6 Diversity, Phylogeny and Classification of *Clusia*

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6.1 Taxonomic Position and Delimitation

Clusia L., with over 300 species, is one of the largest genera of the Clusiaceae (Guttiferae). According to a recent classification system (Stevens 2005), the family comprises the subfamilies Clusioideae and Kielmeyeroideae. In earlier classifications it has often also included *Hypericum* L. and related genera, the Hypericoideae (Engler 1925; Thorne 1976 [using the name Hypericaceae]; Cronquist 1981). There is, however, growing evidence that the Hypericoideae do not form a monophyletic group with other Clusiaceae (Gustafsson et al. 2002; Davis et al. 2005), and in, e.g., the classification system by P. F. Stevens (Stevens 2006), they are treated as a separate family, Hypericaceae. In the following, the name Clusiaceae is therefore used in the narrow sense, excluding *Hypericum* and its relatives.

Clusiaceae comprises two well-defined monophyletic subfamilies, Kielmeyeroideae and Clusioideae. The type genus *Clusia* itself obviously belongs to the subfamily Clusioideae, and tribe Clusieae. The latter is a well-supported, strictly Neotropical group characterized by opposite entire leaves (like the whole subfamily Clusioideae), absence of bud-scales, predominant dioecy, non-fasciculate androecia and fleshy capsules with arillate seeds (Engler 1925; Stevens 2006). Apart from *Clusia*, the largest genus in the tribe, generic delimitation is somewhat problematic. Commonly recognized are *Tovomita* Aubl. (ca. 25 species), *Chrysochlamys* Poepp. (ca. 55 spp.), *Dystovomita* D'Arcy (4 spp.), and sometimes also *Tovomitopsis* Planch. et Triana (2–3 spp.). The sister-group of *Clusia* is to be found among these genera, but still has not been identified with certainty.

Recently, several small genera have been found to have phylogenetic positions nested inside *Clusia*, i.e. *Decaphalangium* Melchior (1 sp.), *Havetia* Kunth. (1 sp.), *Havetiopsis* Planch. et Triana (7 spp. or, more likely, less), *Oedematopus* Planch. et Triana (ca. 15 spp.), *Pilosperma* Planch. et Triana (1 sp.) and *Quapoya* Aubl. (7 spp.). This is based both on morphological cladistic

analyses (Stevens 2006) and molecular studies (all genera except *Pilosperma* sampled; Gustafsson and Bittrich 2003 and unpublished). Most of the necessary recombinations have already been made (Pipoly 1997; Pipoly and Cogollo 1998). The resulting *Clusia* sensu lato is a well supported taxonomic unit, both based on molecular evidence (Gustafsson and Bittrich 2003) and morphology, although it is difficult to point at an uncontradicted morphological synapomorphy for the genus. Most consistent is probably seed length, which is 5 mm or less in *Clusia* while mostly 10 mm or more in other genera of Clusieae. The aril of the seed in these genera is usually vascularized, a condition not seen in *Clusia*. Another synapomorphy with very few, if any reversals, is the presence of a two- to many-layered hypodermis in the leaves (Vesque 1892). Characters occurring in most but not all *Clusia* species, while very rare or absent from the related genera, include hemi-epiphytic life form, long aerial adventitious roots (*Tovomita* has stilt roots, but not long aerial roots), coriaceous-subcarnose leaves with obscure venation, and fruits with more than one seed per carpel.

6.2 Molecular Phylogenetics

In recent years, several widely sampled phylogenetic studies of *Clusia* have been published (Vaasen et al. 2002; Gehrig et al. 2003; Gustafsson and Bittrich 2003). All of these studies have used ITS (Internal Transcribed Spacer, in nuclear ribosomal DNA) sequences for the phylogenetic reconstruction. The number of published ITS sequences of this region for *Clusia* now exceeds 120. Plastid DNA variation has also been investigated (Hale et al. 2004), but all four regions sequenced showed very low levels of variation. ITS is more variable and has proved to be rather informative regarding the interrelationships within *Clusia*.

6.2.1 Combining Published ITS Sequences in a New Analysis

For the present review, ITS sequences published by Gehrig et al. (2003) and Gustafsson and Bittrich (2003) were analyzed together. Outgroups from outside of tribe Clusieae (10 terminals in all), as well as one poor, incomplete sequence of *Chrysochlamys* (GenBank number AY145241), and a highly divergent sequence of *C. sipapoana* (Maguire) Pipoly (AJ312562), were excluded, and the number of samples per species was reduced to one. The remaining 99 sequences were aligned using the program DIALIGN (Morgenstern 1999). The resulting data matrix (indels were not coded) was analyzed cladistically, using PAUP 4b10 (Swofford 2002). A heuristic tree search was performed, and aborted when 130,000 most parsimonious trees (1135 steps, CI=0.47, RI=0.78)
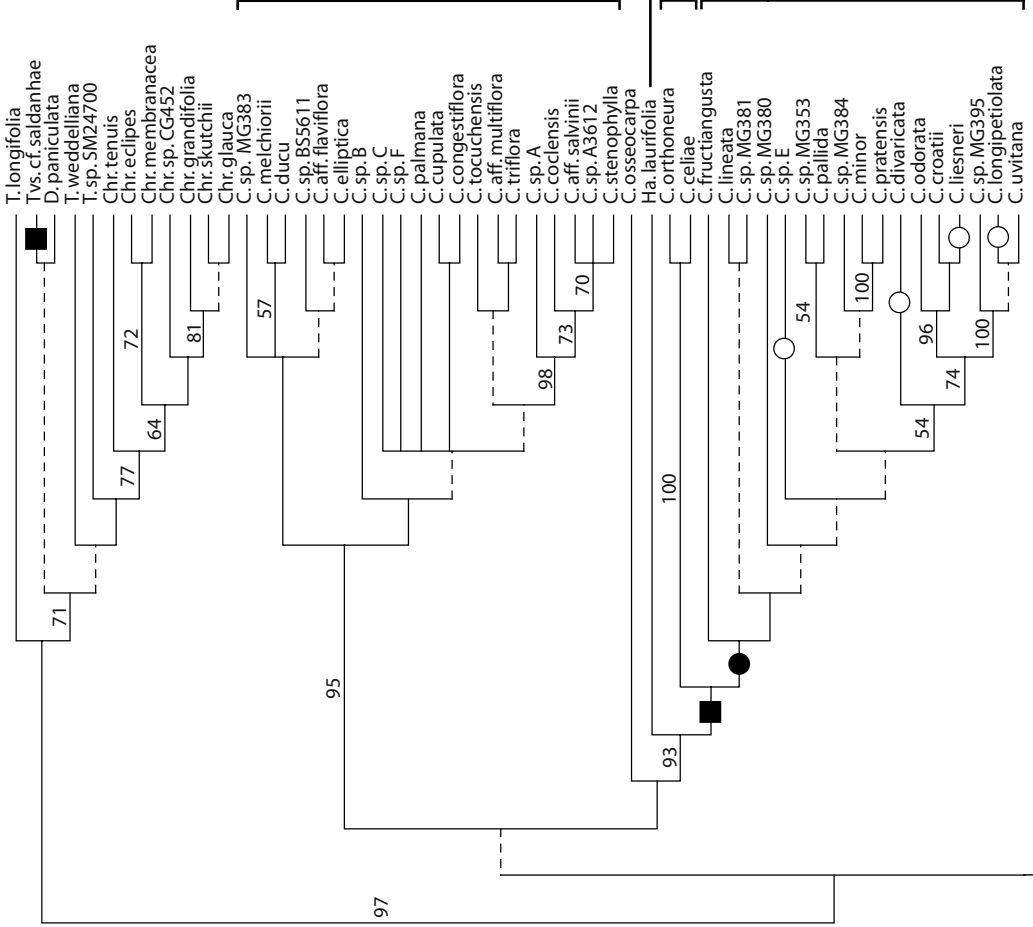
had been found. A jackknife analysis was also performed, as described by Gustafsson and Bittrich (2003). Figure 6.1 shows a single most parsimonious tree, indicating which branches are absent in the strict consensus tree and which have jackknife support.

6.2.2 Character Optimizations

Two characters were optimized onto the selected tree (Fig. 6.1) using Mac-Clade 4.02 (Maddison and Maddison 2001) and PAUP 4b10: resin production in flowers, and CAM photosynthesis.

In the case of resin production the knowledge is fairly complete, as the character is easily observed even on herbarium specimens, and can sometimes be deduced from species descriptions. For most taxa not included by Gustafsson and Bittrich (2003), descriptions in Flora of Panama (D'Arcy 1980) and herbarium specimens were consulted.

Knowledge about the type of photosynthesis is far more patchy, and for many species a question mark had to be entered. None of the outgroup species have been investigated in this respect. In one optimization they were honestly coded as unknown, in another (shown in Fig. 6.1) they were assumed to lack CAM. Information was extracted from Tinoco Ojanguren and Vàzquez-Yanes (1983), Ting et al. (1985), Franco et al. (1990, 1992, 1994, 1996), Borland et al. (1992, 1998), Winter et al. (1992), Roberts et al. (1997), Lüttge (1999), Herzog et al. (1999), and Holtum et al. (2004). Species coded as "CAM present" are those with $\delta^{13}C$ values (see Sect. 8.2) less negative than –20‰, which is indicative of strongly expressed CAM (as seen in, e.g., *C. flava* Jacq., *C. hilariana* Schltdl., *C. fluminensis* Planch. et Triana, *C. major* L., *C. rosea* Jacq., and *C. uvitana* Pittier), and species with $\delta^{13}C$ more negative than –20‰ yet exhibiting nocturnal increases in tissue acidity indicative of weakly expressed CAM (*C. aripoensis* Britton, *C. croatii* D'Arcy, *C. cylindrica* Hammel, *Havetiopsis flexilis* Planch. et Triana=*C. flavida* (Benth.) Pipoly, *C. fructiangusta* Cuatrec., *C. lanceolata* Cambess., *C. lineata* Planch. et Triana, *C. minor* L., *C. odorata* Seem., *C. pratensis* Seem., *C. quadrangula* Bartlett, *C. valerioi* Standl., *C.* sp. D). Species coded as "CAM absent" have $\delta^{13}C$ values normally associated with C_3 photosynthesis (more negative than –20‰) and no evidence of nocturnal increases in tissue acidity (*C. coclensis* Standl., *C. cupulata* Maguire, *C. divaricata* Maguire, *C. liesneri* Maguire, *C. longipetiolata* Schery, *C.* aff. *multiflora*, *C. osseocarpa* Kunth, *C. palmana* Standl., *C. stenophylla* Standl., *C. torresii* Standl., *C.* sp. A, *C.* sp. E), or in which nocturnal levels of tissue acidity have not yet been studied (*C. amazonica* Planch. et Triana, *C. columnaris* Engl., *C. congestiflora* Cuatrec., *C. grandiflora* Splitg., *C. nemorosa* G. Mey., *C. triflora* Cuatrec., *C. salvinii* Donn. Sm., *C.* sp. B, C, F). Although the latter category is currently considered to be C_3, it cannot be excluded that future measurements of tissue acidity may reveal weakly expressed CAM in some of these species.

sect. Clusiastrum

sect. Cordylandra

the flava-group

the Omphalanthera complex

sect. Phloianthera

sect. Chlamydoclusia

sect. Androstylium

sect. Criuvopsis

sect. Criuva

sect. Oedematopus

C. clusioides
C. pusilla
C. burchellii
C. weddelliana
C. diamantina
C. spiritusanctensis
C. aff. pernambucensis
C. fluminensis
C. leprantha
C. panapanari
C. renggerioides
C. paralicola
C. quadrangula
C. sp. D
C. torresii
C. flava
C. scrobiculata
C. columnaris
C. schomburgkiana
C. favum
C. gardneri
C. valerioi
C. major
C. aripoensis
C. hilariana
C. lanceolata
C. mexiensis
C. studartiana
C. viscida
C. insignis
C. rosea
C. platystigma
C. grandiflora
C. palmicida
C. nemorosa
C. fockeana
C. amazonica
Q. sp. MG386
Q. peruviana
C. criuva
C. burlemarxii
C. gundlachii
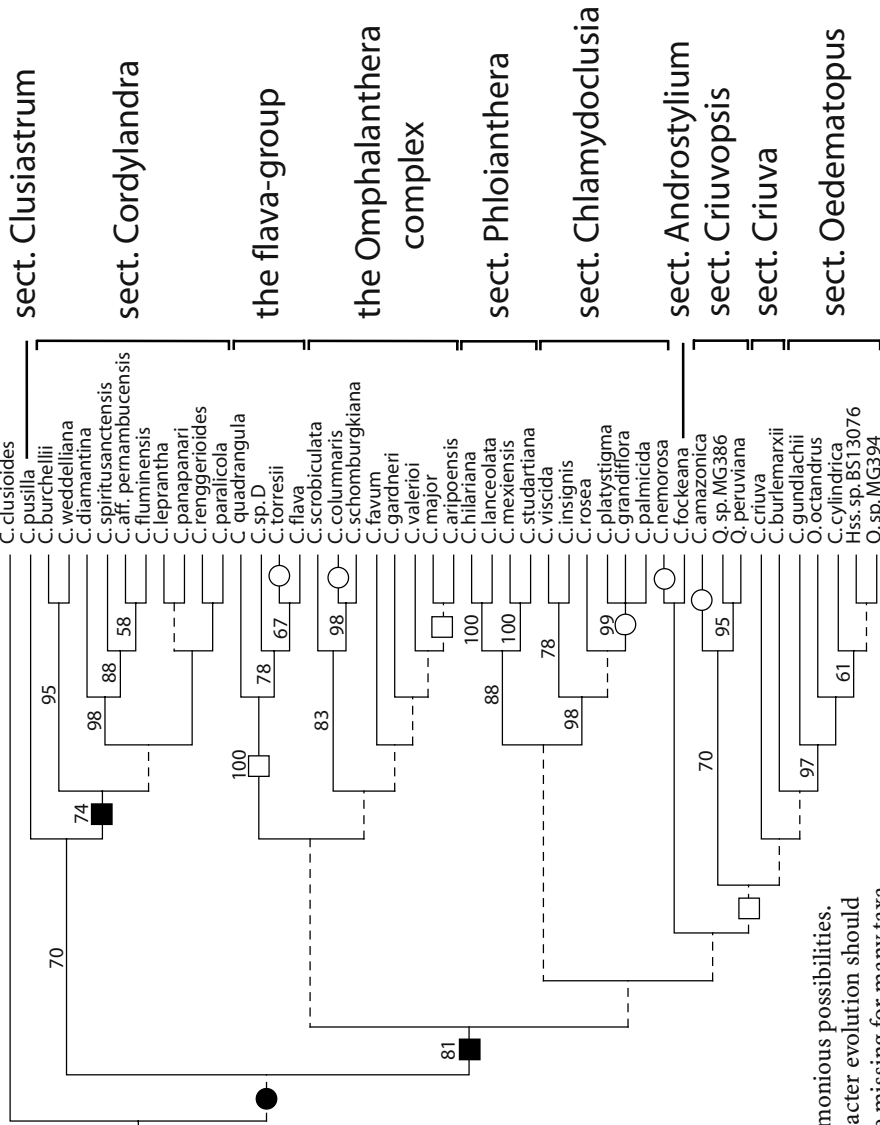O. octandrus
C. cylindrica
Hss. sp. BS13076
O. sp. MG394

Fig. 6.1. One of many most parsimonious trees based on published ITS sequences of *Clusia*, with outgroups from other genera of the tribe Clusieae. Abbreviations: C.=*Clusia*, Chr.=*Chrysochlamys*, D.=*Dystovomita*, Ha.=*Havetia*, Hss.=*Havetiopsis*, O.=*Oedematopus*, Q.=*Quapoya*, T.=*Tovomita*, Tvs.=*Tovomitopsis*. *Dashed branches are absent in the strict consensus tree. Numbers above branches are jackknife support values. The evolutionary history of two characters, reconstructed through parsimonious character optimization, are shown on the trees. Squares show* the evolution of resin pollination (*black box*=gain, *white box*=loss), and *circles* represent CAM photosynthesis (*black*=gain, *white*=loss). In both cases, the reconstruction shown is one of several, equally parsimonious possibilities. In the case of CAM the model of character evolution should be considered preliminary, as data are missing for many taxa, and given that for many of the species coded as "CAM absent" this is based solely on $^{13}C/^{12}C$ ratios (meaning that weak CAM cannot be excluded with certainty; see text)

For each of the two characters, one optimization was selected from several, equally parsimonious possibilities (Fig. 6.1). For the resin-optimization, a scenario intermediate between ACCTRAN and DELTRAN (Swofford 2002) was selected. A "pure" ACCTRAN optimization is very similar, but shows only two origins (with a common origin for *Cordylandra* and subg. *Clusia*; with reversal in *C. pusilla*). Independent origin of resin in *Cordylandra* was considered more plausible given its chemical and physical peculiarities. A DELTRAN model would entail five origins (independently in the *Omphalanthera* complex, *Phloianthera* plus *Chlamydoclusia*, and the *C. fockeana* – *C. nemorosa* clade). The close morphological similarity between *C. nemorosa* and sect. *Chlamydoclusia* makes an independent origin of resin in these taxa seem unlikely.

In the case of CAM photosynthesis, a DELTRAN optimization was chosen. The ACCTRAN alternative is similar, but the whole clade *C. scrobiculata-columnaris-schomburgkiana* (Planch. et Triana) Benth. ex Engl. shows a reversal, and the clade *C. nemorosa* through *Havetiopsis* shows reversal with regain (considered a less plausible complexity) in the clade *C. criuva* through *Havetiopsis*. In Fig. 6.1, outgroups were assumed to lack CAM. If outgroups are coded as unknown with respect to CAM photosynthesis, the number of ambiguous branches increases, but the optimization shown in Fig. 6.1 is still valid (representing one of many maximally parsimonious solutions).

6.3 Species Diversity and Distribution

At the species level *Clusia* must be considered poorly known, at least in parts of its distribution area. Around 300 species are recognized presently (Pipoly et al. 1998), but as many as 100 species may remain to be described, many of which occur in the Andes.

The total distribution for the genus only slightly extends north and south of the tropics (Fig. 6.2). The northern limit is the Bahamas (*Clusia rosea* Jacq.), and to the south it reaches the state of Rio Grande do Sul, Brazil (*Clusia criuva* Cambess.). Species diversity is very unevenly distributed (Fig. 6.2), being highest in areas such as the Northern Andes, the Amazonian lowlands east of the Andes, the Pacific lowlands from NW Ecuador to Panama, and the Guayana Highlands. Least diversity is seen in the peripheral parts of the distribution area, in particular the Caribbean Islands (four species in Puerto Rico), Mexico and Southern Brazil (only *C. criuva* reaches south of the Tropic of Capricorn). The altitudinal range is from near sea level (e.g. *Clusia rosea* and *C. hilariana* Schltdl., in the Caribbean and SE Brazil respectively) to at least 3500 m altitude (*Clusia frigida* Cuatrec. from the Andes of Colombia).

Fig. 6.2. Distribution map for *Clusia*. Estimates of species number are given for individual countries (and for Hispañola and the Lesser Antilles). Numbers are based on field- and herbarium studies and information from flora treatments, taxonomic revisions and checklists such as those by D'Arcy (1980), Liogier (1983), Pipoly et al. (1998), Jørgensen and León-Yánez (1999), and Hammel (2001). The map shows the approximate limits of the distribution; *Clusia* is absent from some regions within the *shaded area*, such as parts of the high Andes

6.4 Habitats and Habits

Habitats vary considerably, and include wet lowland forests, montane forests, paramo, open low forests on coastal sands ("restingas" of Brazil), dry scrub in interandean valleys, and sandstone and granite rocks (Sect. 9.1). *Clusia* species may be early colonizers (and more or less weedy), particularly on various nutrient poor soils, such as laterite or leached sand.

In lowland forests, most species grow predominantly as hemi-epiphytes in the form of shrubs or less commonly trees or climbers (Sect. 2.4). Hemi-epiphytes begin their life as true epiphytes up in a tree, and eventually establish contact with the ground by means of adventitious roots. Eventually, the

adventitious roots may completely surround and encircle the "host" tree, which may die as a result. The life-history of these hemi-epiphytes becoming stranglers is remarkably similar to that of many species of *Ficus*, the well-known strangler figs.

In disturbed habitats in lowland rainforest, particularly on nutrient-poor soils such as in white-sand areas, the same species that grow as hemi-epiphytes in intact forest may be found growing as free-standing trees and shrubs. In montane forests and various open habitats, the growth form is commonly small trees or shrubs.

6.5 Morphological Diversity

Clusia is remarkably variable in floral morphology, as can be seen at a glance from Figs. 6.3–6.32, and the illustrations in Engler (1925) and Gustafsson and Bittrich (2003). The variation concerns size, degree of fusion and number of floral parts, morphology of individual organs, and the overall organization of the flower, such as the position of staminodes (central or peripheral) relative to functional stamens, and presence or absence of a pistillode in the male flowers.

Some species have a highly peculiar stamen morphology, with many unique traits. Often, stamens are fused into synandria of varying shape (Figs. 6.5, 6.7, 6.10, 6.12, and 6.13). This is particularly common in species that offer resin as a pollinator reward (see below), in which case the resin is produced in the androecium. In staminate flowers of some species, there is a clear division of labour between resiniferous staminodes and fertile, pollen-producing stamens (Figs. 6.10 and 6.11), while in other cases resin is produced by the fertile stamens (Figs. 6.5, 6.7, and 6.8). Anther morphology is often modi-

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Figs. 6.3–6.17. Flowers of *Clusia*. ∅=diameter of flower. **6.3–6.14** Staminate flowers of *Clusia*: **6.3** *C. ducu* Benth. (sect. *Anandrogyne*), ∅ 1.2 cm; **6.4** *C. orthoneura* Standl. (sect. *Cochlanthera*; photo by G. Gehrlach), ∅ 5 cm; **6.5** *C. fructiangusta* Cuatrec. (sect. *Retinostemon*), ∅ 2.5 cm; **6.6** *C. pusilla* Steyermark (sect. *Clusiastrum*, photo by H. Balslev), ∅ 5 cm; **6.7** *C. leprantha* Mart. (sect. *Cordylandra*), ∅ 5.5 cm; **6.8** *C. schomburgkiana* (Planch. & Triana) Benth. ex Engl. (the "*Omphalanthera* complex"; photo by H. Balslev), ∅ 4 cm; **6.9** *C. major* L., sect. *Clusia* (part of the "*Omphalanthera* complex"; photo by A. Sloth), ∅ 2.5 cm; **6.10** *C. lanceolata* Cambess. (sect. *Phloianthera*), ∅ 3.5 cm; **6.11** *C. grandiflora* Splitg. (sect. *Chlamydoclusia*), ∅ 13 cm; **6.12** *C. fockeana* Miq. (sect. *Androstylium*), ∅ 2.7 cm; **6.13** *Quapoya* sp. (sect. *Criuvopsis*), ∅ 1 cm; **6.14** *Oedematopus* sp. (sect. *Oedematopus*), ∅ 7 mm. **6.15–6.17** Pistillate flowers of *Clusia*: **6.15** *C. ducu* (sect. *Anandrogyne*), ∅ 8 mm; **6.16** *C. fructiangusta* (sect. *Retinostemon*), ∅ 2.5 cm; **6.17** *C. amabilis* Maguire (sect. *Clusiastrum*), ∅ 5 cm

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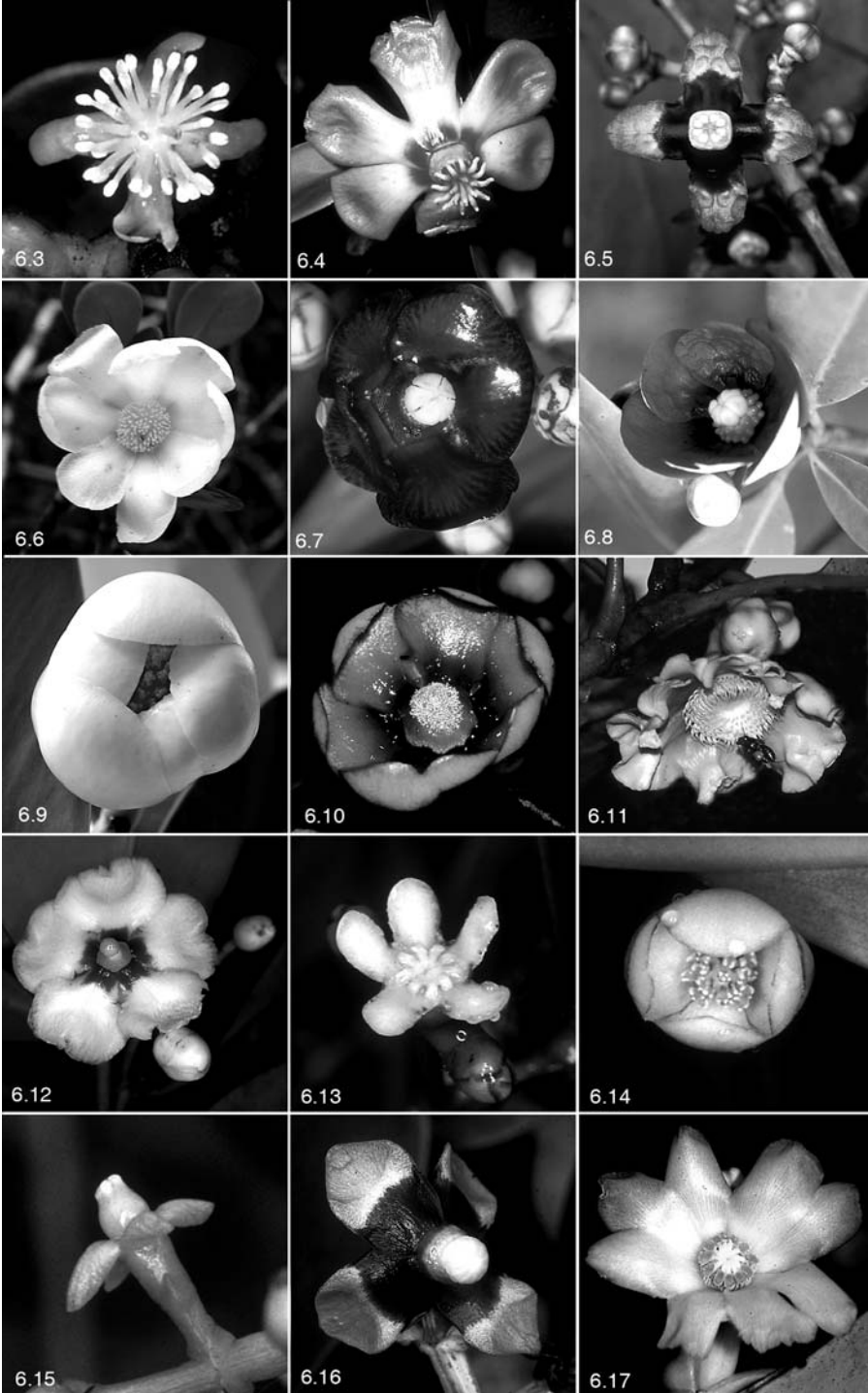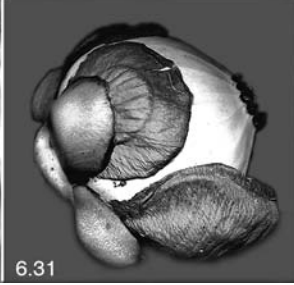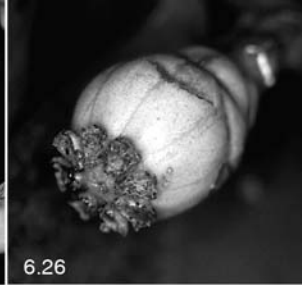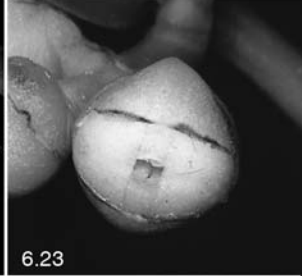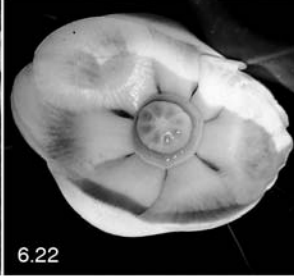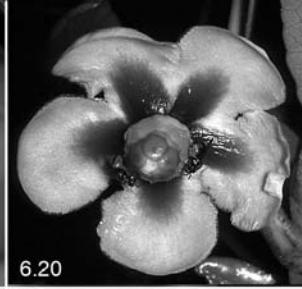
fied to a degree that it is difficult to recognize what represents an individual anther or theca (e.g., Figs. 6.5 and 6.12). Good examples of this are *C. schomburgkiana* and *C. columnaris* Engl., whose bizarre staminal morphology and pollination mechanisms were described by Bittrich and Amaral (1996). In contrast to the apparently fundamental differences in staminal morphology, molecular studies (Gustafsson and Bittrich 2003) have shown that the two species are almost identical in investigated DNA sequences (ITS), and it can be concluded that the morphological differences must have evolved rapidly.

In other floral traits, differences between *Clusia* species are less extreme, but still considerable. Flower diameter varies from ca. 0.5 to around 15 cm. Sepal number is variable and sometimes difficult to determine, as sepals often intergrade with bracteoles. Petals number from four to nine, and their colour can be white to yellow or green, pink to dark red or almost black. The ovary consists of 4–21 carpels, with sessile stigmata (Figs. 6.24, 6.26–6.32), or rarely with short styles (as long as the ovary in one unnamed species from the Andes of Ecuador; Fig. 6.25).

The fruit is invariably a fleshy, thick-walled, septifragal capsule, varying in size from pea to orange (Figs. 6.24–6.32). The number of seeds varies from one (Fig. 6.24) to many (Figs. 6.27 and 6.28) per carpel. Seeds are surrounded by an orange-coloured aril, which is very variable in morphology (Engler 1925). Endosperm is absent at maturity. The embryo is green and consists almost entirely of hypocotyl. Germination begins with elongation of the hypocotyl, and only later do the minute cotyledons expand.

In vegetative characters variation must be said to be moderate, at least compared to the situation for floral morphology, but leaf shape, presence of petiole, latex colour, distribution and morphology of laticiferous ducts in leaves are all variable characters useful for species identification, and sometimes for recognizing larger clades.

Figs. 6.18–6.32 Flowers and fruits of *Clusia*. ∅=diameter of flower or fruit. **6.18–6.23** Pistillate flowers of *Clusia*: **6.18** *C. leprantha* (sect. *Cordylandra*; one petal bent down), ∅ 6 cm; **6.19** *C. major* (sect. *Clusia*, part of the "*Omphalanthera* complex"; photo by A. Sloth), ∅ 2.5 cm; **6.20** *C. columnaris* Engl. ("*Omphalanthera* complex"), ∅ 3.5 cm; **6.21** *C. studartiana* C.M. Vieira & A.G. da Silva (sect. *Phloianthera*), ∅ 3 cm; **6.22** *C. rosea* Jacq. (sect. *Chlamydoclusia*), ∅ 9 cm; **6.23** *Havetiopsis flexilis* Planch. & Triana (sect. *Oedematopus*), ∅ 4 mm. **6.24–6.32** Fruits of *Clusia*: **6.24** *C. ducu* (sect. *Anandrogyne*; open fruits on the left), ∅ 7 mm; **6.25** *C.* sp. (sect. *Anandrogyne*), ∅ 1.5 mm; **6.26** *C.* sp. (sect. *Retinostemon*; immature fruit), ∅ 2.2 cm; **6.27** *C.* sp. (sect. *Retinostemon*; open fruit), ∅ 5.5 cm; **6.28** *C. leprantha* (sect. *Cordylandra*; open fruit; photo by S. Mori), ∅ 4.5 cm (before opening); **6.29** *C. paralicola* (sect. *Cordylandra*), ∅ 3.5 cm; **6.30** *C. major* (sect. *Clusia*, part of the "*Omphalanthera* complex"; photo by A. Sloth), ∅ 3.5 cm; **6.31** *C. grandiflora* (sect. *Chlamydoclusia*), ∅ 7 cm; **6.32** *C. criuva* Cambess. (sect. *Criuva*), ∅ 1.2 cm

6.6 Ecophysiological Variation

As is thoroughly described in Chaps. 8 and 9 of this volume, the genus *Clusia* shows a remarkable diversity in photosynthetic physiology. It is the only truly arborescent genus for which CAM photosynthesis is known, and CAM, C_3-CAM intermediate and C_3 species have been described (Tinoco Ojanguren and Vásquez-Yanes 1983; Franco et al. 1990; Borland et al. 1992; Lüttge 1996, 1999). CAM may be strongly (e.g. *Clusia rosea*) or weakly expressed (e.g. *Clusia minor*), and some species show considerable plasticity in the expression of CAM in relation to plant developmental stage and environmental stress (Sects. 8.1, 9.2, and 9.4; Winter et al. 1992; Lüttge et al. 1993). CAM would appear to be highly adaptive for a rainforest hemi-epiphyte, which begins its life in a periodically very dry micro-habitat on a tree branch, and only later establishes contact with the soil, which ensures a reliable supply of water (Ting et al. 1987).

From the distribution of CAM photosynthesis within *Clusia*, it can be concluded that it has arisen several times independently (Gehrig et al. 2003). If the present optimization (Fig. 6.1) is accepted, there were two independent origins of CAM, one in sect. *Retinostemon*, and another in the ancestor of a group that comprises sect. *Cordylandra* and subgenus *Clusia*. The optimization shown in Fig. 6.1 suggests that there has been no less than nine reversals, which would mean that CAM photosynthesis is a strongly homoplasious character. In some of the species involved, photosynthetic pathway classification is based solely on $\delta^{13}C$ values. Hence, the number of reversals could markedly decrease once detailed studies on tissue acidity are available for all species.

With the present state of knowledge it appears that the occurrences of CAM in *Clusia* are phylogenetically isolated. CAM photosynthesis is absent from other genera of Clusiaceae, as far as is known. This is not surprising given that these comprise mostly terrestrial trees or shrubs in wet to mesic forest. Exceptions are *Clusiella* Planch. et Triana (hemi-epiphytic like *Clusia*) and *Kielmeyera* Mart. (xeromorphic terrestrial of open, dry habitats), both belonging to the subfamily Kielmeyeroideae, and species of *Rheedia* L. (subfamily Clusioideae, tribe Garcinieae) such as the highly xeromorphic *R. ruscifolia* Griseb. from Cuba. Representatives of the two latter genera have been investigated and were found not to have CAM (U. Lüttge et al., unpublished). No examples of CAM are known from the families most closely related to the Clusiaceae, i.e., the Hypericaceae, Podostemaceae and Bonnetiaceae, although the last two families have probably never been investigated in this respect, being aquatics and difficult to access, respectively.

Apart from CAM, *Clusia* also shows other adaptations to (temporarily) dry conditions that are not seen in related genera. Leaves are generally much thicker (Sect. , Tables 2.1 and 2.2), and the hypodermis is two- to many-lay-

ered (as opposed to single-layered) in almost all investigated *Clusia* species (Sect. 2.2, Table 2.2; Vesque 1892).

6.7 Variation in Biological Interactions

Pollination mechanisms, pollinator rewards and pollinators, are all remarkably diverse in *Clusia* (see Chap. 5). Pollinator rewards include nectar, pollen and resins. Floral resin is a rare type of pollinator reward, known only from a few angiosperm genera (Armbruster 1984; Gustafsson et al. 2002; Gustafsson and Bittrich 2003). Of these, three belong to tribe Clusieae: *Clusia* (around half of the species resiniferous, with three independent origins and three reversals according to Fig. 6.1), *Tovomitopsis* (at least 1 species out of 2 or 3), *Chrysochlamys* (at least 1 species, *C. tenuifolia* Cuatrec., out of 55; Hammel 1999). Floral resin is also found in all species of *Clusiella* (7 spp.) of subfamily Kielmeyeroideae. Outside of Clusiaceae it is only known from *Dalechampia* of the Euphorbiaceae. Chemically, the resins of *Clusia* and *Tovomitopsis* flowers consist largely of polyisoprenylated benzophenones, compounds also found in latex (Oliveira et al. 1996) and present in most if not all Clusiaceae. The resin is collected by bees that use it in nest construction (Bittrich and Amaral 1996, 1997) and in the defense of the nest. Flowers offering pollen may be pollinated by beetles (Rodrigues et al. 1993) or bees (Bittrich and Amaral 1996), and nectariferous flowers are visited also by flies and wasps (Gustafsson and Bittrich 2003), lepidoptera (W. S. Armbruster, personal communication) and hummingbirds (Dziedzioch et al. 2003).

The fleshy, brightly orange-coloured aril of *Clusia* is assumed to be an adaptation to dispersal by birds. In *Clusia criuva*, birds are primary dispersers, and seeds are secondarily dispersed by ants (Passos and Oliveira 2002). Arboreal and perhaps other mammals may also act as seed-dispersers (spider monkeys observed by M. v. Roosmalen, personal communication).

6.8 Phylogeny and Sectional Classification

Groups supported by the ITS data are in many cases easily identified based on morphological characters and have sometimes been recognized at the sectional level in previous classifications (Planchon and Triana 1860a, b; Engler 1925; Gustafsson and Bittrich 2003). Around ten such groups are fairly well supported (Fig. 6.1). Morphological synapomorphies for these groups typically concern the androecium, the stigma morphology, and sometimes also characters of the fruit and leaves (often venation and course of latex canals). At higher hierarchical levels, relationships are generally less well supported.

There are, however, a few exceptions. One is the moderately supported sister-group relationship between sects. *Clusiastrum* and *Cordylandra*. Another example is the fairly well-supported group referred to as subgenus *Clusia* (Gustafsson and Bittrich 2003) or "Group I" (Gehrig et al. 2003) (*C. quadrangula* and down in Fig. 6.1). There may also be some weak support (seen in, e.g., the analysis by Gehrig et al. 2003) for a largely Andean and Central American clade comprising the species-rich sections *Anandrogyne* Planch. et Triana and *Retinostemon* Planch. et Triana and a few additional small groups. This "Cordillera-clade" is present in the single mp tree shown in Fig. 6.1.

In the following, the more important subgeneric groups, mostly recognized at the level of section, will be briefly presented.

6.8.1 *Clusia* sect. *Anandrogyne* Planch. et Triana

This may be the most species-rich section in the genus (Pipoly 1995) (Figs. 6.3, 6.13, 6.24, and 6.25). Based on molecular data, it is well supported and distinct from other groups, but the differences in DNA sequence between the species are small (Gustafsson and Bittrich 2003; Frederiksen 2005). The same result was obtained by Gehrig et al. (2003) who referred to them as "Group III". Diversity thus appears to result from a fairly recent radiation. In spite of this recent origin, the group is quite variable, especially in size and shape of flowers, fruits and leaves (Pipoly 1995; Gustafsson and Bittrich 2003; Frederiksen 2005). Stamens are numerous and almost always free (Fig. 6.3). There are usually 4–6 carpels with thick and angular stigmata that are sometimes borne on short styles (Fig. 6.25). Latex canals are often evident on the lower (abaxial) side of the leaves, as darker lines. Pollination biology is very poorly known, but based on scattered field observations, it appears that most species are either nectariferous, or produce copious amounts of pollen, indicating that these may be the pollinator rewards. Floral resin is, as far as is known, absent.

The distribution is predominantly Andean and Central American, with a few species in the Guayana Highlands and in Eastern Brazil. Most grow in montane forests, where they often form a significant component of the vegetation. The altitude record for the genus is held by a member of this section, and above ca. 2500 m no other *Clusia* (or Clusiaceae) occur. Most species are terrestrial and grow in moderately to very wet habitats. Although many species in this section have been investigated (Gehrig et al. 2003; Holtum et al. 2004; K. Winter, unpublished), in none of them has the presence of CAM photosynthesis been conclusively demonstrated. There are indications of CAM activity in *Clusia tocuchensis* Britton (Borland et al. 1992) but further studies are needed to confirm CAM in this species. In the scenario of CAM evolution presented here, the absence of CAM in sect. *Anandrogyne* is plesiomorphic. In the study by Gehrig et al. (2003), CAM seems to have been secondarily lost in

this group, but this is likely an effect of the smaller and geographically biased taxon sample, which primarily comprised Panamanian species.

   Clusia clusioides (Griseb.) D'Arcy, a species from the Greater Antilles that has been included in sect. *Anandrogyne* based on morphological characters (Engler 1925), has been shown to have a more basal and isolated position in molecular phylogenies (Fig. 6.1; Gustafsson and Bittrich 2003). It would be interesting to investigate photosynthesis physiology of this species, as its near-basal position in the genus is probably of importance for the optimization of CAM on the basal node of the genus, i.e., for determining which photosynthesis mechanism was present in the most recent common ancestor of *Clusia*. Given that *C. clusioides* occurs as a terrestrial tree in wet montane forests, it seems unlikely that it would exhibit CAM.

6.8.2   *Clusia* sect. *Retinostemon* Planch. et Triana and Relatives

Like sect. *Anandrogyne*, *Retinostemon* (referred to as "Group II" by Gehrig et al. 2003) is a species-rich group centered in the Andes and Central America (Gustafsson and Bittrich 2003) (Figs. 6.5, 6.16, 6.26, and 6.27). It is notably absent from eastern and southern Brazil. It reaches around 2000 m altitude in the Andes and is quite frequent in montane forests, but also has many species in the lowlands. Representatives of this section are found in some of the driest habitats known for *Clusia*, interandean valleys in rainshadow. Both terrestrial and hemi-epiphytic life-forms are common. Laticifers are usually evident as thin, white lines on the adaxial surface of the leaves. Flowers offer resin as a pollinator reward, and male flowers usually have a fungiform, resin-producing synandrium, with scattered anthers on the distal surface. Female flowers secrete resin from a ring-shaped organ surrounding the ovary, as is also seen in several other sections (e.g. *Chlamydoclusia*). There are usually around eight carpels, and the stigmata can be described as flap-like (Fig. 6.26). The widespread, apomictic *C. minor* belongs to this section. Many species investigated have been shown to have CAM photosynthesis.

   Closely related to sect. *Retinostemon* are the small N. Andean sections *Havetia* (Kunth) Pipoly (one species) and *Cochlanthera* (Choisy) Engl. with seven species (Maguire 1977). *Havetia* appears as a miniaturized (in terms of flowers and fruits) member of sect. *Retinostemon*, while sect. *Cochlantera* is quite different in floral morphology (Fig. 6.4), especially the staminate flowers, which have a resiniferous disk and large, curved anthers (Maguire 1977).

6.8.3   *Clusia* sect. *Clusiastrum* Planch. et Triana

This small (ca. 10 spp) and distinctive section is restricted to the Guayana shield, where the species grow as shrubs in open habitats (Figs. 6.6 and 6.17).

The group can easily be recognized by the bent, short styles and numerous carpels in female flowers (Fig. 6.17), and the dehiscence of the anthers in male flowers, which is by short slits or pores. The pollinators are large bees that vibrate the androecium with their indirect flight muscles which causes the pollen to be released (buzz pollination; Bittrich and Amaral 1996). Representation in molecular studies is poor, but available evidence indicates that it may be the sister-group of sect. *Cordylandra*, from which it differs strongly morphologically. It has so far not been sampled in studies of photosynthesis, but would be highly desirable to include given its phylogenetic position.

6.8.4 *Clusia* sect. *Cordylandra* Planch. et Triana

Most species of sect. *Cordylandra* occur in Eastern Brazil and the Amazon, and the group is, as far as known, absent from the Andes and Central America (Figs. 6.7, 6.18, 6.28 and 6.29). The total number of species known is 17 (P. F. Stevens, V. Bittrich and M. H. G. Gustafsson, revision in preparation). The section is well supported both by molecular and morphological synapomorphies. The sister-group relationship to subgenus *Clusia* (sensu Gustafsson and Bittrich 2003) is not well supported, and the group should perhaps be treated in a subgenus of its own, maybe together with sect. *Clusiastrum*. The mostly five stigmata are covered with acute papillae (unique in the genus), and form a "crown" on the fruit (Fig. 6.29; Bittrich and Amaral 1997; P. F. Stevens in unpublished manuscript). Bracts, bracteoles and sepals are caducous. The endocarp of the fruit is bony, with transversal ridges. The stamens are short and stout (Fig. 6.7) and invariably produce resin, which in male flowers is more fluid than in other *Clusia* species and mixed with pollen.

   Clusia fluminensis Planch. et Triana, from the restingas in southeastern Brazil, is reported to have CAM photosynthesis, and recently CAM has been found to occur also in *C. spiritu-sanctensis* G. Mariz et B. Weinberg (Sect. 9.4.2.10).

6.8.5 *Clusia* sections *Clusia* and *Omphalanthera* Planch. et Triana, and Related Groups

The type species of *Clusia* is *C. major* L., a species from the Lesser Antilles (Bittrich and Stevens 1998; Figs. 6.8, 6.9, 6.19, 6.20, 6.30). It belongs to a small group of Caribbean and Central American species, which should be referred to as sect. *Clusia*. This is part of a diverse and poorly supported complex with somewhat uncertain interrelationships that comprises also sect. *Omphalanthera* Planch. et Triana, with peculiar ring-shaped anthers, which is closely related to sect. *Polythecandra* (Planch. et Triana) Engl., with equally peculiar

but rather different anthers, divided into numerous minute pollen sacs (Bittrich and Amaral 1996). Both groups occur mostly in the Guayana region. Here also belong some additional species with very varying floral morphology and geographical distribution, e. g. *C. gardneri* Planch. et Triana, from Central Brazil, which was placed in its own section, *Gomphanthera* Planch. et Triana, on account of its unique, irregularly dehiscent anthers (Engler 1925), which in other respects are similar to those of *C. schomburgkiana*. Like the floral morphology, the pollination mechanisms are quite variable. Three species in the complex, *C. aripoensis*, *C. major* and *C. valerioi*, are known to have CAM photosynthesis.

Related to the *Omphalanthera* complex is what could be referred to as the flava-group, comprising a few species from Central America and Jamaica. These species all lack resin and are similar in floral morphology to sect. *Oedematopus* (Planch. et Triana) Pipoly, having bud-like flowers with four thick petals. There are some indications that *C. flava* Jacq. (a CAM species) is beetle pollinated (Hammel 1986). It should be pointed out that the "flava-group" of Hammel (1986) also included species here assigned to sect. *Oedematopus*.

6.8.6 *Clusia* sect. *Phloianthera* Planch. et Triana

This is a mostly Eastern-Brazilian group comprising around 10 species (Figs. 6.10 and 6.21). Several North Andean and Amazonian species have also been ascribed to it, although they differ in aspects of androecial morphology. So far, only Eastern Brazilian species have been sampled in molecular studies. There is some weak evidence from molecular studies that the sister group is sect. *Chlamydoclusia*, but morphologically the two groups are strikingly different. In "typical" (Eastern Brazilian) members of the section, the androecium is dome-shaped, covered with numerous minute anthers, and surrounded by a ring of resiniferous staminodes (Fig. 6.10; Bittrich and Amaral 1997). Staminodes of pistillate flowers consist of several series of short, truncate, mostly ananterous, resiniferous staminodes (Fig. 6.21).

One member of this section, *C. hilariana*, is particularly well studied from the point of view of autecology and ecophysiology (Sect. 9.4.2.1.2). It exhibits CAM, and its role in the succession in the restingas of coastal South Brazil is addressed in Chap. 3.

Clusia fockeana Miq. is similar to sect. *Phloianthera* in its floral morphology, differing basically in that the fertile part of the androecium is borne on a "stalk" (Fig. 6.12). Although not supported as member of the section in the ITS phylogenies, *C. fockeana* is part of a clade comprising sects. *Phloianthera* and *Chlamydoclusia* in the most parsimonious tree shown in Fig. 6.1. Historically, it has been placed in its own section, *Androstylium* (Miq.) Engl.

6.8.7 *Clusia* sect. *Chlamydoclusia* Engl.

The most well-known member of sect. *Chlamydoclusia* is *Clusia rosea* (Figs. 6.11, 6.22, 6.31), a frequently cultivated species and a well-known CAM-plant. It is distributed around the Caribbean and throughout Central America, where it is particularly frequent in dry habitats near the sea. At least in most parts of its distribution area it is apomictic, a trait that has evolved repeatedly in the genus (also known in *Clusia minor* L. of sect. *Retinostemon*; Maguire 1976). Apart from *Clusia rosea*, the section comprises a handful of mostly Amazonian and Guayanan species, some of which are very widespread.

The flowers are some of the largest found in the genus, up to 15 cm across in *C. grandiflora* Splitg (Fig. 6.11). Staminate flowers are readily recognized on the androecium, with a central mass of resiniferous staminodes surrounded by basally fused fertile stamens with an apically prolonged connective that secretes tiny oil droplets. Fruits are also characteristic in having connivent stigmata forming a (in most cases) raised ring on the fruit (Fig. 6.31).

The delimitation of sect. *Chlamydoclusia* is somewhat problematic as one species, *C. nemorosa*, shares with sect. *Chlamydoclusia* both the characteristic organization of the androecium, the typical connective and the fruit shape, while there is no support in the ITS data for its inclusion in the section (neither is it strongly contradicted).

6.8.8 *Clusia* sect. *Oedematopus* (Planch. et Triana) Pipoly, and Relatives

Sections *Oedematopus* and *Criuvopsis* are closely related (Figs 6.13, 6.14, 6.23 and 6.32) according to molecular studies, and sections *Criuva* and *Brachystemon* may also be part of this clade (Fig. 6.1). Parts of these sections were previously treated as separate genera, viz. *Quapoya* (Fig. 6.13), *Havetiopsis* (Fig. 6.23) and *Oedematopus* (Fig. 6.14); the old names are used in the figures. Shared characters include small flowers with few stamens (4 to ca. 20; more in sects. *Criuva* and *Brachystemon*), absence of floral resin and often thick, rubber-like, yellow to white petals. Sometimes (in sect. *Oedematopus*) the flowers, during anthesis, only open with a small apical pore and look rather bud-like (Fig. 6.23). The staminodes in the female flowers have sterile anthers and the filaments are dilated at base. The stigmas are densely papillose. Fruits are small with minute, widely spaced, round, ovate or elliptic stigmata (Fig. 6.32). The epidermis on the branchlets disrupts often in characteristic annular segments and the upper leaf epidermis shows a fine scrobiculate pattern in herbarium specimens. Most leaves are distinctly discolorous in vivo, the lower side being greenish-white due to air-filled achlorophyllous subepidermal layers. Life form is usually hemi-epiphytic (at least in *Oedematopus* and *Criuvopsis*) and there are several lianescent

species, particularly in sect. *Criuvopsis*. Most species occur in the Amazon region and Guayana.

6.9 Key Innovations in the Diversification of *Clusia*

If one were to point at the most characteristic and evolutionarily important traits of *Clusia*, they would most probably include resiniferous flowers, hemi-epiphytism, CAM photosynthesis and invasion of montane habitats.

Production of resin in the flowers has evolved no less than three times in *Clusia*, if the evolutionary reconstruction in Fig. 6.1 is accepted. All three origins optimize on deep branches, indicating that resin production is a relatively old phenomenon. In three of the four groups the trait is evolutionarily fixed. The relationship between presence of floral resin and speciation rate is not clear, as there are also species-rich groups (sect. *Anandrogyne*) that lack resin. It is very likely that it has been important to (at least it is correlated with) the floral morphological diversification, as resin-producing flowers are morphologically the most diverse, and show a number of odd and often unique traits. Some of these traits must, judging from the molecular phylogenies, have evolved relatively rapidly, as there may be radical differences between genetically very closely related species.

Clusia, together with *Clusiella* of Kielmeyeroideae (which curiously shares also the resin production in flowers), are the only Clusiaceae that have adopted a hemiepiphytic or lianescent growth form. The exact distribution in *Clusia* is difficult to map, as so many species are plastic in this respect, and may grow terrestrially opportunistically. The predominance of the hemi-epiphytic life form is particularly strong in wet lowland forests, and has evidently been crucial for the success (manifest in numbers of individuals) of *Clusia* in this habitat. Other genera of tribe Clusieae, among which is the sister-group of *Clusia*, are basically from the lowland tropical rainforests, a fact that, together with the widespread occurrence in this habitat by various clades of *Clusia*, suggests that this may have been the habitat of the *Clusia* ancestor, which may or may not have been hemi-epiphytic. *Clusia* may be somehow "predisposed" for the hemi-epiphytic lifestyle, through, e.g., the possession of numerous and smaller seeds than in the outgroups, and a double or multiple hypodermis that serves as an enlarged water storage tissue. Alternatively, these characters, with an evident adaptive value for an epiphyte, may have followed the evolution of hemi-epiphytism. Only careful studies, using character-optimization on well-sampled and well resolved phylogenies can reveal in which order these characters evolved.

Photosynthesis mechanisms have been studied only in a small fraction of *Clusia* species, and the role of CAM in the diversification of the genus is therefore hard to establish with certainty. The present optimization experiment

provides only a very preliminary model. There is no doubt, however, that the ability to perform CAM photosynthesis has been an important factor behind the proliferation of *Clusia* in (periodically) dry habitats (including micro-habitats in tree crowns where hemi-epiphytes often begin their lives), very different from the rainforest understorey where species of most other genera of tribe Clusieae are found.

Final among the assumed key innovations of *Clusia* is the invasion of the tropical montane habitat. No other Clusiaceae come close to the altitudinal limit of *Clusia* at over 3500 m (the closest is probably *Tovomita weddelliana* Planch. et Triana at around 1800 m). Two clades within *Clusia* have invaded high (over 2000 m) habitats, sect. *Anandrogyne* and sect. *Retinostemon*. Both, but particularly *Anandrogyne*, have undergone extensive speciation in the high altitude habitat. This could be referred to as a radiation, given the small genetic differences in combination with the large number of species.

The presence of all of these rare or unique innovations in a single genus, in combination with the evidently exceptionally variable floral morphology, makes it justified to speak of an extraordinary inherent evolutionary plasticity in *Clusia*.

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