species studied to date has an association with *Epicephala*, although the seeds of *P. roseus* are consumed by braconid wasp larvae. The braconid wasp has a very long ovipositor that probably coevolved with the swollen fruit of *P. roseus*; its fruit has a large airspace between the fruit wall and ovule that likely distances the ovule from ovipositing wasps. The association between the *Phyllanthus* fruit and the braconid seed parasite reminds us of the evolutionary arms races between balloonlike fruit of a balloon vine (*Cardiospermum*, Sapindaceae) and its seed-sucking long-proboscid soapberry bugs (Carroll and Boyd 1992) and between the thick fruit pericarp of Japanese camellia and its seed-parasitic weevils with long rostrums and long ovipositors (Toju 2009). *P. mirabilis*, native to Thailand, is the only *Phyllanthus* to be caudiciform, or with a succulent trunk. The species is cultivated as an ornamental plant.

4.6.15 Glochidion

Glochidion (Fig. 4.22) contains some of the tallest plants of all Phyllantheae. In the lowland rainforest of Malaysia, *G. arborescens* commonly exceeds 20 m, and others may reach the canopy layer. However, the majority of *Glochidion* species occur along forest edges or roadsides and are typically small-sized trees or treelets. Few are forest understory shrubs. *G. obovatum*, endemic to Japan, occurs in habitat that is prone to deer browsing, and consequently, the stem apices of young plants are modified to thorns. In areas with large deer populations, *G. obovatum* literally dominates the vegetation due to its effective defense against deer browsing provided by the thorns. All *Glochidion* species studied to date are pollinated by *Epicephala* and share the same basic pollination ecology as described in Chap. 3. As the specialized, fused style morphology is shared among all the members of the genus, it is unlikely that other pollination systems exist in the genus. There is considerable variation in the shape of female flowers among different *Glochidion* species (Fig. 4.23). Although the reason for this variation is unknown, morphological differences may partly facilitate host recognition by ovipositing *Epicephala* females. Even greater variation is found in the fruit size and the number of locules per fruit, which should have major consequences on the proportion of seeds consumed by larvae. Some *Glochidion* species, such as *G. littorale*, have fruits exceeding 2 cm in diameter, each containing >20 seeds. There may be selection on *Glochidion* plants to produce larger fruits and more seeds per fruit to escape seed

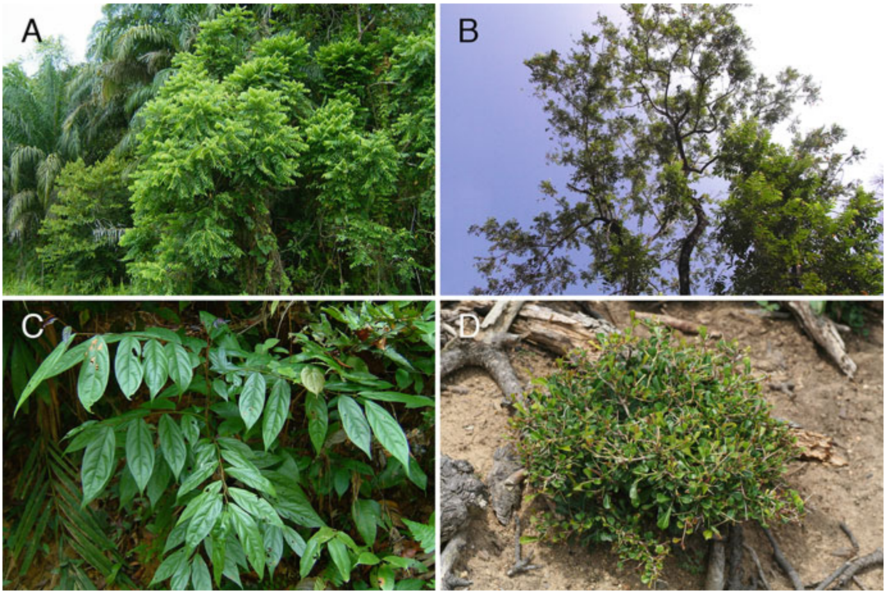

Fig. 4.22 Genus *Glochidion*. (**a**) *G. sumatranum* on forest edge of lowland rainforest in Malaysia. (**b**) Canopy-reaching tree of *G. philippicum* in Taiwan. (**c**) Forest floor shrub of *G.* sp. in lowland rainforest in Malaysia. (**d**) Thorny young plant of *G. obovatum* in temperate Japan

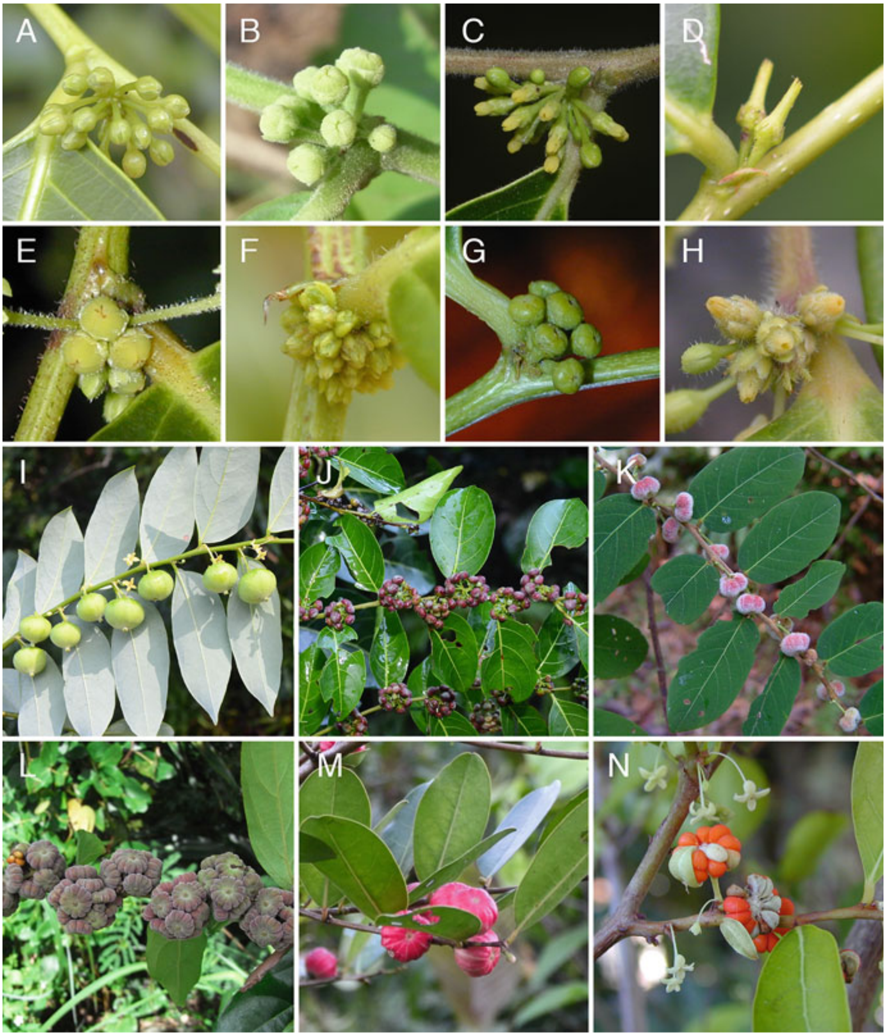

Fig. 4.23 Flowers and fruits of *Glochidion*. (**a**–**h**) female flowers: (**a**) *G. lanceolatum* (Japan); (**b**) *G. philippicum* (Taiwan); (**c**) *G. sumatranum* (Sarawak, Malaysia); (**d**) *G. ferdinandii* (Sydney, Australia); (**e**) *G.* sp. (Laos); (**f**) *G.* sp. (Laos); (**g**) *G. sphaerogynum* (Vietnam); (**h**) *G.* sp. (Laos). (**i**–**m**) fruits: (**i**) *G. obscurum* (Sarawak, Malaysia); (**j**) *G. arborescens* (Sarawak, Malaysia); (**k**) *G. sericeum* (Sarawak, Malaysia); (**l**) *G. philippicum* (Taiwan); (**m**) *G. littorale* (Sarawak, Malaysia). Photographs (**i**–**m**) are in approximately the same scale. (**n**) *G. rubrum* fruit (Japan) showing dehisced capsule and seeds with orange sarcotesta

predation by *Epicephala* larvae. However, if *Glochidion* fruits evolve to become larger, the moths may adapt by laying more eggs per flower to consume a greater proportion of the seeds available. Therefore, it is interesting to examine whether such coevolutionary escalation is the cause of the large variation in fruit size among *Glochidion* species.