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TABLE 4.1 Taxonomic Ranks and Standard Endings Used in Plant, Animal, and Fungi Kingdoms

Taxonomic level	Botanical endings	Zoological endings	Fungi endings
Phylum	-ophyta	NA	-mycota
Class	-opsida[1]	NA	-mycetes
Subclass	-idea[1]	NA	-mycetidae
Order	-ales	-ida or -iformes	-ales
Family	-aceae	-idae	-aceae
Subfamily	-oideae	-inae	-oideae
Genus	NA[2]	NA[2]	NA[2]
Species	NA[2]	NA[2]	NA[2]

NA indicates that there is not a standard ending for that taxonomic rank.
[1] After decades of use, these higher taxonomic ranks have fallen out of favor and are used infrequently.
[2] Generic and specific names are Latinized, so they must follow the rules of Latin grammar for their formation and agreement of the specific epithet with the genus name.

King Philip Came Over For Good Sex.) Each of these groups is known as a **taxon** (plural: taxa). This system is used throughout biology, regardless of whether you are talking about bacteria, fungi, plants, invertebrates, amphibians, reptiles, birds, mammals, or fishes. It has worked well for several hundred years, but recent advances in the analysis of gene sequences have necessitated the use of new terminology for groupings reflecting evolutionary relationships (**clades**). A clade is a group of species that share a common ancestor. Clades can be nested within larger clades. For example, all the genera of the Legume Family constitute a clade (and have pea pod fruits), all the genera of the Mimosa Subfamily constitute a clade (and have shaving brush flowers), and within the Mimosa Subfamily, all the species of *Inga* constitute a clade (and have compound leaves with suction-cup nectaries between the leaflets). Generic and specific names are always latinized, often from Latin or Greek roots. Often, the specific epithet indicates some descriptive feature of the organism in question, but it can also refer to a person being honored by the naming authority. Generic names may be descriptive or honorific. For example, the genus name of the tree *Warszewiczia coccinea* is named in honor of the Polish botanist and tropical explorer Józef Warszewicz, and *coccinea* refers to the scarlet of the enlarged sepals of this plant. For really large groups there are further subdivisions, such as tribe and subfamily. Those will be avoided as much as possible in this book. Each of the taxonomic ranks has a standard ending or suffix. As it happened, different fields of biology, such as botany, zoology, and mycology, were developed independently by scientists working in their own isolated silos. The result is that botanists and zoologists follow a similar hierarchy of large to successively smaller taxonomic ranks, but they use different standard endings. It is worth the effort to learn the taxonomic ranks and their standard endings as shown in Table 4.1. The rules for naming are published in official codes issued by each group, such as *The International Code of Nomenclature for Algae, Fungi, and Plants* and *The International Code of Zoological Nomenclature*. Congratulations if you are still reading! Please realize that this stuff is important. How can we begin to get a sense of the 10 million or more species that make up Earth's biological diversity if we can't first organize the species into similar groups? You need universally accepted rules and schemes for doing this. Hence, all the confusing names.

SORTING OUT CLASSIFICATION AND EVOLUTIONARY RELATIONSHIPS

The science of **taxonomy** is concerned with naming and identifying organisms, whereas the science of **systematics** aims to classify organisms based on their evolutionary histories and to formulate hypotheses about how species are related to one another. The scientists who carry out this work are usually one and the same, but taxonomy and systematics have slightly different goals. Making sense of the ways that taxonomists name and classify organisms is a daunting task, made increasingly difficult by baffling terminology, some of which is understood by only a few specialists; the frequency with which names are changed for seemingly obscure reasons;

and the inability of taxonomists to agree completely with one another. You may ask, "Why bother?" The ultimate goal is the reconstruction of the evolutionary history of organisms, the so-called "tree of life." This evolutionary history is properly called a **phylogeny**. Phylogenies are represented by diagrams known as **trees** (Fig. 4.1). The tips of the trees are species (or genera or families). The point where two branches diverge is a **node**. All of the taxa/species that radiate from a particular node make up a **clade**. All members of a clade are more closely related to one another, as a result of sharing a more recent common ancestor in their evolutionary history, than they are to members of other clades. Phylogenetic trees consist of groups of clades nested within one another or separated from one another. Charles Darwin was the first person to draw a phylogenetic tree as a representation of an evolutionary history showing species relationships. The discipline of **phylogenetics** has come a long way since Darwin sketched a crude drawing in one of his notebooks, but the overall goal of illustrating hypotheses about the relationships and evolutionary history of living organisms has not changed.

Phylogenies are hypotheses (testable scientific explanations) about evolutionary relationships and, as such, are constantly subject to testing and revision. Even with human history, for which we often have a written record and abundant artifacts, there is constant reinterpretation to eliminate previous bias and arrive at the true sequence of events and their interconnections. In flowering plants, the historical events took place over a period of approximately 125 million years, with many of the most important changes happening early in this history. Analysis of the history of life is based on the best data available. What is "best" changes as we develop a finer understanding of the data and, importantly, as we develop technological innovations that allow scientists to examine traits, such as DNA, that were previously unavailable for study. It is no wonder that taxonomy is constantly changing. These same principles and challenges exist no matter what phylum or taxon is being studied.

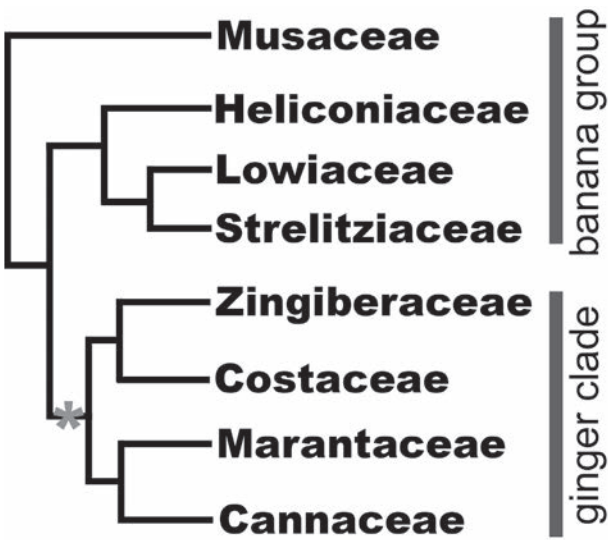

FIG 4.1 Phylogenetic tree showing the evolutionary relationships of families in the Ginger Order, Zingiberales (covered in chapter 10). The gray asterisk indicates evolutionary changes in flower morphology studied in the source article (Almeida et al. 2018). Note that Zingiberaceae, Costaceae, Marantaceae, and Cannaceae share a hypothetical common ancestor (the node by the asterisk) that is not shared by any of the other families. Therefore, they form a clade of closely related families.

TALKIN' 'BOUT A REVOLUTION (SONG TITLE BY TRACY CHAPMAN)

The science of naming and classifying living organisms is indeed in the midst of a revolution. Advances in molecular biology have made it relatively easy for scientists to isolate any organism's DNA and make copies of it in the lab (using thermocyclers and the polymerase chain reaction). With plenty of material to work with, scientists can then read the sequence of nucleotides, the letters that made up the DNA alphabet. Improvements in sequencing technology have made it increasingly easier to decipher the genetic alphabet of a piece of DNA or the entire genome of an organism. This alphabet (AGCT) contains the instructions for making the building blocks of living organisms and for regulating when proteins are made and in what quantities. We often refer to these instructions as genes. DNA also consists of regions that don't seem to code for anything, and these sections and the rates at which they change are useful to biologists. Closely related species will have similar DNA sequences, whereas more distantly related species will be less similar. These genetic traits are now the gold standard used in constructing hypotheses about evolutionary relationships and building phylogenetic trees. Powerful computers and complex algorithms enable scientists to analyze huge amounts of data fairly easily and to construct phylogenies depicting evolutionary history.

The revolution has supported many older ideas about evolutionary relationships. Early biologists working only with morphological traits that could be observed with the naked eye or with primitive microscopes proposed

relationships that have been supported by modern analyses. At the same time, many new relationships are emerging, resulting in the rejection of previously held ideas. The acceptance of new phylogenetic trees often necessitates changes to classification schemes and names that have been in use for more than a century. The rate of discovery and creation of new names is staggering. Many of the family, genus, and species names, as well as common names, used in this book are not the same as those used 10–50 years ago and will probably be different from the ones used in the future.

As a result of this molecular revolution, the names of species and their assignment to genera, families, and orders need to be updated to reflect what we now know to be the best representation of evolutionary relationships. There are sound biological reasons for making these changes, yet it is very frustrating to know that the things I learned in botany class as an undergraduate 40 years ago and what I taught my students just a few months ago are no longer valid. The monkey ladder liana is no longer in the genus *Bauhinia*; the Caesalpinioideae subfamily, where it has resided for more than 100 years, has been divided into a half-dozen new subfamilies. The Blue Jean Frog that I learned as *Dendrobates* is now in the genus *Oophaga* (Fig. 4.2). The bird that I first learned as Scarlet-rumped Tanager was split into two species, only for them to be lumped back together again a few years later. There are good reasons for these changes, but boy can they be frustrating. It is not uncommon to discover that what was once considered a single species with populations in Central America and South America is really two genetically isolated groups. At this point, these groups are determined to be two separate species, a process known as splitting. As a result of all this, it is nearly impossible to keep up with the numbers of species that inhabit a particular region and the various name changes. The numbers and names used in this book were correct at the time of publication, but they will soon become obsolete.

FIG 4.2 ***Oophaga pumilio*** was once known as *Dendrobates pumilio*. Comparisons of DNA and recognition of the unique way that females care for tadpoles necessitated the separation of certain species of poison dart frogs into the genus *Oophaga*.

CHAPTER 5

AN INTRODUCTION TO PLANTS

THEIR PLACE IN THE FOREST AND HOW THEY GROW

It seems rather silly to write a paragraph about how to see plants in a forest (Fig. 5.1). It is impossible not to see plants in a forest! And yet, sorting out individuals, matching trunks with leaves, assigning fallen flowers and fruits to their source plants, seeing the overall shape of the plant, and discerning individual species or families are exceptionally challenging. The first-time visitor can't help but be overwhelmed by the vastness of the rainforest, how green and shady it is, and how everything looks the same yet different at the same time. Dozens of visits later, those same feelings rush over me every time I enter the rainforest. So, how do you best begin to sort out the botanical components of the forest? The answers are the same regardless of what forest type you are visiting, just that it is much more complicated in a tropical forest.

FIG 5.1 Tall canopy tree with the rope-like roots of epiphytes hanging down from branches.

TABLE 5.1 Top Ten Plant Families at La Selva

Top 10 families of flowering plants		Top 10 tree families	
Family	**Species**	**Family**	**Species**
Orchidaceae Orchid Family	136	**Fabaceae Legume Family**	41
Fabaceae Legume Family	117	**Lauraceae Avocado Family**	24
Rubiaceae Coffee Family	109	**Rubiaceae Coffee Family**	22
Araceae Arum Family	106	**Euphorbiaceae Euphorb Family**	18
Piperaceae Pepper Family	84	**Annonaceae Soursop Family**	16
Melastomataceae Black Mouth Family	83	**Melastomataceae Black Mouth Family**	15
Poaceae Grass Family	79	**Arecaceae Palm Family**	13
Asteraceae Aster Family	58	**Moraceae Mulberry Family**	13
Euphorbiaceae Euphorb Family	45	**Meliaceae Mahogany Family**	10
Malvaceae Mallow Family	45	Sapotaceae Sapodilla Family	9

Flowering plant families containing the most species. Adapted from Hartshorn and Hammel (1994) and updated based on the Digital Flora of La Selva website (Castro 2013). The tree families have not been updated (Malvaceae would probably have earned a spot here). Boldfaced families are explored in the following chapters.

La Selva Research Station is home to more than 2,000 species of vascular plants, of which some 300 are trees (Hartshorn and Hammel 1994). The most species-rich families and genera are listed in Tables 5.1 and 5.2. In the following paragraphs, family names marked with an asterisk are explored in greater detail in the following chapters. Fifty common tropical plant families are described in Appendix 1.

TABLE 5.2 Top Ten Plant Genera at La Selva

Genus and family	Species
Piper (Piperaceae)	58
Miconia (Melastomataceae)	40
Philodendron (Araceae)	32
Psychotria (Rubiaceae)	26
Anthurium (Araceae)	25
Inga (Fabaceae—Mimosoideae)	23
Peperomia (Piperaceae)	20
Ficus (Moraceae)	17
Epidendrum (Orchidaceae)	16
Goeppertia (Marantaceae)	12

Flowering plant genera containing the most species. Adapted from Hartshorn and Hammel (1994) and updated based on the Digital Flora of La Selva website (Castro 2013).

PLANTS DO STUFF!

If you have an animal bias, and most people do, you may think that plants just sit there and don't do anything. Nothing could be further from the truth. Plants carry out photosynthesis by multiple biochemical pathways; engage in cellular respiration; transpire water; work hard to conserve precious water (even in the rainforest); mine the soil for nutrients; compete with neighbors, cooperate with neighbors; fall victim to predation; defend themselves against predation; serve as homes for other species of plants, animals, and microbes; engage in sexual reproduction; engage in asexual reproduction; disperse their offspring; are "born" when seeds germinate; struggle to survive; live for long times; contract diseases; get destroyed by violent weather; succumb to the forces of gravity; die; and decompose. *Just about every aspect of biology can be studied using plants!*

FOREST STRATIFICATION AND SEEING THE FOREST

Forests are organized into layers, or **strata** (Fig. 5.2). Start by looking at the forest floor, specifically at the **groundcover layer** (Fig. 5.3). Notice the thin layer of leaf litter. Contrast that with a temperate deciduous or coniferous forest

FIG 5.2 **Dark forest understory** and contrasting light gap showing understory, subcanopy, and canopy strata.

FIG 5.3 The spreading feathery sprays of the lycophyte **Selaginella** are common elements of the rainforest groundcover. At least two species are shown here.

where the litter layer provides a soft cushion of organic matter that is 15–30 cm (6–12 in) deep. In the rainforest this layer is barely a few leaves thick and within just a few centimeters transitions to mineral soil devoid of organic matter. Despite being labeled as "evergreen," tropical rainforest trees are constantly dropping leaves. In forests with a pronounced dry season, leaf drop can be seasonal and synchronous. In the Caribbean lowlands of Costa Rica, seasonal rainfall differences are subtle, and there is wide variation in leaf dropping. Some trees drop a few leaves at a time, whereas others are seasonally deciduous and drop all their leaves over a few days and quickly grow new ones. Once they reach the forest floor, the leaves are quickly decomposed by bacteria and fungi, and the released nutrients are rapidly reclaimed by the roots of living plants.

What plants live in the groundcover layer? Ferns of various sizes grow on the ground layer, on rotting logs, and climbing up the trunks of trees. The next most obvious inhabitants are fern-like plants in the genus *Selaginella*. Despite their fern-like appearance, they are lycophytes, a phylum of spore-producing plants that have only a single vein of vascular tissue in their tiny leaves (responsible for conducting water, nutrients, and sugars throughout the plant). True fern leaves, in comparison, have many veins per leaf. In the case of *Selaginella*, the tiny leaves are arranged in four rows along a spreading stem. Nine species of *Selaginella* are found almost everywhere you look in the La Selva forest. They don't carpet the ground but spread in widely dispersed clumps.

You may also find small seedlings of flowering plants attempting to survive in the ground layer. The goal of many species is to get to the canopy as quickly as possible and before they are eaten or trampled to death. Other species take decades to reach the canopy, growing slowly, tolerating the low light levels, and resisting herbivores. Mosses and liverworts, plants that lack any vascular tissue and, therefore, can't grow more than a few centimeters in height, also grow along the ground and on decaying logs.

The next highest stratum is the **understory** (Figs. 5.4 and 5.5). At maturity, understory plants are knee-high to head-high, with only a few reaching heights twice as high as the average human observer. I like being able to see the entire plant! Ferns, dwarf palms, cyclanths, giant herbs of the Ginger Order, woody shrubs, and saplings are abundant in the understory. Shrubby Piperaceae (Pepper Family)*, Melastomataceae (Black Mouth Family)*, and Rubiaceae (Coffee Family)* are well represented here and have very distinctive characteristics that make recognition of these families quite easy. Species identification, however, is difficult.

FIG 5.4 Ferns, dwarf palms, and saplings are common **understory plants**.

FIG 5.5 **Giant herbs** with leaves shaped like canoe paddles, such as this *Heliconia irrasa*, are common in the understory, especially in treefall gaps.

Approximately 20 species of dwarf palms (Arecaceae)* inhabit the rainforest understory of La Selva (Fig. 5.6). With the use of the palm key (Appendix 2), it is possible to identify all of these to 20 species. The leaves of palms are either simple/bifid (shaped like a fish tail), pinnate (feathery with the leaf split into many leaflets), or palmate (shaped like a fan). Challenge yourself to locate the flowers and fruits on the palms. Some palms are solitary with a single stem, whereas others are clonal and form clumps of stems that are joined by hidden underground connections. Beware, many have needle-like spines along their stems and leaves. Like many dwarf palms, plants in the Cyclanthaceae (Cyclanth Family)* have bifid leaves shaped like a "V" for victory sign (Fig. 5.7). They are easily confused with palms but have secondary veins that run the length of the leaf, rather than running toward the margin of the leaf.

The next highest stratum is the **subcanopy**. The trees here grow taller than the subcanopy shrubs, but they never quite reach the canopy created by their bigger neighbors. Some of these trees are capable of reaching the canopy and are biding their time until a treefall or branchfall enables sufficient light to shine through for them to resume growth and take their rightful place in the canopy. These are the canopy wannabes. The others have reached their maximum height and will spend their entire lives harvesting whatever bits of sunlight they can get in order to survive in the dimly lit subcanopy. Trees and palms occupy this layer.

Look up as far as you can and you are looking at the bottom of the **canopy layer**. In old-growth forest you are witnessing a closed canopy formed by the branches of

FIG 5.6 **Palms** are ubiquitous plants of the rainforest understory, many of which never exceed 2 m in height.

FIG 5.7 Bifid-leaved **cyclanths** are abundant in the understory of old-growth forest. They can be distinguished from palms by the way their veins orient parallel to the long axis of the leaves.

FIG 5.8 View of the forest **canopy** from a 38 m (125 ft) tower. The canopy towers and walkways of La Selva were erected for research and education, but have repeatedly been toppled by falling trees. Note the lavender flowers of *Dipteryx panamensis*, in full bloom in July, and the emergent tree extending far above the rest of the canopy.

adjacent trees meeting and leaving little or no cracks for rays of sunlight to penetrate to the lower strata. Most of the 300-plus species of trees of the La Selva forest occupy this layer. The leaves that you can see are poorly illuminated and barely photosynthesizing enough to overcome their expenditure of energy through respiration. In contrast, the leaves at the top of the tree are bathed in full sunlight. This hidden realm is where monkeys, sloths, lizards, insects, and birds make their living. The best way to see the canopy layer is from a tower, walkway, or bridge that is suspended above the canopy (Fig. 5.8).

And then there are the overachievers. Several tree species are capable of reaching 45–55 m (148–180 ft) in height and stick up far above the canopy level to truly exploit full sunlight coming from above and laterally. These are the giants of the rainforest known as **canopy-emergent trees**. From the ground, they look like massive walls of tree trunks 1.5–2.0 m (5–6 ft) in diameter) and buttresses.

Once you get a feel for the stratified nature of the forest, you are ready to begin exploring plant growth habits, and then you will be ready to attempt family identification and recognition of the most common species in the forest. In some cases, species or genera are distinctive; however, just being able to determine the family to which an individual belongs is an achievement worthy of self-congratulation. To help with this, I have provided an overview of plant growth habits (this chapter), a simple method for examining a plant and noting its distinctive features (chapter 6), an introduction to some of the most common families of flowering plants and their more easily recognized species (chapters 7–11), a somewhat technical description of 50 of the most common families of flowering plants (Appendix 1), a key to the palms of La Selva (Appendix 2), and an introduction to the most common ferns (chapter 12).

GROWTH HABIT AND SEEING THE PLANTS

Not to be confused with "habitat" or the setting where a plant grows, "**habit**" refers to *how* a plant grows, as well

as its overall shape and size at maturity. **Trees**, **shrubs**, **lianas**, **epiphytes**, and **herbs** are possible growth habits.

Trees are woody plants that grow upright. There are 323 different tree species at La Selva (Hartshorn and Hammel 1994). Most trees have a single main trunk or bole (Fig. 5.9). Many tropical trees resemble a child's lollipop drawing with a spherical mass of branches and leaves perched at the top of a single trunk. Very little light penetrates beyond the upper canopy, hence the lack of branches and leaves along most of the trunk. Nonetheless, there is a great amount of variation in branching patterns and overall tree architecture. A distinctive feature of tropical trees is that many have flared trunk bases, known as buttresses (Fig. 5.10). Presumably the buttresses lead to roots and are responsible for helping stabilize a giant tree growing in soil that is shallow and becomes destabilized every time it rains, which happens almost every day.

FIG 5.10 Many tropical trees have **buttresses**, flared extensions of the trunk that presumably help anchor the tree in unstable ground.

FIG 5.9 **Canopy trees** often have a wide-diameter straight trunk with few branches below the canopy. This challenges the observer to match the trunk with the leaves suspended 30 m (98 ft) from the ground.

Trees occupy different levels of the stratified forest. Most of the vegetation in the forest is located roughly 30 m (100 feet) above the ground, in the canopy. Trees that reach this height are called **canopy trees** (Fig. 5.11). The closed canopy formed by crowns of adjacent trees meeting lets very little sunlight through, resulting in a dimly lit understory. Some trees extend above and beyond the canopy and may reach heights of 45–55 m (148–180 ft). These so-called **canopy-emergent trees** are the giants of the rainforest (Fig. 5.12). At ground level all you see of these overachievers is a wall of tree trunk that may be 1.5–2.0 m (5–6 ft) in diameter while the top of the tree is all but invisible (Fig. 5.13). If you are lucky enough to climb to the top of a canopy tower, stroll along a canopy walkway, or go for a ride on a canopy zip-line tour, you will see these enormous trees extending far above the canopy. A list of some canopy-emergent species, their maximum heights, and where to find them at La Selva can be found in Table 5.3. Long-term research on canopy-emergent trees by Clark and Clark (1996) has revealed that emergent trees make up only 2% of the stems in old-growth forest yet contain 27.2% of aboveground biomass and continue to add biomass even after reaching enormous sizes. The Clarks also discovered that the mortality rate of emergent species is far lower than that of other trees in the forest. The ecological importance of canopy-emergent trees in the forest is far greater than their abundance would suggest. The Holdridge Arboretum offers a unique opportunity to view most of these emergent species up close.

Trees below the canopy are called **subcanopy trees** (Fig. 5.14). True subcanopy trees will never attain canopy

FIG 5.11 **Canopy trees**.

FIG 5.12 The extreme size of **emergent trees** is hard to capture in a photograph, but it is easier to grasp when a biologist is included for scale.

FIG 5.13 Often all you can see of an emergent tree is a huge trunk and buttresses.

status. They are tolerant of low light levels and are able to complete their entire life cycle in the dimness below the canopy. Other trees in the subcanopy are patiently waiting for the chance to reach the canopy, either by growing slowly or by waiting for a neighboring tree to drop a large branch, tip over, or die in place. Once this happens, a light gap is formed and the understory trees race to fill the gap. The most common subcanopy tree is the palm *Welfia regia* (corozo, Arecaceae). Another abundant and easily recognizable subcanopy species is *Warszewiczia coccinea* (pastora, Rubiaceae) with its brilliant red inflorescences visible in almost every season of the year.

Understory trees and **shrubs** occupy a stratum that ranges from 1 to 5 m (3–16 ft) in height. Shrubs and dwarf palms are common here (Fig. 5.15). Woody shrubs are defined by their low stature and often having multiple trunks. Woody shrubs from the Piperaceae (Pepper Family)*, Rubiaceae (Coffee Family)*, and Melastomataceae (Black Mouth Family)* are abundant in the forest understory.

Lianas are woody vines (Figs. 5.16–5.18). They lean upon or cling to woody trees for support. Various means are used to attach to host trees. Some stems twine around tree trunks as they grow. Others have hairs that provide a rough surface texture to help grab onto supports, while some species employ tendrils to wrap around the branches of their hosts. Lianas become massive, with diameters reaching the size of a human thigh. Length is almost impossible to measure. Lianas may reach the top

TABLE 5.3 Canopy-emergent Trees of the Caribbean Lowland Rainforest

Species	Family	Common names	Maximum height	Where to see at La Selva
Balizia elegans	Fabaceae Legume Family	Ajilo	55 m	Start of the CC trail
Ceiba pentandra	Malvaceae Mallow Family	Kapok Ceiba	50 m	Near STR trail at 700 m, along major rivers
Dipteryx panamensis	Fabaceae Legume Family	Almendro	54 m	Common throughout; CEN and CCL trails
Hieronyma alchorneoides	Phyllanthaceae Leafflower Family	Pilón	50 m	Cantarana near CCC trail
Hura crepitans	Euphorbiaceae Euphorb Family	Sandbox tree Jabillo	50 m	STR trail
Hymenolobium mesoamericanum	Fabaceae Legume Family	Cola de Pavo	58 m	CES trail at 750 m; tallest tree species of La Selva
Lecythis ampla	Lecythidaceae Brazil Nut Family	Monkey Pot Olla de mono	45 m	SHO trail at 800 m
Terminalia oblonga	Combretaceae Indian Almond Family	Surá	45 m	On alluvial soils near streams and rivers; SUR, STR, SAT trails

Emergent tree size data were taken from Clark and Clark (1992, 2001) and the Digital Flora of La Selva website (Castro 2013). Most of these species can also be found in the Holdridge Arboretum.

FIG 5.14 Canopy and subcanopy trees.

FIG 5.15 **Dwarf palms** are abundant in the forest understory.

of a canopy tree and then continue to spread to other trees. When a tree falls to the ground, it brings lianas with it, and they in turn pull down other trees. The trees will die, but the liana will reorient and new shoots will begin upward growth within a few weeks. Try to follow a liana from where it roots to where it ends. It is a seemingly impossible task. The Bignoniaceae (Trumpet-creeper Family), Fabaceae (Legume Family)*, Sapindaceae (Soapwort Family), Malpighiaceae (Malpighia Family), Aristolochiaceae (Dutchman's Pipe Family), Cucurbitaceae (Squash Family), and Dilleniaceae (Dillenia Family) make up more than half of the 106 species of liana at La Selva (Hartshorn and Hammel 1994).

Epiphytes are plants that grow on other plants ("phyta" means plant and "epi" means on). They grow on the branches and trunks of trees and are everywhere you look in the rainforest (Fig. 5.19). Wind or birds disperse seeds to tree branches and trunks. The epiphytes produce roots that anchor them to the substrate but do not absorb water and nutrients like most roots. Ferns and members

FIG 5.16 Looking like a giant snake coiled on the ground, this **liana** was probably brought down to the ground when a tree fell. The tree rotted away, leaving behind the coiled liana, which simply reoriented, continued to grow, and resumed its exploration of the canopy. The pinnately compound leaves identify this species as *Paullinia ingifolia* (Sapindaceae).

FIG 5.17 *Moutabea gentryi* (Polygalaceae) has young leaves that are dark blue! This individual is resuming growth after being brought down by a treefall (notice the fresh brown dirt of a tip-up mound in the background).

FIG 5.18 Usually all that is visible of lianas is a tangle of arching or loopy stems, offering the observer no clue as to what the rest of the plant looks like.

of the Orchidaceae (Orchid Family)*, Araceae (Arum Family)*, Bromeliaceae (Bromeliad Family)*, Moraceae (Mulberry Family)*, and Cyclanthaceae (Cyclanth Family)* are well represented as epiphytes. Epiphyte species constitute 23% of all vascular plants at La Selva (Hartshorn and Hammel 1994). Some, such as the bromeliads, are true epiphytes that never make contact with the ground. Others, known as **hemiepiphytes**, begin life as a seedling in the canopy and send roots down to the ground. Once they make contact with the ground, they are able to mine the soil for water and mineral nutrients. The most famous of the hemiepiphytes are the strangler figs (Moraceae), which will sometimes encircle the host tree with their roots, eventually killing it and, after the host has rotted away, forming a hollow cylinder of roots (Fig. 5.20). Another group of epiphytic plants, known simply as **climbers**, begins life on the ground and then grows toward the darkest spot formed by the shade of a tree, bringing them into contact with a tree trunk (Fig. 5.21). They then use roots to anchor themselves to tree trunks and climb their way up the side of a host tree. Philodendrons and Monsteras in the Araceae are often climbers. And then there are plants that live on the leaves of other plants! These **epiphylls** are mosses, liverworts, and lichens (Fig. 5.22). The interactions of epiphylls with palm host leaves are described in chapter 9.

Herbs, or herbaceous plants, are plants that do not make wood. Throughout the world, they are mostly small plants that are restricted to high-light environments and are uncommon in shady forests. Most of the epiphytes are also herbaceous. Ferns are by far the most abundant of the herbaceous plants, making up 17% of the herbaceous species at La Selva (Hartshorn and Hammel 1994). Members of the Rubiaceae (Coffee Family)*, Poaceae (Grass Family), Araceae (Arum Family)*, and Marantaceae (Prayer-plant Family)* also exhibit an herbaceous growth habit. While many herbaceous plants are small, there are some unique tropical exceptions. The Ginger Order (Zingiberales: Banana, Ginger, Heliconia, Costa, and Prayer-plant families)* includes a group of **giant herbs** that can grow 1–4 m (3–14 ft) in height and often feature leaves resembling canoe paddles in size and shape (Fig. 5.23). Leaves of

FIG 5.19 Tree branches are often covered in **epiphytes**—literally, plants that live on other plants. This branch is supporting arums (*Anthurium, Philodendron*), several species of fern, and bromeliads.

FIG 5.20 A tree being hugged by two **strangler figs** (*Ficus*).

FIG 5.21 The **Arum Family** (Araceae) includes many species that climb up the trunks of trees.

plants in the Arum Family (Araceae) are some of the largest in the forest. Palms present a conundrum. Are palms herbaceous or woody? Many have woody stems, but this "wood" is made up of fibers and is formed in a different way than that of the wood of true trees. (A plant anatomist would point out that palms are supported by lignified fibers, not secondary xylem; do not make wood; and are not trees. For the purpose of thinking about the forest, if it looks like a tree and functions like a tree, we'll call it a tree.)

ABOVE: FIG 5.23 **Giant herbs** in the Heliconiaceae and Marantaceae are common in gaps and other disturbed areas.

FIG 5.22 The surfaces of the fern and cyclanth leaves are barely visible because of a felt-like growth of **epiphylls**: a mix of mosses, liverworts, and lichens.

CHAPTER 6

HOW TO EXAMINE A PLANT

Many people assume that all plants are the same (Fig. 6.1). They are wrong! Most plants are green and have roots, stems, leaves, flowers, and fruits. But what about the plants like mosses, liverworts, lycophytes, and ferns that disperse by spores and don't make flowers or fruit at all? In addition, not all flowering plants are green or have leaves. Upon entering the rainforest, you are immediately struck by the overwhelming diversity of plants, especially the trees. Then, when you try to identify those trees, you suddenly start to think that they all really do look alike and you will never be able to differentiate one species from the next. Don't despair; with some practice, you can at least discern some of the major families of flowering plants. Coverage of plants in this book will be heavily biased toward flowering plants. There are two species of gymnosperm in the La Selva rainforest, *Zamia neurophyllidia* (Cycadaceae) and *Gnetum leyboldii* (Gnetaceae). A dozen lycophytes and a little more than 170 species of ferns are scattered abundantly across the landscape and will be covered in a subsequent chapter (chapter 12). The following routine is intended to be used to identify flowering plants at least to the level of family.

FIG 6.1 Leaves are not all alike! Each one has a unique shape. Some are broad at the base and narrow at the tip, while others are narrow at the base and broad at the tip or narrow throughout. Some consist of a single blade (simple leaves), whereas others are composed of multiple leaflets (compound leaves). Some have smooth margins; others are toothed. Each one has a venation pattern that is different from all the others. Some are smooth while others are hairy. The pictured leaves are even different shades of green and one is tan due to a coating of rusty hairs.

So, how do you go about the process of identifying a plant? You will need to learn about 25–35 basic botanical terms, follow a routine for examining a new plant, practice using some sort of identification key, and practice some more. The next few chapters provide an overview of the characteristic features and ecology of 20-some of the most common flowering plant families of the rainforest, highlighting some of the more easily recognized genera and species. Appendix 1 offers brief botanical descriptions of 50 of the most common flowering plant families of the rainforest. Chapter 12 describes the most common ferns and how to identify them.

With a moderate amount of effort, you should be able to observe members of each of these families, even during a short visit to the tropics. It is surprising how many different families you can identify in only a few hundred meters of almost any trail at La Selva. The same families, but not necessarily the same species, will be found anywhere you visit in the Neotropics. To identify a plant to the family level, usually all you need is a stem or branch and some leaves. Flowers and fruits would be helpful, but they are produced only at certain times of the year and are often high up in the canopy.

THE HISTORY OF BOTANY AND FLORAL VERSUS VEGETATIVE CHARACTERISTICS

Historically, the naming and classifying of flowering plants was based on flower traits. To a large extent, this is still true today. Carl Linnaeus is credited with developing a classification and identification system based on the numbers of flower parts. The numbers and arrangements of flower parts have been an essential part of plant identification ever since. Perhaps this is not surprising for a science that developed in temperate regions where

annual flowering is highly predictable. In the tropics, however, finding plants in flower can be much more challenging.

Early botanical explorers traveled from Europe to the tropics and spent years at a time collecting plants. They would search for months for the ideal opportunity to collect a plant in flower, press it, and ship it to a European museum. The reliance on flowers is less useful for short-term visitors to the tropics. While some tropical plants produce flowers all the time, most seem to produce flowers when they feel like it and are fickle about when they are in the mood. Some flower annually, whereas others may go years or decades between flowering episodes. Thus, for the boots-on-the-ground botanist, most of those flowers are inaccessible, either because they are 30 m (98 ft) up in the canopy or simply not present at that particular moment in time. Therefore, tropical botanists have been forced to learn plant identification by means of plant parts not associated with flowers or fruits, what we call vegetative characteristics. Family-level identifications are often the best you can hope for. After that, a more detailed botanical key is necessary for genus or species identifications.

Plant family names all end in "-aceae," which is pronounced "ay-see-ee" or like saying the letters "A-C-E." Spanish-speaking botanists pronounce it slightly different, sounding like "ah-see-ah." They maintain that their language is closer to Latin than English and, therefore, their pronunciation is more correct!

The following routine, organized as a series of questions, is used by tropical botanists to identify plants in the field. You can go a long way toward identification of a plant if you learn how to describe a handful of easily observable traits, including its growth habit, leaf type, leaf arrangement, leaf shape, presence or absence of stipules, venation pattern, and various other features of the leaves and stems. If flowers or fruits are present, then that's an added bonus.

WHAT IS THE GROWTH HABIT OF THE PLANT?

"Habit" refers to the way that a plant grows and is covered in chapter 5. Are you looking at a **woody tree**? **Woody shrub**? Woody vine (**liana**)? Or an **herbaceous** plant that lacks wood? Is it firmly rooted in the ground and growing independently? Does it climb up the trunk of a tree? Is it an **epiphyte** perched on the branch or trunk of a tree?

ARE THE LEAVES SIMPLE OR COMPOUND?

Simple leaves consist of a single blade or lamina attached to a branch node by a slender stalk or **petiole** (Fig. 6.2). **Compound leaves** consisting of multiple **leaflets** are very common in the tropics. They in turn come in two basic types, **palmate** and **pinnate**. If you think of the palm of your hand with five fingers radiating from a common point, then you have a good idea of what a palmate leaf looks like (Fig. 6.3). The number of leaflets will vary by species, but they will all originate from a single point at the end of the petiole.

Pinnate means feathery, and pinnate leaves have leaflets arranged much like the barbs coming off the rachis of a bird feather. Pinnate leaves consist of a central **rachis** representing an extension of the petiole and

FIG 6.2 **Simple leaves** consist of a single blade attached to the stem by a petiole. The simple leaves of *Goethalsia meiantha* (Malvaceae) have toothed margins, an elongated drip tip, and stipules and exhibit delayed greening of young leaves.

FIG 6.3 **Palmately compound leaves** consist of a cluster of leaflets all originating from a single point at the tip of a petiole. The genus *Schefflera* (Araliaceae) includes common rainforest plants and houseplants.

FIG 6.4 **Paripinnate leaves** are compound leaves with an even number of leaflets attached to a central rachis. *Inga* is a common genus of trees in the Legume Family. Note the suction-cup-shaped extrafloral nectaries located between each pair of leaflets and the winged rachis.

FIG 6.5 **Imparipinnate** leaves are compound leaves with an odd number of leaflets coming off a central rachis (extension of the petiole).

FIG 6.6 Many mimosoid legumes have **bipinnate leaves**. These compound leaves have leaflets that are compound. *Stryphnodendron* is a common legume tree in lowland rainforest and has pinnules (the leaflets of the leaflets) that are rhomboid in shape.

varying numbers of leaflets that attach to the rachis. The stem that attaches the leaflet to the rachis is called a **petiolule** or little petiole. **Paripinnate** leaves have an even number of leaflets (they are in pairs; Fig. 6.4), whereas **imparipinnate** leaves have an odd number of leaflets (Fig. 6.5). Some leaves are **bipinnate** (Fig. 6.6); in this case the leaflets are also compound. A bipinnately compound leaf is most likely a member of the Mimosoideae subfamily of the Legume Family (Fabaceae). Pinnate leaves are exceedingly common in tropical forests and are found in the Fabaceae, Meliaceae (Mahogany Family), Sapindaceae (Soapwort Family), Simaroubaceae (Tree-of-Heaven Family), and Anacardiaceae (Cashew Family), among others.

It can sometimes be difficult to distinguish simple versus compound leaves in the field. Botanically, what defines a plant part as a single leaf (simple or compound) is the presence of an axillary bud at the base of the petiole where it meets the stem. In practice, axillary buds can be difficult or impossible to see. Look for the smallest repeating unit of leaf tissue—do you always see a certain number of leaflets clustered together? Do you always see a central rachis with leaflets coming off it? If so, it's a compound leaf.

HOW WOULD YOU DESCRIBE THE LEAF ARRANGEMENT, OR PHYLLOTAXY?

Most leaves come off a stem and follow strict rules about how they are arranged relative to one another and to the axis of the stem. They may be opposite, alternate, or whorled. The order of the leaves about the stem is known as **phyllotaxy**. The location on a stem from which a leaf originates is the **node**. **Opposite** leaves are positioned directly across from one another at a node (Figs. 6.7 and 6.8). In some cases, the opposite leaves rotate 90° from one node to the next and are said to be **decussate** (Fig. 6.9).

Opposite leaves are not very common in the tropics, so if you find a plant with opposite leaves, you can quickly narrow down the choices of families. Common families with opposite leaves include Acanthaceae (Acanthus Family), Bignoniaceae (Trumpet-creeper Family), Melastomataceae (Black Mouth Family), Clusiaceae (Mangosteen

FIG 6.7 The orientation of leaves relative to the stem is known as **phyllotaxy**. Leaves may have an opposite, alternate, or whorled phyllotaxy. *Vismia* has opposite leaves with smooth (entire) margins.

FIG 6.8 Plants in the Trumpet-creeper Family (Bignoniaceae) have **opposite compound leaves**. Many members of the family are lianas that use coiling tendrils to attach to other plants.

FIG 6.9 Plants with **opposite decussate leaves** exhibit a 90° rotation in leaf orientation from one node to the next. This is common in the Melastome (shown here), Mint, and Verbena families. The leaves of this melastome are covered in hairs (trichomes).

FIG 6.10 Most plants have **alternate leaves**. Some plants with alternate phyllotaxy are distichous, meaning leaves originate in two rows following a strict left–right alternation with the leaves lying more or less in the same plane. Species of Annonaceae, shown here, have alternate distichous leaves.

Family), Myrtaceae (Myrtle Family), Apocynaceae (Dogbane Family), Verbenaceae (Verbena Family), Rubiaceae (Coffee Family), and Malpighiaceae (Malpighia Family).

When leaves are not paired like this, they are considered **alternate** or **whorled**. Leaves that alternate in a strict left-right–left-right fashion and are arranged in the same plane are **distichous** (Fig. 6.10). If the branch of such a plant with alternate distichous leaves were to be laid on the ground, all the leaves would lie flat. More commonly alternate leaves follow a spiral pattern that may or may not repeat itself around the stem.

In some cases, there will be three or more leaves originating at a node. These are said to be **whorled**, or arranged in a whorl about the stem (Fig. 6.11).

The spacing between nodes, the internode distance, varies among species. If the distance between nodes is very short, distinguishing among the three different leaf arrangements can be tricky. Also notice whether the leaves are scattered regularly along a branch or if they are clustered near the tip.

FIG 6.11 Of the three types of phyllotaxy, the least common is **whorled**, in which more than two leaves originate at each node. *Hamelia patens* has whorled leaves with stipules located between adjacent petioles (interpetiolar stipules characteristic of the Coffee Family).

WHAT IS THE OVERALL SHAPE OF THE LEAF? ARE THE LEAF MARGINS ENTIRE OR TOOTHED?

Botanists employ a bewildering array of terms to describe **leaf shape**: cordate, elliptical, lanceolate, linear, oblong, obovate, ovate, and the list goes on. There are also terms for the shape of the leaf tip, as well as the base of the leaf: acuminate, acute, cordate, oblique, rounded, and sagittate, just to name a few. Many tropical leaves have an elongated point at their tip (acuminate). These structures are called "**drip tips**" and may help leaves shed water, a useful trait in a place where it rains most days and fungal pathogens abound (Fig. 6.2). Leaf shape terminology will be minimized in this book, but if you intend to continue in your study of botany, it will be important to learn these terms.

The **margin**, or edge of a leaf, is usually smooth, or **entire**. However, it may also be **toothed** and be either **serrate** (teeth curved and pointing in one direction, like a serrated knife) or **dentate** (teeth pointed outward) (Fig. 6.12). Toothed leaves are uncommon in the tropics and characteristic of the Malvaceae, Salicaceae, Sapindaceae, and Ulmaceae.

FIG 6.12 A plant from the Mallow Family (Malvaceae) with toothed leaves, large **stipules**, and hairs (trichomes). Closer magnification would reveal the hairs to be shaped like asterisks (stellate trichomes).

ARE MYSTERIOUS LITTLE FLAPS OF TISSUE CALLED STIPULES PRESENT?

Stipules are small (usually) leaf-like flaps of plant tissue that are thought to play a role in protecting developing leaves (Fig. 6.12). Some plants have them and some don't. In some cases, the stipules remain firmly attached to the plant. In other cases, they are ephemeral features that fall off as soon as the leaf being protected unfurls, leaving behind a tiny scar as the only evidence of its existence. Stipules usually come in pairs and are found just below and to either side of the petiole. The presence or absence, shape, and location of stipules and their scars can be valuable plant identification traits. Beware, searching for them can be very frustrating. In figs (*Ficus*), the stipule is located at the tip of a branch, is shaped like a dunce cap, and falls off as the leaf matures, leaving behind a ring-like scar on the stem. The stipules of Balsa trees are persistent, about a centimeter wide, and shaped like a bicycle seat. Plants in the Coffee Family (Rubiaceae) have dozens of stipule shapes and sizes, but they are always present between the opposite leaves (interpetiolar stipules; Fig. 6.13). For most species, stipules are tiny, seemingly insignificant flaps of tissue and require a hand lens to see either the actual stipules or the scars they have left behind.

FIG 6.13 A key feature of the Coffee Family (Rubiaceae) is the presence of **stipules** between the petioles of opposite or whorled leaves (interpetiolar stipules), the size and shape of which can be helpful in species identification.

WHAT PATTERN IS DELINEATED BY THE LEAF VENATION?

You would think that the word should be written *veination*, but as a scientific term it is spelled according to its Latin root *vena*, meaning "vein." **Venation** patterns are usually distinctive and easy to observe. In other cases, the veins are nearly invisible (*Simarouba* or *Clusia*). In monocots (except Araceae) the easily observed veins run parallel to one another. This is the typical pattern in grass-like plants and works well in the temperate zone for separating monocots and dicots but works less well in the tropics, where monocot leaves are often large and broad. Plants in the Ginger Order have large leaves with a central midvein and numerous secondary veins that are parallel to one another as they extend to the leaf margin. The large leaves of the Arum Family (Araceae) don't look like monocots at all (Fig. 8.2). They typically have secondary veins arranged pinnately, while tertiary veins branch repeatedly in a very un-monocot fashion.

Let us consider the other flowering plants, the magnoliids and eudicots, which have veins arranged in a much more complex netted arrangement. There are some distinctive patterns. Leaves with **pinnate venation** have a central primary vein, or midrib, running down the middle of the leaf and secondary veins originating at the midrib and extending at regular angles toward the leaf margin (Fig. 6.14). In some cases, those secondary veins end at the leaf margin. In serrate leaves, they may extend all the way to or just beyond the point of the tooth. In figs (Moraceae), the secondary veins never reach the margin and form loops that join up with a neighboring vein. This loopy venation is called **brochidodromous**, and if you start using that term, you just might be a botanist (Fig. 6.15). In **palmate venation**, multiple veins originate at the base of the leaf, where it attaches to the petiole, and then radiate away from the attachment point. Many Malvaceae

FIG 6.14 **Pinnate venation** is the most common venation pattern in broad-leaved plants.

FIG 6.15 Leaves with **brochidodromous venation** feature secondary veins that extend from the midvein and form a loop without ever reaching the margin of the leaf. Several families feature this venation pattern, including the Moraceae (Mulberry or Fig Family).

have palmate venation (Fig. 6.12). The most striking venation pattern is found in the Melastomataceae, in which 3 to 5 veins originate in a palmate fashion at the petiole, spread out toward the middle of the leaf, and then reconverge at the leaf tip (Fig. 6.9). The tertiary veins, located between the secondaries, are parallel to one another and form a distinctive ladder-like pattern. If you can recognize this venation pattern, then you can identify melastomes.

ARE THERE EXUDATIONS? DON'T GET SAPPY

A cleanly cut stem will often appear shiny because of the presence of sap, consisting mostly of water. Because the sap was under tension when you cut it, the plant doesn't "bleed." In other cases, clear or colored liquid oozes from the cut surface. Some plants have special cells that secrete **latex**, a translucent and sticky substance loaded with toxic defense chemicals (Fig. 6.16). The latex is often pure white, but it may also be cream, yellow, orange, or red in color. In some cases, the color is revealed only upon exposure to the air and oxidation of the chemical constituents. Dabbing the cut stem on a white piece of paper and waiting for the color to set is a good way to test for colored exudations. Snap off a leaf and watch what happens at the cut end of the petiole (or cut a narrow stem with clippers). Apocynaceae gush copious amounts of white latex, whereas figs and other Moraceae often need to have tiny droplets milked out by squeezing a severed petiole. The exudations of Clusiaceae are cream, yellow, or orange colored. Dab some on a notebook page,

FIG 6.16 Oozing milky **latex** from cut stems and leaves is common in Apocynaceae, Clusiaceae, and Moraceae (*Brosimum* [shown here], *Castilla*, and *Ficus*). Photo: Reinaldo Aguilar, Digital Flora of La Selva.

and it will make the pages forever sticky. Myristicaceae (Nutmeg Family), such as *Virola*, produce small amounts of clear exudations, which when streaked onto notebook paper turn pink or red as they oxidize. Do not get any of these exudations in your eyes or mouth! They contain an arsenal of antiherbivore defense compounds and can be quite irritating. Some have been harnessed by humans for use as powerful poisons, medicines, and hallucinogens. Always keep in mind that the difference between a medicine and a poison is the dose.

ARE THE LEAVES OR STEMS COVERED WITH TRICHOMES? A HAIRY SITUATION

For all botanists, a **hand lens** is an essential piece of equipment with which to conduct the examination of hairs, glands, nectaries, teeth, domatia, flowers, and other tiny wonders. The lens should be carried at all times and worn around the neck like a precious pendant. Many, if not most, leaves are covered with **hairs**. Botanists prefer the term **trichome** (Figs. 6.9, 6.12, and 6.22). In extreme cases, the leaves are so hairy that they look and feel fuzzy. Hairs come in different shapes and sizes. The most basic is a stalk without any other ornamentation. **Capitate** trichomes look like a golf ball perched on a tee. The most famous of these are the trichomes found on the flower bracts of *Cannabis*. Like the *Cannabis* trichomes, some hairs are secretory and release aromatic or biologically active compounds, most likely to deter herbivores. The presence or absence of hairs is usually a species-level attribute; that is, it can vary considerably within a genus. The shape of hairs (when present) can be diagnostic at the family level. Leaves of Malvaceae sport **stellate** hairs, which look like miniature stars or asterisks. The Malphigiaceae have **T-shaped** hairs, consisting of a very short stem and looking more like a child's rendition of a flying seagull than the letter T (Fig. 11.88). None of these details would be visible without the use of a hand lens, so *never enter the field without one*.

ARE THERE DOTS OR GLANDS ON THE LEAF BLADE? YET ANOTHER USE FOR THE HAND LENS

Study the surface of a leaf carefully, and you might find that it is covered with dots or **punctations** (Fig. 6.17). These are usually more visible or present only on the undersurface of the blade. Holding a leaf up to bright light—in the forest, holding it up to the sky—can make dots more visible. What are these? If you find them on multiple leaves and in an orderly arrangement, then you can probably rule out disease.

Pellucid dots are usually lighter in color than the rest of the leaf and sometimes a little shiny. They are glands that secrete aromatic compounds. Perhaps the mere whiff of these compounds is sufficient to warn an herbivore that eating this leaf could lead to indigestion or worse. If you find a plant with pellucid dots, tear up the leaf and quickly smell it. Rutaceae (Citrus Family) and Myrtaceae (Myrtle Family) have aromatic leaves and pellucid dots.

FIG 6.17 Some leaves, such as this guava leaf (*Psidium guajava* in the Myrtaceae), are covered with tiny dots that are best seen by holding the leaf up against the sky and peering at it with a hand lens. These **punctations**, also called pellucid dots, are glands that emit aromatic compounds.

Punctations of the Myrsinoideae (Myrsine Subfamily) take the form of streaks.

In other instances, the dots are invaginations in the leaf that are thought to be homes to mites or ants. Mite **domatia** are visible as depressions in the leaf surface and are dark and shadowy. If you actually see mites, you have witnessed a rare event. Sometimes, domatia are little more than a dense collection of hairs at the intersection of a secondary vein with the midvein. Combretaceae (Indian Almond Family) often have domatia, either along the sides of the main vein or near the leaf margins (Fig. 11.13).

IS THE LEAF AROMATIC? TEAR IT UP AND BREATHE DEEPLY—THE NOSE KNOWS

After being handed a leaf, an experienced tropical botanist will often shred a leaf, crush it up, and then take a deep whiff. Many tropical plants, including the ones with glandular punctations as described above, have very distinctive odors. Before the advent of gas chromatography, organic chemists followed their noses in making chemical determinations. That is what tropical botanists are doing in the field. Take a sniff—does the leaf smell like a primitive "ranalean odor," anise, turpentine, unripe avocado, guava, eucalyptus, rank, sweet, green bean, or just plain nasty? Or like crushed leaves? With some practice, you will be able to describe leaf

odor just like an oenophile describing the complex bouquet of a fine merlot. When checking the odor of a leaf, choose one that is relatively young and not covered in epiphylls—many liverworts have a strong, cloying anise odor that can obscure the odor of the leaf itself. Also, check for latex before you rip up a leaf and stick it under your nose to check for an odor. The families with copious latex do not have any strong odor characteristics, and you don't want your face and hands covered in toxic latex!

ARE EXTRAFLORAL NECTARIES PRESENT?

Flowers produce nectar as a sugar reward for pollinators; however, some plants produce nectar elsewhere in **extrafloral nectaries**. These are often bumps along the petiole or base of a leaf. Passionflower vines (*Passiflora*) have extrafloral nectaries at the base of each leaf or along the petioles (Fig. 6.18). Sometimes you can even see a droplet of sugary reward on the nectaries. Reward for whom? Oftentimes the nectar benefits ants that reimburse the plant by fending off potential herbivores. The leaves of *Inga*, one of the largest genera of tropical legume trees, have compound leaves with nectaries resembling suction cups between each leaflet (Fig. 6.4).

FIG 6.18 The leaves of this passionflower vine (Passifloraceae) feature several interesting dots and bumps. The pair of bumps at the base of the petiole are **extrafloral nectaries** that produce a sugary solution that is harvested by ants, which in turn help protect the plant from herbivores. The yellow dots on the leaf mimic butterfly eggs and protect the plant from herbivorous butterflies that hesitate to lay their eggs on a leaf that already has eggs on it.

DO THE STEMS HAVE STRONG OR WEAK BARK?

Cut a stem and then try to peel the bark. If the largest pieces of bark are the ones that are stuck beneath your fingernails, then the bark is said to be "weak." In other cases, the bark will peel in long strips and be fairly difficult to break (Fig. 6.19). This is **strong bark**, and it has been used by people for centuries as a natural rope. The Annonaceae (Soursop Family), Lecythidaceae (Brazil Nut Family), and Malvaceae (Mallow Family) are families that have very strong bark because of the presence of abundant fibers.

IS A PULVINUS PRESENT? WHO SAID PLANTS DON'T MOVE?

Some plants can move their leaves or leaflets in response to certain stimuli, such as touch, sunlight, or time of day. The two best-known examples are the Prayer-plant and the Sensitive Plant. Each night, the Prayer-plant (*Maranta leuconeura*), a common houseplant, folds up its leaves, giving the impression that it is reciting its bedtime prayers. Other members of the Prayer-plant Family (Marantaceae) exhibit similar movements. Some members of the Legume Family also fold up their leaves at night, while some fold up during the day to prevent water loss. If the Sensitive Plant (*Mimosa pudica*) is touched by a

FIG 6.19 Break a twig and see if the bark peels or if it breaks cleanly. **Strong bark** peels in strips and is common in the Annonaceae (shown here along with alternate distichous leaf arrangement), Lecythidaceae, and Malvaceae.

FIG 6.20 The Sensitive Plant, *Mimosa pudica*, has a **pulvinus** in between each leaflet (actually pinnules) and along the petiole. If the leaf is touched, water pressure changes in the cells of the pulvinus, and the leaflets fold up.

human hand or a hungry insect, the leaves quickly fold up. How can a plant that lacks muscles move its leaves? The answer lies in changes in water pressure in the cells of the plant. Leaf movement is controlled by a swelling of tissue known as a **pulvinus**. Many mimosoid legumes have a pulvinus at the base of each leaflet (Fig. 6.20). It will be visible with a hand lens as a tiny sphere. Members of the Prayer-plant Family have an elbow-like swelling on the petiole that enables them to change the orientation of the leaf blade. Plants in the Malvaceae (Mallow Family) and Burseraceae (Frankincense and Myrrh Family) also commonly have a pulvinus associated with their leaves.

ARE ANY FLOWERS PRESENT? IF SO, HOW MANY OF EACH FLOWER PART IS PRESENT?

Flowers and fruits are very helpful for identifying plants, but in the tropics their presence is unreliable. **Flowers** are the reproductive structures of flowering plants and consist of **whorls** of flower parts (Figs. 6.21–6.24). It is easiest to consider these whorls in the order in which they are encountered as you travel up the stem of the plant.

FIG 6.21 The flowers of ***Passiflora*** (Passifloraceae) have 5 sepals and 5 petals (distinguishable only by position), a frilly corona, and a column bearing 5 stamens with yellow anthers and 3 styles with white stigmas. Note the curly tendrils on this passionflower vine. This red-flowered species is pollinated by hermit hummingbirds.

FIG 6.22 ***Lycianthes*** (Solanaceae) flower with 5 petals (sepals are small and hidden), and 5 purple anthers clustered around a central style. Leaves come in two different sizes and are covered in trichomes (hairs). The flowers are pollinated by bees that vibrate the anthers to release pollen.

There is a name for the parts that make up the whorl and a name for the collection of parts taken together. The first whorl is made up of **sepals**, and the collection of sepals is called the **calyx**. Sepals are often green, but they may also be the same color as the petals or may contrast with the petals as a way of advertising the presence of the flower to pollinators. The next whorl is made up of **petals**; the collection of petals is called the **corolla**. The petals may

FIG 6.23 ***Razisea*** (Acanthaceae) flowers consist of 5 tiny green sepals and 5 red petals fused into a 2-lipped corolla tube. Two stamens are visible in this photo. As with many red flowers, they are pollinated by hummingbirds.

FIG 6.24 This hummingbird-pollinated ***Malvaviscus*** (Malvaceae) flower has green sepals and 5 red petals surrounding a central column bearing 10 stigmas at the tip and stamens just below.

be separate from one another (distinct) or fused together to form a tube. The function of petals is to attract pollinators. The size, shape, and degree of fusion of the petals will determine what species of insects and other visitors will be able to access the food rewards provided by the flower. The next two whorls contain the sexual parts of the flower. The **stamens** each consist of a filament or stalk upon which sits a pair of **anthers**. **Pollen** is produced inside the anthers and the pollen in turn contains sperm cells. The collection of stamens is known as the **androecium** (a Greek word meaning "house of man"). **Carpels** consist of a **stigma**, **style**, and **ovary**. The stigma is the surface where pollen lands, and the style consists of elongated tissue that the sperm travels through on its way to the ovary. Eggs are produced inside the ovary and, once fertilized, will develop into seeds while the ovary ripens into a fruit. Carpels may be separate from one another (apocarpous) or they may be fused together (syncarpous). Individual or fused carpels may also be referred to as the **pistil**. The collection of carpels is known as the **gynoecium** ("house of woman"). Many flowers have **nectaries** that provide a dilute sugar reward (**nectar**) to potential pollinators. The process of delivery of pollen to the carpel is known as **pollination**, whereas the fusion of sperm and egg is known as **fertilization**. The parts that make up a flower are often present in multiples of 3, 4, or 5, depending on the species. Botanists sometimes refer to flowers as being on the three-plan or being trimerous, and so on.

Most plants have both male (stamens) and female (carpels) parts on the same flower. Botanists label these flowers as perfect or bisexual. Other plants produce flowers that contain only male parts (staminate flowers) or only female parts (carpellate or pistillate flowers). In some cases, these unisexual flowers are produced on the same plant. These plants are said to be **monoecious** after Greek roots meaning "one house." I think of the males and females inhabiting separate rooms in the same house. In other cases, plants are **dioecious** with some individuals producing only male flowers and others only female flowers. Dioecious means "two houses," and according to my analogy, the males and females are segregated into different houses.

ARE ANY FRUITS PRESENT?

The ovary will ripen into a **fruit** after fertilization of the eggs located within ovules, which in turn are located within the ovary (Figs. 6.25–6.27). The seeds are contained within the fruit. Fruits may be fleshy and contain nutritious sugars or fats (berries, drupes). They attract animals

RIGHT: FIG 6.25 The numerous **tiny berries** of *Anthurium* are dispersed by birds.

FAR RIGHT: FIG 6.26 The relatively **large berry** of Passionflower (*Passiflora*) is consumed by birds and mammals that disperse the many seeds contained within.

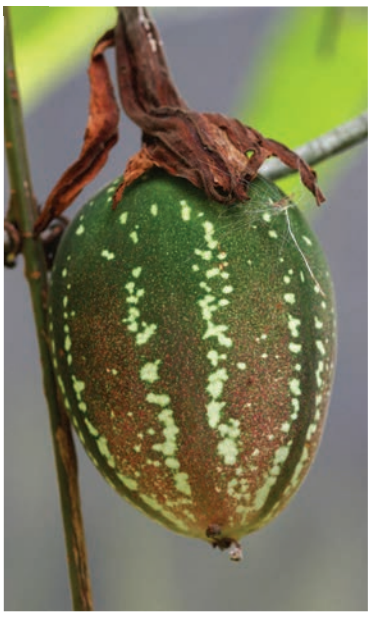

FIG 6.27 Plumose **wind-dispersed seed** released from a dry fruit (capsule).

that consume the flesh and either defecate or regurgitate the seeds. Alternatively, the fruits may be dry at maturity and often split apart to release the seeds contained within (capsules). These seeds may be dispersed by animals, wind, or gravity. There are many variations of flower and fruit characteristics, but they are beyond the scope of this book. Flower and fruit terminology will be minimized.

PUTTING IT ALL TOGETHER

Some plants can be identified by *gestalt*, a German word for shape. A bromeliad with a rosette of sword-shaped leaves forming a central tank simply looks like a bromeliad and is easy to recognize as such. Most plants are much more difficult to identify, hence the need to follow the routine described above and combine it with a botanical key. The key can be a series of photographs, a matrix of traits, or a dichotomous key. The series of short descriptions in Appendix 1 provide a user-friendly way to identify the plants of the lowland rainforest to the family level. By combining several of the different features described above, you stand a good chance of successfully making a family identification. For example, a plant with alternate simple leaves, terminal conical stipules, ringed stipule scars, white exudations, and brochidodromous venation must be a member of the Moraceae family and is probably a fig in the genus *Ficus*. A plant with opposite simple leaves that are shifted 90° from one node to the next, no stipules, secondary veins that radiate from the base only to converge at the tip, and tertiary veins arranged in a ladder-like pattern can only be a Melastomataceae.

EVOLUTIONARY RELATIONSHIPS IN FLOWERING PLANTS

With 320,000 known species in the plant kingdom, it is easy to see why teasing apart evolutionary relationships is a huge challenge that is subject to periodic revision (see chapter 4). The most current **phylogeny** (evolutionary history) of the flowering plants has been constructed by a team of scientists known as the **Angiosperm Phylogeny Group** (APG; Stevens 2001). Using complex computer algorithms, in 2016 they published the fourth revision of this phylogeny, incorporating the latest hypotheses about evolutionary relationships among the flowering plants based on analysis of morphological and molecular data. Classification schemes that have stood the test of time for decades have been rigorously tested against the "new" data resulting from molecular studies. In many cases, the delimitations of genera, families, and orders have been supported. In other cases, they have been radically reorganized as previously accepted groupings have been shown not to be as closely related (monophyletic) as previously thought. A **monophyletic** group *must include all the descendants of a shared common ancestor*, may not *include* species that *do not share that common ancestor*, and may not *exclude* species that *do share that common ancestor*. Groupings that fail to adhere to these rules are not to be tolerated, hence the rearranging of groups and reassessment of relationships in response to the "molecular revolution" that has gripped **plant systematics** since the 1990s. This phenomenon of reinterpreting evolutionary relationships and renaming taxonomic groups is not limited to plants and has been taking place in all groups of living organisms. Previously used, but no longer accepted, names for a species are known as **synonyms**, and in some cases in this book a species name will be followed by the phrase "formerly ..." to indicate a synonym.

The "new" APG phylogeny does away with the standard classes and subclasses of earlier systems, replacing these higher taxa with large clades or monophyletic groupings. In some cases, these groupings are well supported by easily observed morphological features, whereas in others the secret is locked away in the DNA, and distinguishing field traits are lacking. The APG has divided the 416 families of the flowering plant phylum into three large clades: the Magnoliids, Monocots, and Eudicots. Overviews of 20-some of the most common families of flowering plants in each of these clades are presented in the following pages.

A plant with bipinnate leaves and stipule scars is a mimosoid legume. It sounds easy, but it takes practice and discipline. Give it a try.

GOING TO THE NEXT LEVEL

The next chapters highlight some of the most common families of plants found throughout the Neotropics and are intended to be easy to read. Appendix 1 describes the features of 50 families in a terse fashion favored by botanists. Ferns are introduced in chapter 12. To learn more about tropical plants, enroll in the Organization for Tropical Studies Tropical Plant Systematics summer course.

Once you have made a family-level determination, the next logical source to consult is the website Digital Flora of La Selva (https://sura.ots.ac.cr/florula4/index.php), which has photos and descriptions of every species of flowering plant found at La Selva. *A Field Guide to the Families and Genera of Woody Plants of Northwest South America* by Alwyn Gentry (1993) is the "Gentry bible" of Neotropical plant identification and is surprisingly user-friendly. Two field guides provide photographs and descriptions of many of the common plants found throughout Costa Rica (Gargiullo et al. 2008 and Zuchowski 2022). *Trees of Panama and Costa Rica* by Condit et al. (2010) is also helpful, but it is biased toward the drier forests of Panama. *Flowering Plants of the Neotropics* by Smith et al. (2004) is an excellent reference summarizing family traits, natural history, and economic uses. Finally, the definitive work is the multivolume *Manual of Plants of Costa Rica* (Manual de Plantas de Costa Rica, http://legacy.tropicos.org/Project/Costa%20Rica). *Plant Identification Terminology: An Illustrated Glossary* (Harris and Harris 2001) is highly recommended for navigating botanical jargon. Keep in mind that because of the rapid pace of changes in taxonomy described in chapter 4, most of these classic sources use family names and describe evolutionary relationships that have since been revised. Nonetheless, they are still excellent resources for tropical botanists. The best resource for updated taxonomy is probably the Tropicos website (www.tropicos.org).

COMMON PLANT FAMILIES

CHAPTER 7

MAGNOLIIDS

The next four chapters contain overviews of common plant families of the Neotropical rainforest. Each section highlights the key morphological features used to identify each family, the ecology of the family, notable species from the La Selva forest, and how humans make use of plants from that family. Why were these particular families chosen out of the many possibilities? They are the most abundant and the ones you are guaranteed to see, they are disproportionately important ecologically, there's a good story to tell, I find them inherently fascinating, or all of the above.

WHAT ARE MAGNOLIIDS?

For several centuries, botanists adhered to the notion that there were two classes of flowering plants, the monocots and dicots, with the monocots being the more primitive and the most likely ancestors of the dicots. (The names monocotyledon and dicotyledon are based on the numbers of leaves [cotyledons] that first emerge as a seedling begins to grow.) Then it became apparent, based on morphology and DNA comparisons, that about 25 families thought to be dicots based on their broad leaves evolved not only prior to the other dicots but before the monocots, the group previously thought to be the most ancient part of the lineage because of their overall simplicity. This group of "early angiosperms" includes what are now known as the "**magnoliids**." Based on vascular tissue anatomy and pollen traits that differ from those of the rest of the dicots, this group was already known to be somehow different, and their status as a separate monophyletic group (clade) was eventually confirmed with molecular evidence.

Magnoliids are mostly woody plants possessing many ancient traits. They lack vessels in their xylem (the cells that conduct water and mineral nutrients), have simple leaves, and emit aromatic terpenoids (think of the smell of pine). Magnoliid flowers are often white, creamy yellow, or even green, rather than brightly colored. The perianth parts (sepals and petals) are free (not fused) and in multiples of three. The numerous carpels are separate (not fused) as well. All but a few have **protogynous** flowers that are functionally female (stigmas presented for pollination) before entering a male phase (releasing pollen). Flowering is often spread over a 2-day period with flowers being female on the first day and male on the second. Beetles, flies, and thrips are the most common pollinators. Nectar is rarely produced. Instead, pollinators are rewarded with pollen, flower tissue, heat, or a place to hide (Endress 2010). Many magnoliids even smell different, producing volatile ethereal oils that give off a "primitive" or "ranalean" odor. Close examination of leaves sometimes reveals pellucid dots representing the oil glands responsible for producing these chemicals. At one point long ago, botanists recognized that some of these primitive plants grew in wetlands, so they became known as the plants that live with the frogs (*Rana*) or the Ranales. This designation has long since been abandoned, but botanists still talk about the "ranalean odor" that is common in these plants. The peppery odor of Piperaceae, general stink of Lauraceae, and make-you-cough blast of Siparunaceae all point to the importance of olfaction in plant identification. Some of the most common families of magnoliids in Neotropical lowland rainforest include Annonaceae (Soursop Family)*, Aristolochiaceae (Dutchmen's Pipe Family), Lauraceae (Laurel Family)*, Myristicaceae (Nutmeg Family)*, Piperaceae (Black Pepper Family)*, and Siparunaceae (Siparuna Family). Family names marked with an asterisk are explored in detail below, while the distinguishing traits of all of these families are covered in Appendix 1.

SOURSOP FAMILY: ANNONACEAE

The **Annonaceae** (Custard Apple/Soursop Family) comprises trees and shrubs with distinctive branching patterns, leaf arrangement, odor, flowers, and fruits (Fig. 7.1). They are abundant in lowland rainforests throughout the Neotropics. Nine genera and 21 species

FIG 7.1 *Anaxagorea crassipetala* displaying the **alternate distichous leaf arrangement** found in **Annonaceae**.

FIG 7.2 Leaf showing "loopy" **brochidodromous venation** common in Annonaceae.

are found at La Selva, the most common of which are ***Anaxagorea***, ***Annona***, ***Cymbopetalum***, ***Guatteria***, and ***Xylopia***.

Clusters of horizontal branches emerge from a single location on the trunk followed by bare trunk before the next cluster of branches emerges. This tiered branching pattern is referred to as "pagoda" or "myristicaceous branching" (after the Nutmeg Family). The simple leaves are strictly alternate and in the same plane (distichous). The secondary veins extend from the midvein toward the leaf margin but never actually reach the margin. Instead, they form a loop that arches toward the adjacent vein (Fig. 7.2). This loopy pattern is known as brochidodromous venation and is characteristic of relatively few families, including the Annonaceae and Moraceae (Fig Family).

Members of the Annonaceae have a characteristic fruity odor that is due to the presence of essential oils, mostly mono- and sesquiterpernes, in their leaves and bark. These plants have been used extensively in folk medicine and when tested in the laboratory have been shown to have promising anti-inflammatory, antibacterial, antimalarial, and anticancer properties (Cascaes et al. 2021). The bark is very fibrous; a thin slice along the length of a twig will reveal the fibers. The so-called strong bark will peel in long strips when a twig is broken. This feature separates the Annonaceae from the closely related Myristicaceae (Nutmeg Family). Indigenous cultures have long used the bark for making rope.

The distinctive flowers are adapted to pollination by beetles that come to flowers to feed upon pollen, as well as the sepals and petals (Fig. 7.3). An inflorescence consists of a single flower, usually originating from a leaf axil. Flowers bear 3 sepals and 2 whorls with 3 petals each, all of which are fleshy and tough. Stamens and carpels are numerous. Flowers are apocarpous, meaning the many carpels are separate from one another. Like many members of the magnoliid clade, Annonaceae flowers are protogynous, with the female parts being receptive to pollinators a day before the stamens begin to release pollen, an arrangement that avoids self-pollination.

The flowers are white, yellow, or greenish yellow. The petals are thick and tough and therefore resistant to snacking by beetles. The flowers generate heat up to 5° above ambient temperatures, which helps disperse a fruity aroma to attract beetles. Similar thermogenesis occurs in flowers of certain species in the Arum, Palm, and Cyclanth families. In the case of the Annonaceae, as the flower first opens, the petals bend over the stigma

FIG 7.3 Thick-petaled flowers of Annonaceae, such as this ***Guatteria amplifolia***, are pollinated by beetles. Note the 6 yellow petals, many yellow stamens, and many green carpels.

to create a pollination chamber. Beetles attracted by the fruity scent squeeze between the petals and enter the chamber. They become imprisoned here for one day. The trapped beetles don't seem to mind as they nibble on the fleshy petals. Thermogenesis may also put the beetles in the mood for mating. The enclosed space of the pollination chamber provides beetles with a safe space where they can feed and mate without worrying about being discovered by predators. The stigma surfaces are covered by a sticky fluid that serves the dual role of trapping pollen and protecting the stigmas from herbivory. The following day, the petals open up and drop from the flower as the stamens begin to release pollen. The beetles consume some of the pollen while getting a dusting of pollen on their entire bodies. They are then free to fly off and visit another flower, where they will deposit some of the pollen onto the stigmatic surfaces of the new flower.

Annonaceae can be divided into two groups based on the types of beetles they attract (Gottsberger 1999, 2012). Beetle pollination is known as cantharophily. The flowers of *Guatteria*, *Xylopia*, and some *Annona* attract small sap beetles (Nitidulidae). The sap beetles are only a few millimeters in length and feed upon pollen. They normally feed on rotting fruit but are attracted to the flowers by their fruity aromas. In contrast to this small beetle pollination syndrome, the larger flowers of *Annona* and *Cymbopetalum* open at night and attract larger scarab beetles (Dynastinae or rhinoceros beetles) that feed on pollen and the petals.

The apocarpous gynoecium matures into one of two different types of fruits. In the first, the carpels remain distinct, producing a cluster of separate fruitlets (monocarps), each with its own little stalk or stipe. In the case of *Guatteria*, the fruits are indehiscent and never open (Fig. 7.4). *Anaxagorea*, *Cymbopetalum* (Fig. 7.5), and *Xylopia* have dehiscent fruits that split open to reveal the seeds. In the case of *Anaxagorea* the seeds are explosively released from the fruits, whereas the others are dispersed by birds that feed on either the fruit capsule or an aril surrounding the seeds. The lengths of the stipes and shapes of the fruits can be useful for making species identifications.

The second fruit type is found in the genus *Annona*, in which the carpels fuse together to mature into an aggregate fruit, the most famous of which is the edible guanábana (Fig. 7.6). These large, pulpy fruits are mammal dispersed.

Their sheer abundance and nutritious fruits make Annonaceae ecologically important in tropical forests. The tasty fruits of guanábana/soursop (*Annona muricata*), and cherimoya/custard apple (*Annona cherimola*) are

FIG 7.4 As the carpels of ***Guatteria*** (Annonaceae) ripen they remain separate, forming many small fruits, or fruitlets.

FIG 7.5 Finger-like fruitlets of ***Cymbopetalum*** (Annonaceae).

FIG 7.6 Aggregate fruits of ***Annona*** (Annonaceae) originate from a single flower with many separate carpels. As they ripen the carpels fuse together to form a single fruit. Photo: Reinaldo Aguilar, Digital Flora of La Selva.

tropical delicacies for human consumption. You should seek out guanábana ice cream in San José or at a local "Pops" ice cream parlor. The Asian species *Cananga odorata* (Ylán-Ylán) is cultivated as an ornamental tree. Its fragrant flowers are the source of oils that are used in perfumes, such as Chanel No. 5.

AVOCADO FAMILY: LAURACEAE

The **Lauraceae**, commonly known as the **Laurel** or **Avocado Family**, is composed of trees and shrubs that are important components of tropical lowland and montane forests (Fig. 7.7). In addition to their numerical abundance and species diversity, they are important ecologically because of their nutritious fruits. Twenty-nine species of Lauraceae inhabit the La Selva forest, more than half of which belong to the genera ***Nectandra*** (5 species) and ***Ocotea*** (15 species). The descriptions below are for these two genera. Recognizing the family is easy, but differentiating genera is very difficult.

Vegetatively, the plants are easy to overlook. The leaves are elliptic in shape with a pointed drip tip (acuminate). They tend to be glossy on the upper surface and often have wavy margins, as well as a J-shaped petiole. The leaves are arranged in an alternate spiral pattern and are often clustered at the tips of branches. The leaves and twigs contain essential oils and when crushed emit an aroma that may be pleasant or foul, often resembling that of an unripe avocado. Secondary veins are forward arching, initially angled toward the leaf margin but then curving and sweeping forward toward the tip of the leaf. The genus *Nectandra* can be distinguished by tertiary veins that are parallel to one another. Lauraceae lack stipules. Another feature of the family is that the twigs are green and randomly flattened.

FIG 7.7 The **Laurel Family** (**Lauraceae**) is characterized vegetatively by alternate leaves with wavy margins, shiny surfaces, and green stems. Note the drip tips on this species.

Some of the most distinctive features of the family can be found in the flowers, but these are very small and not always available for examination. Flowers are trimerous, meaning that parts tend to occur in multiples of three, a characteristic more common in monocots. The presence of trimerous flowers and the odor of essential oils are two traits that led to placement of the family within the magnoliids. There is no differentiation of sepals and petals, so these parts are referred to as **tepals**. The tepals occur in 2 whorls of 3. There are usually 9 stamens produced in 3 whorls. The anthers release pollen through a series of flap-like valves, a trait unique to the family. Nectaries are produced at the base of the stamens, a feature that is reflected in the name of the genus *Nectandra*, derived from Greek words for "nectary" and "stamen." Depending on the species, the flowers may be bisexual or unisexual. Bees, wasps, flies, and moths visit the flowers.

The Lauraceae produce single-seeded fleshy fruits known as drupes (Fig. 7.8). Unlike most drupes, which form a thick, stony covering around the seed (think peach pit), the endocarp of Lauraceae is nothing more than a thin coating surrounding the seed. Think of an avocado, which has a tough outer skin (exocarp), a thick fleshy mesocarp that is edible, and a seed with an easily overlooked endocarp. In the wild, many Lauraceae are referred to as "little avocados" or "aguacatillos." They differ from the cultivated avocado by being small and sitting in a swollen receptacle or cupule. These fruits look like a soft-boiled egg sitting in an egg cup (or a golf ball perched on a tee). The fruit turns green or dark purple as it ripens. The cupule is usually red, creating a contrast with the fruit that is thought to make the fruit more visible to seed-dispersing frugivores. Like that of the cultivated avocado, the flesh

FIG 7.8 **Lauraceae fruits** are green or black when ripe and sit upon a fleshy cupule or receptacle with contrasting red coloration. Leaves of *Nectandra* have parallel tertiary veins. The writing is part of a long-term research project by Dr. Kellie Kuhn (US Air Force Academy).

of wild aguacatillos is rich in fats and nitrogen. They are favorite foods of birds, bats, and monkeys. Certain frugivorous birds highly sought after by birdwatchers, such as trogons, Snowy Cotinga, and the Resplendent Quetzal of highland forests, specialize on these fruits.

Some species form mutualistic associations with ants. Research conducted at La Selva was the first to document the association between *Ocotea pedalifolia*, ants, and mealy bugs (Stout 1979). Ants live within hollow spaces in the stems of the tree and readily attack insect intruders or remove their eggs from the leaves. The ants encourage the growth of mealy bugs within these chambers. The mealy bugs feed on the phloem of the plant while the ants feed on honeydew excreted by the mealy bugs. Phloem-feeding bugs excrete waste that is essentially dilute phloem that has flowed through the insect faster than it can be digested. Ants often feed on this so-called honeydew. The cost to the plant of hosting mealy bugs is hypothesized to be outweighed by the protective benefits provided by the ants.

Humans value Lauraceae for several purposes. Neotropical trees are the source of valuable timber. Avocados are valued for the fruits as well as for the medicinal properties of their leaves. The cultivated avocado, *Persea americana*, from Central America is unusual for its size and lack of a cupule. Whatever animal once ingested its fruits and dispersed the large seeds is believed to have been driven to extinction by human hunters during the Pleistocene era. Cinnamon is obtained from the bark of the genus *Cinnamomum* from tropical regions of Asia. Bay laurel, *Laurus nobilis*, from the Mediterranean region is used as a culinary herb.

FIG 7.9 Widely spaced whorls of branches that look like the spokes of a bicycle wheel, so-called myristicaceous or pagoda branching, are characteristic of *Virola* and other species of the **Nutmeg Family** (**Myristicaceae**).

FIG 7.10 Alternate distichous leaves of ***Virola sebifera*** (Myristicaceae).

NUTMEG FAMILY: MYRISTICACEAE

Five species of Myristicaceae occur at La Selva. Two species from the ***Virola*** genus, commonly known as nutmeg, will be explored here. The branching patterns of species in the **Myristicaceae** (**Nutmeg Family**) are so distinctive that it is known as "myristicaceous branching" (Fig. 7.9). The pattern is also known as verticillate branching; multiple branches, oriented perpendicular to the main trunk, arise from the same node. They radiate from the stem like the spokes on a bicycle wheel. The pattern is repeated at regular intervals along the length of the trunk. (A similar pattern is exhibited by some Annonaceae.) The medium-sized leaves of *Virola* have a golden-brown hue as a result of a dense coating of hairs. The veins form raised ridges on the leaf underside and are clearly visible even when looking up from the ground. Leaves are alternately arranged along the stem at regular intervals and in the same plane (distichous). The two species of *Virola*, both known as "fruta dorada" in Costa Rica, can be distinguished by the shape of the leaf and the number of secondary veins. The leaves of ***Virola sebifera*** taper gently from the base to a pointed tip (Fig. 7.10). Pairs (more or less) of secondary veins angle off the midvein and are parallel to neighboring veins. The other species, ***Virola koschnyi***, has many more secondary veins spaced much closer together (Fig. 7.11). The overall leaf shape is different as well, with the widest point of the leaf located near the tip, just before tapering to a sharp point (acuminate).

Fruits consist of a thick capsule that splits to reveal a bright red aril (Figs. 7.12 and 7.13). *Virola* arils resemble flattened fingers that wrap around one another and envelop a single hard seed. The arils of *V. sebifera* are rich

FIG 7.11 Alternate distichous leaves of ***Virola koschnyi***. Differences in leaf shape and number of veins distinguish these two species of *Virola*.

FIG 7.13 ***Virola* fruits**, one of which has split to reveal the seed and surrounding aril.

in fats (54%), protein (7%), and carbohydrates (8%) and represent a rich source of nutrients for certain frugivorous birds (Howe 1981). Of all the arils of tropical trees, those of *Virola* trees are among the most nutritious. Capsules open at dawn and almost instantly birds arrive to feed, carrying 85% of the seeds away from the parent plant.

Birds remove the aril-covered seed from the husk of the capsule, swallow it, grind off the aril in their crops,

FIG 7.12 The husks of ***Virola* fruits** split to reveal a hard, marble-sized seed enclosed in a lacy red aril.

and then regurgitate the seed unharmed (Howe and Kerckhove 1981). This sounds like an unpleasant activity for the birds but seems preferable to the alternative once you consider the size of the seed relative to the rest of the bird's alimentary canal and cloacal opening. The crop of a bird is a waystation for food that needs to be processed or temporarily stored before moving further down the digestive system. It also provides a way to reject items like seeds that are hard, bulky, non-nutritious, and potentially dangerous. The time between a bird's ingesting and subsequently regurgitating a seed provides an opportunity for a plant to get its seeds dispersed. If a bird simply sits in the same tree all day eating and regurgitating seeds, then no real dispersal takes place. If, however, the bird flies off to a different location with seeds in its crop and then regurgitates, successful seed dispersal has taken place.

The suite of birds that feed on *Virola* seeds is surprisingly small, consisting of Slaty-tailed Trogon, Rufous Motmot, Collared Aracari, Yellow-throated Toucan, Keel-billed Toucan, and Masked Tityra, and of these only three make a difference. Yellow-throated Toucans and Keel-billed Toucans are the most important seed dispersers (see chapter 15). The Yellow-throated is the larger of the two toucans and will often drive the smaller species away from a food tree. The much smaller Masked Tityra commonly feeds on *V. sebifera*, but they are not effective dispersers because they simply strip the aril away from the seed and drop the seed directly below the parent tree. Toucans, however, are excellent dispersers of *Virola* seeds. They arrive at trees in the early morning just as the fruits split open to reveal the aril-covered seeds. A toucan will use its long bill to pluck the seed from the capsule, toss it up, and then swallow the entire seed and aril. The aril is

(continued...)

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