

STUDIES ON THE SEEDLING TYPES OF DICOTYLEDONOUS PLANTS (MAGNOLIOPHYTA, MAGNOLIOPSIDA)

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ABSTRACT

Seedlings of dicotyledonous plants can be divided into 17 distinct types based on morphological and functional features of the seedling. The most primitive type of dicotyledonous seedling is that characterized by the genus Polyalthia (Annonaceae), herein termed the "Polyalthia type", as its seedling morphology is similar to that found in the seedlings of Cycas and Ginkgo (Pinophyta), and perhaps similar to those of the seed ferns (Pteridospermopsida). The "Magnolia type" is evolutionarily more advanced. From the Magnolia type, several different evolutionary lines of seedling development arose, with the Magnolia type evolving into different seedling types throughout the Magnoliopsida. Minor specialized seedling types evolved within several of the major lines. However, a number of evolutionary "dead ends" arose from the Polyalthia type which are restricted to families of flowering plants belonging to the Magnoliidae. Neoteny has likely played a major role in the developmental evolution of seed plant seedlings from progymnosperm seedling. The origin of the Polyalthia type from the Pinophyta (especially the seed ferns or Pteridospermopsida) can be explained using neoteny hypotheses. Using the most recent phylogenetic scheme for the Magnoliopsida proposed by Cronquist, the known seedling types for each family are noted.

INTRODUCTION

Early in the sixteenth century, botanists began to study the seedlings of vascular plants. Over the next two centuries, studies characterized the morphological and biological features of the seed-

ling, noting in particular the relationships between the embryo and the resulting seedling. These early workers were struck with the diversity of seedlings found among the flowering plants, and particularly so among the dicotyledonous members (Magnoliophyta, Magnoliop-

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sida). As studies continued into the nineteenth century, more exacting details were learned and the diversity of seedling types documented. Soon, systems of seedling classification were proposed (Klebs 1885).

During the course of the present century, numerous studies have been conducted on seedlings, with the majority concentrating on dicotyledonous plants (e.g., Bokdom 1977; Burger, 1972; Duke 1965, 1969; Grushvitskyi 1963; Muller 1978; Vasilezenko 1960; Vogel 1980; Zhou 1955). Only one (Vogel 1980) has attempted to provide a detailed scheme of classification for dicotyledonous seedlings.

THE BASES FOR THE CLASSIFICATION OF SEEDLING TYPES

Seedling features critical to their classification may be found as the seed germinates and seedling grows. These features are mainly expressed morphologically, but can be influenced by their environment or ecological requirements. In the following section, germinational, morphological and ecological factors relating to the classification of mainly dicotyledonous seedlings are reviewed.

I. Germination Features

Seedlings are typically divided into two types, epigeal and hypogeal. In epigeal plants, the cotyledons withdraw from the seed coat and are carried above the soil level by an elongating hypocotyl. At this time the cotyledons are exposed to light and become photosynthetic. In hypogeal plants the cotyledons do not withdraw from the seed coat, and as the hypocotyl does not elongate, the cotyledons remain

below soil level and do not become photosynthetic. Actually, the distinction is not so simple. There is a great deal of diversity in each type, and some seedlings cannot be easily characterized by either condition (e.g., Rhizophora, the mangrove seedling).

II. Morphological Features

Seedling morphology is critical to any scheme of classification of seedling types. Nonetheless, mere morphology is, in and of itself, not the only characters that can be used. Physiological functions often can determine morphology of seedling structures. Photosynthetic cotyledons are generally thin, while cotyledons with a primary storage function tend to be thick and massive. The elongation of the hypocotyl -- an important morphological character -- while a genetic feature of the species, in some cases, is related to ecologically factors associated with the habitat (see below). If the epicotyl does not elongate, the first true leaves of the seedling are arranged in a rosette. Some cotyledons are morphologically similar to mature leaves, but this is the exception. Most cotyledons are simple and lack the elaborate venation patterns or lobing features of mature leaves. Still, some cotyledons may be lobed while the mature leaves are entire.

The embryo is the originator of the seedling. If the embryo occupies the whole seed and is without endosperm or perisperm, the seed is said to be exalbuminous. If the embryo does not occupy the whole of the seed because of the presence of endosperm or perisperm, the seed is said to be albuminous. The presence or absence of these nutritive substances can determine the function of coty-

ledon of the seedling and thus classification of the seedling into specific types. Furthermore, the size of the embryo influences the seedling type. Large seeds often have thick, food storing cotyledons or hypocotyls, or have massive amounts of endosperm. Such plants often belong to the hypogeal types.

The endosperm or perisperm are technically not part of the seedling. Yet their presence affects the function of the parts of the seedling. In exalbuminous seeds, the cotyledons do not have any absorptive function. Exalbuminous seeds that are photosynthetic are always epigeal, while those that have a storage function are always hypogeal. In albuminous seeds, on the other hand, the cotyledons always have an absorptive function no matter if they are epigeal or hypogeal. In albuminous seeds which are epigeal, however, the cotyledons will be photosynthetic once they are exposed to light, while the cotyledons of a hypogeal seedling remains absorptive.

The fruit wall and testa are not part of the seedling, but whether or not the fruit wall or testa persists around the cotyledons is a character that can be used in the classification of seedling types.

III. Ecological Features

The ecological conditions of a given habitat can determine the general kinds of seedlings present. On the floors of tropical rain forests where the rays of the sun rarely penetrate, the epigeal types of seedlings with their photosynthetic requires are scarce. Here the hypogeal types whose cotyledons have the storage function are common. In the grasslands, how-

ever, epigeal seedlings types are often the only kinds found. Some ecological setting have unusual seedlings. The seacoast mangrove forests are characterized by a special viviparied seedling type, whereas parasitic plants, such as *Cuscuta*, have a simplistic seedling type unique to many parasitic plants.

The above characteristics are not equally important. Some may be important for only a single seedling type. Great stress has been placed on the function of the morphological features in this system of seedling classification. The morphology and function of a plant are not isolated but coincide with each other. In short, function determines morphology and morphology embodies function.

A CLASSIFICATION SCHEME FOR THE SEEDLINGS OF MAGNOLIOPSIDA

The proposed new classification of dicotyledonous seedlings is based on my research in the field and laboratory using many species native to the People's Republic of China, as well as those which have been introduced into my native country. In addition, I have consulted a large body of literature (see the literature cited section below) which has concentrated on the study of seedling types in both the temperate and tropical regions of the world. I have concentrated mainly on the works published in English, German and Russian as well as a few studies published to date in Chinese.

The following system tends to stress functional features and not merely morphological ones. The proposed system is somewhat similar to that published by Vogel (1980). In the

appendix, I have attempted to show the areas of agreement and disagreement in the two systems by providing a summary of the seedling types in those families of dicotyledonous plants recognized by Cronquist (1981). Vogel tended to stress seedling development stages and their respective morphologies. This works well when one has seeds in hand and is able to follow the development of the seedling. With the growing need to identify seedlings, especially for agricultural purposes, it is equally important to be able to recognize seedlings "in the field". Therefore, I have given less emphasis to developmental stages than Vogel. In my opinion, knowledge of the general habitat can often allow one to determine the functions associated with the various structures of the seedling. Thus, the combination of function and morphology makes for excellent "field" characters in classifying types of seedlings.

Some efforts, such as that by Muller (1978) who wrote keys to individual species, work well for geographically limited regions of the world -- especially the temperate portions of the world. In the tropics, however, such an effort is at yet impossible although Duke (1965, 1969) and Burger (1972) have presented studies showing the kinds of efforts that can be made for certain groups of tropical species.

My effort is to provide a set of general features which may be used to define groups of seedlings. At this stage, this will be an aid in the study of the phylogeny of the Magnoliopsida. In time, I hope, this system of seedling classification will become more sophisticated and will be able to more exactly define evolutionary units within the dicotyledonous

plants. Finally, with time, it is hoped that a system of classification can be developed for all dicotyledonous plants no matter the species or where, in the world, the plant is found.

A total of 17 seedling types are recognized in the present paper. Vogel (1980) recognized a total of 16 seedling types, with a number of subdivisions within some types. Our definitions of seedling types do not always overlap and a summary table of our similarities and differences is presented below.

1. *Polyalthia* Type (fig. 1)

The mature seed is filled with copious endosperm and the embryo is very small. During germination the cotyledonary petioles elongate first; they push out the radicle, hypocotyl and plumule from the testa. The radicle emerges and develops into a sturdy root system, while the hypocotyl fails to elongate and remains subterranean. The cotyledons have an absorptive function, remain embedded in the testa, and absorb the nutrients from the endosperm. Both the fruit wall and the testa, or only the testa, remain persistent around the cotyledons. The fruit wall and the testa are shed with the cotyledons. The epicotyl and plumule grow upward and elongate into a shoot. Leaves may be spirally arranged, or the first two may be opposite. All leaves may be fully developed at the seedling stage, or the lowest ones may be scale-like.

The *Polyalthia* type of seedling is characteristic of a portion of the Annonaceae, and is the only known type in the Myristicaceae, both members of the Magnoliales. It is found, with the *Magnolia* type, in the Aristolochiaceae. Paeoniaceae only has this type of seedling. The *Polyalthia* type is rare in

the more advanced families, being otherwise found only in Euphorbiaceae.

2. Euryale Type (fig. 2)

The mature seed is filled with copious endosperm and the embryo is very small. During germination the epicotyl elongates and the plumule develops and breaks out of the testa at the apex of the seed. The cotyledons, however, remain in the testa where they serve as a haustorium which absorbs the nutrients from the endosperm. The cataphylla are lanceolate or sagittate. There is a transition from the narrow cataphylla to true leaves which take an orbicular form. The radicle and hypocotyl are abortive, and at the apex of the epicotyl are enormous adventive roots which form the root system of the seedling.

The Euryale type is typical of hydric species. It likely evolved from the *Polyalthia* type. This type is rare and specialized, being recorded so far only from the Nymphaeaceae.

3. Mezzetiopsis Type (fig. 3)

The mature seed is filled with copious endosperm and the embryo is small. During germination the radicle is pushed out from the testa and grows downward developing the root system. The hypocotyl elongates and is either curved in a loop above the ground or is erect and carries the cotyledons, enclosed in the testa, above the soil. The cotyledons have an haustorial function and absorb the nutrients from the endosperm. The cotyledons remain in the testa and attached to the top of the hypocotyl, and thereby block the development of the epicotyl and plumule. In this condition the seedling enters a resting stage during which the nutrients of the endosperm are transferred

into the hypocotyl which becomes rather sturdy. The cotyledons and testa are shed together and then the plumule develops into a shoot. Only rarely does the plumule start to develop before the cotyledons and testa are lost.

This type of seedling is common in Annonaceae. It is otherwise infrequent and rather scattered (e.g. Menispermaceae, Euphorbiaceae, Rubiaceae) in the Magnoliopsida.

4. Magnolia Type (fig. 4)

The mature seed is filled with copious endosperm and the embryo is small. The cotyledons have both the absorptive and photosynthetic functions. During germination the radicle breaks out of the testa and grows downward developing into the root system. At the same time the hypocotyl elongates and brings the cotyledons to a position above the soil level. At first, while the cotyledons are still underground, they have an absorptive function taking nutrients from the endosperm. However, upon reaching the soil level, the cotyledons withdraw from the testa, unfold, expand, and when exposed to light take on a photosynthetic function. The epicotyl and plumule develop into a shoot. In most instances, the first few leaves are well developed and spirally arranged. Occasionally the first two leaves are opposite.

The Magnolia type is the most common in the Magnoliopsida. More than half of the dicotyledonous plant families have this type of seedling, at least in part. The Magnolia type is the only type found in such less advanced families as Magnoliaceae, Illiciaceae, Degeneraceae and Monimiaceae. Likewise, it is the only type in such more advanced families

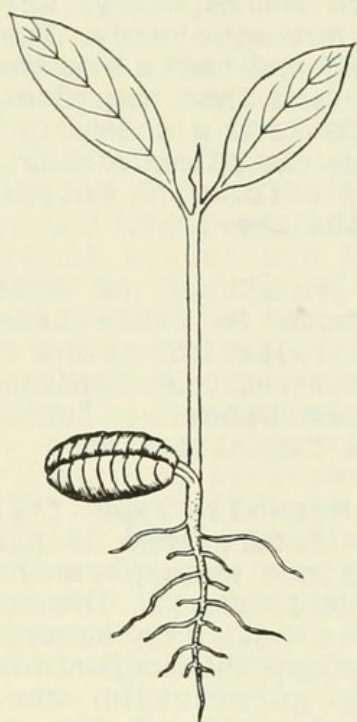


Fig. 1. Polyalthia type
Polyalthia cerasoides (Roxb.)
 Benth. et Hook. f. ex Bedd.
 (Annonaceae)

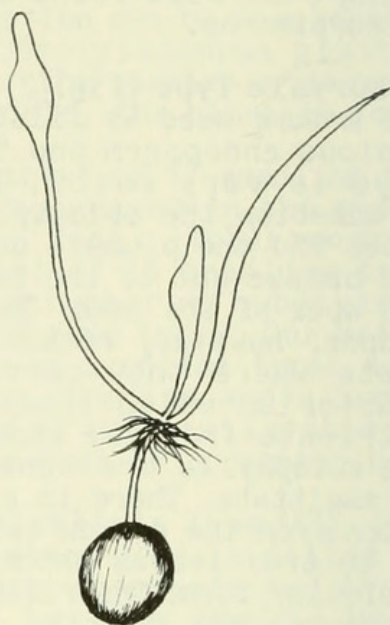


Fig. 2. Eurale type
Eurale ferox Salisb.
 (Nymphaeaceae)

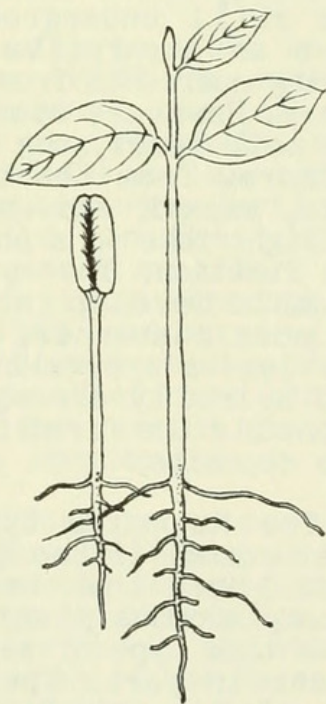


Fig. 3. Mezzettiopsis type
Mezzettiopsis creaghii Ridl.
 (Annonaceae)

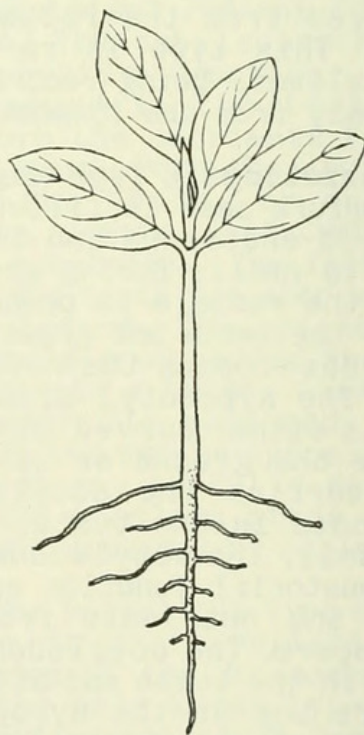


Fig. 4. Magnolia type
Magnolia denudata Desr.
 (Magnoliaceae)

as Convolvulaceae, Scrophulariaceae, Gesneriaceae, Campanulaceae, Caprifoliaceae and Dipsacaceae.

5. *Peperomia* Type (fig. 5)

The mature seed is filled with copious endosperm and the embryo is very small. During germination the cotyledonary petioles elongate and push the hypocotyl and radicle from the testa. The radicle grows downward and forms a tap root. The hypocotyl does not elongate but remains subterranean. One of the cotyledonary petioles continues to elongate, withdraws the cotyledonary blade from the testa, grows upwardly and exposes the blade to light whereupon it assumes a photosynthetic function. The other cotyledon remains in the testa below the soil level and absorbs the nutrients from the endosperm.

The *Peperomia* type has only been recorded from species of *Peperomia* (Piperaceae).

6. *Cyclamen* Type (fig. 6)

The mature seed is filled with abundant endosperm and the embryo is small. During germination the radicle breaks out of the testa first, grows downward and forms a taproot. The hypocotyl does not elongate but remains subterranean where it becomes swollen and tuberlike taking on a food storing function. The cotyledons do not develop well, are generally scale-like, and may even abort. The epicotyl often does not develop and even it will abort. The plumule produces only a single leaf with a long petiole during the seedling stage. When subsequent leaves do emerge, the internodes do not elongate and the leaves are often arranged in a rosette.

The *Cyclamen* type is known only in herbaceous dicotyledonous plants of temperate and

cold regions. To date, it has been found in *Anemone* (Ranunculaceae), *Corydalis* (Fumariaceae), and *Cyclamen* (Primulaceae).

It should be noted that the reports of a "monocotyledonous" embryo for *Cyclamen* (Cronquist 1981) are without foundation (see Vogel 1980).

7. *Sterculia* type (fig. 7)

The mature seed is filled with copious endosperm and a large, thin embryo. During germination the radicle emerges first and grows downward forming the root system. The hypocotyl elongates and extends the cotyledons above the soil level. At first the endosperm surrounds the cotyledons and the cotyledons are absorptive, but as the cotyledons separate, the endosperm adheres to the undersurface of each of the cotyledon blades forming a compound structure which does not separate until shedding. Once the cotyledons are exposed to light, they have a photosynthetic function. The epicotyl and the plumule develop into a shoot. The first two leaves are always opposite, and the subsequent leaves are spirally arranged.

The *Sterculia* type is rare and has been recorded only in *Sterculia* (Sterculiaceae). This type is probably a specialization of the Mezzettiopsis type.

8. *Cinnamomum* Type (fig. 8)

The mature seed is exalbuminous and the embryo is large and occupies the whole of the seed. During germination the radicle emerges first, grows downward and develops a sturdy taproot system. The hypocotyl does not elongate and remains subterranean. Only rarely does it elongate and carry the cotyledons above the soil level. The massive cotyledons are enclosed in

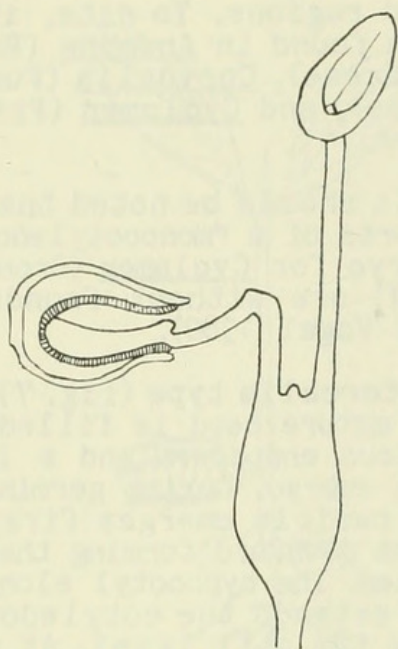


Fig. 5. Peperomia type
Peperomia peruviana Dahlst.
 (Piperaceae)
 (after Hill 1906)

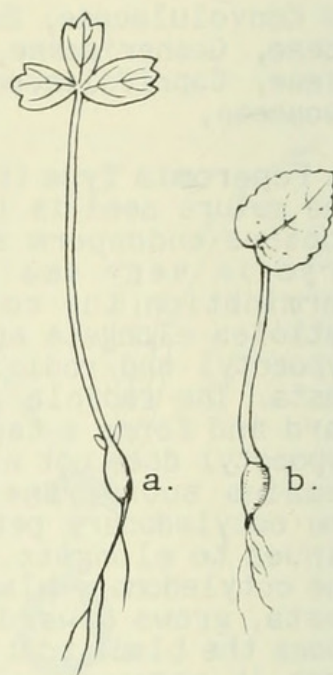


Fig. 6. Cyclamen type
 a. *Anemone nemerosa* L.
 (Ranunculaceae)
 b. *Cyclamen persicum* Mill.
 (Primulaceae - after Csapody 1968)

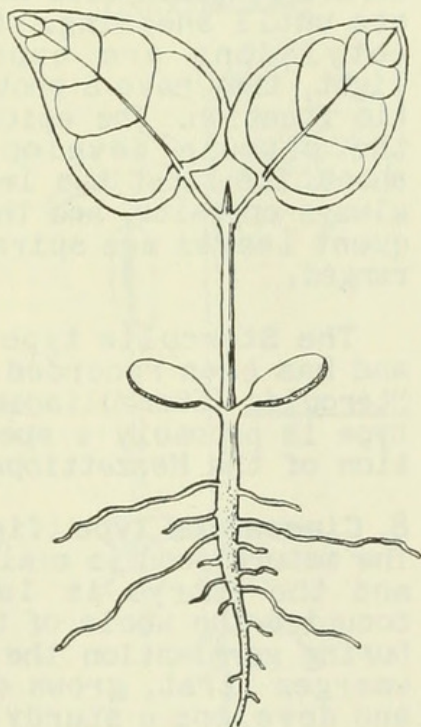


Fig. 7. Sterculia type
Sterculia lanceolata Cav.
 (Sterculiaceae)

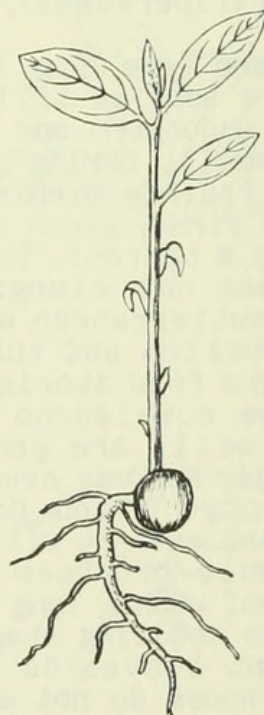


Fig. 8. Cinnamomum type
Cinnamomum camphora (L.) Presl
 (Lauraceae)

the testa and have a food storage function. The epicotyl and plumule emerge opposite the root and gradually develop into a shoot. At first only spirally arranged, scale-like leaves are seen. Gradually, these give way to normal leaf development.

The *Cinnamomum* type is common among families of woody Magnoliopsida with exalbuminous seeds bearing large embryos and massive cotyledons. Seedlings of this type may be seen in Lauraceae, Fagaceae, Juglandaceae, Bombacaceae, Connaraceae, Mimosaceae, Caesalpinaceae, Rosaceae, Combretaceae, Sapindaceae, Burseraceae, Anacardiaceae, Simaroubaceae, and Bignoniaceae. In a strict sense only Lauraceae belongs to the *Cinnamomum* type. As noted below in the discussion of the *Chimonanthus* type, the seedlings of the others families referred to the *Cinnamomum* type (which diagnostically cannot be distinguished from those in the Lauraceae) probably evolved secondarily from the *Chimonanthus* type.

9. *Ceratophyllum* Type (fig. 9)

This type of seedling is a specialized hydric form. Its essential characteristics are the aborted radicle, the poorly developed (or even aborted) hypocotyl, and the exalbuminous seeds. There are two subtypes.

9a. *Ceratophyllum* Subtype (fig. 9a)

The mature seed is exalbuminous and has a small but well developed embryo (*Ceratophyllaceae*) or one that is scarcely differentiated into parts (*Urticularia*). During germination the cotyledons break out of the testa, grow upward, and while still under the water, take only a photosynthetic function when exposed to light. The plumule develops into a shoot. Its leaves are linear, with the

first pair always inserted into the node of the cotyledons; the remaining leaves are whorled. The radicle is aborted, and no adventitious roots are formed.

The *Ceratophyllum* type is reported only in *Ceratophyllaceae* and in the genus *Urticularia* (*Lentibulariaceae*).

9b. *Nelumbo* Subtype. (fig. 9b)

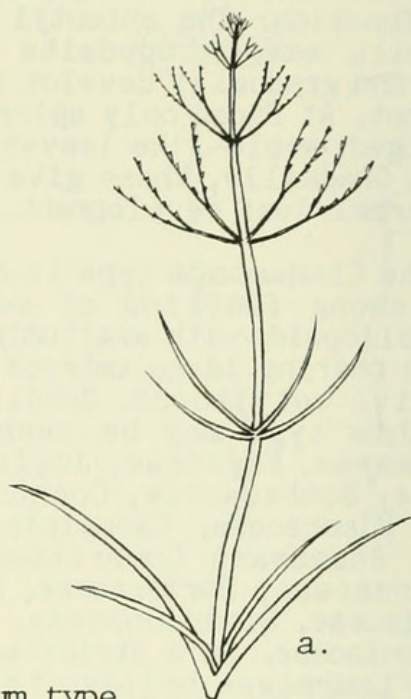
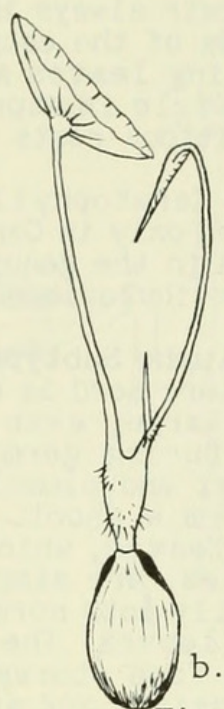
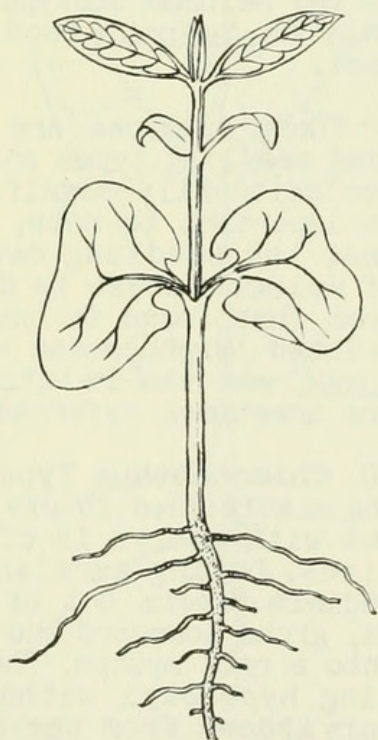
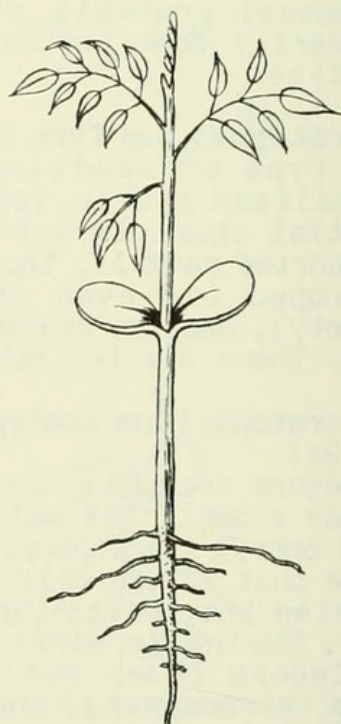
The mature seed is exalbuminous and a large, even edible embryo. During germination the epicotyl and plumule break out and form a shoot. The shoot's first leaves, which have long petioles, are simple and pass gradually into normally developed leaves. The cotyledons have a food storage function, are massive, and are adnate to each other at the base. The radicle and hypocotyl both abort and at the node of the stem, many adventitious roots are formed.

The *Nelumbo* subtype is known only in *Nelumbo* (*Nelumbonaceae*).

These subtypes are specialized seedling types and are not evolutionarily significant. It is important to note, however, that the seedling development of *Nelumbonaceae* is different from that found in the closely related *Nymphaeaceae* where *Nelumbo* and its related genera are sometimes referred.

10. *Chimonanthus* Type (fig. 10)

The mature seed is exalbuminous but with embryo is of various sizes. During germination the radicle breaks out of the testa, grows downward and develops into a root system. The elongating hypocotyl withdraws the cotyledons from the testa and lifts them above the soil level. Subsequently, the cotyledons unfold and assume a photosynthetic function. The epicotyl may or may not deve-

Fig. 9. *Ceratophyllum* typeb. *Nelumbo* subtype*Nelumbo nucifera* Gaertn.
(*Nelumbonaceae*)a. *Ceratophyllum* subtype*Ceratophyllum demersum* L.
(*Ceratophyllaceae*)Fig. 10. *Chimonanthus* type
Chimonanthus praecox (L.) Link
(*Calycanthaceae*)Fig. 11. *Sophora* type
Sophora japonica L.
(*Fabaceae*)

lop. The plumule develops into a shoot and its first leaves generally are well developed and arranged spirally or opposite.

The *Chimonanthus* type, named for the genus *Chimonanthus* of the Calycanthaceae, is essentially the same as the *Macaranga* type proposed by Vogel. Unfortunately, he placed both albuminous and exalbuminous members in his type. The *Chimonanthus* type does resemble the *Magnolia* type, where Vogel placed of his *Macaranga* type families, but the *Chimonanthus* is here defined as those families in which the seeds are always exalbuminous.

This is a common seedling type in both herbaceous and woody members of Magnoliopsida being found with equal frequency in the more primitive and more advance families. Like the *Magnolia* type, this seedling type is exceedingly common and widespread in the Magnoliopsida. The *Chimonanthus* type likely gave rise to the derived *Cinnamomum* type as noted above. The two differ in that the *Chimonanthus* type seedlings are epigeal with thin, photosynthetic cotyledons, while the seedlings of the *Cinnamomum* type are hypogeal with massive, non-photosynthetic cotyledons. An examination of recent phylogenetic systems of classification for the Magnoliopsida (Bedell & Reveal 1983) shows that these two conditions occur in overlapping families. It is likely that in most of the advanced dicotyledonous families, the *Cinnamomum* type secondarily evolved from the *Chimonanthus* type.

11. *Sophora* Type (fig. 11)

The mature seed is exalbuminous and the embryo is fairly large. During germination the radicle breaks out of the testa and

grows downward forming a sturdy taproot. The cotyledons are fleshy and even massive due to their food storing function, yet the hypocotyl elongates and brings the cotyledons to or above the soil level. Once exposed to light, the cotyledons assume a photosynthetic function. Shortly thereafter, the cotyledons are shed. When the epicotyl and plumule develop into a shoot, its first two leaves are always opposite while the subsequent leaves are arranged spirally or are opposite.

The *Sophora* type is derived from the *Chimonanthus* type, differing only in the massive nature of the cotyledons. This seedling type is found in the Rosaceae, Fabaceae, Dipterocarpaceae, Anacardiaceae Meliaceae among other families.

12. *Ternstroemia* Type (fig. 12)

The mature seed is exalbuminous and a large embryo. During germination the seed splits along the margin and the hypocotyl emerges. The radicle grows downward and develops into a root system. The erect hypocotyl is fusiform and has a food storage function. The two cotyledons are either small and scale-like or lacking entirely. When the plumule develops into a shoot, the first leaves are always scale-like, but the next ones are fully developed. The leaves are spirally arranged or the lower two may be opposite.

The *Ternstroemia* type is derived from the *Chimonanthus* type, differing in its reduced or abortive cotyledons and swollen hypocotyl. This type is known only from the Lecythidaceae and the Ternstroemiaceae (included in the Theaceae by Cronquist 1981).

13. *Garcinia* Type (fig. 13)

The mature seed is exalbuminous

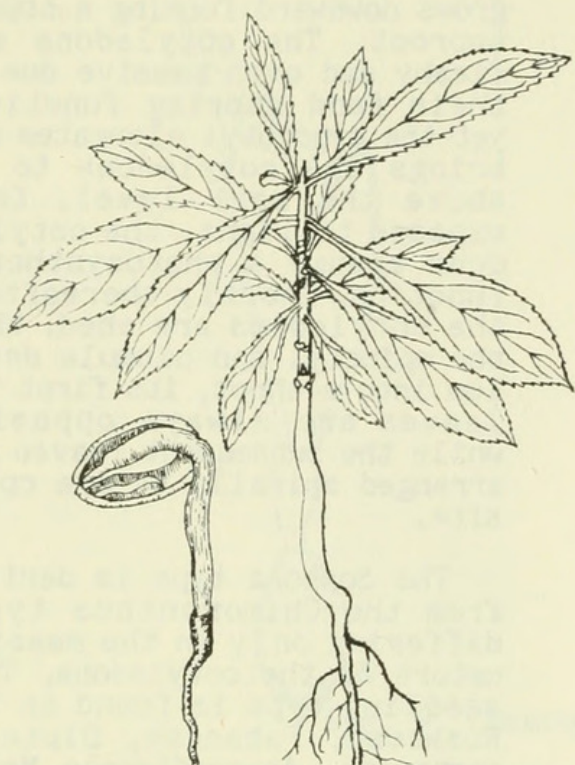


Fig. 12. Ternstroemia type
Ternstroemia elongata (Korth.) Koord
 (Theaceae - after Vogel 1980)

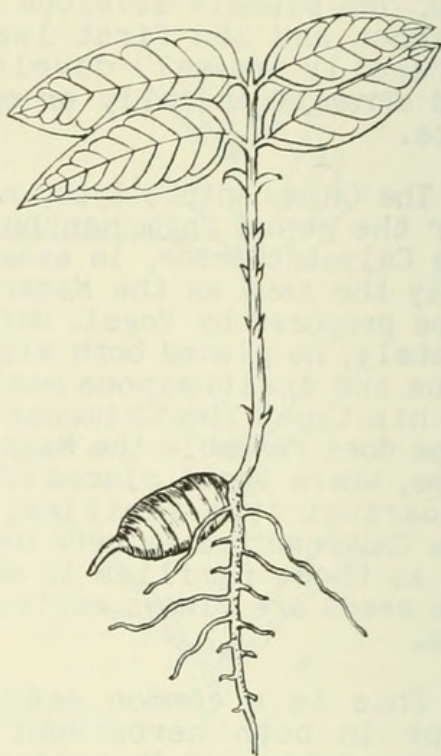
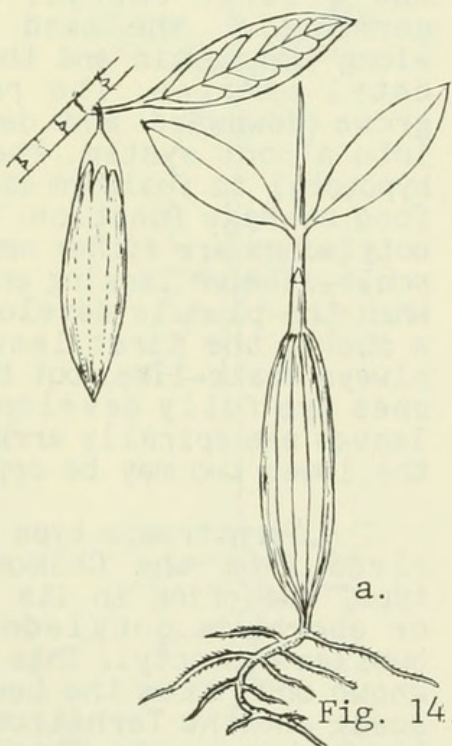
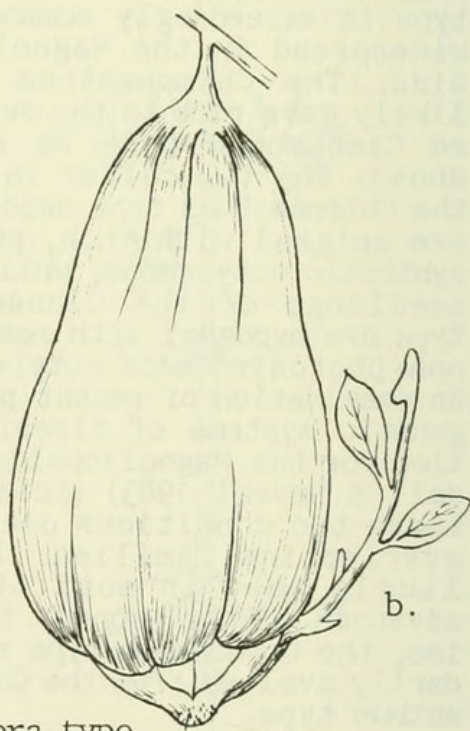


Fig. 13. Garcinia type
Garcinia oligantha Merr.
 (Clusiaceae)



a. Rhizophora subtype
Bruguiera sexangula (Lour.) Poir.
 (Rhizophoraceae)



b. Sechium subtype
Sechium edule Sw.
 (Cucurbitaceae)

and the embryo is mostly large. During germination either the radicle breaks out of the testa and grows downward and develops into a sturdy root system, or the primary root does not develop fully or fails to develop altogether. If the primary root fails, an accessory root can develop at the junction between the epicotyl and the hypocotyl which will replace the primary root. The hypocotyl is a massive, swollen body with a food storing function. It completely fills the testa which remains persistent until long after germination. The cotyledons are rudimentary or absent due to abortion. The epicotyl and plumule develop into a seedling shoot. Its first leaves are always scale-like and spirally arranged or opposite. Such first leaves gradually pass into normal leaves.

The *Garcinia* type of seedling is rare. It has been reported only in the tropical genus *Garcinia* (Clusiaceae) and in *Barringtonia* (Lecythidaceae).

14. Rhizophora Type (fig. 14)

The essential characteristics of this type is the vivipary which is the result of specialized ecological conditions. Two subtypes can be distinguished.

14a. Rhizophora Subtype (fig. 14a)

The mature seed is albuminous and the embryo often large and green. During germination the hypocotyl (with the radicle) breaks out of the testa and fruit wall of the young fruit and grows downward, developing into a large fusiform body which slowly enlarges and accumulates food. The cotyledons are reduced; they have an absorptive function and serve to pass nutrients (including salt) from the parent plant to the growing seedling before it de-

taches. When the fruit is mature (defined as when the cotyledons are detached or the fruit petiole is broken), the seedling drops from the parent plant. The seedling, depending on the weight of the hypocotyl (and the depth of the water under the tree) may either plant itself in the mud or fall into the water, drift ashore, and quickly develop a sturdy root system. Only at this time does the epicotyl and plumule emerge and develop a shoot. All the leaves are decussate, and the lowest pair are always scale-like.

The *Rhizophora* Subtype has been recorded from the mangrove genera of Rhizophoraceae, in *Avicenia* (Verbenaceae), and in *Aegiceras* (Myrsinaceae). Like other types of seedling associated with aquatic habitats, this subtype is a highly specialized modification and is of no particular phylogenetic significance.

14b. Sechium Subtype (fig. 14b)

The mature seed is exalbuminous and the embryo is large. During germination the cotyledons enlarge and break out of the testa from one side, attaching directly onto the fleshy fruit wall and absorbs nutrients from the young fruit. Subsequently, the cotyledons rapidly enlarge 2-3 times their previous size, and push the immature radicle and hypocotyl out of the fruit, but these structures do not develop further. The epicotyl and plumule elongate and develop into a seedling shoot without tendrils. The first leaves are scale-like, but subsequent leaves gradually develop into normal, spirally arranged leaves. The seedling remains in this condition until the parental plant dies. Upon its death, the viviparous seedlings fall to the ground.

The *Sechium* Subtype is known only from a monotype genus, *Sechium* (Cucurbitaceae), native to tropical South America. The edible fruit of *S. edule* Swartz contains one enormous seed.

15. *Loranthus* Type (fig. 15)

The mature seed is filled with copious endosperm and a small embryo. During germination the hypocotyl and radicle (which cannot be readily differentiated) jointly break out of the fruit wall and form a short column. Shortly thereafter the end of the column enlarges and forms a haustorial disk covered with a glutinous substance. The cotyledons, which have an absorptive function, remain in the seed and absorb the nutrients from the endosperm. In some, the cotyledons will withdraw from the fruit wall, but have no significant photosynthetic function. If the seedling germinates on a suitable host, the haustorial disk will attach itself to the host and grow into its tissue. The plumule will then develop into a seedling shoot and eventual produce normal leaves. The resulting plant is hemiparasitic as the mature plant is fully photosynthetic.

The *Loranthus* type is restricted to representative, hemiparasitic genera of Loranthaceae and Viscaceae.

16. *Pyrola* Type (fig. 16)

The mature seeds is filled with copious endosperm and a small embryo. During germination the radicle breaks out of the testa, grows downward, and develops into a taproot. The hypocotyl and the cotyledons abort, or occasionally the hypocotyl elongates and brings the cotyledons above the soil level. The plumule aborts and adventitious buds form the seedling shoots.

The *Pyrola* type is known only from *Pyrola* (Pyrolaceae) and some genera belonging to the Gesneriaceae.

17. *Orobanche* Type (fig. 17)

The mature seed is filled with copious endosperm and a very small, essentially undifferentiated embryo. During germination a slender, unbranched axis develops, yet there is not differentiation between the radicle and the hypocotyl. Before contact with a host, the axis elongates, and when contact is made, a haustorial disk is formed at the point of contact which pierces the epidermis of the host plant and fuses with its tissue. A parastic life thus is established.

The *Orobanche* type is unlike any normal type of seedling development. As such it is of no particular phylogenetic significance. It is reported in *Orobanche* (Orobanchaceae) but should be expected in other genera of the family as well, the monotypic Cuscutaceae, and perhaps some species of Balanophoraceae and Pyrolaceae (notably the genus *Moneses*).

ORIGIN AND EVOLUTION OF THE SEEDLING CONDITION

Seedlings were long divided into two types, epigeal and hypogeal. Little agreement has been reached as to which of these two conditions was the most primitive. Vasilezenko (1946) stated with certainty that the hypogeal condition was the more primitive. This contradicted the earlier conclusion of Compton (1912) and Takhtajan (1948) that the epigeal condition was the less advanced of the two.

Vasilizenko argued that the hypogeal type was found among the primitive families of seed plants, notably Cycadaceae and

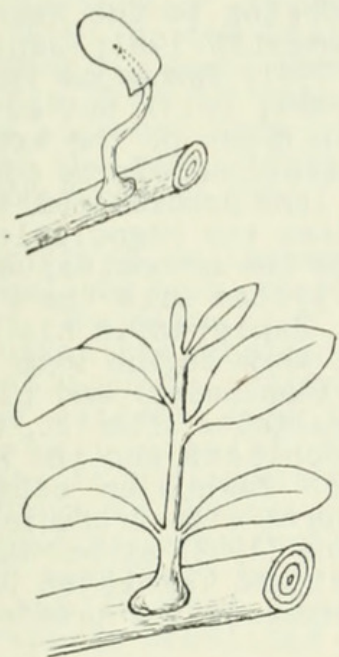


Fig. 15. Loranthus type

Loranthus parasiticus (L.) Merr.
(Loranthaceae)

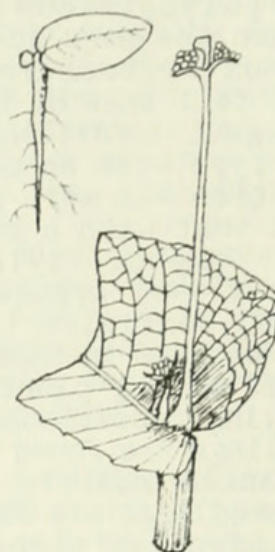


Fig. 16. Pyrola type

Monophyllaea horsfieldii R.Br.
(Pyrolaceae)
(see Serebriakov 1952)

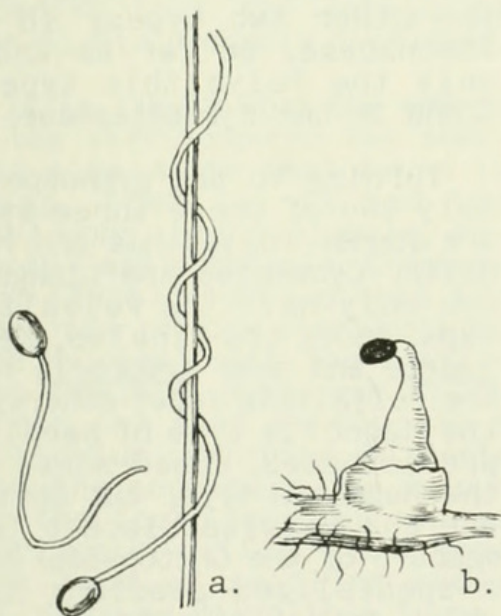
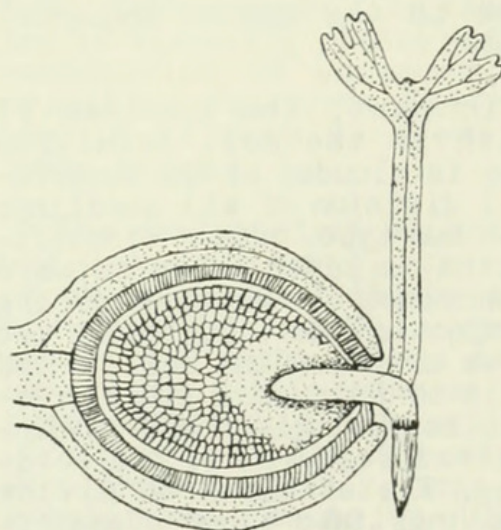


Fig. 17. Orobanche type

a. *Cuscuta chinensis* Lam.
(Cuscutaceae)

b. *Orobanche minor* Sutton
(Orobanchaceae)
(after Caspody 1968)

Fig. 18. The seedling of a
pteridosperm

(after Chamberlain 1935)

Ginkgoaceae, and that in the Magnoliopsida, the hypogeal condition was more predominant among the polypetalous angiosperms than the more advanced gamopetalous members. Grushvitski (1963) felt that of the two major hypogeal conditions, the cotyleon type with an absorptive function was more primitive than that with a storage function. Compton (1912) and Takhtajan (1948) argued that the epigeal condition is more primitive because in those families of flowering plants with both seedling conditions, epigeal seedlings are found in the less advanced members while hypogeal seedlings are found in the more advanced members of the same family. Hill and De Fraine (1913) and Grushvitski argued that the epigeal condition was more primitive because the epidermis of the cotyledons of the hypogeal type (which are located underground) have stomata, and therefore must have evolved from a cotyledon type that had stomata. In short, the exposed epigeal condition gave rise to the hidden hypogeal type.

In part, the problem of which is the most primitive type is clouded by the superficial division of all seedlings into two type. Such a classification is based on an outward phenomenon -- whether during germination the cotyledons are above or below the soil -- and fails to scrutinize other critical morphological and physiological features of the seedling. The attempts to divide seedlings into finer classificatory groupings, such as proposed here, should permit a more exact resolution of the problems relating to the origin and evolution of the seedling.

It is generally agreed that the most primitive of the extant flowering plants are those

belonging to the Magnoliidae (Cronquist 1981; Dahlgren et al. 1981; Takhtajan 1980; Thorne 1981, 1983). Not all concur which order of the extant Magnoliidae should be considered the less specialized. Cronquist defines the Magnoliales to include the Annonales, and begins his system with the Winteraceae. Dahlgren in his most recent work begins with Annonaceae (Annonales) and places the Magnoliales after it, the Aristolochiales and the Rafflesiaceae. Takhtajan essentially concurs with Cronquist, while Thorne (1983) agrees with Cronquist and Takhtajan that Winteraceae is the premiere family.

Among the Magnolales as defined by Cronquist, there are three seedling types: the Polyalthia, Mezzettiopsis and Magnolia types. Winteraceae has the Magnolia type (Lubbock 1892), as does Magnoliaceae itself, and it is found, with the other two types, in the Annonaceae. So far as known, only the Polyalthia type is found in the Myristicaceae.

Turning to the gymnosperms, only two of these three types are found: Polyalthia and Magnolia. Cycadales and Ginkgoaceae only have the Polyalthia type. Among the Pinales, Keteleeria and some Araucaria have the Polyalthia type; otherwise, the Magnolia type of seedling predominates. Ephedraceae has the Magnolia type, but Gnetaceae and Welwitschiaceae (all members of the Gnetopsida) have a specialized seedling type which cannot be compared with those found among the Magnoliopsida.

The Cycadopsida and Ginkgopsida are considered to be more primitive than the Pinopsida, with all three not having "a common ancestor short of the

Archaeopteridales" (Cronquist 1971, p. 419). On the basis of this finding, it would seem the *Polyalthia* type of seedling would be somewhat more primitive than the more widespread and common *Magnolia* type.

The origin of angiospermous plants has long been considered a mystery. The majority of most modern botanists consider that the Magnoliophyta originated from the extinct seed ferns (e.g., see Cronquist 1968, 1981), the Pteridospermopsida of the Pinophyta. Unfortunately, no pteridosperm fossil embryos or seedlings have been found, and in fact, Taylor (1981) reports seedlings only for fossil members of Araucariaceae (it is the *Polyalthia* type of seedling!). This is not surprising for like *Cycas* and *Ginkgo* of today, the seeds of pteridosperms likely matured and were dropped from the parent plant before the embryo developed. It was only after ripening that the embryo of such plants probably developed.

It is likely that the embryo of the pteridosperms was somewhat similar to that found in *Cycas*, that is, it had two cotyledons, and a plumule, hypocotyl and a radicle. Chamberlain (1935) proposed that the seedlings of the pteridosperms were hypogeal with the cotyledons remaining subterranean and within the seed serving as a haustorium absorbing nutrients from the endosperm. He drew a hypothetical seedling for a pteridosperm (fig. 18), and this type of seedling would fall into my *Polyalthia* type.

From the above evidence, the *Polyalthia* type of seedling must be considered the most primitive. That is, the seedling arose from an albuminous seed, with the cotyledons remaining subterranean and absorp-

tive. Among the early Magnoliopsida, this kind of seedling is the only type found in the Myristicaceae, and occurs with two other seedling types in the Annonaceae. The Myristicaceae are not the most primitive type of angiosperm as the plants are dioecious and this is a specialization. Although Dahlgren and his fellow workers (1981) argue that Annonaceae is the most primitive family, I believe the most ancient surviving angiosperm is the Winteraceae which has a *Magnolia* type of seedling.

How does one explain this? In evolutionary processes, the speed of each stage in the development of morphological features of the plant body is not necessarily in concert. Thus, in some families with more specialized (or advanced) flowers (features which tend to be emphasized in systems of angiosperm classification), other less obvious features (such as anatomical characteristics) may not be so specialized. Thus one can find families of flowering plants with a combination of advanced and primitive features. The same should be true to seedling types as well.

The most ancient angiosperm was likely a small tree or shrub (Stebbins 1965; Doyle & Hickey 1976), with a xylem system consisting only of tracheids, and a flowering structure composed of many parts (Cronquist 1968). The seeds were probably fairly large and albuminous (Takhtajan 1964), and the resulting seedling was of the *Polyalthia* type.

Although I have affirmed that the *Polyalthia* type of seedling is the most ancient, how can the existence of stomata on the cotyledons of hypogeal seedlings, and those of

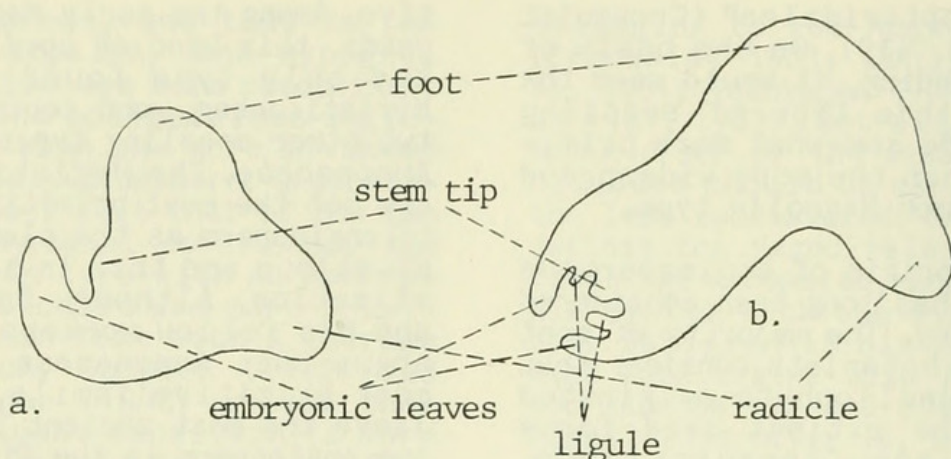


Fig. 19. The embryo structure of the fern. (a.) *Pteridium aquilinum* (b.) *Selaginella martensii*. Both figures simplified; see Smith 1955.

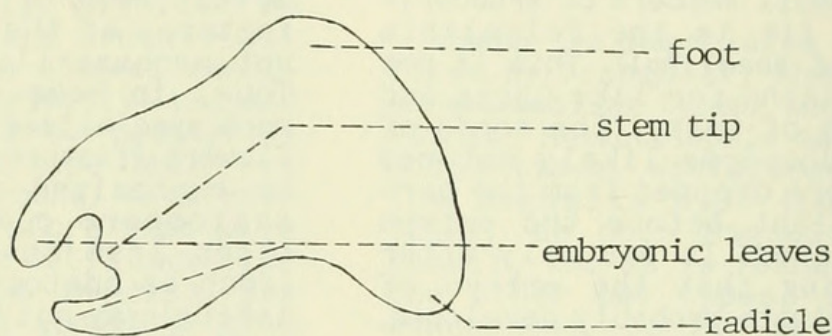


Fig. 20. The hypothetical structure of a progymnosperm embryo.

Cycas and Ginkgo be explained? This condition must be traced back to a fern group known as the progymnosperms or Archaeopteropsida of Polypodiophyta. It is likely that the seed ferns evolved from the progymnosperms, and therefore the embryo of both taxa were not only different (as obvious by the fact one formed seeds and the other did not), but that they were related as well (if one evolved from the other). The embryo of the true fern may be generally divided into a stem tip, an embryonic leaf, a radicle and a foot (fig. 19a). I believe the embryo of the progymnosperm (fig. 20) was not

like that of the true ferns, however, but rather more like Selaginella (fig. 19b) where one also finds a stem tip, a radicle and a foot as before, but now two embryonic leaves. While I do not suggest that the progymnosperms evolved from the Lycopodiophyta, the similarities are striking. The stem tips develops into the shoot; the radicle develops into a primary root; the foot is a haustorium which absorbs nutrients from the female gametophyte; and, the embryonic leaves develop into seedling leaves (which are in the position of cotyledons) which have stomata. I postulate that the

embryo of the seed fern lacked a foot, that the plumule of the seed fern corresponded to the stem tip of the progymnosperm, that the radicles corresponded in each taxon, and that the cotyledons of the seed ferns correspond to the first two embryonic leaves of the progymnosperms.

I am the first to admit that the morphological shifts represented by the evolution of the seed habit was a qualitative leap, and certainly the embryonic changes from the progymnosperms to the seed ferns must have been a qualitative leap as well. This was manifested in the loss of the foot, and in the embryonic leaves remaining in the female gametophyte where they served as an haustorium to replace the function of the foot. We can use the neoteny hypothesis to explain this process (see Takhtajan 1976). When the embryo of the progymnosperm evolved into the embryo of the seed fern, the foot of the former disappeared in the developmental process of the embryo. The two embryonic leaves at the early period of the differentiation matured quickly so that they did not have to enlarge further, and thus (1) did not have to grow above the soil level, and (2) were not required to assume a photosynthetic function. In short, the seed leaves later period of development was arrested, and their function changed from a photosynthetic one to an absorptive one. Thus, the photosynthetic first leaves of epigeal progymnosperm seedlings were changed, via neoteny, into the haustorial cotyledons of hypogeal seed ferns. Evolutionarily, the stomata of the cotyledons that have remained in hypogeal seedlings likely have done so because they have been neither selected for or against (Grant 1971).

EVOLUTIONARY RELATIONSHIPS AMONG DICOTYLEDONOUS SEED- LING TYPES

There are four basic types of dicotyledonous seedlings, namely *Polyalthia*, *Magnolia*, *Chimonanthus* and *Cinnamomum*. Within the primitive families of the Magnoliopsida, all four types are found. In fact, three of the four types occur in the Magnoliales and nine of the 17 types recognized in this paper are found in the Magnoliidae as defined by Cronquist (1981). As can be seen, even the most primitive angiosperms displayed a wide array of seedling plasticity.

Like the evolution of the dicotyledonous subclasses, the evolution of the seedlings found in the Magnoliidae produced an array to dead ends, with only a single successful line of development continuing into the Asteridae (fig. 21). It was the *Magnolia* type that gave rise to a series of addition basic groups, notably the *Chimonanthus* type which can be separated into four groups each of which is associated with a major dicotyledonous subclasses, notably an expression here-in called the *Hamamelis* group (*Hamamelididae*), a *Thea* group (*Dilleniidae*), a *Rosa* group (*Rosidae*), and finally a *Aster* group (*Asteridae*). A small number of additional types evolved as more specialized seedling expressions (*Sophora*, *Garcinia* and *Ternstroemia*). All of these came from various groups of the *Chimonanthus* type.

The loss of endosperm allowed the *Magnolia* type to evolve into the *Chimonanthus* type. It was through a series of minor modifications, all within the *Chimonanthus* theme, that the *Chimonanthus* type gave rise repeatedly to the *Cinnamomum* type. These are not technically

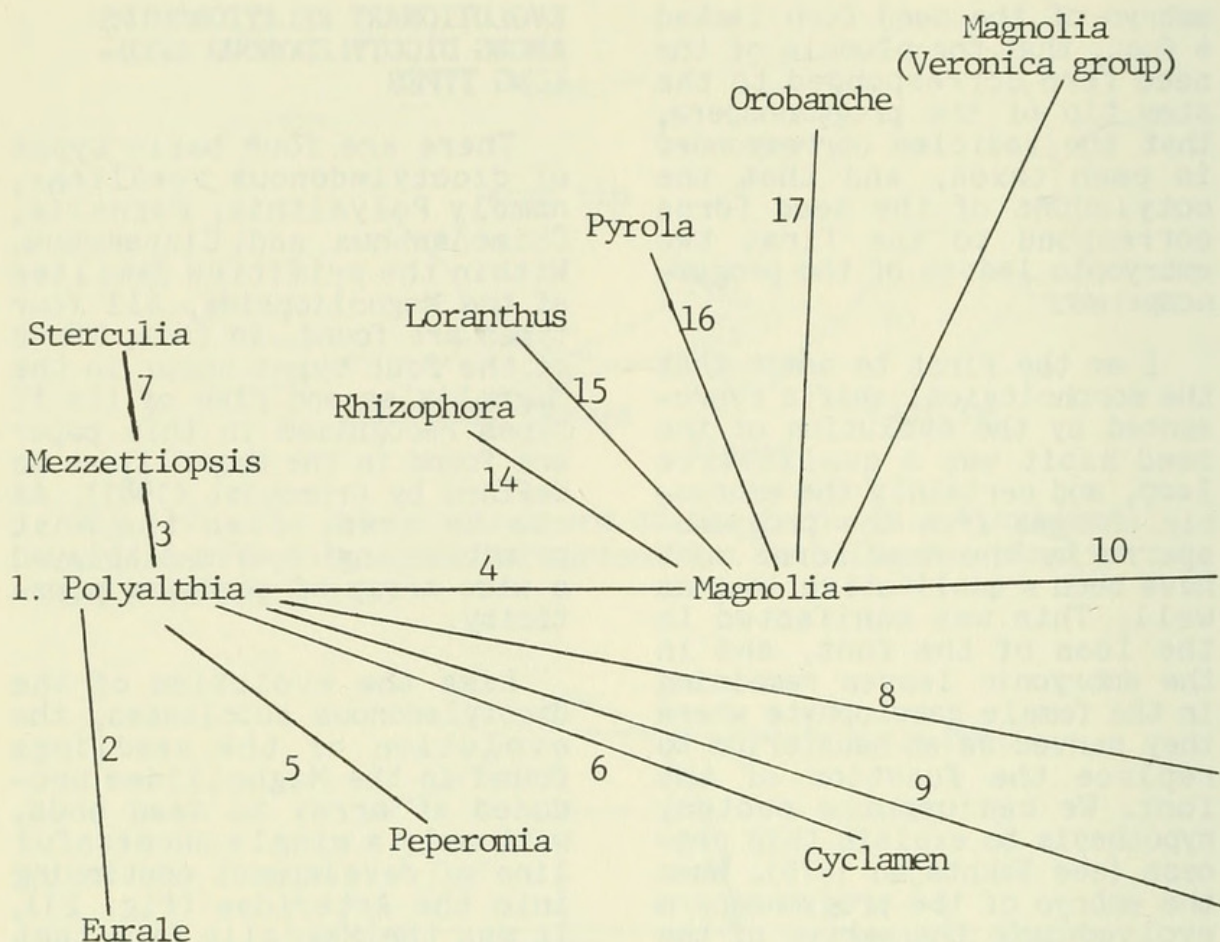
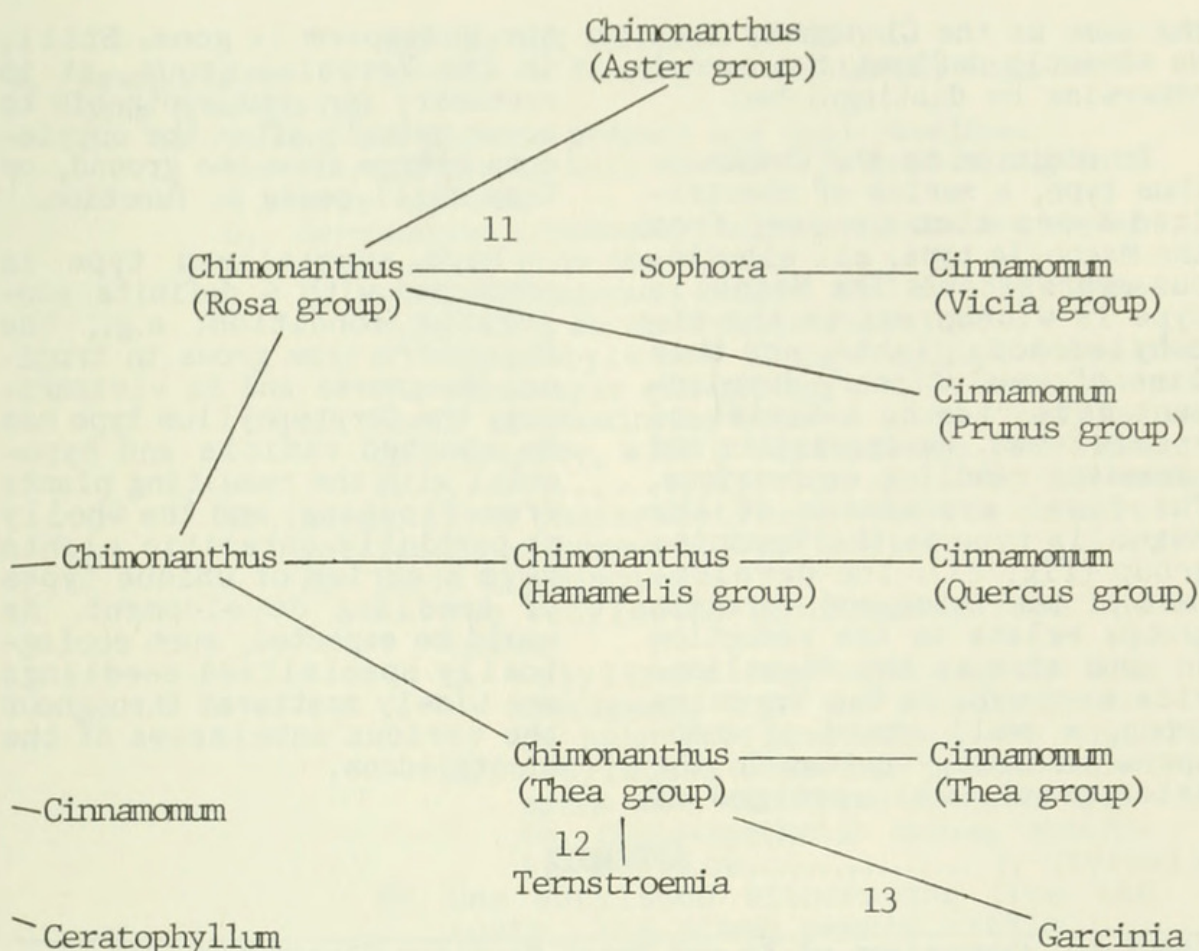


Fig. 21. Evolutionary Relationship of Magnoliopsida Seedling Types. -- From the original Polyalthia type evolved a number of specialized lines of seedling development. Only the Magnolia type evolved further. Line 2 is an aquatic form of the Polyalthia type, evolving into the Eurale type as a result of the abortion of the hypocotyl and radicle. In line 3, the Mezzettiopsis type, the hypocotyl of the Polyalthia type elongates and extends the cotyledons, endosperm and testa to a point above the soil level. From this type, line 7 to the Sterculia type, evolved with the cotyledons and its surrounding endosperm withdrawing from the testa, but with the endosperm adhering to the lower surface of the cotyledons. Line 5 to the Peperomia

type evolved as a specialized line from the Polyalthia type in which one cotyledon extends above the soil level and is photosynthetic, while the other remains in the testa. In line 6, to the Cyclamen type, the hypocotyl become swollen and forms a tuber, with poorly developed or aborted cotyledons. The resulting seedling has but a single leaf. In lines 8 and 9, the endosperm is lost. Line 8 consists of plants with massive cotyledons which have a storage function (Cinnamomum type), while in line 9 (Ceratophyllum type) the hypocotyl and radicle are aborted. Line 4 to the Magnolia type is representative of seedlings in which the hypocotyl elongates from the endospermous seed, and the cotyledons become photosynthetic. As with the Polyalthia type, a



number of specialized lines evolved from the Magnolia type. Those plants with viviparous seedlings formed line 14, the Rhizophora type. In line 15, the Loranthus type, the radicle end of the seedling forms a haustorium. In line 16, the Pyrola line, the plumule aborts and the adventitious buds form the seedling shoot. A truly parasitic line (line 17) leads to the Orobanche type. Here the seedling becomes simple and the end of the radicle forms an haustorium. The final expression of the Magnolia type is its Veronica group in which small seeds with little endosperm occur. Line 10, the Chimonanthus line, evolved from the Magnolia type and may be recognized by the absence of endosperm. From various expressions within the epigeal Chi-

monanthus type, herein called the Rosa, Hamamelis and Thea groups, specialized seedling types developed involving a change to a hypogeal condition with the cotyledons becoming massive and assuming a storage function. This resulted in the formation of a series of isolated groups all of the Cinnamomum type. The Sophora type, line 11, differs from the Chimonanthus type only the somewhat swollen cotyledons. The Ternstroemia type (line 12) is a line of epigeal seedlings with aborted cotyledons and a swollen hypocotyl. The Garcinia type, line 13, is a line of hypogeal seedlings with aborted cotyledons and a massive hypocotyl. The ultimate line in the exalbuminous seedlings is the Aster group of the Chimonanthus type which has small seeds.

the same as the *Cinnamomum* type as strictly defined, but cannot otherwise be distinguished.

In addition to the *Chimonanthus* type, a series of specialized types also evolved from the *Magnolia* type, all albuminous expressions. The *Magnolia* type is widespread in the dicotyledonous plants, and this line of evolutionary development gave rise to a series of specialized, hemiparasitic and parasitic seedling expressions. The final expression of the *Magnolia* type is the *Veronica* group (fig. 21). The development of the *Aster* and *Veronica* groups relate to the reduction in seed size as the *Magnoliopsida* evolved. In the *Veronica* group, a small amount of endosperm persists, whereas in the *Aster* group, all vestiges of

the endosperm is gone. Still, in the *Veronica* group, it is necessary for photosynthesis to occur quickly after the cotyledons emerge from the ground, or they shall cease to function.

Each specialized type is concerned with a definite ecological condition; e.g., the *Rhizophora* type grows in tropical mangroves and is viviparous; the *Ceratophyllum* type has an aborted radicle and hypocotyl with the resulting plants free-floating; and the wholly or partially parasitic plants have a series of unique types of seedling development. As would be expected, such ecologically specialized seedlings are widely scattered throughout the various subclasses of the dicotyledons.

APPENDIX

TABLE I. Comparison of Ye and Vogel Seedling Classification

Ye	Vogel	Vogel	Ye
1 Polyalthia	6a, 7a	1 Macaranga	4, 10
2 Eurale	--	2a Sloanea	4, 11
3 Mezzettiosis	7b, 8, 10	2b Palagium	8
4 Magnolia	1, 2a	3 Sterculia	7
5 Peperomia	11c	4 Ternstromia	12
6 Cyclamen	5	5 Cyclamen	6
7 Sterculia	3	6a Heliciopsis	1, 8
8 Cinnamomum	2b, 6a, 6b, 7a, 7b, 8, 11b, 12	6b Koordersiodendron	8
9a Ceratophyllum	--	7a Horsfieldia	1, 8
9b Nelumbo	--	7b Pseudavaria	3, 8
10 Chimonanthus	1	8 Blumeodendron	3, 8
11 Sophora	2a, 11a	9 Rhizophora	14a
12 Ternstromia	4	10 Coscinium	3
13 Garcinia	13, 14	11a Eudertia	11
14a Rhizophora	9	11b Chisocheton	8
14b Sechium	--	11c Streblus	5
15 Loranthus	--	12 Cynometra	8
16 Pyrola	--	13 Barringtonia	13
17 Orobanche	16	14 Garcinia	13
		15 Hodgsonia	--
		16 Orobanche	17

KEY TO THE SEEDLING TYPES

- A. Seedling not viviparous or forming an haustorial tip; seedling free-living.
- B. Cotyledons and plumule present and well developed.
- C. Terrestrial plants with the radicle developing into a sturdy taproot.
- D. Germination cryptocotylar, the cotyledons never withdrawing from the testa.
 - E. Seeds albuminous; embryo small; cotyledons thin, with an absorptive function.
 - F. Hypocotyle not elongating.....1. Polyalthia
 - FF. Hypocotyle elongating..... 3. Mezzettiopsis
 - EE. Seeds exalbuminous; embryo large; cotyledons massive, with a foodstorage function..... 8. Cinnamomum
- DD. Germination phanerocotylar, with one or more cotyledons withdrawing from the testa.
 - E. Seeds albuminous.
 - F. Two cotyledons withdrawing from the testa.
 - G. Cotyledons not adhering to the endosperm, thin and photosynthetic on both surfaces..... 4. Magnolia
 - GG. Cotyledons adhering to the endosperm when withdrawn from the testa, photo-synthetic above, absorptive below..... 7. Sterculia
 - FF. One cotyledon withdrawing from the testa, the other remain within..... 5. Peperomia
 - EE. Seeds exalbuminous.
 - F. Cotyledons thin and leaf-like, only with a photosynthetic function..... 10. Chimonanthus
 - FF. Cotyledons somewhat thick and fleshy, with foodstorage and some photosynthetic functions..... 11. Sophora
- CC. Aquatic plants with the radicle and hypocotyl aborted and never emerging from the seed.
 - D. Seeds albuminous; cotyledons with an absorptive function..... 2. Eurale
 - DD. Seeds exalbuminous; cotyledons with a food storage or photosynthetic function.
 - E. Cotyledons with a photosynthetic function, thin and green..... 9a. Ceratophyllum
 - EE. Cotyledons with a food storage function, massive and yellowish..... 9b. Nelumbo
- BB. Cotyledons or plumule reduced or absent; seedling with only a single leaf, or if more, then the cotyledons reduced or absent and the hypocotyl swollen.
- C. Plumule not aborted.
 - D. Seedling with a single leaf..... 6. Cyclamen
 - DD. Seedlings with more than a single leaf; cotyledons reduced or absent; hypocotyl swollen.
 - E. Seedling free from both the testa and the fruit wall..... 12. Ternstroemia
 - EE. Seedling not free from the testa and/or the fruit wall which remains persistent around

- the swollen hypocotyl..... 13. *Garcinia*
 CC. Plumule aborted; cotyledons sometimes reduced.....
 16. *Pyrola*
 AA. Seedlings viviparous or forming an haustorium.
 B. Seedlings viviparous.
 C. Hypocotyl fusiform..... 14a. *Rhizophora*
 CC. Hypocotyl not fusiform..... 14b. *Sechium*
 BB. Seedlings forming an haustorium.
 C. Seedlings green..... 15. *Loranthus*
 CC. Seedlings non-photosynthetic..... 17. *Orobanche*

The following appendix attempts to summarise the known seedling types (according to the system presented in this paper) for the Magnoliopsida. The families not represented indicate families of flowering plants which remain to have their seedling examined. I would appreciate reprints of papers dealing with families which have been examined but for which I have not seen the published reports. The system of classification here is that proposed by Cronquist (1981). I have not attempted to bring his system up to date (see Cronquist 1983).

I. Magnoliidae

1. Magnoliales
 1. Winteraceae - 4
 2. Degeneriaceae - 4
 3. Himantandraceae
 4. Eupomatiaceae
 5. Austrobaileyaceae
 6. Magnoliaceae - 4
 7. Lactoridaceae
 8. Annonaceae - 1, 3, 4
 9. Myristicaceae - 1
 10. Canellaceae
2. Laurales
 11. Amborellaceae
 12. Trimeniaceae
 13. Monimiaceae - 4
 14. Gomortegaceae
 15. Calycanthaceae - 10
 16. Idiospermaceae
 17. Lauraceae - 8
 18. Hernandiaceae - 8
3. Piperales
 19. Chloranthaceae
 20. Saururaceae
 21. Piperaceae - 4, 5
4. Aristolochiales
 22. Aristolochiaceae - 1, 4
5. Illiciales

23. Illiciaceae - 4
24. Schisandraceae
6. Nymphaeales
 25. Nelumbonaceae - 9b
 26. Nymphaeaceae - 2
 27. Barclayaceae
 28. Cabombaceae
 29. Ceratophyllaceae - 9a
7. Ranunculales
 30. Ranunculaceae - 4, 6
 31. Circaeasteraceae
 32. Berberidaceae - 4
 33. Sargentodoxaceae
 34. Lardizabarabaceae - 4
 35. Menispermaceae - 3, 4
 36. Coriariaceae
 37. Sabiaceae - 4
8. Papaveraceae
 38. Papaveraceae - 4
 39. Fumariaceae - 4, 6
- II. Hamamelididae
9. Trochodendrales
 40. Tetracentraceae
 41. Trochodendraceae
10. Hamamelidales
 42. Cercidiphyllaceae
 43. Eupteleaceae
 44. Platanaceae - 4
 45. Hamamelidaceae - 4
 46. Myrothamnaceae
11. Daphniphyllales
 47. Daphniphyllaceae
12. Didymelales
 48. Didymelaceae
13. Eucommiales
 49. Eucommiaceae - 4
14. Urticales
 50. Barbeyaceae
 51. Ulmaceae - 4, 10
 52. Cannabaceae - 4
 53. Moraceae - 4, 8, 11
 54. Cecropiaceae
 55. Urticaceae - 10
15. Leitneriales
 56. Leitneriaceae
16. Juglandales
 57. Rhoipteleaceae

58. Juglandaceae - 8,
10
17. Myricales
59. Myricaceae - 10
18. Fagales
60. Balanopaceae
61. Fagaceae - 8, 10
62. Betulaceae - 8, 10
19. Casuarinales
63. Casuarinaceae - 10
- III. Caryophyllidae
20. Caryophyllales
64. Phytolaccaceae - 4
65. Achatocarpaceae
66. Nyctaginaceae - 4
67. Aizoaceae - 4
68. Didiereaceae
69. Cactaceae - 4
70. Chenopodiaceae - 4
71. Amaranthaceae - 4
72. Portulacaceae - 4
73. Basellaceae - 4
74. Molluginaceae - 4
75. Caryophyllaceae - 4
21. Polygonales
76. Polygonaceae - 4
22. Plumbaginales
77. Plumbaginaceae - 4
- IV. Dilleniidae
23. Dilleniales
78. Dilleniaceae - 4
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