

OBSERVATIONS ON THE STRUCTURE AND
CLASSIFICATION OF THE PYROLEAE

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Having discussed the natural classification of the Monotropoideae (1941) and Rhododendroideae (1944), as indicated by studies of the microscopic structure, I now deal in the same fashion with a third distinct group within the same order of plants. I believe that it is right to call this order by the first name applied to it as such, namely Bicornes L. The rule that a group cannot be published by enumeration of the included groups seems merely an excuse for breaches of priority and not entitled to respect.

HISTORY

The tribe Pyroleae coincides with the genus *Pyrola* as delimited by Linnaeus (1753). Radius (1821) tells us that the name *Pyrola* was introduced by Brunfels, and cites those naturalists who first discovered or recognized the six species named by Linnaeus: only the names were original with the latter. These species are moderately divergent, and most subsequent authorities have distributed them among two or more genera. All agree, however, that none of them is to be placed quite apart from the others, and that no additional forms, belonging with them and conceivably representing additional genera, have been discovered. The names of the species of *Pyrola* known to Linnaeus, and those of the genera subsequently based upon them, are as follows.

1. *Pyrola rotundifolia* is the obvious type of *Pyrola* and has been construed as such by all authorities except one. Alefeld (1856) made the group typified by it a distinct genus *Thelaia*.

2. *Pyrola minor* is typical of the genera *Erxlebenia* Opiz, 1852¹, and *Amelia* Alefeld.

3. *Pyrola secunda* was treated by Alefeld as the typical *Pyrola*. As a segregate from *Pyrola*, it has been named *Ramischia* Opiz and *Actinocyclus* Klotzsch (1851).

4, 5. *Pyrola umbellata* and *P. maculata* belong to the genus *Chimaphila* Pursh (1814).

6. *Pyrola uniflora* typifies the genus *Moneses* Salisbury, 1821.

Linnaeus (1764) placed *Pyrola* in the natural order Bicornes; Jussieu (1789) placed it in order Ericae. I have not had access to various other early essays in natural classification, and draw a part of the following information from a discussion by Domin (1915). The Pyroleae were so named as a separate order or

¹Dates in parentheses are references to literature cited. Dates not in parentheses are those of publications which I have not been able to consult, and do not list.

family by Lindley, 1821, and this group was renamed Pyrolaceae by Agardh, 1825. In 1830, Lindley included the monotropoid plants in his order Pyroleae. De Candolle (1839) admitted as distinct orders both Monotropeae and Pyrolaceae. He misplaced among the latter the genus *Galax*; this mistake gave him occasion to apply to the typical examples the name Pyroleae as that of a tribe. Asa Gray (1848) included both Pyroleae and Monotropeae in Ericaceae; Bentham and Hooker (1876), while maintaining a separate order Monotropeae, included Pyroleae in Ericaceae. Klotzsch (1851) had followed Lindley to the extent of combining the pyrolid and monotropoid plants in a separate order which he called Hypopithieae. Drude (1889) maintained the same group as the family Pirolaceae, placing it before Ericaceae as if definitely more primitive.

The most recent comprehensive treatment of the group is by Andres (with whom, in happier times, I had the honor and benefit of regular correspondence) in a series of papers (1909–1936) the main item of which (1914) is in effect my point of departure and primary object of criticism. In it, Andres followed in many respects the usage of Drude. He conscientiously misspelled *Pyrola* and the names derived from it; declared the family typified by it to be primitive as compared with Ericaceae; and construed this family as including the Monotropoideae. The system of the pyrolid plants was in outline as follows:

Pirolaceae subfamily 1. *Pirolloideae* Dumortier. This is to be understood as including a single tribe *Piroleae*.

Genus 1. *Ramischia* Opiz. 1. *R. secunda* (L.) Garcke, in all northern continents; 2. *R. truncata* Andres in eastern North America.

Genus 2. *Pirola* Salisb. [!]

Subgenus 1. *Amelia* Hook. f. 1. *P. minor* L., in all northern continents.

Subgenus 2. *Thelaia* Hook. f.

Section 1. *Ampliosepala* Andres. Sepals short, triangular. The subsections are distinguished by details of the texture and form of the leaves.

Subsection 1. *Elliptica* Andres. 2. *P. elliptica* Nuttall in North America; 3. *P. alpina* Andres in Japan and North America.

Subsection 2. *Obscura* Andres. 4. *P. chlorantha* Swartz in all northern continents; 5. *P. renifolia* Maximowicz, 6. *P. soldanellifolia* Andres, 7. *P. morrisoniana* Hayata, 8. *P. gracilis* Andres, 9. *P. atropurpurea* Franchet, all in eastern Asia.

Subsection 3. *Scotophylla* Andres. 10. *P. spathulata* (Alefeld) Andres; 11. *P. aphylla* Smith; both from western North America.

Subsection 4. *Rotundoides* Andres. 12. *P. uliginosa* Torrey, in North America.

Anomalous species: 13. *P. oxypetala* Austin, in New York.

Section 2. *Euthelaia* (Alefeld) Andres. Sepals elongate.

Subsection 1. *Erxlebenia* (Opiz) Andres. Sepals tongue-shaped, more than one-third and less than half as long as the corolla. 14. *P. sororia* Andres in eastern Asia; 15. *P. media* Swartz in northern Europe and Asia; 16. *P. Faurieana* Andres, 17. *P. Corbieri* Leveillé, 18. *P. nephrophylla* Andres, in eastern Asia; 19. *P. Sartorii* (Alefeld) Hemsley in Mexico; 20. *P. paradoxa* Andres in western North America.

Subsection 2. *Alefeldiana* Andres. Sepals lance-acuminate, at least half as long as the petals. The three included groups are distinguished by details of the form of the leaves.

Group 1. *Genuina* Andres. 21. *P. Forrestiana* Andres in eastern Asia; 22. *P. rotundifolia* L. in all northern continents; 23. *P. japonica* Siebold; 24. *P. americana* Fernald [actually of Sweet]; 25. *P. subaphylla* Maximowicz in eastern Asia; 26. *P. asarifolia* Michaux in eastern North America; 27. *P. bracteata* Hooker in western North America.

Group 2. *Amoena* Andres. 28. *P. decorata* Andres and 29. *P. alba* Andres in eastern Asia.

Group 3. *Pictoides* Andres. 30. *P. septentrionalis* Andres, 31. *P. blanda* Andres, and 32. *P. Conardiana* Andres, in western North America.

Genus 3. *Moneses* Salisbury. 1. *M. uniflora* (L.) Salisb., in all northern continents.

Genus 4. *Chimaphila* Pursh.

Section 1. *Aristata* Andres. 1. *C. japonica* Miquel.

Section 2. *Campanulata* Andres. 2. *C. umbellata* (L.) Nuttall [actually of Barton] in all northern continents; 3. *C. maculata* (L.) Pursh in eastern North America; 4. *C. Menziesii* Sprengel in western North America.

In Andres' other papers one finds minor variations from the framework of classification just set forth. In 1936 he added *P.*

coreana (said to be a subspecies, though designated by a binomial) and *P. sumatrana*, both placed next to *P. japonica*. His elaborate system of categories was extended downward into an elaborate subdivision of the collective species *P. rotundifolia*. This complication of classification is objectionable as a matter of taste and expediency rather than of fact and hypothesis. One can express the opinion that certain species are related by placing them under a common key-heading and by listing them in succession; it is not necessary to make of every such cluster a named subgeneric group.

Rydberg (1914) referred duly to Andres when dealing with the North American pyrolid plants in a work which goes to the extreme in avoiding recognition of subsidiary categories. In his treatment, these plants were the family Pyrolaceae, of five genera, *Pyrola*, *Erlebenia* (*Pyrola minor* L.), *Ramischia*, *Moneses*, and *Chimaphila*. Under *Pyrola*, eighteen species were recognized; three of Andres' species were reduced, two new species were described, and six older ones reduced or overlooked by Andres were restored.

Henderson (1919) studied extensively the macroscopic and microscopic structure of the pyrolid and monotropoid plants, and concluded that these groups are not primitive, but derived from Ericaceae.

Fernald has discussed specific limits in the group of *Pyrola rotundifolia* (1904) and has shown (1941) that *P. virens* Schweigger is the right name of the species generally known as *P. chlorantha*. Camp has dealt with specific limits in *Chimaphila* (1939) and among the allies of *Pyrola picta* (1940).

Several morphological contributions, old and new, will be cited below.

MATERIAL AND METHODS

Alefeld opened his classic paper with the words, "Im Sommer 1845 fand ich einmal auf einem ganz kleinen Raume 6 deutsche Arten von *Pyrola* L. beisammen. Dies veranlasste mich, diese Pflanze näher zu untersuchen und vergleichen." My introduction to the group was by a quite similar experience: in the summer of 1920, I saw at Jonesville (a locality in Butte County, California, at an altitude of about 1500 m.) seven distinct races of Pyroleae.

The plants growing at Jonesville have afforded the mass of my material. This has been supplemented by the generous contributions of correspondents. On the present occasion as on former ones, it is a pleasure to acknowledge a cordial obligation to the Juneau Botanical Club, of Juneau, Alaska, and particularly to the secretary, Mrs. Lucille Stonehouse; and to Dr. W. H. Camp of the New York Botanical Garden. By their contributions, the available material has amounted to a fair representation of the range of the group.



PLATE 9. STRUCTURE OF THE PYROLEAE. Plants, approximately natural size, photographed by E. B. Copeland at Jonesville, Butte County, California, July, 1920. FIG. 1. *Chimaphila Menziesii*. FIG. 2. *Pyrola picta*.

The races of which material in histological fixatives has been available are listed below. As it seems expedient to designate these races by the names which appear correct, and to place them in the sequence which appears best as a representation of natural classification, the listing implies some of the conclusions which are to be stated explicitly in the sequel.

1. *Ramischia secunda* (L.) Garcke, collected at Jonesville; on

Mount Rainier, Washington, by Camp; and on the Mendenhall Flats, near Juneau, Alaska, by the Juneau Botanical Club.

2. *Chimaphila umbellata* (L.) Barton, collected at Jonesville; and in Oregon and in the Alleghany National Park, New York, by Camp.

3. *Chimaphila maculata* (L.) Nuttall, collected at Chilhowees, Tennessee, by Camp.

4. *Chimaphila Menziesii* Sprengel, collected at Jonesville; and on Mount Rainier by Camp.

5. *Pyrola minor* L., collected on the Mendenhall Flats by the Juneau Botanical Club.

6. *Pyrola virens* Schweigger, collected on Mount Rainier by Camp.

7. *Pyrola picta* Smith, collected at Jonesville; and on Mount Rainier by Camp.

8. *Pyrola dentata* Smith, collected on Mount Rainier by Camp.

8a. *Pyrola dentata* var. *integra* Gray, collected at Jonesville.

8b. *Pyrola dentata* var. *apophylla* n. var.,² collected at Jonesville.

9. *Pyrola americana* Sweet, collected in Alleghany Park by Camp.

10. *Pyrola uliginosa* Torrey and Gray, collected at Jonesville.

11. *Pyrola bracteata* Hooker, collected by Camp on Mount Rainier. A plant collected by the Juneau Botanical Club on Mendenhall Flats, and sent under the name of *P. asarifolia* Michaux, appears to represent the same species.

12. *Moneses uniflora* (L.) Gray, collected at Lena Cove and the Shelten Islands by the Juneau Botanical Club. The material from the Shelten Islands is said to represent var. *reticulata* (Nuttall) Blake.

The material listed has been used principally in study by routine histological methods. The necessary herbarium and library study has been facilitated by the continued, unstinted, and

² *Pyrola dentata* var. *apophylla* n. var., laminis foliorum reductis. Jonesville, Butte County, Calif., H. F. Copeland, s.n., July 28, 1935; type in the Herbarium of the University of California.

Aphyllous forms of *Pyrola* have repeatedly been collected in western North America; they have generally been referred to *P. aphylla* Smith. Fernald (1920, 1941), however, has described and named one of these forms as a variety of *P. virens*, and Camp (1940) has identified the classic *P. aphylla* as a form of *P. picta*. The aphyllous plants of Jonesville appear, by their distribution in the woods, to represent *P. dentata* var. *integra*. It is not possible from Hooker's (1834) plate of *P. aphylla*, and it would probably be impossible from Smith's type specimen, to decide whether this name belongs to a variant of *P. virens*, *P. picta*, or *P. dentata* var. *integra*: the loss of leaves obliterates the distinctive characters. Under these circumstances it appears best arbitrarily to treat Camp's action as sound, that is, to consider the classic *P. aphylla* as a form of *P. picta*; and to give the new name here published to the leafless variant of *P. dentata* var. *integra*. The plant which Holm (1898) described as *P. aphylla* appears, by the characters of its sporadically occurring foliage leaves, to represent the present variety.

cordially appreciated hospitality of the Herbarium and Biology Library of the University of California.

The observations lead to conclusions as to the proper place of these plants in the taxonomic system, and as to their expedient arrangement in genera. Specific limits remain obscure in some parts of the group, and the present observations are of little help in clarifying them.

VEGETATIVE GROSS STRUCTURE

Linnaeus noted certain Pyroleae as undershrubs, and others as perennial herbs; all are in fact rather of the latter character, their aerial shoots being less enduring than the underground structures. The main underground structure, in all members of the group except *Moneses*, is a rhizome. The rhizome is slender, not more than a few millimeters in diameter, yellow to brown in color, bearing distant small scales. The scales subtend scaly buds; associated with each of these, as Henderson noted, there is usually a single root, springing from within the rhizome, and usually brief and less than one millimeter in diameter. Most buds remain dormant; the rhizome is sparsely branched, though often quite elongate. I found one of *Chimaphila umbellata* which was approximately 2.5 meters long, connecting two leafy shoots near one end with a single one at the other. Occasionally, the tip of a rhizome turns toward the surface of the soil; produces, at the end of a growing season, a scaly bud; and gives rise, during the following growing season, to an aerial shoot.

In *Moneses uniflora*, the aerial shoots grow upward directly from slender roots, within which they originate, of course, as adventitious buds. This habit was first reported by Irmisch (1855). It is the same as that of the monotropoid plants. Irmisch reported that in *Ramischia secunda* and *Pyrola virens* the aerial shoots may arise either from rhizomes or from roots; Holm (1898) states that this occurs also in *P. aphylla* (that is, as I suppose, *P. dentata* var. *apophylla*), and in *P. picta*, *Chimaphila umbellata*, and *C. maculata*. Henderson could not confirm this, nor have I done so in digging up a moderate number of specimens. It seems safe, nevertheless, to accept these observations as sound: it is inherently probable that the roots are capable of the occasional production of adventitious buds throughout the group.

Various observers, as Wydler (1860), Drude (1889), and Henderson (1919), have noted the habit of the Pyroleae, of producing a winter bud at the end of each season of growth; with the effect (the scales being persistent) that the stem is found to bear, alternately, series of scales and of leaves. In *Ramischia*, the leaves of each year are distributed along a few centimeters of stem. In *Chimaphila*, they are typically crowded near the summit of the year's growth of stem, and give a superficial appearance of being whorled. In *Pyrola* and *Moneses*, the year's growth of stem is

usually very brief; all the leaves on one shoot are crowded in a single rosette.

Growth as described continues until the year in which the growing point is used up in inflorescence. This occurs sooner or later, characteristically in different species. In *Chimaphila umbellata* and *Chimaphila Menziesii* it may be delayed until after the production of seven or eight annual pseudo-whorls of leaves. In the group of *Pyrola rotundifolia*, the shoots seem most often to flower in the fourth growing season, after bearing leaves during three. *Ramischia*, *Chimaphila maculata*, *Pyrola picta*, *P. dentata* var. *integra*, and *Moneses uniflora* flower most often in the third growing season. *P. virens* flowers usually after producing a single series of foliage leaves. Shoots of the various aphyllous races flower in the season in which they come up.

Axillary buds do not usually open before the terminal bud above them is ready to produce an inflorescence. If they open in the same year, it is usually to produce additional inflorescences. This they do rather commonly in *P. virens* and the group of *P. picta*. In *Ramischia*, *Chimaphila*, and the group of *P. rotundifolia*, they usually open the year after the stem bearing them has produced flower and fruit, and produce leaves during two or three years before bearing flowers in turn. In *Moneses*, the shoots usually die after flowering and fruiting.

The leaves are alternate. I examined a few plants and found the leaves to form a regular spiral: starting from any given leaf, the third leaf or bract above it stands somewhat to one side, say the left, of directly above it; the fifth falls a smaller distance to the right, the eighth a yet smaller distance to the left, and so forth. Wydler (1860) has noted irregularities in the phyllotaxy of this group: such irregularities are common in all groups of plants.

The size, shape, and texture of the leaves, their characters as petioled or sessile, entire or dentate, are duly set forth in the manuals and need not be recounted. As noted, the stalked leaves of *Pyrola* form rosettes. Usually, both leaves and bracts are persistent; Pease (1917) has found green leaves up to seven years old on shoots of *Chimaphila umbellata*, and up to eight years old in *C. Menziesii*. In this genus, the bracts, and later the leaves, are finally allowed to fall by the action of a disjunction mechanism. In *Pyrola*, the leaves wither in place. In the group of *P. rotundifolia*, this occurs usually after they have been green for two years.

EXPLANATION OF THE FIGURES. PLATE 10.

PLATE 10. STRUCTURE OF THE PYROLEAE. Anatomical features of *Chimaphila Menziesii*. FIG. 3. Longitudinal section of root tip, $\times 200$. FIG. 4. Cross section of young root, $\times 200$. FIG. 5. Cross section of older root, $\times 200$. FIG. 6. Cross section of rhizome, $\times 25$. FIG. 7. The marked area of fig. 6, $\times 200$. FIG. 8. Cross section of young stem, $\times 25$. FIG. 9. The marked area of fig. 8, $\times 200$.

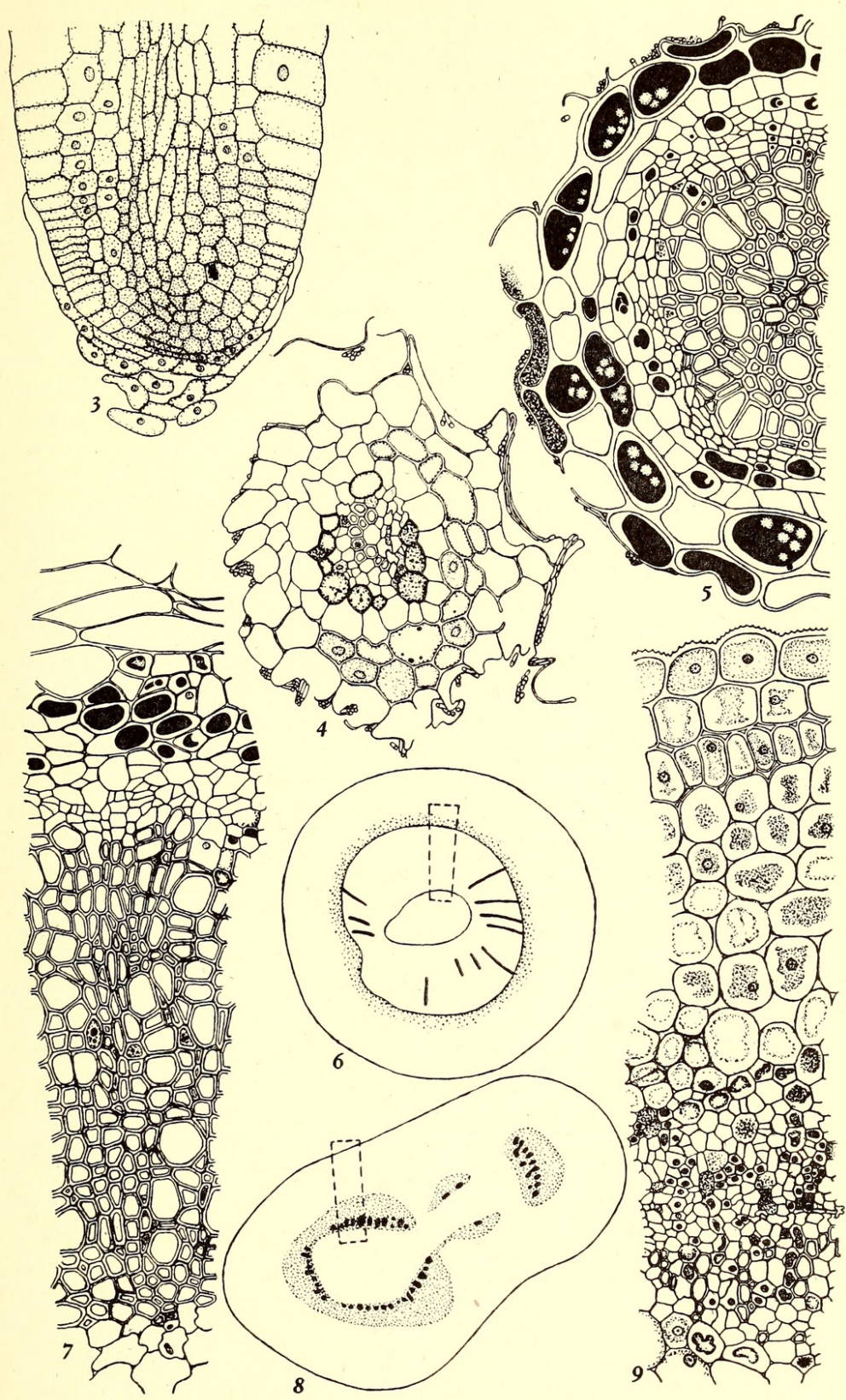


PLATE 10. STRUCTURE OF THE PYROLEAE.

As the shoot usually produces no leaves in the year in which it flowers, there are bud scales above the highest foliage leaves as well as below the lowest. Irmisch, Wydler, and Henderson have reported *Chimaphila umbellata* as an exception. Of this species and of *C. Menziesii*, I find that they may or may not bear foliage leaves above the highest bud scales, in the same year as the flowers. Wydler and Andres have reported the same variability in *Pyrola virens* and *P. minor*.

ANATOMY OF THE VEGETATIVE STRUCTURES

The structure of well-developed primary roots has never to my knowledge been observed in any pyroloid plant. The roots examined by Henderson, of *Chimaphila umbellata*, *C. maculata*, *Pyrola rotundifolia* (that is, presumably, the scarcely distinct *P. americana*), and *P. elliptica*, and by myself, of *Ramischia secunda*, *Chimaphila Menziesii*, *Pyrola minor*, and *P. uliginosa*, were either adventitious roots springing from the rhizome or secondary roots springing from these. The elongate roots of *Moneses uniflora*, seen by Henderson and myself, were not traced to their origin; presumably they spring from other roots.

The structure observed presents no particular peculiarities. In the root tips (pl. 10, fig. 3) there is a definite dermatogen as distinct from an inner body of meristematic cells. The root cap is very scant. The epidermal cells grow considerably in the radial direction as soon as they emerge from the protection of the cap. In almost all examples, they presently become beset, both externally and internally, with a mycorrhiza of fine hyphae. It is a familiar and probable theory, that the mycorrhiza contributes significantly to the nutrition of the plants. This has not been demonstrated experimentally in the present group. Eventually, the epidermal cells die and disappear; this may be true also of the outer layers of the cortex.

The inner meristematic tissue produces, of course, a cortex and a stele surrounded by it. In most examples, the cortex is of only about three layers of cells in addition to the endodermis. In *Moneses*, the root being the permanent organ of the plant, the cortex is of several layers of cells. The cortical cells are generally thin-walled; in *Chimaphila Menziesii*, the innermost ones are thick-walled. The cells of the endodermis are thin-walled. In some specimens, the radial walls resist staining, being apparently of the nature of Casparian strips.

There is no pith. Henderson described the primary xylem as

EXPLANATION OF THE FIGURES. PLATE 11.

PLATE 11. STRUCTURE OF THE PYROLEAE. FIG. 10. *Chimaphila Menziesii*, cross section of mature stem, $\times 200$. FIG. 11. *Ramischia secunda*, cross section of leaf, $\times 400$. FIG. 12. *Chimaphila Menziesii*, cross section of leaf, $\times 400$. FIG. 13. *Pyrola picta*, cross section of leaf, $\times 400$. FIG. 14. *Chimaphila Menziesii*, cross section of mature peduncle, $\times 25$. FIG. 15. Part of same, $\times 200$.

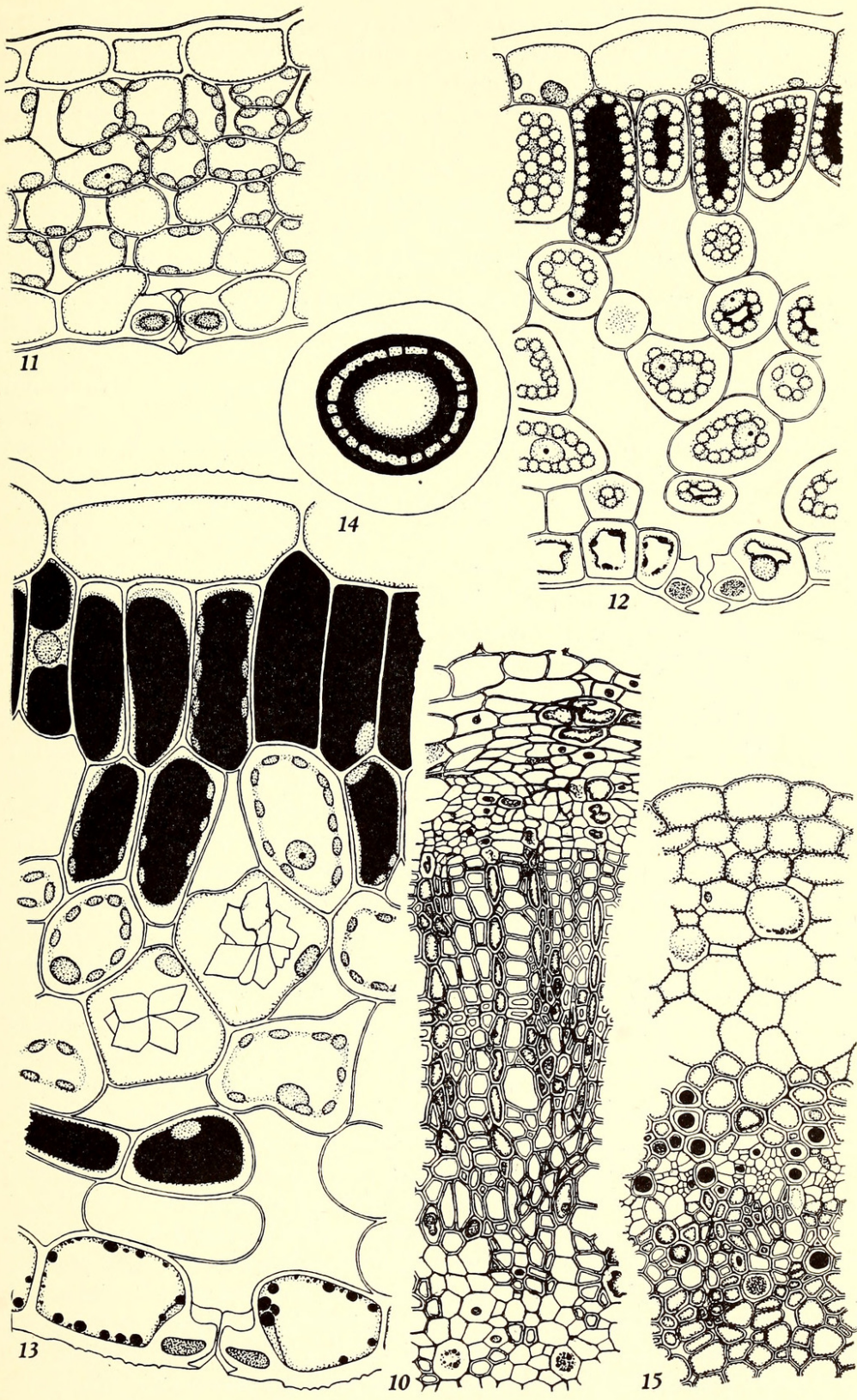


PLATE 11. STRUCTURE OF THE PYROLEAE.

usually 4- or 5-arch, but found a diarch specimen of *Moneses*. So far as my own observations go, roots are always diarch at their origin (pl. 10, fig. 4). Usually they remain diarch, but my specimen of *Moneses* is triarch. By the production of secondary xylem, a cylinder of wood is formed (pl. 10, fig. 5). Phloem, and a pericycle of thin-walled tanniniferous cells, were noted between xylem and endodermis. As lateral growth goes forward, the endodermis becomes divided by radial walls. No cork is formed.

The rhizome and the aerial stem are essentially alike in structure. They do not attain great thickness, nor develop a considerable mass of wood: further differences from the stems of typical *Bicornes* are noted below. During the annual brief period of active growth, the cortex, procambial cylinder, and pith become differentiated immediately back of the growing point. Scattered spiral tracheids become differentiated at the inner boundary of the procambial cylinder (pl. 10, fig. 9). These may be few, or may become fairly numerous; in the latter case, there is a radial transition from tracheids with an extended spiral, scattered in parenchyma, to others with a compact spiral and scant associated parenchyma. A typical cambium begins to function. The secondary xylem produced by it consists, as to the tracheary elements, of cells whose walls are marked by compact spiral striations and bordered pits with elliptic included openings, horizontal or oblique. These are the characters both of the numerous fiber-tracheids and of the fewer and only slightly broader vessels; in the latter, the spiral ridges are less prominent, and there are commonly two alternate columns of pits on each face. The vessels have strongly oblique ends with numerous scalariform perforations. The numerous rays are essentially uniseriate. The cells of which they consist are vertically elongate, and there may be several tiers to the ray; the tiers may overlap at the margins, producing a biseriate appearance in cross sections. Except in the rays, no parenchyma was found in the wood.

In rhizomes (pl. 10, fig. 7), spring wood and summer wood are scarcely distinguishable. In aerial stems (pl. 11, fig. 10), the annual rings are evident, though neither prominent nor numerous.

These rhizomes and stems differ notably from those of typical *Bicornes* in two anatomical features. No pericycle, that is, no layer of fibers at the outer margin of the phloem, is differentiated, and no cylinder of cork is formed.

The cortex is mostly of thin-walled cells, but on aerial stems the outermost layers are thick-walled, constituting a differentiated hypodermis. The epidermis also is thick-walled and bears a longitudinally striate cuticle. The growth of the cylinder of wood, so long as it continues, results in a crushing of the thin-walled inner cells of the cortex. The epidermis and hypodermis are neither ruptured nor reinforced by a layer of cork: they persist as long as the shoot does. The plants are not totally incapable of producing cork. This tissue may be formed in response to wounding,

and is formed regularly as a disjunction layer at the bases of the bracts and leaves of *Chimaphila*.

The nodes are unilacunar. A single trough-shaped bundle, unaccompanied by fibers, enters each petiole. The bundle which enters a bud or branch is formed by a junction of two bundles springing from the sides of the leaf gap.

As to the leaves, Table 1 gives, for the species of which I have seen cross sections (pl. 11, figs. 11-13), the thickness and the numbers of layers of palisade tissue observed.

TABLE 1. COMPARISON OF CERTAIN LEAF CHARACTERS IN THE PYROLEAE

Species	Approximate thickness of leaves in microns	Number of layers of palisade
<i>Ramischia secunda</i>	80-100	0
<i>Chimaphila umbellata</i>	200-250	1
<i>C. maculata</i>	320	2
<i>C. Menziesii</i>	200-300	1-2
<i>Pyrola minor</i>	140	0
<i>P. virens</i>	250	1
<i>P. picta</i>	275-300	2
<i>P. dentata</i> var. <i>integra</i>	275-300	2
<i>P. americana</i>	180	0
<i>P. uliginosa</i>	150	0
<i>P. bracteata</i>	150	0
<i>Moneses uniflora</i>	150	0

Henderson found three layers of palisade tissue in *Chimaphila umbellata* and cited European authorities who had made the same observation. As to several other species, her observations agree with mine. She cited European authority for the absence of palisade tissue in *Pyrola rotundifolia*; her own agreeing observation applies, I assume, to the race here called *P. americana*. She found the same condition in *P. elliptica*. Holm found about two layers of palisade tissue in the foliage leaves of his "*Pyrola aphylla*": this would be true whether the plant in question was related to *P. virens*, *P. picta*, or *P. dentata*.

On thick leaves with palisade tissue, the epidermis bears a thick cuticle; the stomata are confined to the lower epidermis and open at the level of the outer surface of the cuticle. Thin leaves without palisade tissue bear a thin cuticle and the stomata project moderately from the lower surface. As Henderson noted, stomata in small numbers may be found on the upper surfaces of these leaves. The outer opening of the stomatal pore is marked by a prominent knife-like ridge; a less prominent ridge was found at the inner opening in some specimens.

There is usually an accumulation of tannin in the uppermost cells of the mesophyll, whether or not these are of the character of a palisade, and a less considerable accumulation in the lowest

cell-layers. In many cells of the less tanniniferous intermediate layers, there are star-shaped crystals.

The leaf contains no fibers, though there are more or less considerable bodies of collenchyma associated with the veins and in the margins.

The thin leaves, lacking palisade tissue and bearing projecting stomata, are evidently adapted to life in moist and shaded places. According to my understanding of the relationships of the species, I would suppose that this set of characters has developed more than once within this limited group.

INFLORESCENCE

The typical inflorescence of the group is a bracted raceme embraced at the base by the outer bud scales of the winter bud from which it grew. The peduncle bears usually a few "scales," that is, scattered lower bracts which do not subtend flowers. Abortive buds can usually be found in their axils. Bud scales, scales on the peduncle, and bracts are all of quite the same character. The pedicels are without bractlets.

The typical inflorescence thus described occurs in *Ramischia* and in *Pyrola* (pl. 9, fig. 2). The occasional presence of foliage leaves above the highest bud scales in some species of *Pyrola* was noted above. Rydberg and Henderson took careful note of the numbers of flowerless lower bracts in the species with which they dealt. In *Ramischia secunda* the number is variable, from one to four; in *Pyrola elliptica* and *P. virens*, it is often just one; aphyllous shoots bear several; in the remaining American species, the number is two or three, the species not being distinguishable by this character.

The occasional presence of foliage leaves above the highest bud scales in *Chimaphila* has been noted. In this genus, the peduncle bears no scales and the bracts are adnate to the pedicels. The inflorescence of *Chimaphila umbellata* is no umbel, but a condensed raceme, a corymb; Pursh (1814), in introducing the genus *Chimaphila*, undertook to change the epithet of this species, calling it *C. corymbosa*. In *C. maculata* and *C. Menziesii* (pl. 9, fig. 1), the inflorescence is a cyme-like cluster of two or three flowers. The bracts of *C. Menziesii* are suborbicular, pale, fleshy, with a dentate margin.

EXPLANATION OF THE FIGURES. PLATE 12.

PLATE 12. STRUCTURE OF THE PYROLEAE. Flowers, $\times 5$; stamens and anthers, $\times 10$. FIG. 16. Flower of *Ramischia secunda*. FIG. 17. Flower of *Chimaphila Menziesii*. FIG. 18. Flower of *Pyrola minor*. FIG. 19. Flower of *Pyrola americana*. FIGS. 20, 21, 22. Stamens and anthers of *Ramischia secunda*, respectively in early bud, older bud, and in open flower. FIGS. 23, 24. Stamens of *Chimaphila Menziesii*, respectively in older bud and in open flower. FIGS. 25, 26. Younger and older stamen of *Pyrola minor*. FIGS. 27, 28. *Pyrola americana*, mature anther seen from within and stamen seen laterally. FIGS. 29, 30. Stamens of *Moneses uniflora*.

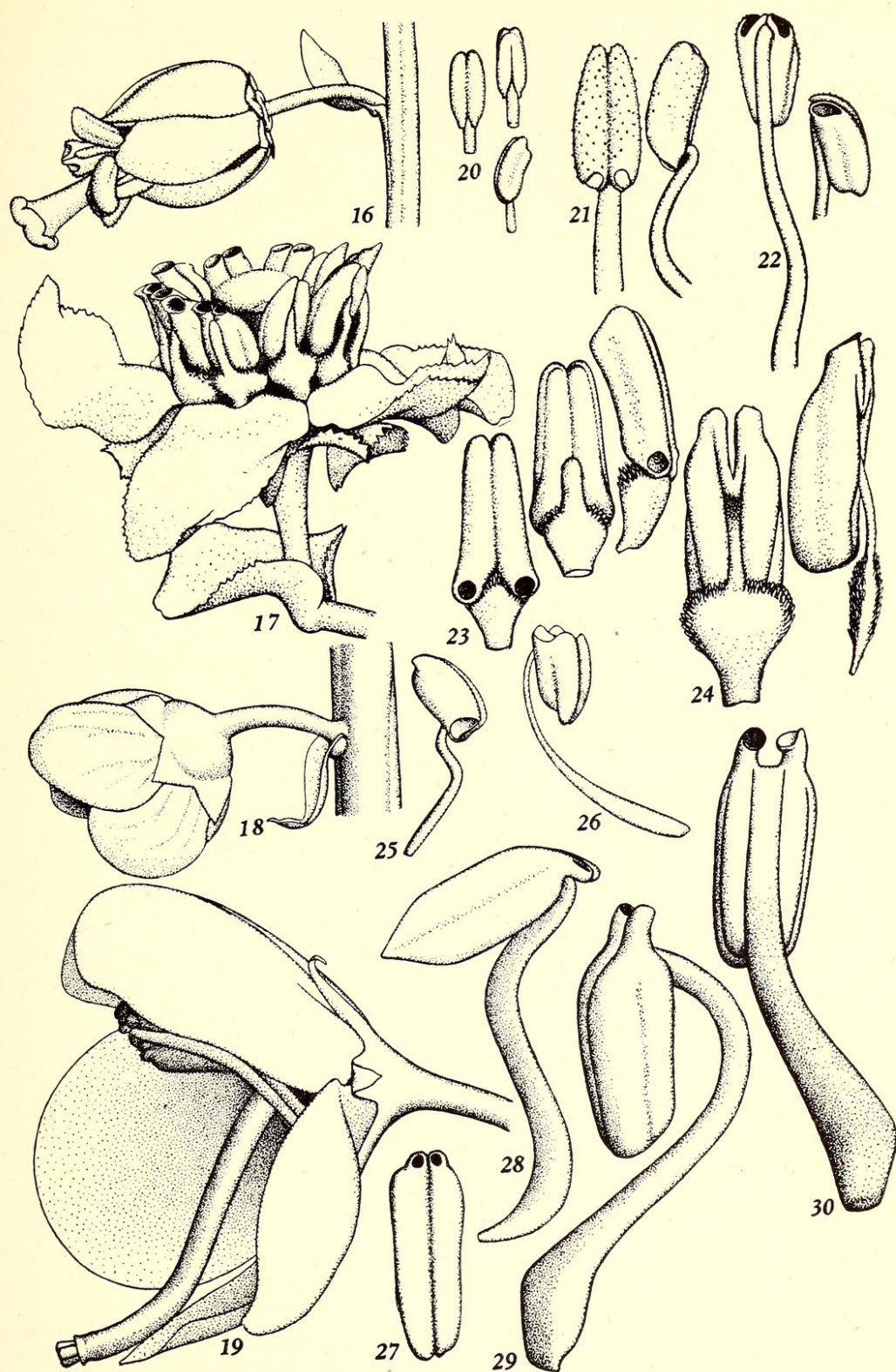


PLATE 12. STRUCTURE OF THE PYROLEAE.

The inflorescence of *Moneses* consists of a solitary flower terminal on a peduncle which may bear no scales or one or two.

The peduncle differs anatomically from vegetative stems in showing scant secondary tissue or none, and in the presence of a sheath of fibers outside the phloem (pl. 11, figs. 14, 15). In *Ramischia secunda*, *Chimaphila Menziesii*, and *Pyrola minor*, the development of this sheath is scant and tardy, so that it may not be recognizable in young peduncles. The sheath does not extend into the pedicels.

The nodal anatomy of the peduncle is in *Ramischia* the same as in the vegetative stems: each bract is supplied by a single bundle leaving a single gap, and each flower by a vascular cylinder formed in the base of the pedicel by the junction of two bundles running from the sides of the gap.

In *Chimaphila*, each pedicel is entered by a broad and trough-like band of vascular tissue, like a leaf trace, but differing in the fact that the margins of the trough coalesce, not far above the base of the pedicel, to form a cylinder. Some distance up the pedicel, the cylinder emits the single scant bundle which supplies the bract. In *Pyrola* (*P. minor* and *P. uliginosa* were studied) the structure is similar except that each bract is supplied by three small bundles. One might say that in these genera the physiological dominance of the axillary structure, the flower, has resulted in reduction of the subtending leaf to an accessory status, so far as the vascular supply is concerned.

FLOWERS: THE PERIANTH

The flower is choripetalous, pentacyclic, pentamerous, actinomorphic or essentially so in *Ramischia*, *Chimaphila*, and *Pyrola minor*, zygomorphic in most species of *Pyrola* and in *Moneses*. Perianth, stamens, and the disk if any is present, are hypogynous. The median sepal is on the upper or adaxial side of the flower (pl. 12, fig. 19; pl. 17, fig. 56). The petals are alternate with the sepals, and the median one is accordingly on the lower or abaxial side. The stamens of the outer cycle are opposite the petals. Stamens of the inner cycle and carpels are alternate, each with the leaves of the preceding cycle, so that the carpels lie in the radii of the petals.

The aestivation of the petals is imbricate. Roeper (1852) studied the phyllotactic sequence of the petals, and found it variable.

The sepals are ovate to lanceolate. In *Chimaphila* they are irregularly finely dentate. In *Ramischia* and *Moneses* they are finely ciliate. In *Pyrola* they are strictly entire and glabrous; shape of sepals is a character of subgeneric groups in this genus.

The petals are glabrous, rotund to obovate, generally with obtuse or rounded apices. American floras recognize a single local species, *Pyrola oxypetala*, with acute petals. In color, they

are white, cream, greenish, pink, or red, the main variations distinguishing subgeneric groups in *Pyrola*. In *Ramischia* only, each petal bears a pair of minute tubercles on the inner surface near the base. This obscure distinction was discovered by Alefeld. The tubercles project from each petal into the spaces between the three filaments lying within the petal. Sectioned and stained, they are found not to be of the microscopic character of glands. Their function is not evident; possibly it is that of the lodicules of grasses, namely to effect the opening of the flower.

STAMENS

The lower half of the filament of *Chimaphila* is laterally expanded and beset, particularly on the margins, with rather coarse white hairs which are outgrowths of epidermal cells (pl. 12, figs. 23, 24). In the remaining genera, the filaments taper smoothly and are glabrous (pl. 12, figs. 20-22, 25-30).

The stamens of *Ramischia*, *Chimaphila*, and of a few of the species of *Pyrola*, are nearly uniform in length and dorsiventrally symmetrical. In most of the species of *Pyrola*, the petalad stamens are perceptibly the shorter, and all of the filaments are so bent as to gather the anthers in a cluster on the upper side of the flower. A similar inclination is present in *Moneses*, but the clustering of the anthers is less pronounced; in many specimens, the filaments of the sepalad stamens are so bent that the anthers are born in pairs opposite the petals.

Throughout the group, the summits of the filaments in bud are sigmoidally bent, outward and upward. The filament merges into the lower part of the inner side of the anther. The two areas which are to become the pores of the anther are located on the outer side near the base. At anthesis, the summit of the filament bends inward and inverts the anther, so that instead of standing erect on the filament it hangs from it, into the interior of the flower, with the pores at the top. Undoubtedly, the juvenile position of the anther expresses its true morphology, this in spite of the fact that Asa Gray (1846) once stated the contrary opinion. It is not true that the stamens are formed in an inverted position, nor that they right themselves at maturity: they are formed right side up and later turn upside down.

The pores are of various shapes, and may or may not be born at the ends of tubes of various shapes.

In *Ramischia*, the pores are not circular, but elongate, crossing the proximal ends of the anthers in the direction of the radial planes of the flower; these ends are scarcely extended as tubes (pl. 12, fig. 22).

In *Chimaphila* the circular pores are terminal on brief conical tubes (pl. 12, figs. 23, 24).

In *Pyrola minor* (pl. 12, figs. 25, 26) the pores are widely open and tubes are scarcely developed. Similar pores were seen in her-

barium specimens of *P. media* and *P. grandiflora*, and are reported in an Alaskan species, *P. occidentalis*.

In other species of *Pyrola* which are available to me in preservative, the small pores are on the dorsal (at maturity, inner) surfaces of brief tubes (pl. 12, figs. 27, 28). In two Mexican species, *P. Sartorii* and *P. angustifolia*, Alefeld described the pores as almond-shaped (*amygdaliformes*), that is, elongate, rounded above, narrowed to a slit below. This character is perceptible in herbarium specimens of the latter species, together with another peculiarity: there is a slight protuberance on the ventral side of each tube. It is as though the tubes bore the rudiments of horns like those of the *Andromedaeae*.

In *Moneses* (pl. 12, figs. 29, 30) the pores terminate definite tubes which are so curved as to diverge below and converge above.

The internal structure of the young anthers is in most respects that of flowering plants in general. There are four masses of pollen mother cells surrounded by tapetum, inner wall cells, and epidermis. In *Ramischia*, some of the epidermal cells project as papillae, principally in vertical bands on the front and back of each lobe of the anther. In *Chimaphila*, the microscope reveals a tendency to this papillose character; it is so obscure as not to be evident when the anthers are examined under the dissecting lens. In *Pyrola* and *Moneses*, the epidermis of the anthers is essentially smooth.

The epidermis of the areas of dehiscence is of small, thin-walled, darkly-staining cells, and is underlain by further cells of the same character, extending to the tapetum at the proximal ends of both the pollen sacs in the same lobe of the anther. The entire body of darkly-staining cells, conceived in space, is roughly a triangle several cells thick, with one angle at the area of dehiscence, the other two respectively at the proximal ends of the pollen sacs. Because the two pollen sacs of the lobe are not in the same radial or tangential plane of the flower, longitudinal sections of the flower do not usually show the whole extent of this body of cells, but merely sections through it (pl. 13, figs. 32–35), which may appear to extend from the area of the pore to one pollen sac or the other. The entire structure appears to be homologous with the body of resorption tissue described in *Arbutus* and *Arctostaphylos* by Matthews and Knox (1926), and again in the latter genus by Doyel (1942); but differs in being more than a single

EXPLANATION OF THE FIGURES. PLATE 13.

PLATE 13. STRUCTURE OF THE PYROLEAE. Sections of the proximal ends of anthers, $\times 125$. FIG. 31. *Chimaphila Menziesii*, cross section through the tubes of the young anther with the filament ascending between them. FIGS. 32–35: Sagittal sections of young anthers. FIG. 32. *Ramischia secunda*. FIG. 33. *Chimaphila umbellata*. FIG. 34. *Pyrola picta*. FIG. 35. *Moneses uniflora*. FIG. 36. Sagittal section of open tube of anther of *Chimaphila umbellata*.



PLATE 13. STRUCTURE OF THE PYROLEAE.

layer of cells, and in being extended to include a broad area of epidermis.

Stages in the development of the pollen grains have been seen in the anthers of *Chimaphila umbellata*, *C. Menziesii*, and *Pyrola picta* (pl. 14, figs. 37-42). They occur, as Hagerup (1928) noted, in spring (in the mountains of California, in June) not long before anthesis. They are perfectly normal. The haploid chromosome number in both species of *Chimaphila* is 13; that of *Pyrola picta* is 23. The latter number had been reported by Hagerup in *P. grandiflora*, *P. rotundifolia*, and *P. minor*; but Samuelsson (1913) had reported 16 in *P. virens*, *P. rotundifolia*, and *Moneses uniflora*. I confess to having held both reports in doubt, expecting to find either 13 or 26, but have unmistakably found in *P. picta* the number reported by Hagerup.

The pollen grains of *Ramischia* are solitary; those of *Chimaphila* occur in easily disrupted tetrads; those of the remaining Pyroleae are firmly united into permanent tetrads, as in most Bicornes. In *Ramischia*, the pollen grains are tricolpate. In *Pyrola*, as in most Bicornes, the wall of each individual grain is marked by three half-grooves, continued as half-grooves on the three associated grains. Mature pollen grains are binucleate, with one of the nuclei lying in a clear area, the generative cell.

The tapetal cells become binucleate and then shrivel to nothing. The inner wall cells disappear as far as, but not including, the layer next within the epidermis. The septum between the pollen sacs of the same lobe breaks down. The connective—the septum between the lobes, traversed by a bundle—persists.

Artopoulos (1903) and Matthews and Knox (1926) distinguished two tissues involved in the opening of the anthers of Bicornes. Both tissues originate as small, thin-walled, darkly-staining cells, as already described. In some circumstances, these cells undergo disappearance by collapsing successively, each against the one which is to disappear next. The tissue which behaves in this fashion may be called collapse tissue. It is essentially the same thing as the inner wall tissue of the anthers of flowering plants in general, and of the present group. It may be held to be present in the anthers of all Bicornes.

Under other conditions, the small cells do not collapse. They become granular and undergo deliquescence, forming a granular, apparently slimy mass, which gradually disappears. The cells which undergo this process constitute resorption tissue. It is present in the anthers of some Bicornes but not others.

As to the Pyroleae:

In *Ramischia*, the epidermis where the pores are to form, together with several layers of the underlying cells, consist of resorption tissue (pl. 13, fig. 32); but the inner part of the mass of differentiated tissue which extends to the tapeta at the proximal ends of the pollen sacs is of collapse tissue. This is to say that the outermost plugs of the anther pores disappear by deli-

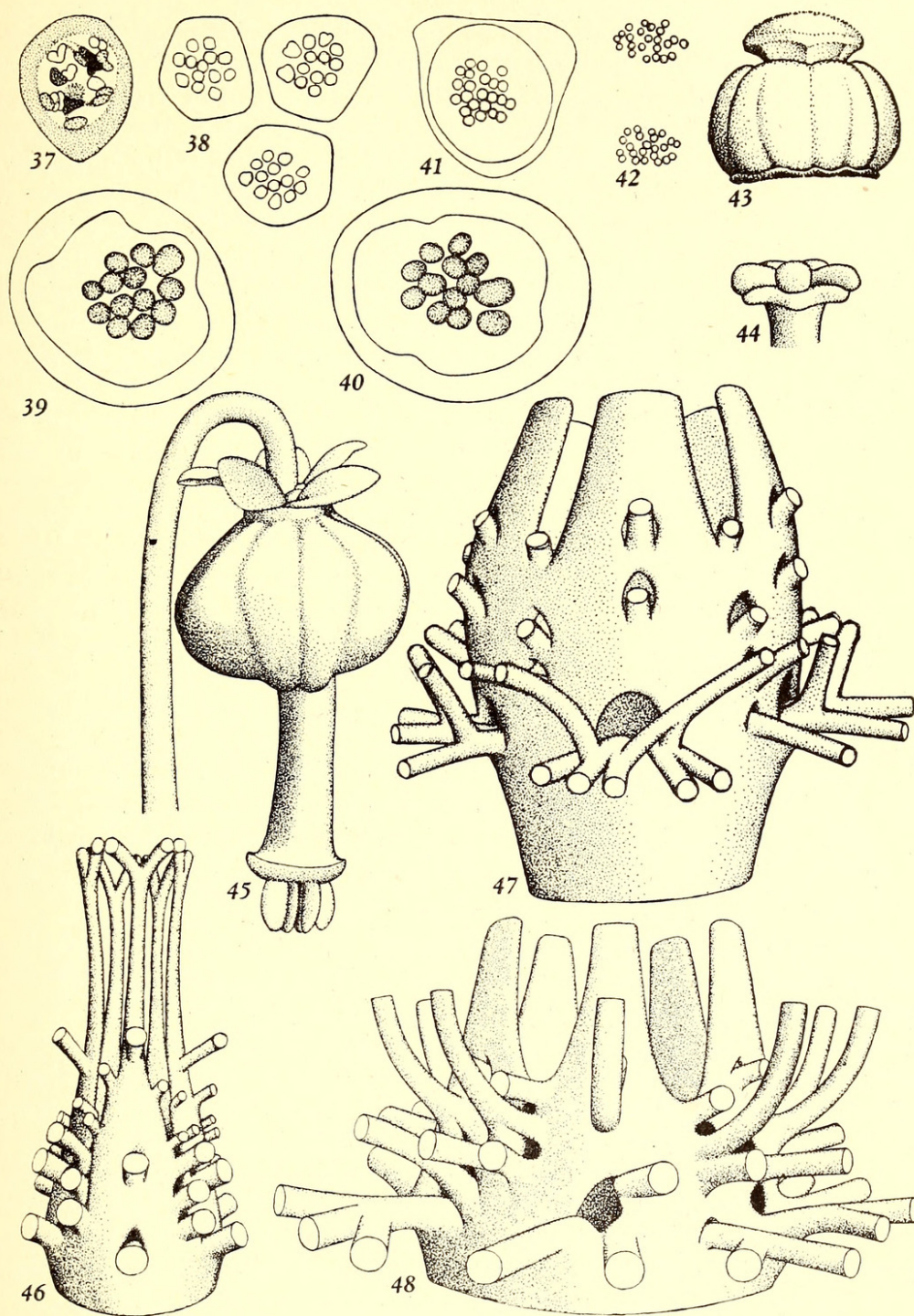


PLATE 14. STRUCTURE OF THE PYROLEAE. Details of microsporogenesis. FIG. 37. *Chimaphila umbellata*, diakinesis, $\times 900$. FIG. 38. *Chimaphila umbellata*, heterotypic metaphase, $\times 900$. FIGS. 39, 40. *Chimaphila Menziesii*, heterotypic metaphases, $\times 1200$. FIG. 41. *Pyrola picta*, heterotypic metaphase, $\times 1000$. FIG. 42. *Pyrola picta*, chromosomes in heterotypic anaphase, the two groups from a single spindle, $\times 1000$. FIG. 43. *Chimaphila Menziesii*, pistil, $\times 5$. FIG. 44. *Pyrola minor*, stigma, $\times 10$. FIG. 45. *Moneses uniflora*, pistil, $\times 5$. FIGS. 46-48: Models of the vascular system in the floral receptacle, $\times 50$. FIG. 46. *Ramischia secunda*. FIG. 47. *Chimaphila umbellata*. FIG. 48. *Chimaphila Menziesii*.

quescence; the further disappearance of tissue within the anther, as already described, is by collapse.

In *Chimaphila*, the entire body of differentiated tissue, from the area of dehiscence to the tapeta, is resorption tissue. The disappearance of further tissue within the anthers is by collapse.

In various species of *Pyrola*, and in *Moneses*, I have searched material, less abundant than the available material of *Ramischia* and *Chimaphila*, and have found no resorption tissue. In *Pyrola picta* I found anthers in which dehiscence was barely beginning to take place, by a process of collapse forming a cleft within the differentiated tissue. I am convinced that resorption tissue does not occur in these genera.

The persistence of the hypodermal cell layer of the anthers has been mentioned. In the proximal end of the anther but not in the distal, and excluding, of course, the area of the pores, the cell walls of the hypodermal layer develop reticulate thickenings and constitute a rigid lining maintaining the form of the anther tubes (pl. 13, fig. 36). This mechanical layer occupies a part of the position of the endothecium in the anthers of typical flowering plants, but it is not necessarily homologous with it. It is a rigid structure, not a dynamic one, and the reticulate thickening of the cell walls is distinctly different from the ribbing of a typical endothecium.

In *Ramischia*, a rather scant extent of hypodermis develops reticulate thickenings, but this genus has the peculiarity that reticulate thickenings are developed in the epidermis throughout its extent.

DISK. PISTIL

Respected authorities have differed as to the presence of a disk in the flowers of certain Pyroleae. The facts were set forth correctly by Irmisch (1856), being as follows.

In *Ramischia* there is a rather massive disk of glandular tissue forming a complete ring below the base of the pistil and projecting between the bases of the filaments.

In *Chimaphila* there is a well-developed disk like a collar about the base of the pistil (pl. 14, fig. 43). Its margin is nearly entire, scarcely impressed by the filaments nor projecting between them.

Neither in *Pyrola minor*, nor in the typical species of *Pyrola*, nor in *Moneses*, is there any disk whatever; there is no projection at the base of the pistil nor any glandular tissue in this region.

The ovary (pl. 14, figs. 43, 45) is subglobular with ten distinct vertical grooves in the planes both of the sepals and of the petals. It is deeply impressed at the summit, the style springing from within the impression.

The style and stigma of *Pyrola minor* (pl. 14, fig. 44) are much like those of the Rhododendroideae. An extended cylindrical style flares at the summit to form a circular platform whose mar-

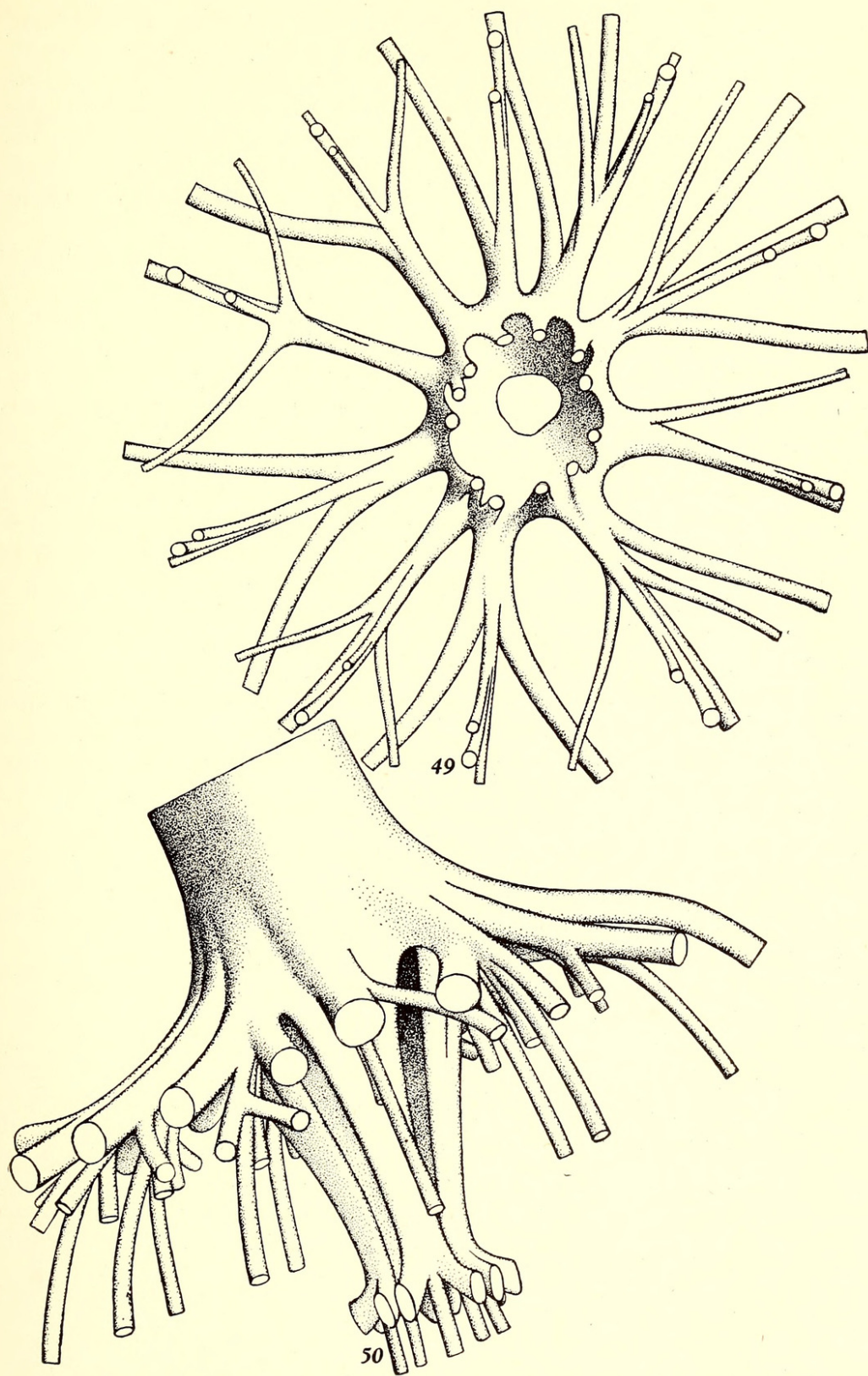


PLATE 15. STRUCTURE OF THE PYROLEAE. Models of the vascular system in the floral receptacles, $\times 50$. FIG. 49. *Pyrola minor*. FIG. 50. *Pyrola bracteata*.

gin is describable as a collar; upon the surface there are five projecting knobs in the planes of the sepals; between them, in the planes of the petals, there are five clefts, meeting in the center, all leading into the open style passage. By what circumstance some authorities have been led to describe the stigma of *P. minor* as having no collar, I do not know. The arcs of collar between the knobs are the extremities of the carpels; each knob represents the end of the coalescent margins of two adjacent carpels.

The style and stigma of *Moneses* are similar, except that the knobs are remarkably prominent (pl. 14, fig. 45).

Those of the typical species of *Pyrola* (pl. 12, fig. 19) are of the same structure but on a finer scale; and the style is bent to the shape of an old-fashioned italic *j*, or an integral sign: the flower standing nearly horizontally, the style is bent downward, toward the median or abaxial petal, and then outward.

The style of *Chimaphila* is brief and broadly flaring (pl. 14, fig. 43). The stigma is of the same structure as before, but with the proportions greatly modified. It is bordered by an obscure collar. The coalescent margins of adjacent carpels do not form projecting knobs, but merely sectors, separated by clefts, of a domed surface.

The extended style of *Ramischia* flares to a domed stigma divided into five sectors by radiating clefts which lie, of course, in the planes of the petals. The margin of the stigma at the ends of the clefts does not project and form lateral extensions coalescent below the knobs; hence it is descriptively correct to say that the stigma is without a collar. This stigma is simpler than that which is typical of the *Bicornes*, as if primitive; more probably, it is reduced.

As in most *Bicornes*, the style is traversed by an open channel. Five lengthwise flanges of tissue project into this channel. These represent the coalescent margins of adjacent carpels; they are continuous with the knobs on the stigma above and with the septa in the ovary below. The grooves between the flanges are continuous with the locules.

There are, of course, five locules, located opposite the petals. They are nearly filled by massive placentae each of which is radially divided into two by a vertical cleft. Above the middle of the ovary, the clefts in the placentae meet in the center of the ovary. Thus, in the upper half of the ovary, the placentation is parietal. The structure thus described is the same as the usual structure of the ovaries of *Monotropeae*; Henderson has duly noted its occurrence in both groups. Typical *Bicornes* are different in the fact that the locules are in communication with the style channel only at the summit of the ovary.

The placentae are densely beset with numerous minute ovules. The inner surfaces of the ovary walls are clad with about two layers of slender fiber-like cells with thick walls.

THE RECEPTACULAR VASCULAR SYSTEM

The vascular cylinder which ascends from the pedicel into the receptacle of *Ramischia* (pl. 14, fig. 46) emits there, in succession from proximal to distal, the following whorls each of five bundles: (1) sepal bundles, each soon forking into three; (2) petal bundles, each forking into three some distance from its origin; (3) petalad stamen bundles, close above the petal bundles; (4) sepalad stamen bundles, some distance above the sepal bundles; (5) carpel dorsals, in the radial planes of the petals, in a horizontal plane close above the two whorls of sepal bundles; (6) carpel laterals, at a considerably higher level: each of these belongs, it is clear, jointly to two adjacent carpels. At levels between the carpel dorsals and the carpel laterals, sporadic small bundles run out into the disk. Columnar placental bundles ascend the central column of the ovary beyond the carpel laterals, reaching approximately the level at which the central column is broken up by radial clefts. There each placental bundle splits into two which depart radially to supply two half-placentae lying in different locules but attached to the same septum. These ultimate bundles which supply the placentae are carpel ventrals, and the description just given means that each carpel ventral is fused in the central column with that of the adjacent carpel, and, lower down, with the carpel laterals of both. The style is supplied by the carpel dorsals, which dip under the groove about its base and ascend it in the tissue between the flanges. The carpel laterals ascend the ovary wall in the planes of the septa and fade out before reaching the base of the style.

The gaps above the petal bundles are rather profound and divide the vascular tissue which ascends past them into five almost distinct parts. Petalad stamen bundles and carpel dorsals spring often from one side of a gap instead of being formed by strands from both sides. Except in this respect, and in the fusion of the lateral and ventral bundles of adjacent carpels, the vascular system just described is almost precisely the theoretically ideal or primitive vascular system of a pentamerous pentacyclic flower.

In *Chimaphila* (pl. 14, figs. 47, 48), the vascular supply of each sepal and petal is normally of three bundles. The origin of these bundles is quite variable. Each may spring from a separate gap, or more than one from a single gap; or an originally single bundle may split into two or three, supplying the same organ or different ones; frequently rather than usually, bundles both of a sepal and a petal may be of the same origin. Above the median bundles of the petals, the ascending tissue is more or less definitely divided into five bands in the planes of the sepals. From these bands spring the following whorls of bundles in fairly regular fashion: petalad stamen bundles, sometimes from the petal bundles but characteristically from paired branches from the margins of ad-

jacent bands; sepalad stamen bundles, from the faces of the bands; carpel dorsals from the margins of adjacent bands; and carpel laterals from the faces of the bands. The remnants of the bands ascend the central column of the ovary, as in *Ramischia*, approximately to where it breaks up; then each of them supplies two half-placentae in adjacent locules. Both the carpel dorsals and the carpel laterals ascend the ovary wall, dip under the groove about the base of the style, and ascend the latter.

To speculate as to things of which we know very little, one would say that the genetic and physiological system which determines the receptacular vascular system in Bicornes in general has become modified in *Chimaphila*; and that in becoming modified it has lost precision. One may imagine that the tendency of evolution would be to fix it in a definite pattern different from that of the related plants; but that this has not yet happened in the present genus.

In *Pyrola*, including *P. minor*, and in *Moneses*, the vascular cylinder flares within the receptacle and emits ten large bundles which lie in the median planes of the perianth parts but are not the definitive bundles of the respective perianth parts (pl. 15, figs. 49, 50; pl. 16, fig. 51). Characteristically, though with many exceptions, the petal laterals arise from the sepal dorsals and the sepal laterals from the petal dorsals; in general, then, each petal lateral passes diagonally above a sepal lateral, and each sepal lateral passes diagonally below a petal lateral. Stamen bundles, and carpel dorsals and laterals, arise in fairly regular fashion, either from the upper sides of main perianth bundles or from the vascular tissue which ascends above their departure. This tissue becomes organized, finally, as five bands ascending the central column of the ovary in the planes of the sepals.

The vascular supply of the style of *Pyrola* is peculiar in consisting of five bundles lying in the flanges projecting into the style passage. These bundles are upward continuations of the placental bundles beyond the level where each of these emits two branches to half-placentae in adjacent locules. It is as though the distal ends of the carpel laterals had lost connection with their bases, and had established connection with the placental bundles. This peculiarity, illustrated in *P. bracteata* (pl. 15, fig. 50), was observed also in *P. minor*, *P. virens*, *P. picta*, *P. dentata*, and *P. americana*.

In species of *Pyrola* other than *P. minor*, the vascular system of the flower is bent so that it is of dorsiventral symmetry, in keeping with the slight zygomorphy of the flower (pl. 15, fig. 50).

In *Moneses* the style is supplied as in *Chimaphila* by ten bundles, being both the carpel dorsals and the carpel laterals.

Thus, in *Pyrola* and *Moneses* the receptacular vascular system shows specializations, some of which, however, are not so firmly established as to exclude many exceptions.

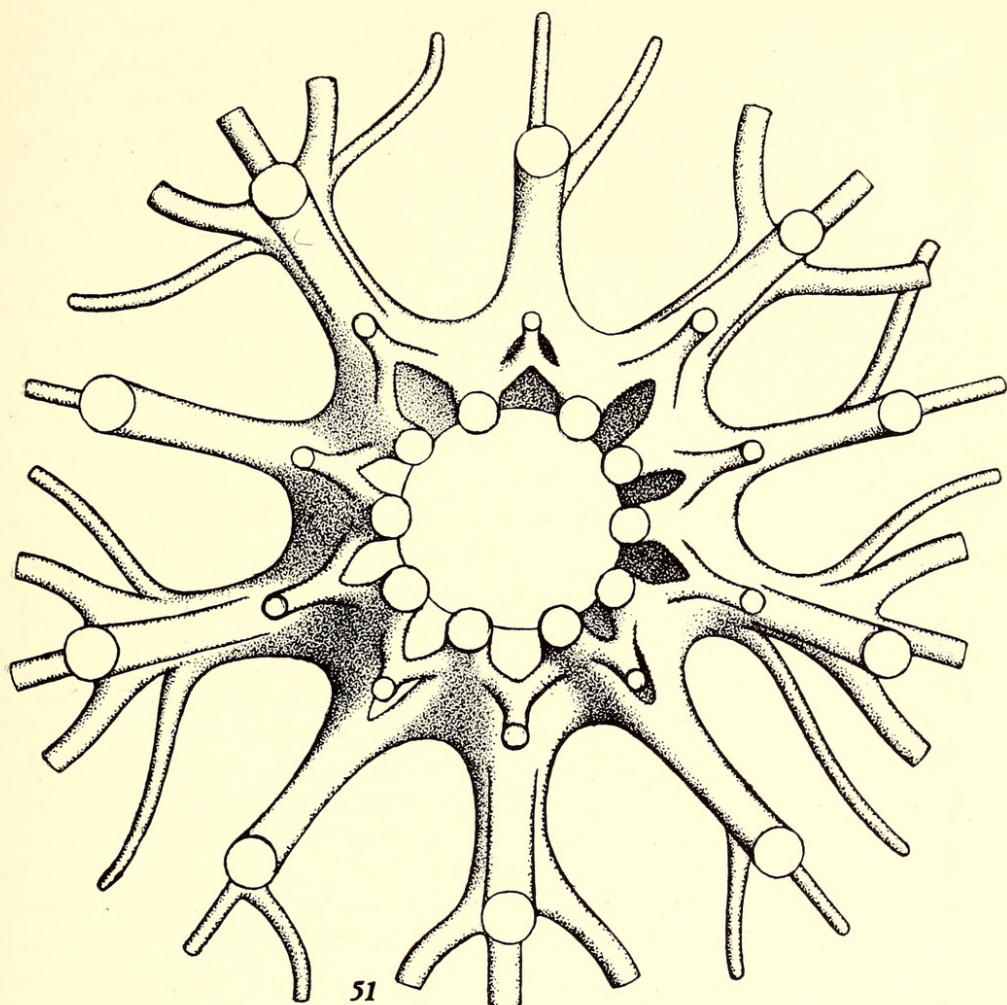


PLATE 16. STRUCTURE OF THE PYROLEAE. FIG. 51. *Moneses uniflora*, model of the vascular system in the floral receptacle, $\times 50$.

EMBRYOGENY

The embryogeny of the Pyroleae, as of the Bicornes in general, has been studied by Peltriset (1904) and by Samuelsson (1913). The anatropous ovules have a single integument of only two layers of cells. The nucellus consists of a single ephemeral superficial layer of cells and of a single megaspore mother cell enclosed by it. Reduction division takes place later than in the pollen mother cells, and results as usual in three ephemeral non-functional megaspores in the micropylar end, together with a single large functional megaspore. This develops through normal stages into a slender embryo sac of normal structure. The inner cell-layer of the integument, where it lies against the embryo sac, is perceptibly of the character of a jacket layer.

After fertilization, the triploid endosperm mother nucleus divides once and again. A transverse cell wall is formed after each nuclear division, with the result that the developing endo-

sperm passes through a stage in which it consists of four cells in a row. The terminal cells of this row do not enlarge considerably, and do not divide; the two middle cells divide and produce a globular mass of several cells. The zygote does not begin to grow until after the endosperm has passed the four-celled stage. It then becomes elongate and penetrates into the mass of endosperm cells (pl. 17, fig. 52). It becomes divided into a suspensor and a terminal cell, and the latter develops into a mass of smaller cells enclosed in the endosperm (pl. 17, fig. 53). The embryo develops no distinct parts, but eventually absorbs all of the endosperm except a single layer of cells (pl. 17, fig. 54).

The external cells of the integument develop moderately thick walls marked by elliptical pits on their inner and lateral surfaces; their external cell walls remain thin. Along the sides of the seed, the inner cells of the integument are absorbed by the endosperm; in the ends of the seed, the inner integumental cells die and remain in existence only as more or less shrivelled empty spaces. The undivided terminal cells of the endosperm are called haustoria. They become darkly-staining, and remain prominent for some time, but eventually shrivel. Thus, in the ripe seed, there is a central ellipsoid mass, consisting of an embryo covered by a single layer of cells of endosperm. This ellipsoid body lies within a cylindrical epidermis of cells with partially thickened walls, which contains, for the rest, the collapsed remains of the haustoria and the empty walls of a few other cells.

The features described are in most respects those of typical Bicornes such as the Rhododendroideae. The present group is distinguished by the integument of only two layers of cells; by the failure of those cells of the endosperm which lie next to the haustoria to become converted into "plugs"; by the rudimentary state of the embryo in the mature seed: in short, by small size, fewness of cells, and scant differentiation in every part. Every peculiarity of the embryogeny of the Pyroleae is shared by some or all of the Monotropeae.

THE FRUIT. GERMINATION

The locules of the fruit are jacketed on the inner surface, as in many other Bicornes, by about two layers of fibers constituting the mechanical layer which effects dehiscence. As a marked difference from the Rhododendroideae, the mechanical tissue of each locule does not act as a single body producing septicial dehiscence: the adjacent fibrous layers in each septum maintain their

EXPLANATION OF THE FIGURES. PLATE 17.

PLATE 17. STRUCTURE OF THE PYROLEAE. FIGS. 52-54: developing seeds, $\times 400$. FIG. 52. *Moneses uniflora*. FIG. 53. *Chimaphila Menziesii*. FIG. 54. *Ramischia secunda*. FIGS. 55, 56: fruits, $\times 5$. FIG. 55. *Chimaphila umbellata*. FIG. 56. *Pyrola minor*.

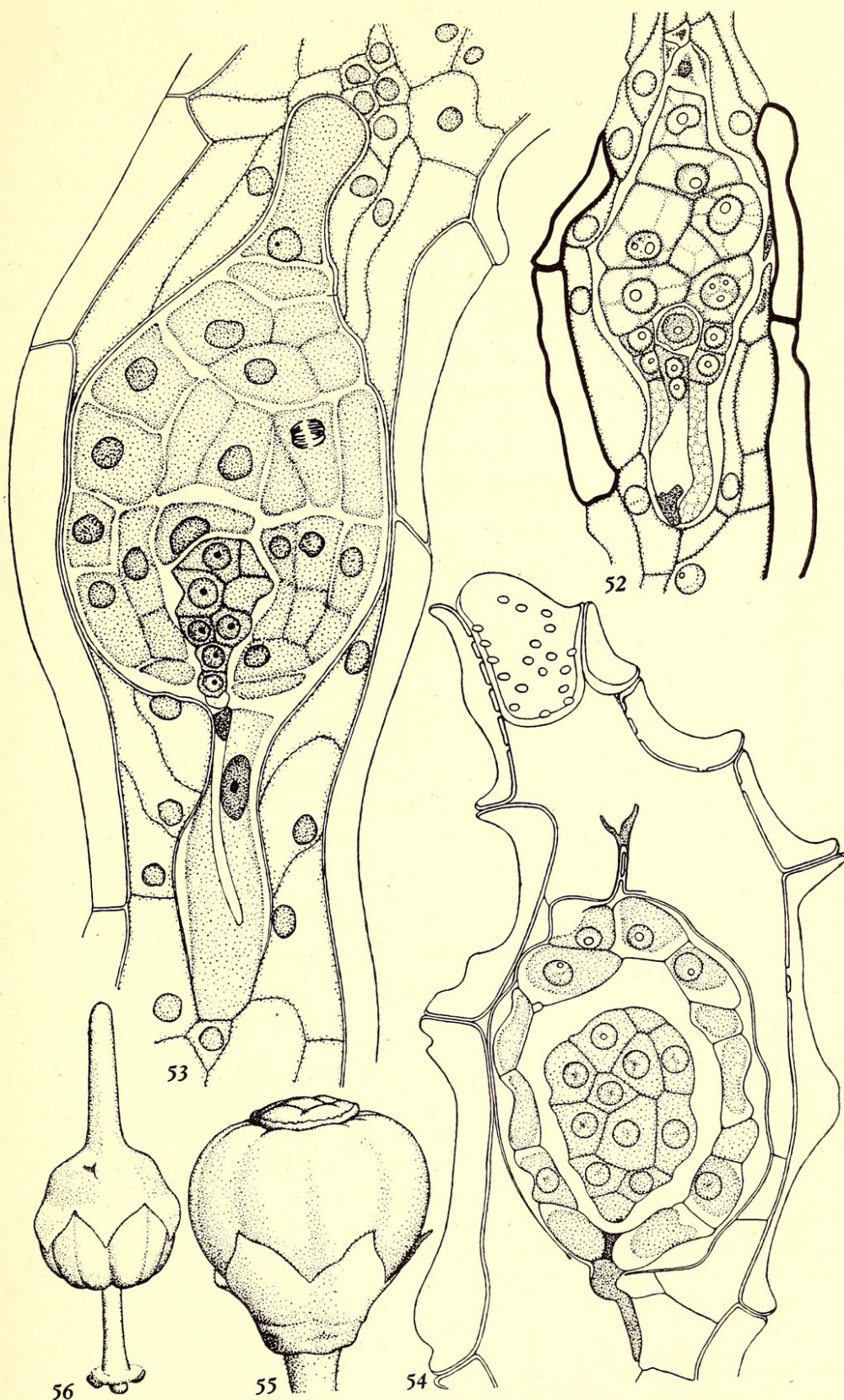


PLATE 17. STRUCTURE OF THE PYROLEAE.

connection, and the wall of each locule is ruptured in the median radial plane, so that dehiscence is loculicidal.

Rydberg (1914) distinguished *Ramischia*, *Erxlebenia*, and *Pyrola* as having capsules splitting from below upward; and *Chimaphila* and *Moneses* as having capsules splitting from above downward. I cannot persuade myself, from a study of herbarium specimens, that this difference exists. Certainly, none of these plants have capsule valves which tear loose at the base as they do in *Ledum*. One rarely sees capsules in the act of splitting; herbarium specimens which appear to be in this state seem usually to show splitting both from above and from below toward the middle.

Rydberg further distinguished the three former genera as having cobwebby hairs between the separating valves, and the two latter as lacking these. This distinction is valid. The scant wefts of white or tawny hairs seen between the separating valves consist of torn fragments of the fibrous layer. Their absence in *Chimaphila* and *Moneses* is a derived character, a matter of the more definite establishment of loculicidal dehiscence by the formation of a more definite line of splitting.

To the best of my knowledge, the process of germination has never been followed through in this group. Christoph (1921) induced seeds of *Pyrola rotundifolia* to germinate, to the extent that the micropylar end of the embryo grew forth as a root bearing a cap. He could induce no further development. His figures leave no doubt as to the validity of his observation, though Andres (1929) was unable to repeat it. Fürth (1920) observed, in a pot seeded with *Moneses*, a body resembling a brief length of root with secondary roots and an adventitious bud. Holm (1898) identified certain young plants as seedlings of *Chimaphila*.

Velenovsky is said to have affirmed, in works which I have not seen, that the germinating seed gives rise to an underground cylindrical structure, neither stem nor root, but more primitive than either, and to be known as the procaulon. I affirm that there is in the Pyroleae no such thing as a procaulon; there is a definitely cauline rhizome, except in *Moneses*, whose permanent member is a perfectly definite root. The Monotropoideae likewise have no procaulon, but definite roots.

THE CLASSIFICATION OF THE PYROLEAE

As noted, the generally accepted classification of plants, being that of Engler and Prantl, or, as to the Bicornes, that of Drude, combines the Pyroleae and the Monotropoideae in a separate family Pyrolaceae which is listed before most of the other families of the order, as if primitive. Andres, the leading authority of the Pyroleae, has accepted this arrangement. My own observations as just set forth, together with previous studies of the Monotropoideae (1941), have led me to quite other conclusions. These are in general the same as those of Henderson (1919).

The Pyroleae, many of the Monotropoideae, and a third group, the Clethraceae, have choripetalous flowers and loculicidally dehiscent fruits. All three were placed as primitive Bicornes on the basis of the floral character, the character of the fruit being overlooked. The further characters of the Clethraceae—that they are woody plants, with a true endothecium in the anthers and primitive features in the stigma—substantiate this placement of this group.

Choripetalous flowers are not, however, necessarily a primitive character among Bicornes. Costerus and Smith (1916) and Camp and Gilly (1943) have shown that choripetaly occurs occasionally in *Vaccinium* as a teratological phenomenon, presumably by a mutation. I am convinced that the choripetalous flowers of *Hypopitys* and *Monotropa* are derived from a sympetalous ancestry represented among living plants by *Monotropsis*, and that the choripetalous flowers of *Ledum* represent a deviation from the sympetalous flowers of *Rhododendron*.

If among the Bicornes choripetalous flowers are frequently derived from sympetalous, we may consider the possibility of associating the Pyroleae and Monotropoideae with that group of Bicornes which is particularly characterized by loculicidal capsules, namely the tribe Andromedae. The Andromedae have not been subjected to a thorough survey of the microscopic characters, and I am not able to show that they agree with the Pyroleae and Monotropoideae in any of those striking positive details which are accepted as convincing evidence of relationship. Nothing in the gross characters of the groups contradicts it. Mention was made above of the characteristic dehiscence mechanism of the anthers of the Arbuteae, a group related to, and presumably derived from, the Andromedae. This mechanism appears quite probably to be related to the corresponding mechanism of the Pyroleae, as though it were a specialized derivative of the same original type.

Henderson was inclined to regard the Pyroleae as representing a stage in the evolution of the Monotropoideae (she was aware that some of the genera listed in the latter group are quite isolated, as though of independent origin). The most striking common characters of the Pyroleae and Monotropoideae are the peculiar placentation, axile in the lower half of the ovary and parietal in the upper, and the numerous, minute, and delicately constructed ovules and seeds. These characters are much more readily interpreted as derived than as primitive, and one must recognize the possibility that they have had a repeated independent origin. In fact, the Pyroleae and Monotropoideae exhibit only a general similarity: there are no striking identities in positive details. The genera demonstrably related to *Monotropa* are marked by a pairing of the lobes of the disk, by petals with saccate bases, and by obsolescence of the petal dorsal bundles. Nothing

of these characters occurs in the Pyroleae; these characters can be traced back to *Monotropsis*, a genus with sympetalous flowers, obviously not descended from the Pyroleae. So, likewise, *Pterospora* and *Sarcodes* have sympetalous flowers, and the latter genus has ovules with an integument of several layers of cells. As to *Allotropa* alone among the accepted genera of Monotropoideae, a derivation from the Pyroleae is a reasonable possibility; and even as to this genus, an independent origin it at least equally probable.

The Pyroleae and Monotropoideae are accordingly not to be combined in one group. I abide by my former suggestion, that the Monotropoideae be construed as a subfamily of Ericaceae and placed after subfamily Arbutoideae, as presumed descendants of Andromedeae. The strong probability that the group includes more than one line of descent from Andromedeae must be kept in mind. The group is maintained pending further knowledge, for the accommodation of various genera, *Allotropa*, *Sarcodes*, *Pterospora*, and *Pleuricospora*, whose detailed relationships remain obscure.

The Pyroleae are to be construed as a rather inconsiderable but thoroughly natural tribe of Ericaceae, to be placed in subfamily Arbutoideae after tribe Andromedeae as presumably derived from the latter.

We have seen that five genera have been distinguished within the original genus *Pyrola* of Linnaeus. Among these, *Chimaphila* (*Pyrola umbellata* and *P. maculata* of Linnaeus) and *Ramischia* (*Pyrola secunda* L.) are quite decidedly distinct. Whether *Erxlebenia* (*Pyrola minor* L.) and *Moneses* (*Pyrola uniflora* L.) are tenable is more questionable. Andres has decided to maintain the latter but not the former. This decision is tenable, *P. minor* being distinct merely in the fact that the flowers are not definitely zygomorphic, whereas *Moneses* has a different type of underground structure as well as a different inflorescence. Accordingly, I maintain Andres' list of genera.

It appears that *Ramischia* exhibits many primitive characters, and may be interpreted as a moderate modification of what one would postulate as the original form of the group. *Chimaphila* likewise exhibits primitive characters, but is in other respects specialized, more highly so than *Ramischia*, and in different features. I would differ from Andres by listing it second rather than last among the genera of the tribe. *Pyrola minor* represents the transition from our hypothetical original form to the typical species of *Pyrola*. *Moneses* appears to be a derivative of something much like *Pyrola minor*.

The following is the taxonomic system of the Pyroleae which best represents the natural system of the group as far as I am able to infer it:

Order Bicornes L. Gen. Pl. ed. 6 (1764).

Family Ericaceae de Candolle in Lamarck and de Candolle,

Fl. Franc. ed. 2, 3: 675 (1805).

Subfamily Arbutoideae Drude in Engler and Prantl, Nat. Pflanzenfam. 4 (1): 32 (1889).

Tribe Pyroleae (Lindley) DC. Prodr. 7: 772 (1839).³ Plants essentially perennial herbs with permanent underground parts, mostly with green leaves; stems without pericycle or a continuous layer of cork; the inflorescences racemes or reduced racemes, the peduncle with a pericycle, bracts present, bractlets absent; flowers choripetalous; anthers without horns, with brief tubes or none, opening through pores actually basal and external, appearing by inversion of the anthers to be terminal and internal, the lobes lined near the pores with a hypodermis of cells with reticulately thickened walls; ovary with the placentation axile below, parietal above; ovules minute and numerous, with an integument of two layers of cells; embryo without differentiated parts; fruit a loculicidal capsule.

I. Disk present. Dehiscence of anthers effected, at least in part, by resorption tissue. Permanent underground structure of the plant a rhizome.

1. *RAMISCHIA* Opiz. Plants with ovate, finely-toothed leaves lacking palisade tissue; inflorescence racemose, the vascular supply of the flowers originating in the same manner as that of axillary buds; flowers small; each perianth part supplied by a separate bundle which forks into three; sepals ciliate; petals concave, ascending, each with two ventral basal tubercles, collectively forming an ovate corolla; anthers sparsely papillose, the epidermal cell walls with reticulate thickenings, tubes essentially absent, pores elliptic, opening to some distance from the surface by resorption tissue, for the rest by collapse tissue; style elongate, traversed by the five carpel dorsal bundles; stigma without a collar; capsule valves connected by cobwebby hairs.

Ramischia secunda (L.) Garcke (*R. secundiflora* Opiz), occurring around the world in the northern part of the north temperate zone, is perhaps the only tenable species. I have been unable to locate a formal description of *R. truncata* Andres.

2. *CHIMAPHILA* Pursh, Fl. Am. Sept. 1: 279 (1814). Leaves ovate to oblanceolate, serrate, with palisade tissue; inflorescence a condensed raceme, the bracts adnate to the pedicels, each bract supplied by a single bundle springing from the stele in the pedicel; flowers larger than those of *Ramischia*; each perianth segment supplied by three bundles, the origin of which is quite variable;

³ Some botanists declare a new combination upon transferring a subfamily to a different family or a tribe to a different subfamily or family. This practice is unsound because the names of subfamilies and tribes are not combinations at all. De Candolle first applied to the present group a name in *-eae* as that of a tribe; and he is authority for this name as that of a tribe in whatever subfamily or family it may be included.

sepals finely dentate; petals spreading, so that the corolla is saucer-shaped; anthers obscurely papillose, the epidermal cell walls not thickened, the tubes brief, tapering, opening from the pores to the tapetum by resorption tissue; style brief, obconic, supplied by both the carpel dorsal bundles and the carpel laterals; stigma dome-like with an obscure collar; capsule valves without cobwebby hairs.

There are four generally recognized species, *Chimaphila japonica* Miquel in Japan, *C. Menziesii* Sprengel in western North America, *C. maculata* (L.) Pursh in eastern North America, and *C. umbellata* (L.) Barton general in the northern north temperate zone. The latter occurs respectively in Europe, in eastern North America, and in western North America as obscurely distinguishable races which have been treated as species but are scarcely tenable as such. Camp (1939) has reduced a number of other proposed species; whether any further species, as *C. dominguensis* Blake in Jour. of Bot. 52: 169 (1914), are tenable, I do not know.

II. Disk absent; anthers without resorption tissue, their epidermis not papillose, its cell walls not thickened. Perianth supplied by ten bundles, each typically forked into three which are respectively the dorsal bundle of one perianth part and the laterals of the two adjacent ones. Style elongate, stigma with a collar.

3. PYROLA L. Sp. Pl. 396 (1753). Underground permanent member of the plant a rhizome; flowers racemose, the bract subtending each supplied by three bundles from the stele in the pedicel; sepals glabrous, entire; style supplied by five bundles springing from the placental bundles; capsule valves connected by cobwebby hairs.

This genus is widely distributed in the north temperate zone, with outliers in Sumatra and Mexico. There are rich arrays of distinguishable forms in northern North America and in eastern Asia, and the list of tenable species may exceed forty. Among these, a small minority typified by *P. minor* are distinguished by essentially actinomorphic flowers. The majority, with zygomorphic flowers, were subdivided by Alefeld with emphasis on the shape of the anther pores; by Andres, with emphasis on the shape of the sepals; and by Rydberg with emphasis on the color of the flowers. The following arrangement is merely tentative. In recognizing three sections, it is a simplification of that of Andres.

A. Flowers essentially actinomorphic.

SECTION 1. *Amelia* (Alefeld) Benth and Hooker, Gen. Pl. 2: 603 (1876). Andres cites Hooker as authority for this group as a subgenus; but in the *Genera Plantarum* the name is applied definitely to a section.

Pyrola minor L. and various races in eastern Asia, together, probably, with *P. media* Swartz.

B. Flowers definitely zygomorphic.

1. Sepals essentially ovate, scarcely longer than broad.

SECTION 2. *Scotophila* Nuttall in Trans. Am. Phil. Soc. n. s. 8: 271 (1843), based on *P. aphylla*. Section *Ampliosepala* Andres. Often producing aphyllous forms.

a. Leaf blades if present bright green, containing one layer of palisade tissue or none.

Pyrola virens Schweigger (*P. chlorantha* Swartz), supposedly around the world, though with variations; *P. renifolia* Maximowicz Prim. Fl. Amur. 190 (1859), and other species in eastern Asia; *P. elliptica* Nuttall in eastern North America.

b. Leaf blades if present dull green or with dull green mottling, containing two layers of palisade tissue.

Pyrola picta Smith, *P. dentata* Smith, and variations (*P. aphylla* Smith is treated as one of these), in western North America. Alefeld combined the two species here accepted under the name of *Thelaia spathulata*. His action was justified by the practice of the times, but Andres was not justified in using Alefeld's epithet under *Pyrola*.

2. Sepals essentially lanceolate, distinctly longer than broad. Leaves without palisade tissue.

SECTION 3. *Thelaia* (Alefeld) Bentham and Hooker, l. c. Subgenus *Euthelaia* Alefeld, in part; section *Euthelaia* (Alefeld) Andres. In the usage of everyone except Alefeld, this is the type group of the genus *Pyrola*.

a. Flowers white.

Pyrola rotundifolia L.; *P. americana* Sweet, scarcely distinguishable from the foregoing; other races in Canada and eastern Asia.

b. Flowers with more or less considerable red pigment.

The first species to be distinguished in this group was *P. asarifolia* Michaux, Fl. Bor. Am. 1: 251 (1803). As to *P. uliginosa* Torrey and Gray in Torrey Fl. New York 1: 453 (1843), Fernald (1904) has found it to intergrade with the preceding and has reduced it; Rydberg, on the other hand, has maintained it and has reduced to it *P. elata* Nuttall in Trans. Am. Phil. Soc. n. s. 8: 270 (1843), a perfectly definite race in western North America. I have applied the name in Rydberg's sense: the plant here called *P. uliginosa* is not positively representative of that species; it is positively representative of *P. elata* Nuttall. *Pyrola bracteata* Hooker, Fl. Bor. Am. 2: 47 (1834) is a definite though not profoundly distinct race in western North America. Further races of this group occur in Mexico and in eastern Asia; the oldest name for the latter is *P. incarnata* Fischer apud DC. Prodr. 7: 773 (1839).

4. *MONESSES* Salisbury ex S. F. Gray. Permanent underground structure a root; leaves without palisade tissue; flowers solitary, terminal on an extended peduncle; sepals ciliate; stamens inclined toward the upper side of the flower, as in the species of *Pyrola* with zygomorphic flowers; anthers with the tubes curved, diverging and converging; style supplied both by carpel dorsal bundles and by carpel laterals; capsule valves without cobwebby hairs.

Moneses uniflora (L.) A. Gray, around the world in northern regions, is presumably the only species. *Moneses reticulata* Nuttall in Trans. Am. Phil. Soc. n. s. 8: 271 (1843), described from western North America, was reduced by Piper (1906) to complete synonymy and restored as a variety by Blake (1915); it is very feebly if at all distinct.

SUMMARY

The Pyroleae and the Monotropoideae agree in having chori-petalous flowers, parietal placentation in the upper part of the ovary, the ovules and seeds numerous, minute, and delicately constructed, and septicidally dehiscent capsules (actually, most of these characters extend only to a part of the Monotropoideae). All of these characters appear to be derived, not primitive, and the two groups appear not properly to be united into one; rather, they represent parallel lines of descent from a common origin, presumably the tribe Andromedeae.

The Pyroleae are an undoubtedly natural small group best construed as a tribe of Ericaceae to be placed in subfamily Arbutoideae after tribe Andromedeae.

It is expedient to recognize four genera, as Andres did. *Ramischia* (*Pyrola secunda*) is definitely distinct from *Pyrola* proper. It is the most primitive genus of the group. *Chimaphila* is also primitive in most respects. These genera are distinguished by a disk below the ovary and by the presence of resorption tissue in the anthers. *Pyrola minor* has actinomorphic flowers but agrees in all other respects with *Pyrola* proper, and may properly be left among the moderately numerous species of that genus. *Moneses*, with shoots springing from roots instead of from rhizomes, solitary flowers, and styles supplied by ten bundles, is tenable as a distinct genus.

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