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A Monograph on Foliar Anatomy of the Genera Connellia, Cottendorfia, and Navia (Bromeliaceae)

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ABSTRACT

Harold Robinson. A Monograph on Foliar Anatomy of the Genera *Connellia, Cottendorfia,* and *Navia* (Bromeliaceae). *Smithsonian Contributions to Botany,* 2: 1–41. 1969.—The 102 presently known species of the pitcairnioid genera *Connellia, Cottendorfia,* and *Navia* are discussed, illustrated, and keyed on the basis of cross sections and epidermal peels of leaves. Comparison with other genera of the bromeliad subfamily Pitcairnioideae indicates *Connellia, Cottendorfia,* and *Navia* belong in a series with *Ayensua, Brocchinia, Fosterella, Pitcairnia,* and *Puya* that have sharply demarcated chlorenchyma and water-storage layers in the mesophyll. *Abromeitiella, Deuterocohnia, Dyckia, Encholirium,* and *Hechtia* seem to be another related series without such sharp demarcation. *Connellia* is considered related to a series of *Cottendorfia* species having elongate stomata. Many *Cottendorfia* species show abaxial water-storage tissue of a structure similar to *Puya* and some Amazonian species of *Pitcairnia.* In *Navia,* the species with paniculate or racemose inflorescences are found to represent three rather distinct groups, one of which seems close to *Cottendorfia.* Species of *Navia* with vascular bundles more completely enclosed in chlorenchyma, with scales replaced by trichomes, with sessile or glomerate inflorescences, or with connate and partially reduced sepals are considered specialized. A great number of substomatal variations are recorded in *Navia* that distinguish species or groups of species. *Navia lopezii* is shown to have a very modified epidermal structure with simple stomata and no scales, characters unlike any other bromeliad presently known.

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Harold Robinson

A Monograph on Foliar Anatomy of the Genera Connellia, Cottendorfia, and Navia (Bromeliaceae)

The pitcairnioid genera, *Connellia, Cottendorfia,* and *Navia,* are restricted almost entirely to the remote and relatively inaccesible part of South America known as the Guayana Highland. While one species of *Cottendorfia* and two species of *Navia* were described as early as 1830 and a few additional species from 1846 to 1929, the vast majority have been described during the years since 1930, mostly by Lyman B. Smith working with collections of Tate, Steyermark, Maguire, and others. The most complete treatments for the genera may be found in the recent summary of the Bromeliaceae of the Guayana Highland (Smith, 1967a). About eight species have been described since the 1967 work.

As presently accepted, the three genera, *Connellia, Cottendorfia,* and *Navia,* are distinguished as broad but apparently natural groups on the basis of floral and seed characters. However, rather marked characters have been observed within genera, such as the lack of a scape in *Cottendorfia navioides* (in a genus where it is normally well developed), and the presence of a long scape in various species of *Navia* (a genus in which it is usually lacking). In the single species, *Navia parvula,* the anterior sepal is totally aborted, a character that might be considered very significant in other groups of plants. One species, *Cottendorfia florida,* is unique in its distribution, being found in eastern Brazil, far from the Guayana Highlands and all other species of the group.

One of the primary concerns of this study was a search for anatomical characters that might support or refute suspected relationships derived from floral characters alone. In the process any evidence of natural or related groups has been sought to decrease the reliance on the artificial though workable key characters that are now prevalent. It is hoped that the series of keys and notes produced in the process will be useful in the determination of sterile or otherwise incomplete material. To these ends, Dr. Lyman B. Smith of the Smithsonian Institution staff, with his continuing interest, has provided time, material, and constant encouragement. Dr. Edward S. Ayensu, also of the Smithsonian, who has concerned himself increasingly with the anatomy of the Bromeliaceae has likewise provided much needed assistance.

A general anatomical treatment of the family Bromeliaceae is available in the work of Solereder and Meyer (1929); however, the work does not include any of the species of *Connellia, Cottendorfia,* or *Navia.* I have seen, in manuscript form, some parts of the treatment of the family by P. B. Tomlinson for the series on the Anatomy of the Monocotyledons edited by C. R. Metcalfe, Oxford University Press. This latter work does include a few of the species in the above complex.

Methods

Many characters are available in studies of bromeliad leaf anatomy, but the present effort emphasizes epidermal and stomatal structure along with the leaf structures seen in cross section. Scales and trichomes

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are used to distinguish some species, but no critical review of variations in scale structure has been attempted.

The leaf sections and epidermal preparations for this study were all made free hand and mounted in Hoyer's Solution (Anderson, 1954). All specimens were obtained from fragments of dried herbarium material soaked in tap water. The final slides used in the study were unstained temporary mounts. Preparations kept more than two years clearly show the original limits of the chlorenchyma and the resinous deposits.

In taking epidermal strips and leaf sections, the leaf base has been strictly avoided. In the leaf base the chlorenchymatous mesophyll is poorly differentiated and air chambers are highly developed. The vascular bundles are surrounded with irregular groupings of small parenchyma cells, and the epidermal layers are greatly thickened. It is at a higher level that stomata begin to appear and finally are densely organized into definite bands underlying the smaller bundles or intervening mesophyll regions. In some species internal features at this higher level may still show some disorganization characteristic of the leaf base, and for critical observations only those sections from midleaf or above have been relied on.

The present study constitutes a preliminary effort with definite limitations. Even in the case of *Cottendorfia,* where sections of leaves have often been taken at various levels, conclusions must be drawn with care. Rarely are more than two levels sampled or more than one leaf, and few of the species are even known from more than one collection. In *Navia,* with its far greater number of species, observations are based on far less thorough sectioning, and the stomatal characters, which happen to be of particular interest in the genus, are emphasized.

For a list of specimens examined during this study, see page 19.

Generic Limitations

Of the three genera, *Navia, Cottendorfia,* and *Connellia,* the first, *Navia,* is distinguished almost entirely on the basis of the unappendaged seeds. *Connellia* is close to *Cottendorfia* but distinguished by the subbasifixed anthers and showier flowers.

This study has involved only the most cursory examination of flower parts, but what has been seen tends to indicate uniformity of these structures in such genera as *Pitcairnia, Brocchinia, Cottendorfia,* and *Connellia.* Only the last, a small genus of four species, shows such uniformity in leaf anatomy. All the other genera listed show two or more distinct types of leaf structure. Some of the types that appear in more than one genus might indicate relationships, but some are probably the result of parallel development. There is not, at present, any reason to question that present genera represent natural groups, but there is considerable reason to regard them as very broad concepts that may be subject to some subdivision.

After observing transverse sections of the leaves of over twenty species selected by Dr. Lyman B. Smith to represent the variation in the genus *Pitcairnia,* and of nearly all species of *Brocchinia,* these genera seem relatively uniform with only two very distinct types in *Pitcairnia* and three types in *Brocchinia.* This is contrary to the impression that is given by the macroscopic leaf variation in *Pitcairnia* where the basic anatomical unity is obscured by broad bladed and slenderly petiolate, narrow bladed and deciduous, and heterophyllous variants. The variation in transverse sections in *Cottendorfia* seems at least as great, although there are certain types totally lacking, reflecting a basic uniformity in the genus. The genus *Navia* is, from all indications, the most richly varied in almost all structures, patterns of leaf cross section, stomata, and scales. One might conclude that although restricted to a climatic and topographic area lacking any great antiquity, *Navia* may represent one of the oldest lines of development in the subfamily.

The leaf anatomy does not clearly demarcate the existing generic concepts of the genera *Connellia, Cottendorfia,* and *Navia,* but it does show distinctive trends within the latter two genera. These trends are discussed in the following section but they are summarized as follows.

Characters sometimes found in *Navia,* not in *Connellia* or *Cottendorfia:* (1) Vascular bundles separated from adaxial water-storage cells by a layer of chlorenchyma; (2) substomatal pores with large or long intrusions or reduced to a slit; (3) leaves bearing radially symmetrical uniseriate trichomes.

Character sometimes found in *Cottendorfia,* not in *Connellia* or *Navia:* Vascular bundles in contact with well-developed areas of water-storage tissue both abaxially and adaxially.

Key to Basic Distinctions of the Pitcairnioid Genera (adapted from Smith, 1967b)

1. Epigynous tube absent.
  2. Plants monoecious with perfect flowers or if rarely polygamodioecious (*Dyckia maritima* and *D. selloa*) then petals yellow or orange and plants native of southernmost Brazil and Uruguay.
    3. Bases of the filaments separate from each other, but sometimes individually adnate to the petals and sepals.
      4. Seeds appendaged.
        5. Petals not tightly coiled after anthesis.
          6. Ovary wholly superior; petals regular.
            7. Petals naked.
              8. Seeds with a falciform or broad apical appendage; plants of northeastern Brazil . . . . . ***Encholirium***
              8. Seeds bicaudate-appendaged.
                9. Anthers basifixed, linear, coiled at anthesis; inner filaments adnate to base of petals; leaf blades thin, more or less contracted at base; mesophytic plants of Mexico to Argentina . . . . . ***Fosterella***
                9. Anthers subbasifixed to equitant, stout, straight; filaments usually free; leaf blades firm, not contracted at base; plants of the Guayana Highland and northeastern Brazil.
                10. Anthers subbasifixed; petals brightly colored, more or less massed together after anthesis but not twisted; sepals large and firm . ***Connellia***
                10. Anthers equitant; petals white, separate after anthesis; sepals not over 7 mm long, thin, flat . . . . . ***Cottendorfia***
            7. Petals appendaged with a single basal scale each; plants of the southern Andes from Peru to Chile and Argentina.
              11. Scape evident; inflorescence usually well developed; plants ring-forming so far as known . . . . . ***Deuterocohnia***
              11. Scape lacking; inflorescence one–few-flowered; plants polster-forming . . . . . ***Abromeitiella***
          6. Ovary partially to wholly inferior, or if superior then the petals zygomorphic (*Pitcairnia mirabilis*).
            12. Petals large, naked or appendaged, usually zygomorphic and forming a hood over the anthers; sepals convolute with the left side of each overlapping the right of the next one; plants of Mexico and the West Indies to Argentina and Brazil . . . . . ***Pitcairnia***
            12. Petals minute, regular; sepals cochlear with both posterior ones overlapping the anterior; plants of the Guayana Highland . . . . . ***Brocchinia***
        5. Petals tightly coiled together after anthesis; Andean plants of open summits from Costa Rica and Venezuela to Chile and Argentina . . . . . ***Puya***
      4. Seeds naked at maturity.
        13. Sepals convolute; petals zygomorphic (*Pitcairnia aphelandrifolia*) . . ***Pitcairnia***
        13. Sepals cochlear; petals regular, naked; ovary superior (in most species) to nearly inferior; plants of the Guayana Highland . . . . . ***Navia***
    3. Bases of the filaments forming a tube and adnate to the petals; petals yellow or orange; sepals cochlear; plants of eastern South America . . . . . ***Dyckia***
  2. Plants dioecious with functionally unisexual flowers; petals rose or white; plants of Texas, Mexico, and northern Central America . . . . . ***Hechtia***
1. Epigynous tube present; plants of the Guayana Highland . . . . . ***Ayensua***

In addition to these general trends there are many individual characters by which species can be distinguished, as indicated in the keys to the species of each genus. There are many species, however, that possess an intermediate type of leaf anatomy that cannot be placed in the proper genus without referring to floral characters.

Anatomical Structures

ZONATION.—As seen in transverse section, all the species of *Navia, Cottendorfia,* and *Connellia,* except the very aberrant *N. lopezii,* have the chlorenchymatous mesophyll and the adaxial water-storage tissue sharply demarcated from each other (Figures 1, 4, 9, 12, 15,

253, 256, 261, 266). This is in contrast to the genera *Hechtia, Dyckia, Encholirium, Deuterocohnia,* and *Abromeitiella,* which have an area of poorly differentiated cells between, forming a transition zone. In dried material this can be very difficult to observe since water-storage cells can collapse and become obliterated or compacted into a layer that looks like a demarcation line. I would refer to sections lacking a sharp demarcation as a *Dyckia* type, which in its most typical form is very thick-leaved with vascular bundles remote from the abaxial surface, and the abaxial surface deeply ridged with stomata restricted to the deep furrows. There has not been much tendency to relate the South American genera of this group with the Mexican and northern Central American *Hechtia* because of their very divergent and rather remote distributions. On the basis of leaf anatomy, however, these genera together seem to form a related series well out of the *Navia, Cottendorfia, Connellia* relationship.

EXPOSURE OF VASCULAR BUNDLES.—The extent to which the chlorenchyma surrounds the vascular bundles seems to be a variable factor that can differ in closely related groups, at least in *Navia* (Figures 232, 239, 242, 243, 253, 256, 261, 266). In *Pitcairnia,* at least two species, *P. punicea* and *P. oaxacana,* have chlorenchyma covering the smaller bundles adaxially, while most of the species, including many seemingly closely related, have bundles all emergent against or into the adaxial water-storage tissue.

In spite of such variation between related species, the overall trends indicate the exposure of the vascular bundles is of considerable significance. The extreme situations are quite contrasting and are not found in related groups. Also, in some cases whole groups do show uniformity in the character. The bundles are covered adaxially with chlorenchyma in most species of *Navia* or show a tendency toward such cover with only the larger bundles being exposed (Figures 92, 100, 106, 109, 116, 117, 124, 128, 132, 133). I would refer to such sections as the *Navia* type. A marked exception in *Navia* is a group of perhaps primitive species having a paniculate inflorescence of the *N. reflexa* (Figure 70), *N. hohenbergioides* (Figure 79), *N. ramosa* (Figure 69) relationship, which all have bundles definitely exposed. This group is so marked that the few species that have paniculate inflorescences but with bundles covered with chlorenchyma adaxially seem only distantly related.

Such distinctly covered bundles appear elsewhere in the Pitcairnioideae in the recently described genus, *Ayensua* (Ayensu, 1969; Smith, 1969), in at least two species of *Fosterella,* and in *Brocchinia vestita, B. maguirei, B. delicata, B. melanacra,* and *B. cowanii.* In *Brocchinia* the covered bundles are highly characteristic of the particular series, but the probable primitive type, *B. serrata,* and the series including the type, *B. paniculata,* have bundles not covered with chlorenchyma adaxially.

In what I would call the *Cottendorfia*-type cross section, the chlorenchyma may form large masses extending upward between the vascular bundles, but with rare exceptions there is a group of water-storage cells reaching the adaxial surface of each bundle (Figures 1, 4, 9, 15, 61, 64). This pattern is found in all species of *Cottendorfia* and *Connellia.* In *Cottendorfia* the appearance can become greatly accentuated with the development of large abaxial water-storage canals that also reach the vascular bundles (Figure 43). This extreme type of *Cottendorfia* cross section seems unlikely to have evolved very often, if more than once, and I find it significant that similar sections occur in *Puya* as represented by *P. santosii* and *P. sodiroana,* and in a small section of rather distinctive *Pitcairnia* species as represented by *P. nuda, P. bulbosa,* and *P. armata.* The latter three *Pitcairnia* species are from the part of the extensive range of their genus in which *Cottendorfia* is found.

The abaxial water-storage canals occur in a part of the leaf in which they are often replaced by a fibrous region connecting the vascular bundle to the abaxial epidermis. Such extensions of the sclerenchyma occur in three species of *Cottendorfia*—*C. florida* (Figure 4), *C. thyrsoidea* (Figure 24), and *C. minor* (Figure 25)—and in *Navia immersa* (Figure 136), *N. serrulata* (Figure 182), and various species of the *Navia reflexa* group (Figure 79). In these two genera there is no indication that any of the species are particularly closely related except for those in the *Navia reflexa* group. In neither of these genera do the fibrous bundle groups extend adaxially to reach or nearly reach the epidermis as sometimes happens in *Pitcairnia* or *Brocchinia.*

PLACEMENT OF VASCULAR BUNDLES.—In some species of *Navia* the central portion of the leaf may be rather distinctly thickened, but there is none of the marked alteration in arrangement or shape of the vascular bundles that is so prominent in the costa-like central portion of the leaves of many species of

Pitcairnia. The differentiation of the middle part of the leaf in *Navia* is so slight that there is no reason to assume any close relationship to that in *Pitcairnia*. In the latter genus this pseudocostate or what I would call the *Pitcairnia*-type arrangement has been present to some extent in most species seen, except those in the previously mentioned group including *P. nuda, P. bulbosa,* and *P. armata*. I have seen nothing I would call a *Pitcairnia*-type section in any other genus, and it seems to have evolved completely within the genus *Pitcairnia*.

The review of the various Pitcairnioideae has left the impression that the *Cottendorfia*-type leaf section, at least in its less specialized form, is primitive within the group. In *Brocchinia, Pitcairnia, and Navia* the less specialized species all or mostly seem to show such sections, and the *Navia*-type section seems to be only in obviously derived groups of species.

STOMATA.—The guard cells and subsidiary cells, except for those of the very distinctive *Navia lopezii,* are relatively uniform. They vary in relative width in both *Navia* and *Cottendorfia*. In *Cottendorfia* the genus seems divisible into natural groups on this basis (Figures 5, 7, 10, 13, 16, 19, vs. 22, 27, 29, 31, 34, 37, 41, 44, 46). No such pattern is evident in *Navia* though obviously related species tend to be alike.

In *Navia lopezii* the guard cells are very narrow and have similarly shaped lateral subsidiary cells that are broadly exposed on the outer surface (Figures 275, 277). This pattern of narrow guard cells and exposed subsidiary cells is not seen elsewhere in *Navia,* but resembles the amazingly uniform stomatal type found in most species of *Pitcairnia*. In *Pitcairnia,* only three species observed, *P. nuda, P. bulbosa,* and *P. armata,* which have other cottendorfioid characters, tend to have broader guard cells and more included subsidiary cells. Variation between stomata of the *Navia lopezii* type with only the two lateral subsidiary cells (paracytic) and those such as seen in other bromeliads with both lateral and polar subsidiary cells (tetracytic) has been noted by Stebbins and Khush (1961) in various families, but not previously between species of a single genus.

It is notable that the developmental influence of the stomata of most bromeliads extends laterally to the cells of the adjacent rows to the same extent it does to the polar cells, usually resulting in a true total of six subsidiary cells. In some cases the true inner lateral subsidiary cells seem to become completely included (Figures 215, 216, 218, 219), and the outer laterals directly contact the guard cells becoming subsidiary cells in the strictest sense of the term.

SUBSTOMATAL INTRUSIONS.—The pore immediately inside the stoma is usually rounded or only slightly misshapen in most genera of the Pitcairnioideae. It has slight intrusions in some *Hechtia* or *Pitcairnia* species and is rather reduced in *Cottendorfia florida* (Figure 6). It is in the genus *Navia,* however, that the pore is subject to incredibly rich variation in shape. One totally unique variant is the special case of *N. lopezii* in which the pore does not occur because an inner layer of subepidermal cells is not formed (Figure 275). Other variations in *Navia* concern the types of intrusions projecting inward from surrounding cells. These variations include *N. breweri* (Figure 236) and *N. involucrata* (Figure 108) types in which the surrounding cells are thick-walled and intrude leaving only a small slitlike opening or no opening that can be seen from face view. In the *N. reflexa* type (Figures 72, 75) hooked thick-walled intrusions reduce the opening to a double-anchor shape. The *N. subpetiolata* type (Figure 204) shows similar but thin-walled projections. The *N. cretacea* type (Figure 161) is similar to that of *N. subpetiolata* but bears many extra lobes or papillae. The *N. parvula* type (Figure 102) consists of four separate instrusions that reduce the opening to a cruciate form. The *N. abysmophila* type (Figure 153) has the opening divided into a number of separate round pores. There are in addition a large number of species of *Navia* such as *N. myriantha* (Figure 264) with the simple structure most often found in other genera.

In *Navia* there are strong indications that stomatal types are stable not only in species but species groups. The stomatal type in *N. reflexa* is rather characteristic of the group of species, and the *Navia subpetiolata* group seems to be a natural one showing stomatal uniformity. In most of the species related to *N. myriantha* the substomatal pore is simple. The distinctive substomatal pore of *N. parvula* is correlated with the distinctive aborted sepal in the flower but *N. lepidota* with a reduced sepal has a stomatal type that is as near as any seen to that in *N. parvula*. Still, a case of obvious failure of the character is in the unmodified opening of *N. ramosa,* a species rather obviously related to *N. reflexa* and its relatives with their otherwise distinctive pore type. The similarity of the substomatal pore in *N. breweri* and *N. cardonae* might indicate

close relationship, but here the character is in conflict with the occurrence of trichomes, and in the present treatment I have given the latter character priority.

In many species (Figures 6, 141, 166, 252) I have observed a series of stomata in a row in which an extra cell is interposed in the substomatal layer that forms a bridge across the pore. The fact that this seems to occur erratically without regard to species and that it appears in a series of six to eight stomata in direct line, indicates that it is a common aberration that acts in the manner of a small chimera.

EPIDERMAL CELLS.—On the basis of material examined the epidermal cells of the Pitcairnioideae seem to hold amazingly to a normal type with oblong shape and sinuous walls. The walls tend to be straighter around the stomata and more sinuous in the part of each wall nearer the outer surface. There is considerable variation in size as can be seen in the various figures which, except for *Navia lopezii,* are drawn to the same scale. Among the smallest cells are those of *N. abysmophila* (Figure 152) while the largest epidermal cells of normal structure occur in *Navia intermedia* (Figure 134).

It is remarkable that all marked departures from this basic pattern, even though stable within a species, are presently each known only from a single species. In *Cottendorfia florida* only, the walls of the epidermal cells appear to be straight throughout. In a species outside the immediate study, *Brocchinia paniculata,* one end of each epidermal cell is much enlarged and thick-walled and sinuous walls are mostly lacking. In this species a very distinctive pattern of interlocking fish-shaped cells is formed. Other closely related species of *Brocchinia* lack this pattern.

The most distinctive form of epidermal cell is that of the unique species, *Navia lopezii* (Figures 275–277). Here the cells are extremely large, individual cells reaching nearly 1 mm in length. These cells are visible under a dissecting microscope. Similar large epidermal cells are seen in the outer floral bracts and the character is reflected to some extent in the carpel wall in the fruit. I have concluded on the basis of the epidermal structure that these cells are the result of the failure of protoderm cells to subdivide fully before maturing. As a result whole layers of tissues fail to differentiate. As illustrated in surface view (Stebbins and Khush, 1961), members of some genera in other families, *Juncus* (Juncaceae) and Anigosanthus (Haemodoraceae), have similar structure and may have arisen in a similar way. A similar process was probably responsible for the peculiar sporophyte development in the moss genus *Archidium,* where there are only eight large spores and there is no central columella. The evolution of fern sporangia and of leaves of Hymenophyllaceous ferns have also involved a reduction in numbers of cells, but these examples involve more long term trends than the abrupt development of *Navia lopezii.*

A central silica body is characteristic of the epidermal cells of most Bromeliaceae as well as some other monocot families. As seen in the Pitcairnioideae this is generally distinct in such genera as *Dyckia, Hechtia,* and *Navia,* and it tends to be weaker or lacking in species of *Cottendorfia, Pitcairnia,* and *Brocchinia.* This is only a trend, however, with many exceptions. In both *Navia lopezii* (Figures 276, 277) and *N. cataractarum* (Figure 95) the silica body seems to be entirely lacking.

SCALES.—The scales are one of the primary characteristics of the family Bromeliaceae, being found somewhere on the plant in all but one species. The most common type is similar to those seen in *Cottendorfia argentea* (Figure 40), *Navia serrata* (Figure 183), and *N. caulescens* (Figure 194), platelike with elongate cells at least toward the margin. The scales may be reduced to a plug as seen in *N. garcia-barrigae* (Figure 89) where it sits in the center of a pit covering a circle of stomata. Vestigial scales as shown in *Cottendorfia savannensis* (Figure 58) are undoubtedly common in the family, but only evident under the compound microscope. The scale type in *Navia arida* with its thin-walled rounded cells and partially resorbed margin of small cells is unique among the species in the three-genus complex, but somewhat similar ones have been seen in *Pitcairnia* and *Brocchinia.*

The most distinctive type of emergence encountered in the study is the trichome (Figures 244, 262, 265, 271, 274) seen only in certain species of *Navia.* The radially symmetrical uniseriate structure seems very distinct from all scales seen, but might represent a single branch of some of the deeply cleft types occurring in a few other species. For the present it seems reasonable to treat species so armed as a related complex, but like other characters this may vary in expression within the part of the genus where it occurs.

Even in species with leaves that seem glabrous, microscopic examination will usually reveal vestigial scales with distinct basal plugs set in the leaf. In one

species, *Navia lopezii,* the highly modified epidermis of the leaf has resulted in the elimination of all traces of scales. This species is the one bromeliad now known in which there seems to be no trace of scales on any part of the plant.

Comparative Evaluation of Floral Characters

Some floral characters used in previous keys, such as shape of sepals, have been admittedly artificial. Three characters used by Smith (1967a) in his treatment of the genus *Navia,* however, are worthy of special consideration: (1) connate versus free sepals; (2) inferior versus superior ovary; and (3) paniculate versus glomerate inflorescence.

Connate sepals, as seen in the Smith key, are characteristic of a series of Colombian species, including *Navia heliophila* and *N. graminifolia,* a fact called to my attention by Dr. Smith. In spite of some differences in general aspect, all these Colombian species show similar basic anatomy and three, *N. heliophila, N. acaulis,* and *N. bicolor,* are unquestionably closely related. The connate sepals prove to be characteristic of another group of closely related species, the *Navia subpetiolata* group. Here, the cross section, substomatal intrusions, and general aspect all agree and close relationship is unquestionable. Only *N. caricifolia* of this series seems particularly different and it differs only by the adaxial exposure of the vascular bundle and the somewhat more sinuous walls of the epidermal cells. There is no reason now to believe all species of *Navia* with connate sepals are closely related, but I have nevertheless grouped them together in my survey of the genus.

The inferior ovary is an important character used to distinguish *Pitcairnia* and *Brocchinia* from most other genera of the Pitcairnioideae. The character varies considerably, however, in the genus *Navia.* The species of *Navia* having inferior or partially inferior ovaries include a diverse lot of which only *N. parvula* and *N. lepidota* seem particularly closely related. Others include *N. aloifolia* which has open substomatal pores and trichomes, *N. arida* which has open substomatal pores and very distinctive scales, *N. immersa* with closed pores and vascular bundles fused to the abaxial epidermal layers, and *N. scopulorum* which has closed pores and free bundles. *Navia fontoides* has closed pores, but, like only *N. parvula* and *N. lepidota* of the series, has chlorenchyma completely covering the vascular bundles adaxially. In addition, the degree of inferiority of the ovary in the group varies. No basic unity is evident between the species involved, and I have been inclined to relegate them to various groups on the basis of other characters. It is significant, of course, that while these species show no close relationship among themselves, neither do they show close relationship to any other species in the genus. They are an assemblage of some of the most singularly distinctive species in the genus.

The paniculate inflorescence is certainly primitive in the Pitcairnioideae compared to the condensed and usually sessile inflorescence of most *Navia* species. One of the basic aims of this study involved the analysis of the few *Navia* species having a paniculate inflorescence. As indicated in the discussion of the chlorenchyma distribution, these species of *Navia* are divided into two probably not too closely related groups. The group including *N. ramosa, N. reflexa, N. hohenbergioides,* and *N. garcia-barrigae* has *Cottendorfia*-type cross sections and no tendency toward the *Navia* type. This group seems to be a side branch of *Navia* evolution that, but for the unappendaged seeds, would be called *Cottendorfia.* An additional character suggesting closer relationship to *Navia* is the development of marked substomatal instrusions in many but not all of the species. In the remaining species of *Navia* having paniculate inflorescences, the cross sections are of the *Navia* type. This series of three species, *N. lindmanioides, N. rupestris,* and *N. cataractarum,* may represent a more primitive group near the main line of *Navia* development.

Systematic Review

Floral characters in the following generic descriptions are taken partially from Smith (1967a).

Genus *Connellia*

Flowers showy; sepals free, much shorter than the petals; petals free with a narrow claw, the blades suborbicular, brightly colored, spreading at anthesis, not twisted together afterward; stamens included, free, the anthers subbasifixed; ovary superior, glabrous, the style slender, elongate; placentae elongate, nearly the height of the locule; capsule septicidal; seeds narrow, bicaudate.

Leaves thin with reduced scales (except in *C. quel-*

chii), margins incurved; stomata distinctly longer than wide with narrow guard cells; vascular bundles contiguous with adaxial water-storage tissue, sometimes with poorly differentiated abaxial water-storage canals.

As presently recognized the genus contains four species which occur in the eastern Guayana Highlands from Ptari-tepui in Venezuela to Roraima.

The leaf anatomy of the species of *Connellia* appears quite uniform (Figures 1-3) and seems basically indistinguishable from the group of *Cottendorfia* species having elongate stomata. Among these latter species epidermal scales are generally reduced, abaxial water-storage canals are usually shallow and often indistinct, and leaves in some species have distinct cartilaginous margins, all these characters being found among the species of *Connellia*. One species, *Cottendorfia longipes*, from the group with longer stomata, is possibly a *Connellia*. This species is known only from fruiting material, and flowers will be necessary for final generic placement.

Vegetative Key to Species of *Connellia*

1. Upper leaf margins with a dense fringe of scales . . . . . ***C. quelchii***
1. Leaf margins without noticeable scales.
   2. Leaf blade with prominent white cartilaginous margins . . . . . ***C. caricifolia***
   2. Leaf blade without differentiated white cartilaginous margins . . ***C. angustae, C. nutans***

I have not discovered any foliar characters distinguishing *C. angustae* and *C. nutans*. The abaxial water-storage canals are most highly developed in the distal part of the leaves of *C. quelchii* (Figures 1–3). They are most rudimentary in *C. caricifolia*. In all species the vascular bundles are covered by chlorenchyma abaxially in at least the lower part of the leaf.

Genus *Cottendorfia*

Floral bracts minute; flowers small; petals free with a narrow claw, the blades elliptical, white, separate and not twisted after anthesis; anthers versatile; filaments usually free; ovary superior, glabrous, the style slender; placentae short, subbasal; capsule septicidal; seeds narrow, bicaudate.

Leaves thin to rather thickened, often with dense cover of scales, margins incurved or recurved, sometimes essentially flat; stomata elongate with narrow guard cells or wider than long with broad guard cells; vascular bundles contiguous with adaxial water-storage tissue, sometimes contiguous with abaxial water-storage canals.

As presently recognized the genus contains 24 species, mostly in the eastern Guayana highlands. *Cottendorfia thyrsoidea* and some of the *Lindmania* group extend into central and southern Venezuela.

The majority of *Cottendorfia* species show the abaxial water-storage canals in the leaf. In one large group of species these canals are highly developed and the vascular bundles very high and narrow giving a very characteristic appearance to the leaf cross section not seen in *Navia* or *Connellia* (Figure 43). These species have short broad stomata (Figures 22, 27, 29, 31, 34, 37, 41, 44, 46, 48, 50, 52, 54, 56, 59) and often have a dense cover of epidermal scales on the leaf surface. Another group of species with less distinct water-storage canals, more rounded vascular bundles, more elongate stomata (Figures 5, 7, 10, 13, 16, 19), without obvious scales, and in a few cases bearing a narrow pale border, shows a strong relationship to *Connellia*. The two other very divergent elements in the genus show, each in its own way, resemblance to *Navia*, *Cottendorfia florida* by the partially closed substomatal orifice (Figure 6), and *C. navioides* by the lack of a scape in the inflorescence.

Vegetative Key to Species of *Cottendorfia*

1. Epidermal cells of leaf with straight walls (Figure 5); stomata having inner opening usually narrow, partially closed by outgrowth of surrounding cells (Figure 6) . . . . . ***C. florida***
1. Epidermal cells of leaf with sinuous walls (Figure 7); stomata with inner pore oval or circular, fully or almost fully open (Figure 8).
   2. Leafy stems elongate, usually much longer than leaves; leaves in cross section with upper surface contoured over the massive subdermal cells (Figure 64); leaves often glaucous . . . . . ***C. navioides***

2. Stems short; leaves in section with upper surface showing contours of epidermal cells only (Figure 61); leaves not glaucous.
   3. Stomata elongate, longer than wide (Figures 16, 19); leaf surface never covered with obvious scales; leaves often with narrow cartilaginous border.
      4. Leaves strongly involute . . . . . ***C. steyermarkii***
      4. Leaves mostly plane or narrowly revolute.
         5. Leaves with a layer of resinous cells internally, at least adaxially (Figure 12).
            6. Vascular bundles deeply recessed in the chlorenchyma (Figure 9) . ***C. longipes***
            6. Adaxial surface of major vascular bundles even with upper level of chlorenchyma (Figure 12) . . . . . ***C. dyckioides***
         5. Leaves without layers of resinous cells (Figure 15).
            7. Leaves distinctly toothed near base . . . . . ***C. wurdackii***
            7. Leaves nearly or completely entire margined.
               8. Most leaves 2 cm or more broad at the base, apex broadly acute . . . . . ***C. brachyphylla***
               8. Most leaves about 1 cm broad at the base, apex very narrowly acute . . . . . ***C. tillandsioides***
   3. Stomata short, as wide as long or wider (Figures 22, 27, 29); leaf surface often densely covered with scales; leaves without distinct border.
      9. Vascular bundles (as seen in cross section) continuous with abaxial epidermal layers or separated by a single row of thinner walled cells (Figures 24, 25).
         10. Leaves mostly over 20 cm long, leaf margins plane or recurved . . . ***C. thyrsoidea***
         10. Leaves less than 20 cm long, margins slightly incurved . . . . . ***C. minor***
      9. Vascular bundles separated from lower epidermis by at least two rows of enlarged or thin-walled cells (Figures 33, 36, 39, 43).
         11. Vascular bundles (as seen in cross section) covered by chlorenchyma abaxially (Figures 33, 36).
            12. Leaves completely without abaxial water-storage canal (Figure 36); upper leaf margin with few or no teeth . . . . . ***C. subsimplex***
            12. Leaves with small abaxial water-storage canals (Figure 33); leaf margins distinctly and closely serrate throughout . . . . . ***C. serrulata, C. gracillima***
         11. Abaxial water-storage canals reaching the vascular bundles, the bundles in contact with water-storage tissue both abaxially and adaxially (Figure 43).
            13. Leaf margins incurved . . . . . ***C. guianensis, C. stenophylla***
            13. Leaf margins mostly recurved.
               14. Leaves with prominent scales on the adaxial surface . . . . . ***C. paludosa***
               14. Leaves without distinct scales, adaxially, scales often prominent on abaxial surface . . . . . ***C. argentea, C. cylindrostachya, C. dendritica, C. geniculata, C. maguirei, C. nubigena, C. phelpsiae,*** and ***C. savannensis***

The genus *Cottendorfia* can be subdivided into the following four groups and eight subgroups.

GROUP A: Inflorescence scapose; epidermal cells with straight walls; stomata elongate with narrow guard cells; substomatal orifices partially closed; occurring in northeastern Brazil.

Subgroup I: One species with leaf margins entire or nearly entire; vascular bundles connected to abaxial epidermis; sepals cochleate (anterior sepal included).

Cottendorfia florida (Figures 4–6), the type species of the genus, seems unique in the group studied by the straight walls of the epidermal cells. These are often difficult to see but can be demonstrated best by viewing torn edges of the epidermis. The cochleate sepals and the partially closed substomatal pores are reminiscent of *Navia* where there are a few species with scapose inflorescence and half-buttressed vascular bundles as in *C. florida*. Cochleate sepals and partially buttressed vascular bundles are found elsewhere in the genus *Cottendorfia,* but not combined as in the paniculate *Navia* species. It is on the basis of the appendaged seeds that the present species is most clearly distinct from *Navia*.

GROUP B: Inflorescence scapose; epidermal cells with sinuous walls; stomata elongate with narrow guard cells; substomatal orifices oval or rounded; occurring in the eastern Guayana Highlands.

Subgroup II: One species with leaf margins involute, not cartilaginous, entire; vascular bundles

not buttressed abaxially, separated by chlorenchyma from abaxial water-storage canals; sepal imbrication not determined.

In anatomical structure *C. steyermarkii* is very similar to *C. tillandsioides* (Figures 13–15) but the relatively short, incurved, and involute leaves seem very distinct. *Cottendorfia tillandsioides* along with other species of the following subgroup seem very consistent in their flattened or revolute leaves.

Subgroup III: Five species with leaf margins usually plane or reflexed, often cartilaginous, entire or sometimes toothed near the base; vascular bundles not buttressed abaxially, separated by chlorenchyma from abaxial water-storage canals; sepals where determined are convolute.

The five species share many characters with the genus *Connellia* and close relationship seems likely. The generic status of one species, *Cottendorfia longipes* (Figures 7–9), remains uncertain until flowering material is discovered. All species of the group including *C. longipes, C. dyckioides* (Figures 10–12), *C. tillandsioides* (Figures 13–15), *C. brachyphylla* (Figures 16–18), and *C. wurdackii* (Figures 19–21) have distinct abaxial water-storage canals.

Group C: Inflorescence scapose; epidermal cells with sinuous walls; stomata as wide as long or wider, with broad guard cells; substomatal orifices oval or rounded; occurring in the central and eastern Guayana Highlands.

Subgroup IV: Two species with leaf margins often distinctly but remotely serrate; major vascular bundles buttressed abaxially; sepal arrangement not determined.

Though *Cottendorfia thyrsoidea* (Figures 22–24) and *C. minor* (Figures 25–28) share the half-buttressed vascular bundles, they may not be particularly closely related. This condition occurs also in *C. florida* and in a few species of *Navia,* species of rather remote relationship. In *C. minor* the half-buttressed condition seems to be present only in the upper half of the leaf. In other species showing the character, it seems less restricted.

Subgroup V: Two species with leaf margins closely and finely serrate; vascular bundles covered by chlorenchyma abaxially; abaxial water-storage canals present; sepal arrangement not determined.

There can be no question of the close relationship of *C. serrulata* (Figures 29–30) and *C. gracillima* (Figures 31–32). They seem to agree in all structures other than size of inflorescence parts. In addition, they seem closely related to the members of the following two subgroups of *Cottendorfia,* being distinguished by the arrangement of chlorenchyma and water-storage tissue in the abaxial half of the leaf.

Subgroup VI: One species with leaf margins nearly entire; vascular bundles completely enclosed in chlorenchyma abaxially; without abaxial water-storage canals; sepal arrangement not determined.

The single species, *C. subsimplex* (Figures 34–36), has all the characters of the following subgroup except for the dense and continuous chlorenchyma found in the abaxial half of the leaf.

Subgroup VII: Eleven species with leaf margins entire or with teeth restricted to near the base; vascular bundles contiguous abaxially with well-developed water-storage canals; sepal imbrication where determined usually convolute, rarely cochleate.

The subgroup contains *Cottendorfia guianensis* (Figures 44–45), type-species of the old genus *Lindmania.* This widely distributed and variable species, along with *C. argentea* (Figures 40–43), *C. cylindrostachya* (Figures 48–49), *C. dendritica* (Figures 46–47), *C. geniculata* (Figures 50–51), *C. maguirei* (Figures 52–53), *C. nubigena* (Figures 54–55), *C. paludosa* (Figures 59–60), *C. phelpsiae* (Figures 61–63), *C. savannensis* (Figures 56–58), and *C. stenophylla* (Figures 37–39), have the rather thick leaves with high contiguous abaxial water-storage canals (Figure 43) that I have come to think of as most characteristic of *Cottendorfia.* I have not seen such sections in either *Navia* or *Connellia,* though they occur in those *Puya* species I have seen, and in a small group of *Pitcairnia* species. The species of this subgroup seem very closely related and most of them cannot be distinguished from each other by vegetative characters.

Group D: Inflorescence nonscapose, corymbose; epidermal cells with sinuous walls; stomata as wide as long or wider, with broad guard cells; substomatal orifices oval or rounded; occurring in the eastern Guayana Highlands.

Subgroup VIII. One species with leaf margins entire; vascular bundles somewhat buttressed abaxially; sepal arrangement not determined.

Cottendorfia navioides (Figures 64–66) is named for the *Navia*-like short, nonscapose inflorescence, a structure not otherwise known in *Cottendorfia*. The species is distinguished from *Navia* by the presence of appendaged seeds. The species seems unique and can easily be determined by the contour of the adaxial leaf surface as seen in cross section.

Genus *Navia*

Inflorescence of one or more distinct or agglomerated heads or in a few species paniculate; flowers large or small, sessile or pedicellate; sepals cochlear, the anterior covered by the two posterior or rarely the anterior wholly aborted; petals free with a claw, broad, naked, connate in a slender tube, blades spreading at anthesis, often cucullate with an inflexed acute apex; anthers linear, filaments usually free; ovary usually superior, sometimes partially or wholly inferior; style slender; placentae linear; ovules naked or nearly so; capsule septicidal; seeds naked or with a vestigial wing, reticulate or corrugated.

Leaves thin to much thickened, often with dense cover of scales or trichomes, margins incurved, recurved or flat, entire to strongly toothed; stomata with narrow or broad guard cells, substomatal pore often with intrusions from surrounding cells; vascular bundles either exposed to adaxial water-storage tissue or partially to completely covered by chlorenchyma, abaxial water-storage canals sometimes present but not reaching vascular bundles.

As presently recognized the genus contains 74 species, and occurs throughout the Guayana Highlands.

Many of the species have vascular bundles covered with chlorenchyma abaxially (Figures 92, 100, 106, 109, 116, 117, 124, 128, 132, 133), a character not seen in *Cottendorfia* or *Connellia*. The character seems somewhat variable in its development, but it is completely lacking from the species that seem most like *Cottendorfia* (Figures 69, 70, 79, 88), and is well developed in almost all species with connate sepals or trichomes. The species lacking the character include most of those with a paniculate inflorescence. Also common in the genus but not found in *Cottendorfia* or *Connellia* is a rich variation in the structure of the substomatal pore (Figures 72, 75, 102, 108, 153, 161, 204, 236, 264). The types are itemized in the morphological discussion. Distinctive trichomes (Figures 265, 271, 274) are found in one series of species, most of which have large rounded substomatal pores and vascular bundles covered adaxially by chlorenchyma. I have not seen such trichomes in other bromeliad genera. *Navia* is otherwise notable for a great variety of individual species or small species groups that apparently all represent diverse rather unrelated lines of development. The most distinctive species, *N. lopezii* (Figures 275–277), could not be assigned to the genus or the family on the basis of leaf anatomy alone, having an outer surface of extremely large epidermal cells, no scales, simple paracytic stomata, and a relatively undifferentiated mesophyll.

Vegetative Key to Species of *Navia*

1. Epidermal cells extremely large, up to 800μ long, without separate subepidermal layers (Figures 275–277) . . . . . ***N. lopezii***
1. Epidermal cells small, usually near size of stomata, rarely over 50μ long, subepidermal layers distinct.
  2. Leaves 50 cm or more long, at least 2 cm and usually 3 cm or more wide near the base (inflorescence paniculate).
    3. Substomatal openings large and rounded (Figure 68) . . . . . ***N. ramosa***
    3. Substomatal openings nearly closed by large thick-wall intrusions (Figures 75, 83).
      4. Vascular bundles separated from the abaxial epidermis by many rows of thin-walled cells (Figure 70).
        5. Adaxial leaf surface bearing many stomata (Figures 71–73) . . . . . ***N. reflexa***
        5. Adaxial leaf surface with few or no stomata . . . . . ***N. hechtioides***
      4. Vascular bundles connected or nearly connected to abaxial epidermis by a region of fibers (Figure 79) . . . ***N. brocchinioides, N. diffusa, N. gracilis, N. hohenbergioides***
  2. Leaves distinctly less than 50 cm long or less than 2 cm wide.
    6. Stomata clustered in pits, each cluster protected by a small rather conical scale (Figure 90) (inflorescence paniculate) . . . . . ***N. garcia-barrigae***
    6. Stomata not grouped in pits with protective scale.

Vegetative Key to Species of *Navia*—Continued

7. Leaves bearing distinct erect stiff trichomes, at least on the abaxial surface (Figures 265, 271, 274).
  8. Leaves with only small cells abaxial to the vascular bundles (Figures 239, 242, 243); substomatal openings partially to almost completely closed (Figures 236, 238, 241).
    9. Substomatal openings divided into many small pores (Figure 238) . ***N. colorata***
    9. Substomatal openings not completely divided or at most divided in two (Figures 236, 241).
      10. Chlorenchyma covering the adaxial surface of the vascular bundles (Figure 232) . . . . . ***N. navicularis, N. breweri***
      10. Larger vascular bundles exposed to adaxial water-storage tissue (Figures 242, 243) . . . . . ***N. pauciflora, N. steyermarkii, N. wurdackii, N. xyridiflora***
  8. Leaves with large cells forming water-storage canals abaxial to the vascular bundles (Figures 253, 256, 261); substomatal openings large and rounded (Figures 252, 255, 258).
    11. Larger vascular bundles exposed to water-storage tissue adaxially (Figure 253); leaves succulent in appearance . . . . . ***N. aloifolia***
    11. Chlorenchyma covering adaxial surface of vascular bundles (Figures 256, 261); leaves usually rather thin.
      12. Leaves with only vestigial marginal teeth.
        13. Lower leaf margins densely pubescent . . . . . ***N. lanigera***
        13. Lower leaf margin with only scattered hairs or teeth . . . ***N. myriantha***
      12. Leaves with strongly serrate margins.
        14. Leaf margins strongly reflexed . . . . . ***N. phelpsiae***
        14. Leaf margins plane.
          15. Leaves up to 2 cm wide, with long erect spinose marginal teeth . . . . . ***N. stenodonta***
          15. Leaves 1 cm or less wide.
            16. Leaves stiff, with prominent tufts of trichomes in axils of all the marginal teeth . . . . . ***N. trichodonta***
            16. Leaves lax, without prominent tufts of trichomes in axils of the teeth . . . . . ***N. crispa, N. viridis***
7. Leaves with branching, platelike, or vestigial scales (Figures 58, 183, 184, 194).
  17. Substomatal opening cruciate (Figure 102) or 4-lobed (Figure 104); anterior sepal of flower much reduced or aborted.
    18. Substomatal opening cruciate (Figure 102); leaves with only small scales abaxially; anterior sepal aborted . . . . . ***N. parvula***
    18. Substomatal opening with 4 broad lobes (Figure 104); leaves with large round scales abaxially; anterior sepal only reduced . . . . . ***N. lepidota***
  17. Substomatal opening not cruciate or 4-lobed; anterior sepal not reduced or aborted.
    19. Substomatal openings single, rather rounded, without obvious intrusions, usually large (Figures 186, 189, 192, 217, 220, 226).
      20. Leaves with large cells abaxial to the vascular bundles (Figures 193, 218, 222, 227).
        21. Abaxial subepidermal cells very thick-walled (Figure 217); large vascular bundles exposed to adaxial water-storage tissue (Figure 218) . . ***N. mima***
        21. Abaxial subepidermal cells with relatively thin walls (Figures 226, 229, 231); vascular bundles covered by chlorenchyma adaxially (Figures 221, 222, 227).
          22. Leaves entire, narrowed in basal half; epidermal cells thin-walled, without silica bodies (Figure 95); inflorescence racemose . . . ***N. cataractarum***
          22. Leaves at least slightly toothed, not narrowed below; epidermal cells with silica bodies (Figures 191, 225, 228); inflorescence not racemose.
            23. Abaxial water-storage canals with one layer of very high vertical cells (Figure 193); leaf bearing prominent asymmetric scales (Figure 194); inflorescence long scapose . . . . . ***N. caulescens***
            23. Abaxial water-storage canals with 2 or 3 layers of equal sized cells (Figures 222, 227); scales various; inflorescence not long scapose.

24. Leaves less than 5 cm long . . . . . *N. schultesiana*
24. Leaves mostly over 5 cm long.
25. Leaves 1–3 mm wide; abaxial water-storage cells usually in 3 layers (Figure 222) . . . . . *N. graminifolia*
25. Leaves 7–15 mm wide; abaxial water-storage cells usually in 2 layers (Figure 227) . . . . *N. acaulis, N. bicolor, N. heliophila*

20. Leaves with only small cells abaxial to the vascular bundles (Figures 99, 187, 190).
26. Leaves bearing large scales with small rather isodiametric cells (Figure 184); vascular bundles narrowly fused to abaxial epidermis (Figure 187) . . . . . *N. arida*
26. Leaf scales vestigial or with elongate cells (Figure 183); vascular bundles variously shaped.
27. Vascular bundles broadly fused to abaxial epidermis (Figure 182) . . . . . *N. serrulata*
27. Vascular bundles separated from the abaxial epidermis by distinct layers of small chlorenchymatous cells (Figures 99, 179, 190).
28. Adaxial water-storage tissue with 1 or 2 layers of cells (Figure 99); inflorescence paniculate . . . . . *N. lindmanioides*
28. Adaxial water-storage tissue composed of 3 to many layers of large cells (Figures 179, 190); inflorescence glomerate, sessile.
29. Chlorenchyma continuous over adaxial surface of vascular bundles (Figure 190) . . . . . *N. saxicola*
29. Larger vascular bundles exposed to adaxial water-storage tissue (Figure 179) . . . . . *N. umbratilis*

19. Substomatal openings reduced, multiple, or with obvious intrusions (Figures 94, 126, 135, 153, 163, 173, 176, 214).
30. Substomatal opening multiple, with many separate scattered pores (Figures 94, 153).
31. Chlorenchyma covering adaxial surface of vascular bundles (Figure 92); inflorescence racemose . . . . . *N. rupestris*
31. Vascular bundles mostly exposed to adaxial water-storage tissue (Figures 151, 156); inflorescence not racemose.
32. Stomata about 20μ wide; subepidermal cells mostly 10–15μ wide (Figure 152) . . . . . *N. abysmophila*
32. Stomata about 25μ wide; subepidermal cells mostly 15–20μ wide (Figure 154) . . . . . *N. duidae*
30. Substomatal opening not multiple, sometimes divided in the middle or completely obscured (Figures 126, 135, 163, 173, 176, 202, 214).
33. Substomatal opening large though sometimes divided in half, intrusions usually thin-walled (Figures 163, 173, 176, 202, 214).
34. Abaxial subepidermal cells and the projections into the substomatal cavity thick-walled (Figure 214) . . . . . *N. pungens*
34. Abaxial subepidermal cells and the projections into the substomatal cavity rather thin-walled (Figures 163, 173, 176, 202).
35. Projections into the substomatal cavity multifid, bearing many papillae (Figures 163, 168).
36. Adaxial water-storage tissue composed of 3 or more layers of large cells, leaves thick (Figure 156) . . . *N. brachyphylla, N. glauca*
36. Adaxial water-storage tissue composed of 1 or 2 layers of large cells (Figure 157); leaves thin, broad and flat.
37. Leaves narrowed near the base, not chalky below . *N. nubicola*
37. Leaves not noticeably narrowed near base, often chalky on abaxial surface . . . . . *N. cretacea, N. latifolia*
35. Projections into substomatal cavity usually paired, smooth (Figures 176, 202, 212).
38. Stomata as broad as long or broader (Figures 169, 172, 175); sepals separate.

Vegetative Key to Species of *Navia*—Continued

39. Leaves 3–5 mm wide; larger vascular bundles exposed to adaxial water-storage tissue (Figure 171); stomata about 20μ wide; distinct rounded scales present . . . . . ***N. semiserrata***
39. Leaves about 1 cm wide; adaxial surface of vascular bundles covered by chlorenchyma (Figure 174); stomata 25μ wide or more; scales much dissected or vestigial.
40. Leaf margins with teeth erect to antrorse . . . ***N. octopoides***
40. Leaf margins with teeth close-set, mostly retrorse . ***N. caurensis***
38. Stomata longer than broad (Figures 205, 207, 209, 211, 213); sepals connate.
41. Larger vascular bundles exposed to adaxial water-storage tissue (Figure 197); abaxial epidermal cells with extremely sinuous walls (Figure 195) . . . . . ***N. caricifolia***
41. Vascular bundles usually covered adaxially by chlorenchyma (Figure 200); walls of abaxial epidermal cells strongly to laxly sinuous (Figures 205, 207, 209, 211, 213).
42. Leaf margins entire or with mostly vestigial teeth . ***N. affinis, N. connata, N. gleasonii, N. maguirei, N. subpetiolata***
42. Leaf margins sharply serrate.
43. Leaf blade very narrow, about 2.5 mm wide, with a short broad base . . . . . ***N. ocellata***
43. Leaf blade up to 1 cm or more wide, base not markedly wider . . . . . ***N. sandwithii***
33. Substomatal opening obscure, or reduced to a narrow slit or dumbbell-shaped pore by thick-walled intrusions (Figures 108, 126, 135).
44. Adaxial water-storage tissue composed of 1 or 2 layers of large cells (Figure 150) . . . . . ***N. angustifolia***
44. Adaxial water-storage tissue composed of many layers of large cells (Figures 139, 156).
45. Larger vascular bundles exposed to adaxial water-storage tissue (Figures 133, 136, 139).
46. Vascular bundles broadly fused to abaxial epidermis (Figure 136) . . . . . ***N. immersa***
46. Vascular bundles separated from lower epidermis by distinct layers of small chlorenchyma cells (Figure 139).
47. Stomata 40–50μ long, about 30μ wide; walls of abaxial epidermal cells extremely sinuous (Figure 134) . . . . . ***N. intermedia***
47. Stomata 20–30μ long; walls of abaxial epidermal cells strongly to weakly sinuous (Figures 140, 142).
48. Stomata as wide as long, about 30μ by 30μ (Figure 146). . . . . ***N. scopulorum***
48. Stomata longer than wide, about 25μ long by 20μ wide (Figures 140, 142).
49. Leaves less than 5 cm long . . . . . ***N. pulvinata***
49. Leaves over 5 cm long . . . . . ***N. cucullata***
45. Vascular bundles usually covered adaxially by chlorenchyma (Figures 128, 132).
50. Substomatal opening completely obscured from face view (Figure 108); leaf with branching scales covering adaxial surface. . . . . ***N. involucrata***
50. Substomatal opening distinct as a narrow slit (Figures 121, 123, 126); scales on adaxial surface of leaf sparse or vestigial.
51. Abaxial leaf surface densely covered with branching scales.
52. Scales not completely obscuring abaxial leaf surface; leaf margins strongly incurved with sharp teeth; leaf interior without obvious resinous cells (Figure 117) . . . . . ***N. robinsonii***

52. Scales of abaxial leaf surface forming a dense woolly cover; leaves very stiff with erect margins and vestigial teeth; leaf interior with numerous resinous cells (Figures 127, 128, 131, 132).
53. Leaves broadly lanceolate, with many layers of narrow thick-walled resinous cells adaxially (Figure 131) . . . . . *N. incrassata*
53. Leaves narrowly lanceolate, with 2 or 3 layers of rounded thick-walled resinous cells adaxially (Figure 127) . . . . . *N. lasiantha*

51. Scales of abaxial leaf surface sparse or vestigial.
54. Leaves narrow with very large teeth at the base; ovary almost wholly inferior . . . . . *N. fontoides*
54. Leaves without larger teeth at the base, ovary superior.
55. Leaves broad without broader base; marginal teeth very erect and close, about as long as the distance between them.
56. Abaxial subepidermal cells with very thick walls, lumens very small (Figure 111) . . . . . *N. barbellata*
56. Abaxial subepidermal cells with rather thin walls (Figure 113) . . . . . *N. splendens*
55. Leaves narrow with a very broad base; marginal teeth short, shorter than the distance between them.
57. Lower teeth of leaf margins with prominent tufts of trichomes in axils; interior of leaf with many layers of thick-walled subepidermal cells abaxially (Figure 124) . *N. aurea*
57. Lower teeth of leaf margins without tufts of prominent trichomes; interior of leaf with only 1 or 2 layers of distinct subepidermal cells abaxially (Figure 117) . . *N. cardonae*

The genus *Navia* can be subdivided into the following 7 groups and 26 subgroups.

GROUP A: Inflorescence paniculate; vascular bundles not covered adaxially by chlorenchyma; occurring in the western and central Guayana Highlands of Colombia and southern Venezuela.

Subgroup I: One species with substomatal pore large, oval or rounded; vascular bundles free from abaxial epidermis.

The single species, *N. ramosa* (Figures 67–69), can be distinguished from *Cottendorfia* only by the unappendaged seeds.

Subgroup II: Six species with the substomatal pore reduced to a narrow double-anchor shape by pairs of hooked thick-walled intrusions.

In habit, the six species are like the preceding *N. ramosa* and like many species of *Cottendorfia,* but they can be distinguished by the shape of the substomatal pore. As presently known, *N. reflexa* (Figures 70–76) and *N. hechtioides* (Figures 77–78) have free vascular bundles while those of *N. hohenbergioides* (Figures 79–81), *N. gracilis* (Figures 82–83), *N. brocchinioides* (Figures 84–85), and *N. diffusa* (Figures 86–87) are connected to the lower epidermis by areas of sclerenchyma. Stomata seem rather common on the adaxial leaf surface of *N. reflexa* where the surrounding cells of the third subepidermal layer show a rather distinctive structure (Figure 73). A few adaxial stomata have been observed in *N. gracilis,* but they have not been observed in any other bromeliads examined.

Subgroup III: One species with stomata clustered in pits around thick pluglike scales; substomatal pores irregularly rounded to partially closed by short thick-walled intrusions.

The arrangement of stomata in the single species, *N. garcia-barrigae* (Figures 88–91), seems distinctive. The single specimen available has only a few separate leaves, which may not be representative of the fully vegetative parts of the plant.

GROUP B: Inflorescence racemose to paniculate; vascular bundles nearly or completely covered adaxially by chlorenchyma.

Subgroup IV: Two small species with racemose inflorescence; leaves rather thick; silica bodies small or lacking; occurring in the eastern Guayana Highlands in British Guiana.

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In *N. rupestris* (Figures 92–94) the substomatal openings are usually divided into three or more small rounded pores. In *N. cataractarum* (Figures 95–96) the pores are large and simple.

Subgroup V: One rather large species with large panicle bearing racemose branches; leaves thin; silica bodies distinct; occurring in central Venezuela.

Navia lindmanioides (Figures 97–99) has simple rounded substomatal pores. The species is quite distinct from others with paniculate or racemose inflorescences, and vegetatively resembles many having glomerate inflorescences.

GROUP C: Inflorescence glomerate; vascular bundles covered adaxially by chlorenchyma; anterior sepal reduced or absent; scales platelike or branching.

Subgroup VI: Two species with substomatal pore cruciate or 4-lobed; ovary partly inferior; occurring on Cerro Neblina in southern Venezuela.

Navia parvula (Figures 100–102) shows the extreme conditions of the anterior sepal absent and the substomatal pore cruciate. In *N. lepidota* (Figures 103–106) the anterior sepal is present in reduced form and the substomatal pore has only slight intrusions from each of the four corners. In both mentioned characters the latter species seems transitional, but the species is very distinct in other characters such as its large rounded scales.

GROUP D: Inflorescence glomerate; sepals equal, free; scales platelike, branching, or vestigial.

Subgroup VII: One species with substomatal opening completely obscured from face view; vascular bundles covered adaxially by chlorenchyma; occurring in the Guayana Highlands of central Venezuela.

The intrusions into the substomatal pore of *N. involucrata* (Figures 107–108, section as in 106) are so complex and thick-walled that it is impossible to determine any opening or any pattern. The broad involute leaves with a grayish cover of adaxial scales are also rather distinctive.

Subgroup VIII: One species with substomatal pore reduced to a short narrow slit; vascular bundles covered adaxially by chlorenchyma; leaves with a few very large teeth near the base; ovary almost wholly inferior; occurring in the Guayana Highlands of Colombia.

Navia fontoides (Figures 114–116) seems readily distinguishable by its narrow leaves bearing large teeth near the base. The species also seems rather distinct in its inferior ovary and in its geographical distribution.

Subgroup IX: Two species with substomatal pore reduced to a short narrow slit; vascular bundles covered adaxially by chlorenchyma; leaves broad and smooth with closely and finely serrulate margins; ovary superior; occurring in the eastern Guayana Highlands of British Guiana and adjacent Venezuela.

Navia barbellata (Figures 109–111) and *N. splendens* (Figures 112–113, section as in 109) are similar in most vegetative characters. The material seen of *N. barbellata* has much thicker walled subepidermal cells.

Subgroup X: Five species with substomatal pore reduced to a short narrow slit; vascular bundles covered adaxially by chlorenchyma; leaves mostly with evident scales on abaxial surface; ovary superior; occurring in the Jáua-Duida area of south-central Venezuela.

Navia lasiantha (Figures 125–128) and *N. incrassata* (Figures 129–132) both have nearly entire-margined leaves with a very dense abaxial cover of scales. The three remaining species of the group have less prominent scales. Of these three, *N. robinsonii* (Figures 120–121, section as in 117) has broader involute leaves while *N. cardonae* (Figures 117–119) and *N. aurea* (Figures 122–124) both have narrow blades born on broad sheathing bases. *Navia aurea* is quite distinct in the many layers of thick-walled convoluted cells adjacent to the lower epidermis.

Subgroup XI: One species with substomatal pore reduced to a pair of small hidden pores; epidermal cells large with very sinuous walls; vascular bundles not all covered adaxially by chlorenchyma; ovary superior; occurring on Serranía Jáua in south-central Venezuela.

The epidermal cells of *N. intermedia* (Figures 133–135) are the largest in the genus that are of normal structure. The substomatal structure is also rather distinctive, but is very closely related to that in the immediately preceding and following groups. The leaves are very narrow but thick and nearly entire-margined, unlike any others seen in the genus.

Subgroup XII: Five species with substomatal pore reduced to a short narrow slit; vascular bundles not completely covered by chlorenchyma adaxially; occurring in the Guayana Highlands of British Guiana and Venezuela.

Three of the species, *N. cucullata* (Figures 139–141), *N. pulvinata* (Figures 142–144), and *N. angustifolia* (Figures 148–150), have superior ovaries. Two, *N. scopulorum* (Figures 145–147) and *N. immersa* (Figures 136–138), have partially inferior ovaries. *Navia immersa* is further distinguished by the vascular bundles being broadly fused to the lower epidermis. The subgroup represents the greatest concentration of the leaf type in which the blade is very narrow and stiff from a broad rounded sheathing base. Such leaves are also seen in *N. cardonae* and *N. aurea* of Subgroup X, *N. saxicola* of Subgroup XVI, and *N. graminifolia* of Subgroup XX.

Subgroup XIII: Two species with the substomatal opening divided into few or many small rounded pores; vascular bundles not completely covered adaxially by chlorenchyma; occurring in southern Venezuela.

The two species, *N. abysmophila* (Figures 151–153) and *N. duidae* (Figures 154–156), have slightly different habits but very similar basic anatomy. The epidermal cells are among the smallest seen in the genus.

Subgroup XIV: Five species with substomatal intrusions short but distinct, thin-walled, much divided or bearing many papillae; vascular bundles usually covered adaxially by chlorenchyma; occurring in the Duida-Neblina area of southern Venezuela.

Two of the species, *N. brachyphylla* (Figures 165–166, section as in 156) and *N. glauca* (Figures 167–168, section as in 156), have rather thick leaves. In *N. nubicola* (Figures 157–159), *N. cretacea* (Figures 160–161, section as in 157), and *N. latifolia* (Figures 162–164, section as in 157) the leaves are very thin. *Navia cretacea* and *N. latifolia* are obviously closely related and cannot be distinguished vegetatively.

Subgroup XV: Three species with substomatal intrusions rather short but distinct, thin-walled, simple; vascular bundles partially to completely covered adaxially by chlorenchyma; occurring in the Rio Caura-Rio Ventuari-Duida area of south-central Venezuela.

The subgroup seems unnatural with species differing somewhat in both habit and anatomy. *Navia semiserrata* (Figures 169–171) differs by its stiff leaves and vascular bundles not completely covered by chlorenchyma. In *N. caurensis* (Figures 172–174) and *N. octopoides* (Figures 175–176, section as in 157) the vascular bundles are covered by chlorenchyma adaxially, but the former has broad relatively short thick leaves and the latter has much longer and thinner leaves.

Subgroup XVI: Five species with substomatal pores rounded or oval, without distinct intrusions; occurring in various parts of the Guayana Highlands from British Guiana to Colombia.

The five species included in the subgroup are sufficiently distinct that each could constitute a separate subgroup of its own. *Navia umbratilis* (Figures 177–179), of Cerro Yutaje in south-central Venezula, has long slender nearly entire-margined leaf blades from a rounded sheathing base. The substomatal pores are slightly narrowed, and the larger vascular bundles are not completely covered adaxially by chlorenchyma. The substomatal pores of the other species are not at all obstructed. In both *N. serrulata* (Figures 180–183), of southern Venezuela, and *N. arida* (Figures 184–187), of British Guiana, the vascular bundles are not completely covered with chlorenchyma. In the former species the leaves are narrow from a broad base, but are strongly serrulate, and the scales have oblong cells. In the latter species the leaves are broad and strap-shaped, the scales are rounded with very distinctive small rounded cells and an eroded margin, and the ovary, unlike other species in the subgroup, is partly to wholly inferior. In both *N. saxicola* (Figures 188–190), of southern Venezuela, and *N. caulescens* (Figures 191–194), of Colombia, the vascular bundles are completely covered adaxially by chlorenchyma. The former species has stiff narrow leaf blades from rounded sheathing bases, while the latter has broad strap-shaped leaves. *Navia caulescens,* the type-species of the genus, is most distinct by the elongate inflorescence with several moniliform heads born on a scape.

Group E: Inflorescence glomerate; sepals connate; scales platelike, branching, or vestigial.

Subgroup XVII: Eight species with substomatal pores partly closed by long, paired, thin-walled intrusions; vascular bundles covered adaxially by

chlorenchyma in all but one species; abaxial water-storage canals absent; occurring in the eastern half of the Guayana Highlands from Cerro Sipapo and Neblina in Venezuela to Tafelberg in Surinam.

One species, *N. caricifolia* (Figures 195–197), is distinct in the vascular bundles not being covered adaxially by chlorenchyma, and in the more sinuous walls of the epidermal cells. In other characters such as the long strap-shaped usually nearly entire leaves having somewhat sheathing bases and the structure of the substomatal pore, *N. caricifolia* is like *N. ocellata* (Figures 198–200), *N. maguirei* (Figures 201–202, section as in 200), *N. subpetiolata* (Figures 203–204, section as in 200), *N. gleasonii* (Figures 205–206, section as in 200), *N. sandwithii* (Figures 207–208, section as in 200), *N. connata* (Figures 209–210, section as in 200), and *N. affinis* (Figures 211–212, section as in 200).

Subgroup XVIII: One species with substomatal pores partly closed by short, paired, thick-walled intrusions; vascular bundles covered adaxially by chlorenchyma, abaxial water-storage canals absent; occurring on Cerro Guanay and Cerro Yutaje in south-central Venezuela.

The single species, *N. pungens* (Figures 213–215), is distinct among *Navia* species with a sessile inflorescence by the small but distinct thick-walled intrusions. The leaves are thick and stiff, and the plant closely resembles *N. mima* of the following subgroup in habit.

Subgroup XIX: One species with substomatal pore only slightly obstructed; vascular bundles not completely covered adaxially by chlorenchyma; with distinct large cells forming water-storage canals abaxially; occurring on Cerro Sipapo in south-central Venezuela.

The one species, *N. mima* (Figures 216–218), resembles the preceding, *N. pungens,* in habit, but it has the substomatal pores only slightly obstructed by the surrounding thin-walled resinous cells.

Subgroup XX: Five species with substomatal pore rounded, not obstructed; vascular bundles completely covered adaxially by chlorenchyma; distinct large cells forming abaxial water-storage canals; occurring in the western Guayana Highlands in Colombia.

The five species, *N. acaulis* (Figures 230–231, section as in 227), *N. bicolor* (Figures 228–229, section as in 227), *N. heliophila* (Figures 225–227), *N. graminifolia* (Figures 222–224), and *N. schultesiana* (Figures 219–221), all share the same basic anatomy and the same rather distinctive geographic distribution. Still, the habits of the various species in the subgroup are quite diverse. The first three species are much alike with long, broad, strap-shaped leaves having no distinct central thickening. These three species cannot be distinguished vegetatively. *Navia graminifolia* in contrast has the very different slender-leaved form found most often in Subgroup XII. *Navia schultesiana* has distinctive small rosettes of serrate stiffly spreading leaves, bearing little superficial resemblance to the preceding types. In this study of *Navia,* most attempts to use vegetative habit as an indication of relationship have failed. Most subgroups established on the basis of anatomy have contained many variations in habit. In this subgroup there is some basis to suspect real relationship and therefore potentially good evidence of the erratic nature of the vegetative habit.

Group F: Inflorescence glomerate; sepals equal, separate; scales lacking, large erect trichomes present.

Subgroup XXI: Two species with substomatal pores reduced to a short narrow slit; vascular bundles covered adaxially by chlorenchyma; without distinct water-storage canals abaxially; ovary superior; occurring in the Jáua-Ichún area of south-central Venezuela.

The two species, *N. navicularis* (Figures 232–234) and *N. breweri* (Figures 235–236, section as in 232), seem indistinguishable vegetatively. They and the five species in the following two subgroups, and *N. viridis* and *N. crispa* of Subgroup XXV, show a long, thin, strap-shaped leaf often with a distinct central thickening. While this rather distinctive leaf type is most common among species with trichomes, it is also found in *N. octopoides* of Subgroup XV and *N. lindmanioides* of Subgroup V. Some species like *N. arida* of Subgroup XVI and *N. nubicola* of Subgroup XIV are similar but lack the distinct central thickening.

Subgroup XXII: One species with substomatal opening divided into many small usually rounded pores; with few or no distinct water-storage cells abaxially; vascular bundles covered adaxially by chlorenchyma; ovary superior; occurring in the Rio Ventuari area of south-central Venezuela.

The species, *N. colorata* (Figures 237–239), agrees in habit and in most anatomical characters with the species of the preceding subgroup, but it differs markedly in the thin-walled substomatal cells which form multiple openings. This species is probably most closely related to *N. viridis* and *N. crispa* of Subgroup XXV.

Subgroup XXIII: Four species with substomatal opening obstructed by distinct, long, thin-walled, paired intrusions; vascular bundles not completely covered adaxially by chlorenchyma; with few distinct water-storage cells abaxially; ovary superior; occurring in the Chimanta-Marahuaca-Duida areas of eastern and south-central Venezuela.

The four species, *N. pauciflora* (Figures 247–248, section as in 243), *N. steyermarkii* (Figures 249–250, section as in 243), *N. wurdackii* (Figures 243–246), and *N. xyridiflora* (Figures 240–242), seem indistinguishable vegetatively. The failure of the chlorenchyma to completely cover the adaxial surface of the vascular bundles in this series of species seems to be of relatively little significance, since the organization of the tissues is similar to that in the related subgroups that have covered bundles.

Subgroup XXIV: One species with substomatal pore large and unobstructed; vascular bundles mostly not covered adaxially by chlorenchyma; large cells forming distinct water-storage canals abaxially; ovary inferior; occurring on Cerro Neblina in southern Venezuela.

The species, *N. aloifolia* (Figures 251–253), seems very distinct in the habit, thick leaves, vascular bundles distinctly exposed to the adaxial water-storage tissue, and the inferior ovary. The trichomes on the backs of the leaves are perhaps the best examples of such structures in the genus.

Subgroup XXV: Seven species with substomatal pores large and unobstructed; vascular bundles covered adaxially by chlorenchyma; large cells usually forming distinct water-storage canals abaxially; ovary superior; occurring in south-central and southern Venezuela and adjacent Brazil.

Two species, *N. viridis* (Figures 254–256) and *N. crispa* (Figures 257–258, section as in 256), have the appearance of the species in Subgroups XXI, XXII, and XXIII, but in addition to differences in stomata they show a greater development of water-storage cells abaxially. The remaining five species, *N. stenodonta* (Figures 259–262), *N. myriantha* (Figures 263–266), *N. trichodonta* (Figures 267–268, section as in 266), *N. lanigera* (Figures 269–271), and *N. phelpsiae* (Figures 272–274), have rather diverse leaf types, but all have rather well-developed water-storage canals abaxially.

Group G: Inflorescence glomerate; sepals equal and separate; scales completely absent from leaves.

Subgroup XXVI: One species with broad entire-margined leaves; epidermal cells extremely large, subepidermal layers absent; stomata paracytic; mesophyll not forming distinct layers; occurring in the central and western Guayana Highlands of southern Venezuela and adjacent Brazil and Colombia.

All the most distinctive features of *N. lopezii* (Figures 275–277) could be related to the lack of subdivision of initial cells. This is most pronounced in the epidermal cells of the leaves and floral bracts, but is also somewhat reflected in the structure of the walls of the fruits. The modified epidermis has resulted in complete elimination of scales, a condition that is in exception to the generally accepted definition of the family.

List of Specimens Examined

(Specimens used for illustrations are marked with an asterisk.)

Species	*Collector and Number*	*Locality*	*Herbarium*
Abromeitiella brevifolia (Griseb.) Castellanos	*Cabrera 16333*	Argentina: Prov. Jujuy: Tumbaya	US
Ayensua uaipanensis (Maguire) L. B. Smith	*Steyermark 93940*	Venezuela: Bolívar: Auyán-tepuí	US
Brocchinia acuminata L. B. Smith	*Maguire 32785*	Venezuela: Bolívar: Cerro Guaiquinima	US
Brocchinia cowanii L. B. Smith	*Maguire, Cowan, & Wurdack 30924*	Venezuela: Amazonas: Cerro Moriche, Río Ventuari	US holotype

List of Specimens Examined—Continued

Species	*Collector and Number*	*Locality*	*Herbarium*
Brocchinia cryptantha L. B. Smith	*Maguire, Cowan & Wurdack 30709*	Venezuela: Amazonas: Cerro Yapacana, Río Orinoco	US holotype
Brocchinia delicatula L. B. Smith	*Maguire, Wurdack & Maguire 42207*	Venezuela: Amazonas: Cerro Neblina, Río Yatua	US holotype
Brocchinia hechtioides Mez	*Maguire & Politi* 27603	Venezuela: Amazonas: Cerro Sipapo	US
Brocchinia hitchcockii L. B. Smith	*Phelps & Hitchcock 522*	Venezuela: Amazonas: Serranía Parú, Río Ventuari	NY holotype
Brocchinia maguirei L. B. Smith	*Maguire & Politi 27950*	Venezuela: Amazonas: Cerro Sipapo	US
Brocchinia melanacra L. B. Smith	*Maguire, Phelps et al. 31691*	Venezuela: Amazonas: Río Manapiare, Río Ventuari	US
Brocchinia micrantha (Baker) Mez	*Steyermark 89564*	Venezuela: Bolívar: Sierra de Lema, Cabeceras de Río Chicanán	US
Brocchinia paniculata Schult. f.	*Schultes & Cabrera 17131*	Colombia: Vaupés: Río Piraparaná	US
Brocchinia prismatica L. B. Smith	*Maguire, Cowan, & Wurdack 30596*	Venezuela: Amazonas: Cerro Yapacana, Río Orinoco	US
Brocchinia reducta Baker	*Maguire 33185*	Venezuela: Bolívar: Ilu-tepuí	US
Brocchinia secunda L. B. Smith	*Steyermark 59863*	Venezuela: Bolívar: Ptari-tepuí	F isotype
Brocchinia serrata L. B. Smith	*Garcia Barriga 15096*	Colombia: Vaupés: Río Kubiyú	US
Brocchinia steyermarkii L. B. Smith	*Maguire, Tillett, & Tillett 43808*	British Guiana: Upper Mazaruni	US
Brocchinia tatei L. B. Smith	*Maguire 32874*	Venezuela: Bolívar: Cerro Guaiquinima, Río Paragua	US
Brocchinia vestita L. B. Smith	*Maguire, Wurdack,* etc. *42168*	Venezuela: Amazonas: Cerro Neblina, Río Yatua	US
Connellia angustae (Rich. & Schomb-ock) N. E. Brown	*Steyermark & Nilsson 745*	Venezuela: Bolívar: Cerro Venamo	US
Connellia caricifolia L. B. Smith	*Steyermark 58846*	Venezuela: Bolívar: Mt. Roraima	F holotype
Connellia nutans L. B. Smith	*Steyermark 59933*	Venezuela: Bolívar: Ptari-tepuí	F holotype
Connellia quelchii N. E. Brown	**Im Thurn 315*	Venezuela: Bolívar: Mt. Roraima	US isotype
Cottendorfia argentea (L. B. Smith) L. B. Smith	**Steyermark & Wurdack 677*	Venezuela: Bolívar: Chimantá-tepuí	US holotype
Cottendorfia brachyphylla (L. B. Smith) L. B. Smith	**Wurdack 34134–B*	Venezuela: Bolívar: Sarvén-tepuí	US holotype
Cottendorfia cylindrostachya (L. B. Smith) L. B. Smith	**Maguire 35280*	Venezuela: Amazonas: Serranía Yutaje, Río Manapiare	US holotype
Cottendorfia dendritica L. B. Smith	**Maguire, Pires, & Maguire 60543*	Brazil: Amazonas: Serra da Neblina	NY holotype
Cottendorfia dyckioides L. B. Smith	*Steyermark 93186*	Venezuela: Bolívar: Auyán-tepuí	US
	**Steyermark 93188*	Venezuela: Bolívar: Auyán–tepuí	US holotype
Cottendorfia florida Schultes f.	**Martius 1938*	Brazil: Bahia: Serra do Sincorá	M holotype
Cottendorfia geniculata (L. B. Smith) L. B. Smith	**Steyermark 75774*	Venezuela: Bolívar: Chimantá-tepuí	US holotype
Cottendorfia gracillima L. B. Smith	**Steyermark & Nilsson 436*	Venezuela: Bolívar: Cerro Venamo	US holotype
Cottendorfia guianensis (Beer) Klotzsch ex Baker var. *vestita* L. B. Smith	**Steyermark & Nilsson 567*	Venezuela: Bolívar: Uarama-tepuí	US holotype
Cottendorfia longipes L. B. Smith	**Steyermark 93790*	Venezuela: Bolívar: Auyán-tepuí	US holotype
Cottendorfia maguirei L. B. Smith	**Maguire, Pires, & Maguire 60478*	Brazil: Amazonas: Serra da Neblina	US holotype
Cottendorfia minor (L. B. Smith) L. B. Smith	**Steyermark & Wurdack 678–A*	Venezuela: Bolívar: Chimantá-tepuí	US
Cottendorfia navioides (L. B. Smith) L. B. Smith	**Steyermark & Wurdack 677*	Venezuela: Bolívar: Chimantá-tepuí	US holotype
Cottendorfia nubigena L. B. Smith	**Maguire, Wurdack, & Magiure 42151*	Venezuela: Amazonas: Cerro de la Neblina, Río Yatua	US holotype
Cottendorfia paludosa (L. B. Smith) L. B. Smith	**Maguire 33034*	Venezuela: Bolívar: Cerro Guaiquinima Río Paragua	US holotype

List of Specimens Examined—Continued

Species	*Collector and Number*	*Locality*	*Herbarium*
Cottendorfia phelpsiae (L. B. Smith) L. B. Smith	**Phelps & Hitchcock 501*	Venezuela: Bolívar: Cerro Parú	NY holotype
Cottendorfia savannensis L. B. Smith	**Maguire, Wurdack, & Maguire 42167*	Venezuela: Bolívar: Cerro de la Neblina, Río Yatua	US holotype
Cottendorfia serrulata (L. B. Smith) L. B. Smith	*Cardona 1587*	Venezuela: Bolívar: Cerro Apacara, Río Caroní	US holotype
Cottendorfia serrulata var. *reducta* (L. B. Smith) L. B. Smith	**Steyermark & Wurdack 1167*	Venezuela: Bolívar: Chimantá-tepuí	US holotype
Cottendorfia stenophylla (L. B. Smith) L. B. Smith	**Steyermark & Wurdack 951*	Venezuela: Bolívar: Chimantá-tepuí	US holotype
Cottendorfia steyermarkii (L. B. Smith) L. B. Smith	*Steyermark & Wurdack 827*	Venezuela: Bolívar: Chimantá Massif	NY holotype
Cottendorfia subsimplex (L. B. Smith) L. B. Smith	**Steyermark 75924*	Venezuela: Bolívar: Chimantá Massif	US holotype
Cottendorfia thyrsoidea (L. B. Smith) L. B. Smith	*Maguire & Maguire 35385*	Venezuela: Amazonas: Serranía Yutaje	NY holotype
Cottendorfia tillandsioides (L. B. Smith) L. B. Smith	**Steyermark 74863*	Venezuela: Bolívar: Abácapa-tepuí	US holotype
Cottendorfia wurdackii (L. B. Smith) L. B. Smith	**Maguire, Cowan, & Wurdack 29637*	Venezuela: Amazonas: Cerro Duida	US holotype
Deuterocohnia longipetala (Baker) Mez	*Castellanos 26/448*	Argentina: San Juan: Quebrada del Zonda	US
Dyckia brevifolia Baker	*Reitz 3979*	Brazil: Santa Catarina: Salto Blumenau	US
Dyckia choristaminea Mez	*Rambos s. n.* (PACA *48832*)	Brazil: Rio Grande do Sul: Pôrto Alegre	US
Dyckia duckei L. B. Smith	*Eiten & Eiten 4659*	Brazil: Maranhão: Mun. de Lorêto	US
Dyckia maritima Baker	*L. B. Smith & Reitz 5824*	Brazil: Rio Grande do Sul: Mun. Tôrres	US
Dyckia reitzii L. B. Smith	*Reitz & Klein 2690*	Brazil: Santa Catarina: Serra do Oratório S. Joaquim	US holotype
Encholirium densiflorum Ule	*Foster 2474*	Brazil: Bahia: Amargosa, Milagres	US
Fosterella penduliflora (C. H. Wright) Stapf.	*Venturi 5474*	Argentina: Jujuy: Sierra de Santa Barbara	US
Fosterella schidosperma (Baker) L. B. Smith	*Killip & Smith 25326*	Peru: Junín: Río Paucartambo Valley	US
Hechtia integerrima M. B. Foster	*Foster 3072*	Mexico? cultivated	US holotype
Hechtia lundelliorum L. B. Smith	*Van Hyning 6066*	Mexico: San Luis Potosí Tamazunchale	US
Hechtia montana Brand.	*Ferris 8747*	Mexico: Sonora: San Carlos Bay, near Guayamas	US
Hechtia tillandsioides (Andrè) L. B. Smith	*Foster* June 1950	Mexico: cultivated	US
Navia abysmophila L. B. Smith	**Maguire, Wurdack, & Maguire 42471*	Venezuela: Amazonas: Cerro de la Neblina, Río Yatua	US holotype
Navia acaulis Martius ex Schultes f.	**Idrobo & Schultes 644*	Colombia: Vaupés: Mesa la Lindosa, Ajaju River	US
Navia affinis L. B. Smith	**Maguire, Wurdack, & Maguire 42470*	Venezuela: Amazonas: Cerro de la Neblina, Río Yatua	US holotype
Navia aloifolia L. B. Smith	**Maguire, Wurdack, & Bunting 37146*	Venezuela: Amazonas: Cerro de la Neblina, Río Yatua	US holotype
Navia angustifolia (Baker) Mez	**Appun 1055*	British Guiana: Marima	K holotype
Navia arida L. B. Smith & Steyermark	**Steyermark 89698*	Venezuela: Bolívar Sierra de Lema	US holotype
Navia aurea L. B. Smith	**Steyermark 58219*	Venezuela: Amazonas: Cerro Duida	F holotype
Navia barbellata L. B. Smith	**Tillett 45557*	British Guiana: Essequibo, Karowtipo, Mazaruni River	US isotype

List of Specimens Examined—Continued

Species	*Collector and Number*	*Locality*	*Herbarium*
Navia bicolor L. B. Smith	**Schultes 5444*	Colombia: Vaupés: Cerro Chiribiquete, Río Macaya	US
Navia brachyphylla L. B. Smith	**Tate 571*	Venezuela: Amazonas: Cerro Duida	NY holotype
Navia breweri L. B. Smith & Steyermark	**Brewer 248*	Venezuela: Bolívar: Cerro Jáua, Río Caura	US holotype
Navia brocchinioides L. B. Smith	**Maguire & Politi 28787*	Venezuela: Amazonas: Cerro Sipapo	US holotype
Navia cardonae L. B. Smith	*Cardona 349*	Venezuela: Bolívar Río Canaracuni	US holotype fragment
	**Brewer 249*	Venezuela: Bolívar: Cerro Jáua, Río Caura	US
Navia caricifolia L. B. Smith	**Maguire & Maguire 35437*	Venezuela: Amazonas: Serranía Yutaje, Río Manapiare	US holotype
Navia cataractarum Sandwith	**Whitton 51*	British Guiana: Essequibo, Amatuk Falls, Potaro River	K holotype
Navia caulescens Martius ex Schultes f.	**Schultes 5859*	Colombia: Amazonas: Cerro de Cupatí, Río Caqueta	US
Navia caurensis L. B. Smith	**Cardona 2985*	Venezuela: Bolívar: Cerro Pauo, Río Caura	US holotype
Navia colorata L. B. Smith	**Cowan & Wurdack 31417*	Venezuela: Amazonas: Serranía Parú, Río Ventuari	US holotype
Navia connata L. B. Smith & Steyermark	**Steyermark 90223*	Venezuela: Bolívar: Sierra Ichún	US isotype
Navia cretacea L. B. Smith	**Maguire, Cowan, & Wurdack 29882*	Venezuela: Amazonas: Cerro Huachamacari	US holotype
Navia crispa L. B. Smith	**Maguire, Cowan, & Wurdack 30966*	Venezuela: Amazonas: Cerro Moriche, Río Ventuari	US holotype
Navia cucullata L. B. Smith	**Maguire 32766*	Venezuela: Bolívar: Cerro Guaiquinima, Río Paragua	US holotype
Navia diffusa L. B. Smith	**Maguire, Wurdack, & Maguire 42537–E*	Venezuela: Amazonas: Cerro de la Neblina, Río Yatua	US holotype
Navia duidae L. B. Smith	**Tate 404*	Venezuela: Amazonas: Cerro Duida	NY holotype
Navia fontoides L. B. Smith	**Schultes & Cabrera 15391*	Colombia: Amazonas: Rauda Yayacopi, Río Apaporis	US holotype
Navia garcia-barrigae L. B. Smith	**Garcia Barriga & Schultes 14137*	Colombia: Amazonas: Araracuara, Río Caqueta	US holotype
Navia glauca L. B. Smith	**Steyermark 58320*	Venezuela: Amazonas: Cerro Duida	F holotype
Navia gleasonii L. B. Smith	**Maguire & Fanshawe 32389*	British Guiana: Essequibo	US
Navia gracilis L. B. Smith	**Wurdack & Adderley 43275*	Venezuela: Amazonas: Maroa, Río Guainia	US holotype
Navia graminifolia L. B. Smith	**Schultes 5492*	Colombia: Vaupés: Cerro Chiribiquete, Río Macaya	US isotype
Navia hechtioides L. B. Smith	**Maguire & Politi 27574*	Venezuela: Amazonas: Cerro Sipapo	US holotype
Navia heliophila L. B. Smith	**Schultes 12085*	Colombia: Amazonas: Raudel de Jirijirimo, Río Apaporis	US holotype
Navia hohenbergioides L. B. Smith	**Maguire Cowan, & Wurdack 30970*	Venezuela: Amazonas: Cerro Moriche, Río Ventuari	US holotype
Navia immersa L. B. Smith	**Maguire, Cowan, & Wurdack 30325*	Venezuela: Amazonas: Cerro Huachamacari, Río Cunucunuma	US holotype
Navia incrassata L. B. Smith & Steyermark	**Steyermark 97881*	Venezuela: Bolívar: Meseta de Jáua, Río Caura	US holotype
Navia intermedia L. B. Smith & Steyermark	**Steyermark 97865*	Venezuela: Bolívar: Cerro Jáua, Río Caura	US holotype
Navia involucrata L. B. Smith	**Cowan & Wurdack 31359*	Venezuela: Amazonas: Serranía Parú, Río Ventuari	US holotype
Navia lanigera L. B. Smith	**Maguire et al. 31794*	Venezuela: Amazonas: Cerro Camani, Río Ventuari	US holotype

List of Specimens Examined—Continued

Species	*Collector and Number*	*Locality*	*Herbarium*
Navia lasiantha L. B. Smith & Steyermark	**Steyermark 97865–A*	Venezuela: Bolívar: Cerro Jáua, Río Caura	US holotype
Navia latifolia L. B. Smith	**Maguire, Cowan, & Wurdack 29642*	Venezuela: Amazonas: Cerro Duida	US holotype
Navia lepidota L. B. Smith	**Maguire, Wurdack, & Bunting 37288*	Venezuela: Amazonas: Cerro de la Neblina, Río Yatua	US holotype
Navia lindmanioides L. B. Smith	**Maguire, Cowan, & Wurdack 30650*	Venezuela: Amazonas: Cerro Yapacana, Río Orinoco	US holotype
Navia lopezii L. B. Smith	**Schultes & Lopez 9956*	Brazil: Amazonas: Serra Dimití	US holotype
	Maguire & Politi 27497	Venezuela: Amazonas: Cerro Sipapo	US
	Wurdack & Adderly 43564	Venezuela: Amazonas: Río Siapa	US
Navia maguirei L. B. Smith	**Maguire 24575*	Surinam: Tafelberg	US isotype
Navia maguirei var. *minor* L. B. Smith	*Maguire 24334*	Surinam: Tafelberg	US isotype
Navia mima L. B. Smith	**Maguire & Politi 27590*	Venezuela: Amazonas: Cerro Sipapo	US holotype
Navia myriantha L. B. Smith	**Schultes & Lopez 9955*	Brazil: Amazonas: Serra Dimití	US holotype
Navia navicularis L. B. Smith & Steyermark	**Steyermark 90199*	Venezuela: Bolívar: Sierra Ichún	US isotype
Navia nubicola L. B. Smith	**Maguire, Wurdack, & Bunting 37392*	Venezuela: Amazonas: Cerro de la Neblina, Río Yatua	US holotype
Navia ocellata L. B. Smith	**Maguire & Politi 27500*	Venezuela: Amazonas: Cerro Sipapo	US holotype
Navia octopoides L. B. Smith	**Maguire & Maguire 29151*	Venezuela: Amazonas: Cerro Duida	US holotype
Navia parvula L. B. Smith	**Maguire, Wurdack, & Bunting 37326*	Venezuela: Amazonas: Cerro de la Neblina, Río Yatua	US holotype
Navia parvula var. *expansa* L. B. Smith	*Maguire, Wurdack, & Maguire 42246*	Venezuela: Amazonas: Cerro de la Neblina, Río Yatua	US holotype
Navia pauciflora L. B, Smith	**Maguire & Maguire 29154*	Venezuela: Amazonas: Cerro Marahuaca, Río Cunucunuma	US holotype
Navia phelpsiae L. B. Smith	**Maguire, Phelps et al. 31762*	Venezuela: Amazonas: Cerro Guanay, Río Ventuari	US isotype
Navia pulvinata L. B. Smith	**Maguire 29111*	Venezuela: Amazonas: Cerro Duida	US holotype
Navia pungens L. B. Smith	**Maguire et al. 31652*	Venezuela: Amazonas: Cerro Guanay, Río Ventuari	US holotype
Navia ramosa L. B. Smith	**Cardona 2997*	Venezuela: Bolívar: Cerro Pauo, Río Caura	US holotype
Navia reflexa L. B. Smith	**Schultes & Lopez 9321*	Colombia: Vaupés: San Felipe (El Castillo) Río Negro	US holotype
Navia robinsonii L. B. Smith	**Brewer 250*	Venezuela: Bolívar: Cerro Jáua, Río Caura	US holotype
Navia rupestris (Gleason) Sandwith	**Maguire & Fanshawe 32360*	British Guiana: Essequibo Macreba Falls, Kurupung River	US isotype of *N. fluviatilis*
Navia sandwithii L. B. Smith	**Maguire & Fanshawe 23435*	British Guiana: Kaieteur Falls	US
Navia saxicola L. B. Smith	**Maguire, Cowan, & Wurdack 30680*	Venezuela: Amazonas: Cerro Yapacana, Río Orinoco	US holotype
Navia schultesiana L. B. Smith	**Schultes 5655*	Colombia: Vaupés: Cerro del Castillo, Río Apaporis	US isotype
Navia scopulorum L. B. Smith	**Steyermark 75613*	Venezuela: Bolívar: Chimantá Massif	US holotype
Navia semiserrata L. B. Smith	**Maguire, Cowan, & Wurdack 30959*	Venezuela: Amazonas: Cerro Moriche, Río Ventuari	US holotype
Navia serrulata L. B. Smith	**Maguire, Cowan, & Wurdack 30521*	Venezuela: Amazonas: Cerro Yapacana, Río Orinoco	US holotype

List of Specimens Examined—Continued

Species	*Collector and Number*	*Locality*	*Herbarium*
Navia splendens L. B. Smith	•*Tillett 45841*	British Guiana: Essequibo, Utschi Falls, Kamarang River	US isotype
Navia stenodonta L. B. Smith	**Cowan & Wurdack 31357*	Venezuela: Amazonas: Serranía Parú, Río Ventuari	US holotype
Navia steyermarkii L. B. Smith	**Steyermark 58012*	Venezuela: Amazonas: Cerro Duida	F holotype
Navia subpetiolata L. B. Smith	**Cowan & Wurdack 31368*	Venezuela: Amazonas: Serranía Parú Río Ventuari	US holotype
Navia trichodonta L. B. Smith	**Maguire, Cowan, & Wurdack 30228*	Venezuela: Amazonas: Cerro Huachamacari, Río Cunucunuma	US holotype
Navia umbratilis L. B. Smith	**Maguire & Maguire 35406*	Venezuela: Amazonas: Serranía Yutaje, Río Manapiare	US holotype
Navia viridis L. B. Smith	**Maguire & Maguire 29078*	Venezuela: Amazonas: Cerro Duida	US holotype
Navia wurdackii L. B. Smith	**Wurdack 34324*	Venezuela: Bolívar: Sarvén-tepuí	US holotype
Navia xyridiflora L. B. Smith	**Steyermark 58152*	Venezuela: Amazonas: Cerro Duida	F isotype
Pitcairnia altensteinii (Link ex Kl. & Otto) Lem.	*Degado 45*	Venezuela	US
Pitcairnia angustifolia Soland.	*Sargent 443*	Puerto Rico: Maricao	US
Pitcairnia archeri L. B. Smith	*Killip 35255*	Colombia: Chocó: Upper Río San Juan	US
Pitcairnia armata Maury	*Maguire, Wurdack, & Bunting 36094*	Venezuela: Amazonas: Great Rapids of Orinoco, Palomal	US
Pitcairnia atrorubens (Beer) Baker	*Moore & Bunting 8704*	Mexico: Nayarit: Tepic to Jalcocotán	US
Pitcairnia brunnescens L. B. Smith	*Asplund 19060*	Ecuador: Pichincha: El Paso to El Volante	US
Pitcairnia brongniartiana André	*Killip 34835*	Colombia: Valle: Río Engaña	US
Pitcairnia brittoniana Mez	*Steyermark & Aristeguieta 15*	Venezuela: Bolívar: El Dorado to Luepa	US
Pitcairnia bulbosa L. B. Smith	*Maguire, Wurdack, & Bunting 36083*	Venezuela: Amazonas: Great Rapids of Orinoco, Puerto Ayacucho	US
Pitcairnia caricifolia Martius ex Schultes f.	*Cuatrecasas 7520*	Colombia: Vaupés: Río Guayabero	US
Pitcairnia gracilis Mez	*Stehlé 1804*	Guadeloupe: Ste. Rose, near Callas	US
Pitcairnia heterophylla (Lindl.) Beer	*Wilbur & Wilbur 2295*	Mexico: Jalisco: Autlán	US
Pitcairnia macrochlamys Mez	*Breedlove 6359*	Mexico: Chiapas: Mun. Tenejapa, Tanaté River	US
Pitcairnia micheliana André	*H. E. Moore 8165*	Mexico: Jalisco: Colima to Puente San Pedro	US
Pitcairnia multiflora L. B. Smith	*Cuatrecasas 23948*	Colombia: Valle: Hoya del Río Dígua, Río San Juan	US
Pitcairnia nigra (Carr.) André	*Asplund 20040*	Ecuador: Tungurahua: Río Verde Grande	US
Pitcairnia nuda Baker	*A. C. Smith 3644*	British Guiana: Mt. Iramaikpang, Kanuka Mts.	US
Pitcairnia oaxacana L. B. Smith	*Moore & Bunting 8763*	Mexico: Michoacan: Arteaga	US
Pitcairnia paniculata (R. & P.) R. & P.	*Macbride 5114*	Peru: Huánuco: Pampayacu	US
Pitcairnia pungens H. B. K.	*Pittier 1028*	Colombia: Cauca: Tacueyó, Río Palo Valley	US
Pitcairnia punicea Scheidw.	*Breedlove & Raven 13569*	Mexico: Chiapas: Ocozocoautla	US
Pitcairnia ringens Kl. ex Link	*Van Hyning 599*	Mexico: Veracruz: La Joya	US
Pitcairnia valerii Standley	*Allen 2414*	Panama: Panama: Cerro Campana	US
Puya santosii Cuatrecasas	*Cuatrecasas & Jaramillo 12042*	Colombia: Cundinamarca: Sabana de Bogotá	US
Puya sodiroana Mez	*Foster 2605*	Ecuador: Azuay: Cuenca to Oña	US

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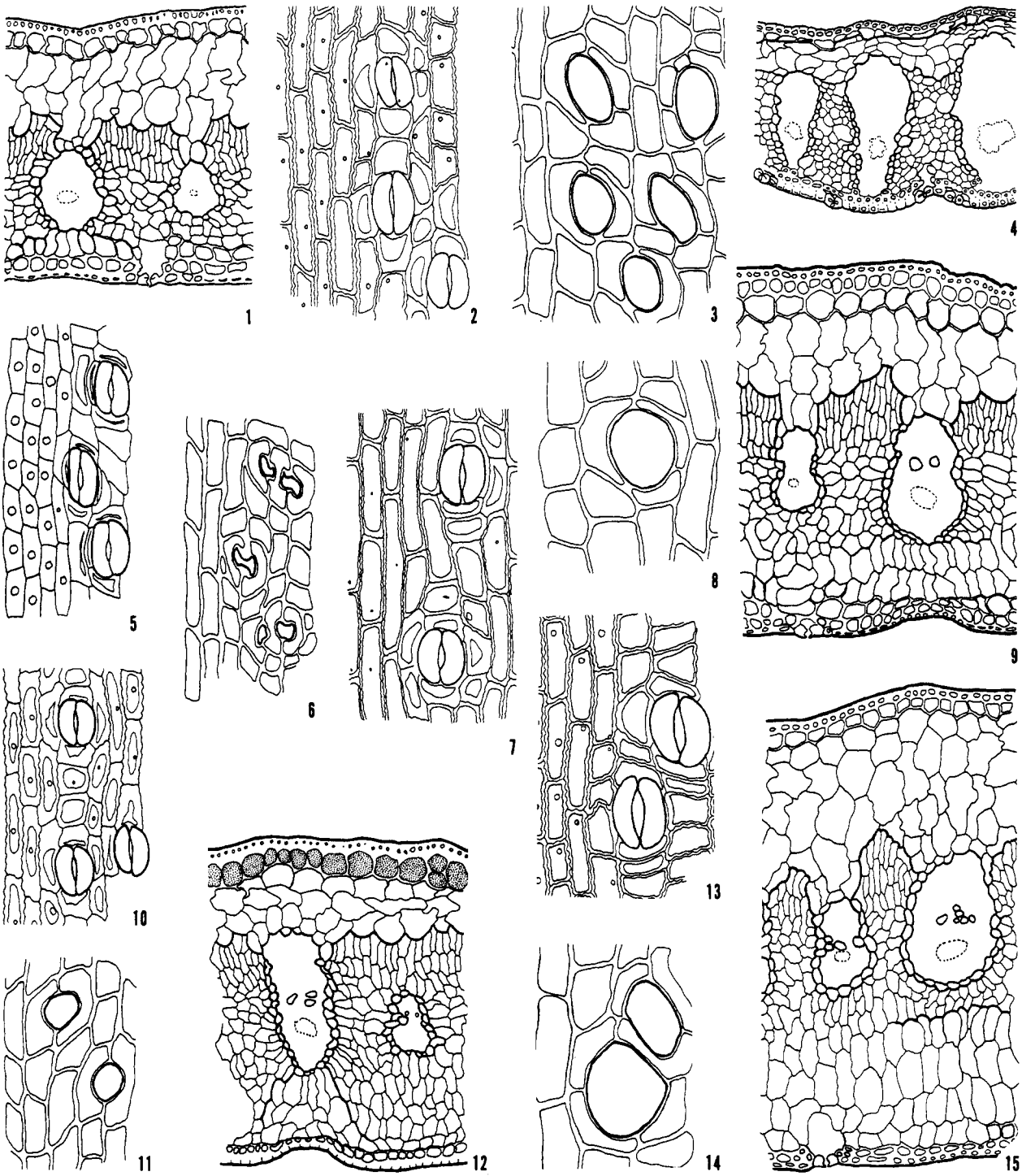
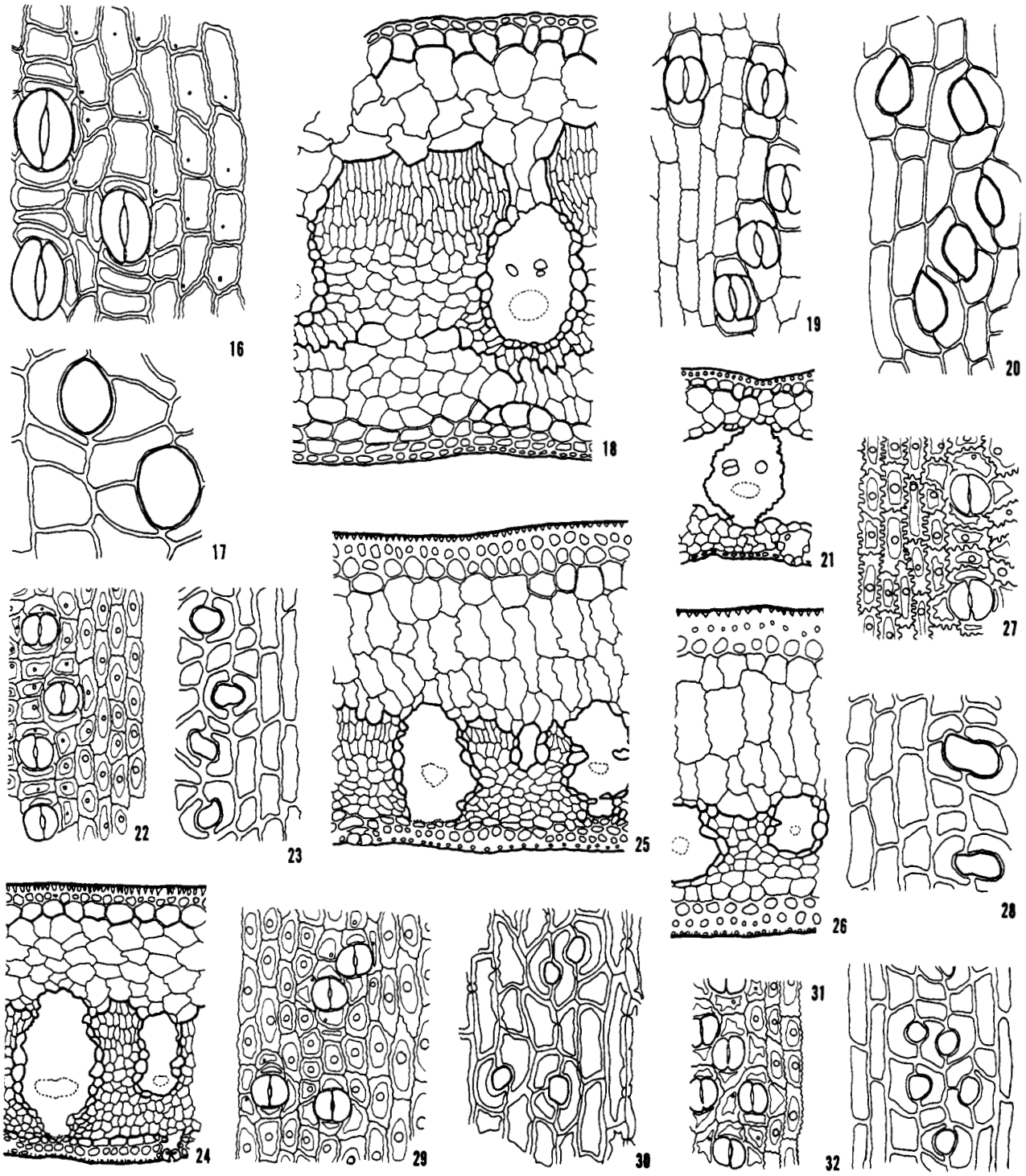
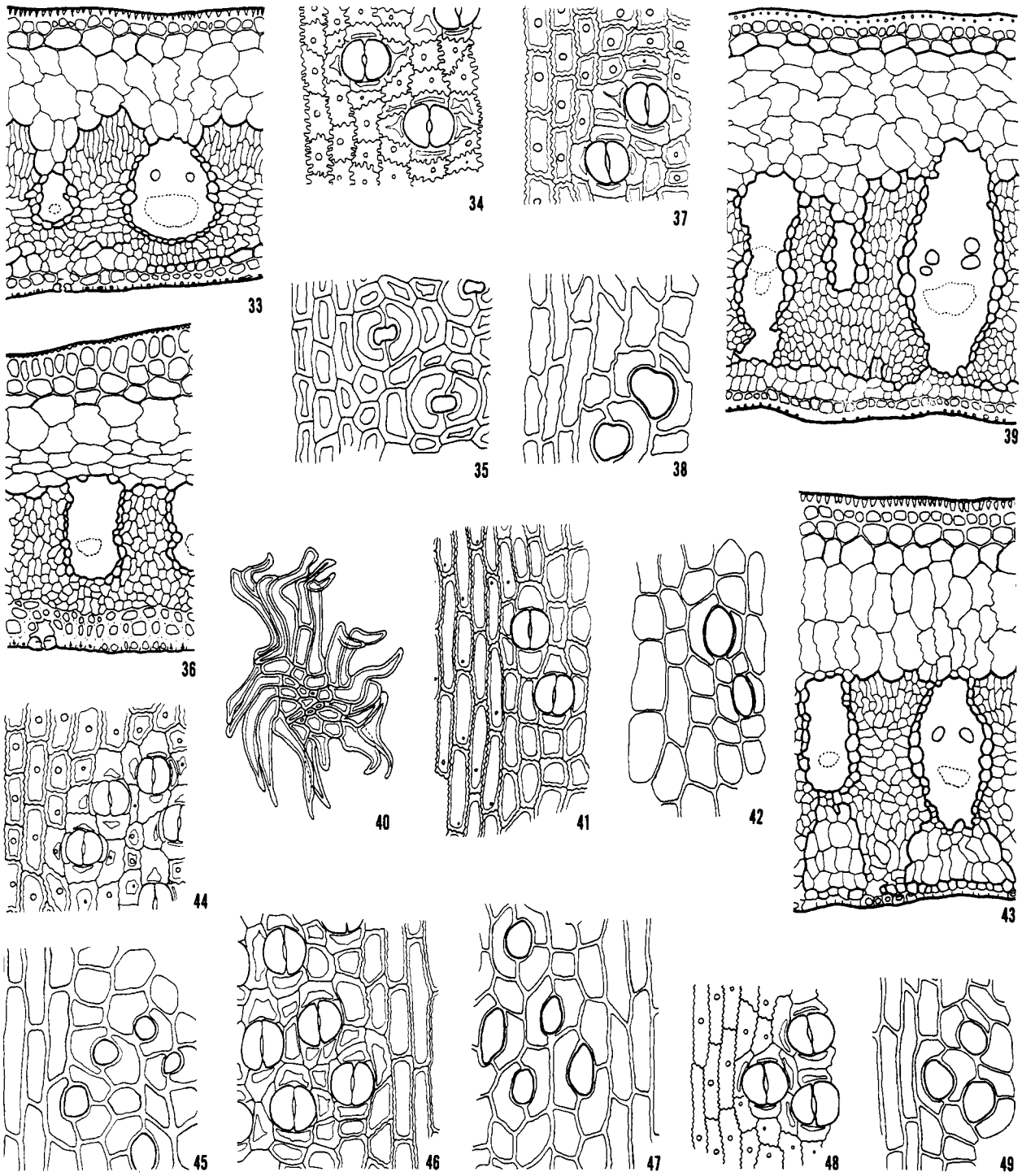


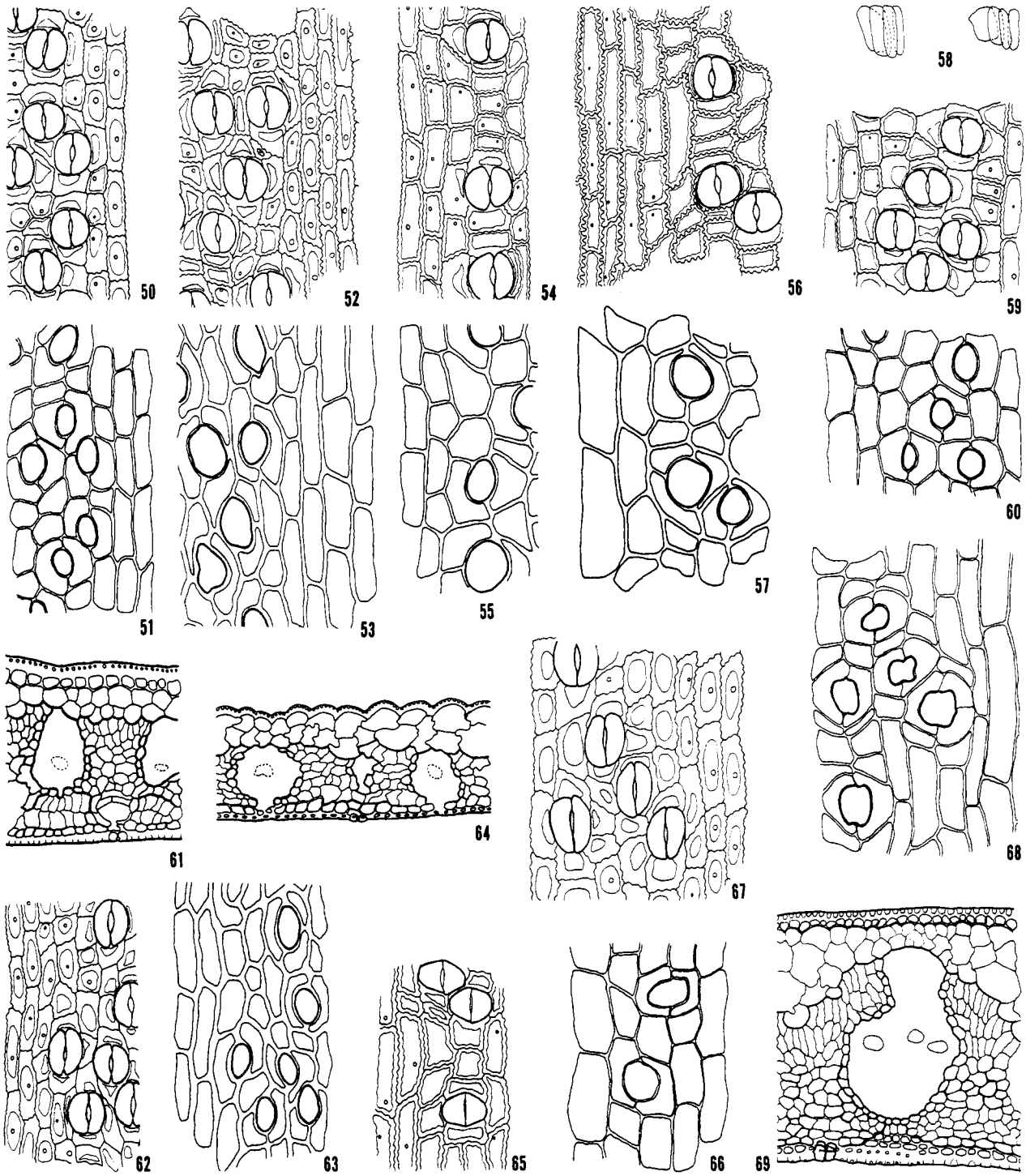
FIGURES 1–15.—*Connellia* and *Cottendorfia,* leaf anatomy. *Connellia guelchii*: 1, cross section, × 133; 2, abaxial epidermis, × 267; 3, abaxial subepidermis, × 267. *Cottendorfia florida:* 4, cross section, × 133; 5 abaxial epidermis, × 267; 6, abaxial subepidermis, × 267. *C. longipes:* 7, abaxial epidermis, × 267; 8, abaxial subepidermis, × 267; 9, cross section, × 133. *C. dyckioides:* 10, abaxial epidermis, × 267; 11, abaxial subepidermis, × 267; 12, cross section, × 133. *C. tillandsioides:* 13, abaxial epidermis, × 267; 14, abaxial subepidermis, × 267; 15, cross section, × 133.



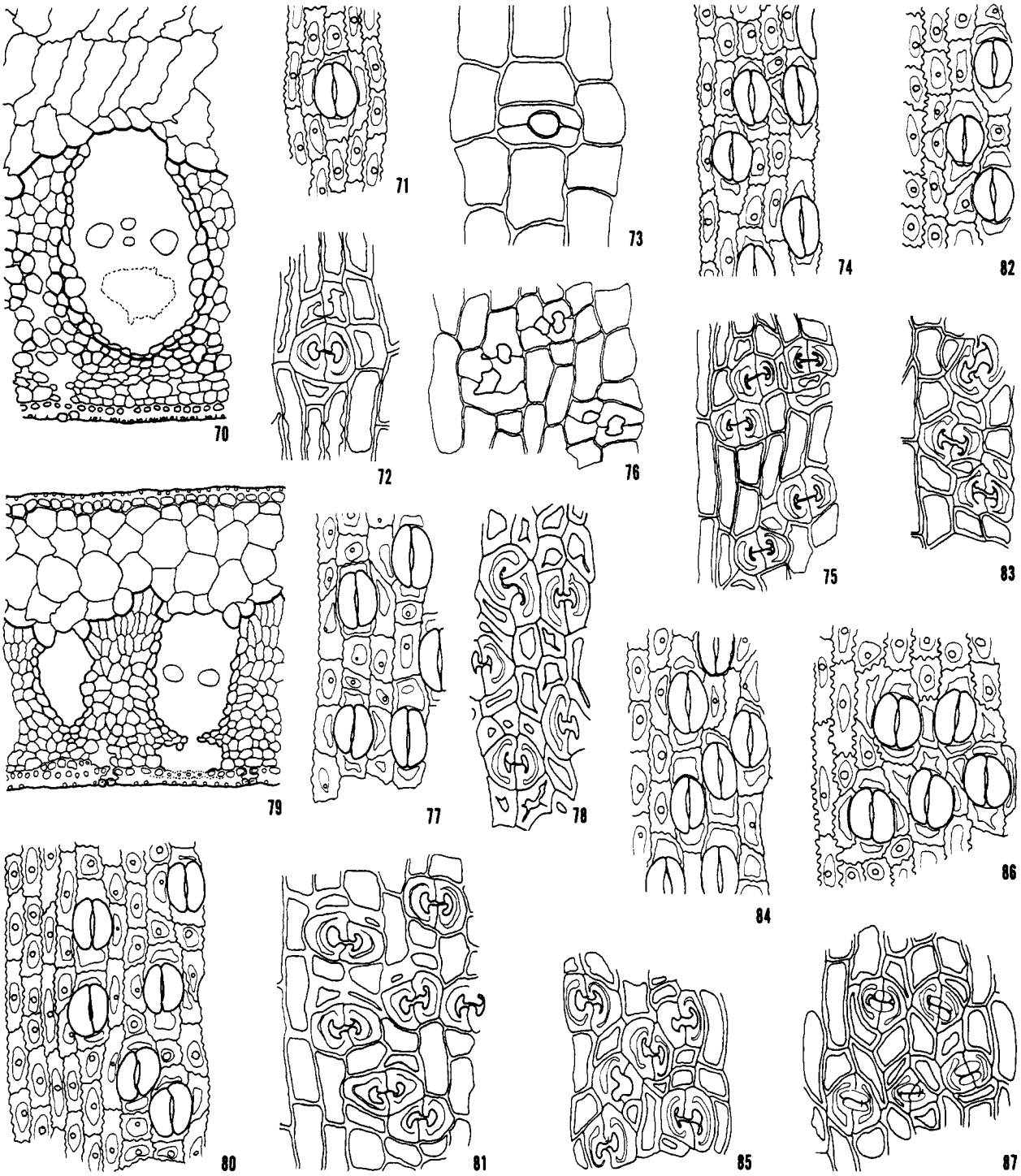
FIGURES 16–32.—*Cottendorfia,* leaf anatomy. *C. brachyphylla:* 16, abaxial epidermis, × 267; 17, abaxial subepidermis, × 267; 18, cross section, × 133. *C. wurdackii:* 19, abaxial epidermis, × 267; 20, abaxial subepidermis, × 267; 21, cross section, × 133. *C. thyrsoidea:* 22, abaxial epidermis, × 267; 23, abaxial subepidermis, × 267; 24, cross section, × 133. *C. minor:* 25, cross section from near midleaf, × 133; 26, cross section from near lower fourth, × 133; 27, abaxial epidermis, × 267; 28, abaxial subepidermis, × 267. *C. serrulata* var. *reducta;* 29, abaxial epidermis, × 267; 30, abaxial subepidermis, × 267. *C. gracillima:* 31, abaxial epidermis, × 267; 32, abaxial subepidermis, × 267.



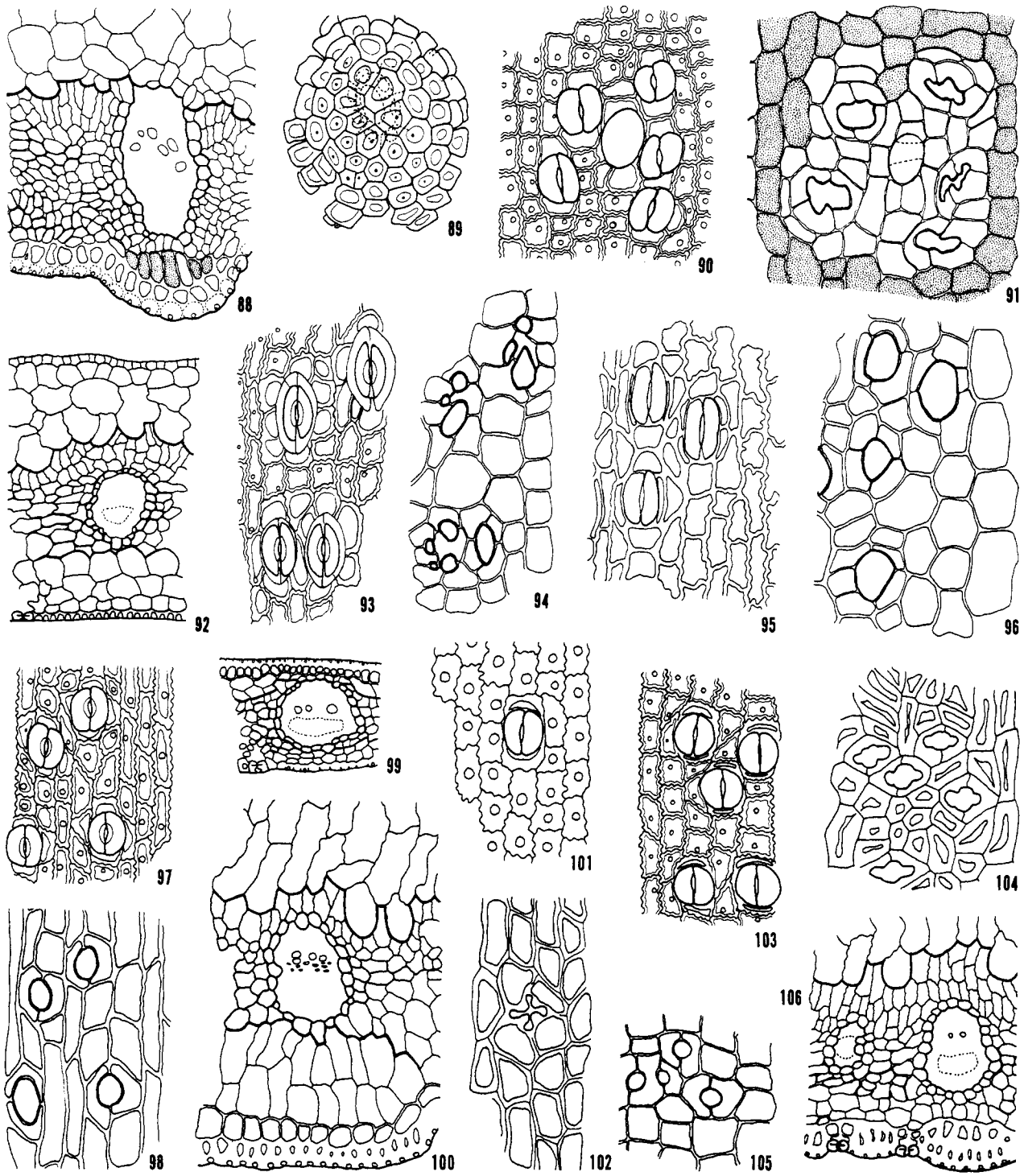
FIGURES 33–49.—*Cottendorfia,* leaf anatomy. *C. serrulata* var. *reducta:* 33, cross section, × 133. *C. subsimplex:* 34, abaxial epidermis, × 267; 35, abaxial subepidermis, × 267; 36, cross section, × 133. *C. stenophylla:* 37, abaxial epidermis, × 267; 38, abaxial subepidermis, × 267; 39, cross section, × 133. *C. argentea:* 40, scale, × 267; 41, abaxial epidermis, × 267; 42, abaxial subepidermis, × 267; 43, cross section, × 133. *C. guianensis:* 44, abaxial epidermis, × 267; 45, abaxial subepidermis, × 267. *C. dendritica:* 46, abaxial epidermis, × 267; 47, abaxial subepidermis, × 267. *C. cylindrostachya:* 48, abaxial epidermis, × 267; 49, abaxial subepidermis, × 267.



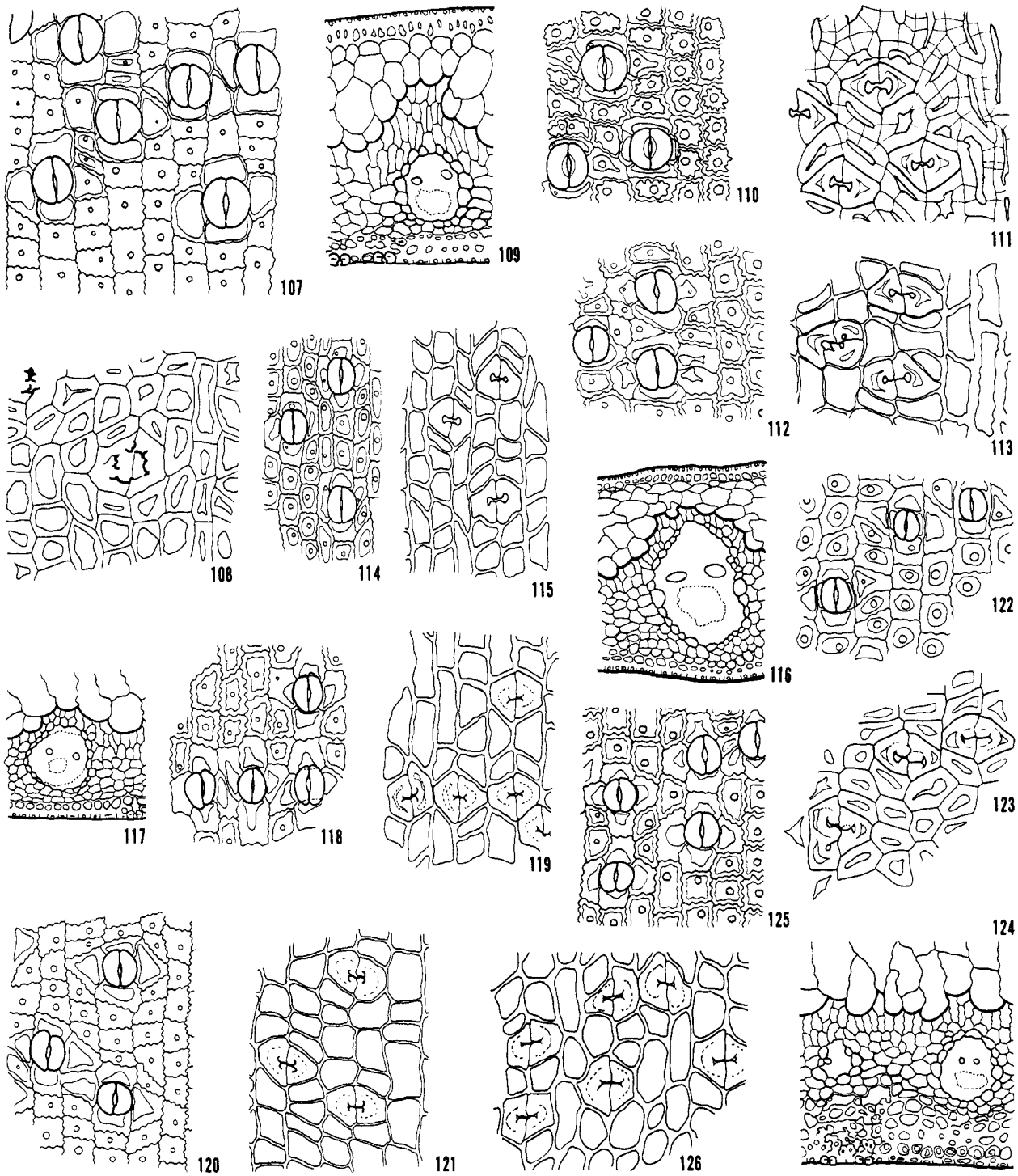
FIGURES 50–69.—*Cottendorfia* and *Navia*, leaf anatomy. *Cottendorfia geniculata:* 50, abaxial epidermis, × 267; 51, abaxial subepidermis, × 267. *C. maguirei:* 52, abaxial epidermis, × 267; 53, abaxial subepidermis, × 267. *C. nubigena:* 54, abaxial epidermis, × 267; 55, abaxial subepidermis, × 267. *C. savannensis:* 56, abaxial epidermis, × 267; 57, abaxial subepidermis, × 267; 58, scales, × 267. *C. paludosa:* 59, abaxial epidermis, × 267; 60, abaxial subepidermis, × 267. *C. phelpsiae:* 61, cross section, × 133; 62, abaxial epidermis, × 267; 63, abaxial subepidermis, × 267. *C. navioides:* 64, cross section, × 133; 65, abaxial epidermis, × 267; 66, abaxial subepidermis, × 267. *Navia ramosa:* 67, abaxial epidermis, × 267; 68, abaxial subepidermis, × 267; 69 cross section, × 133.



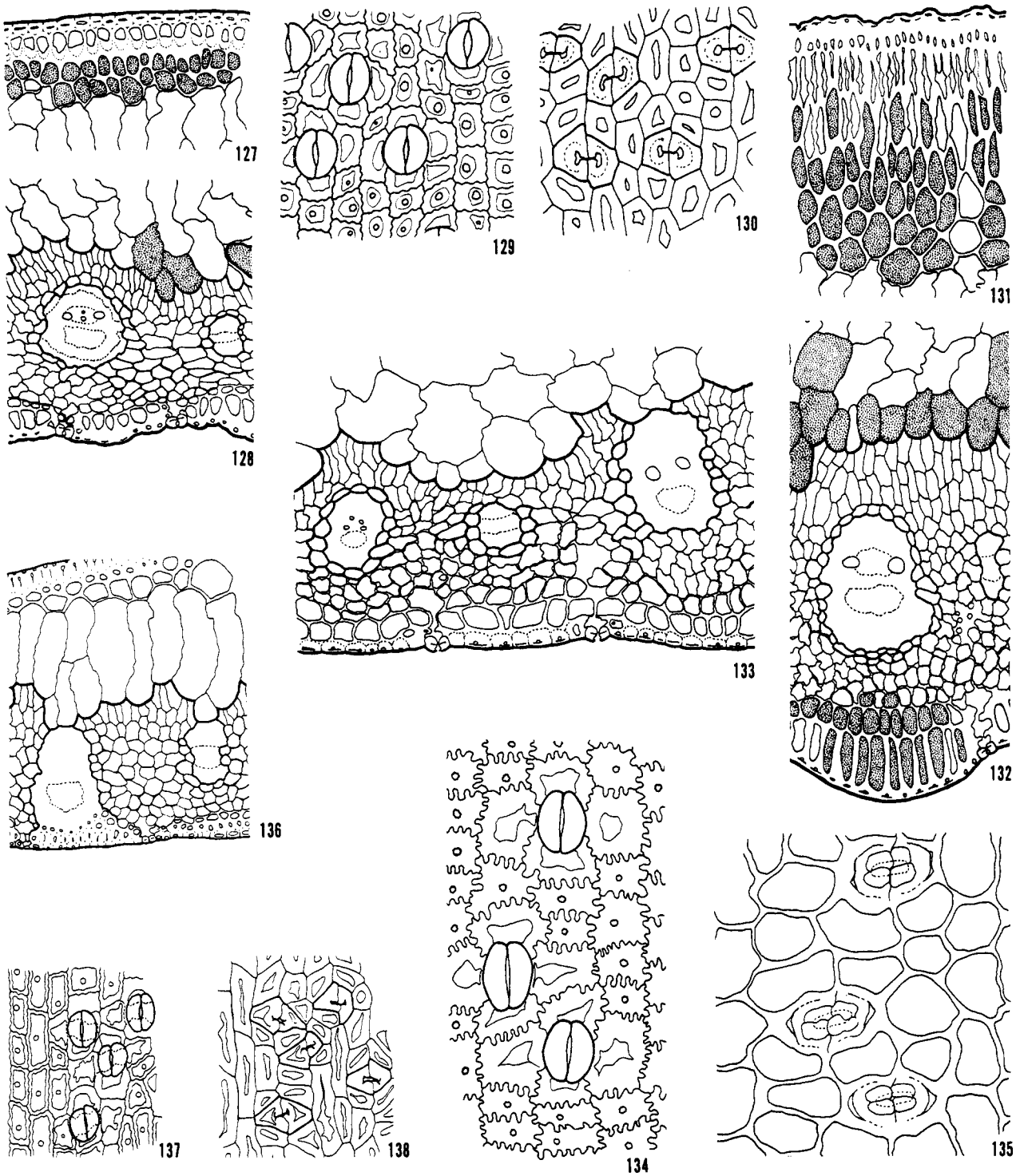
FIGURES 70–87.—*Navia,* leaf anatomy. *N. reflexa:* 70, cross section, × 133; 71, adaxial epidermis, × 267; 72, adaxial subepidermis, × 267; 73, adaxial third cell layer, × 267; 74, abaxial epidermis, × 267; 75, abaxial subepidermis, × 267; 76, abaxial third cell layer, × 267. *N. hechtioides:* 77, abaxial epidermis, × 267; 78, abaxial subepidermis, × 267. *N. hohenbergioides:* 79, cross section, × 133; 80, abaxial epidermis, × 267; 81, abaxial subepidermis, × 267. *N. gracilis:* 82, abaxial epidermis, × 267; 83, abaxial subepidermis, × 267. *N. brocchinioides:* 84, abaxial epidermis, × 267; 85, abaxial subepidermis × 267. *N. diffusa:* 86, abaxial epidermis, × 267; 87, abaxial subepidermis, × 267.



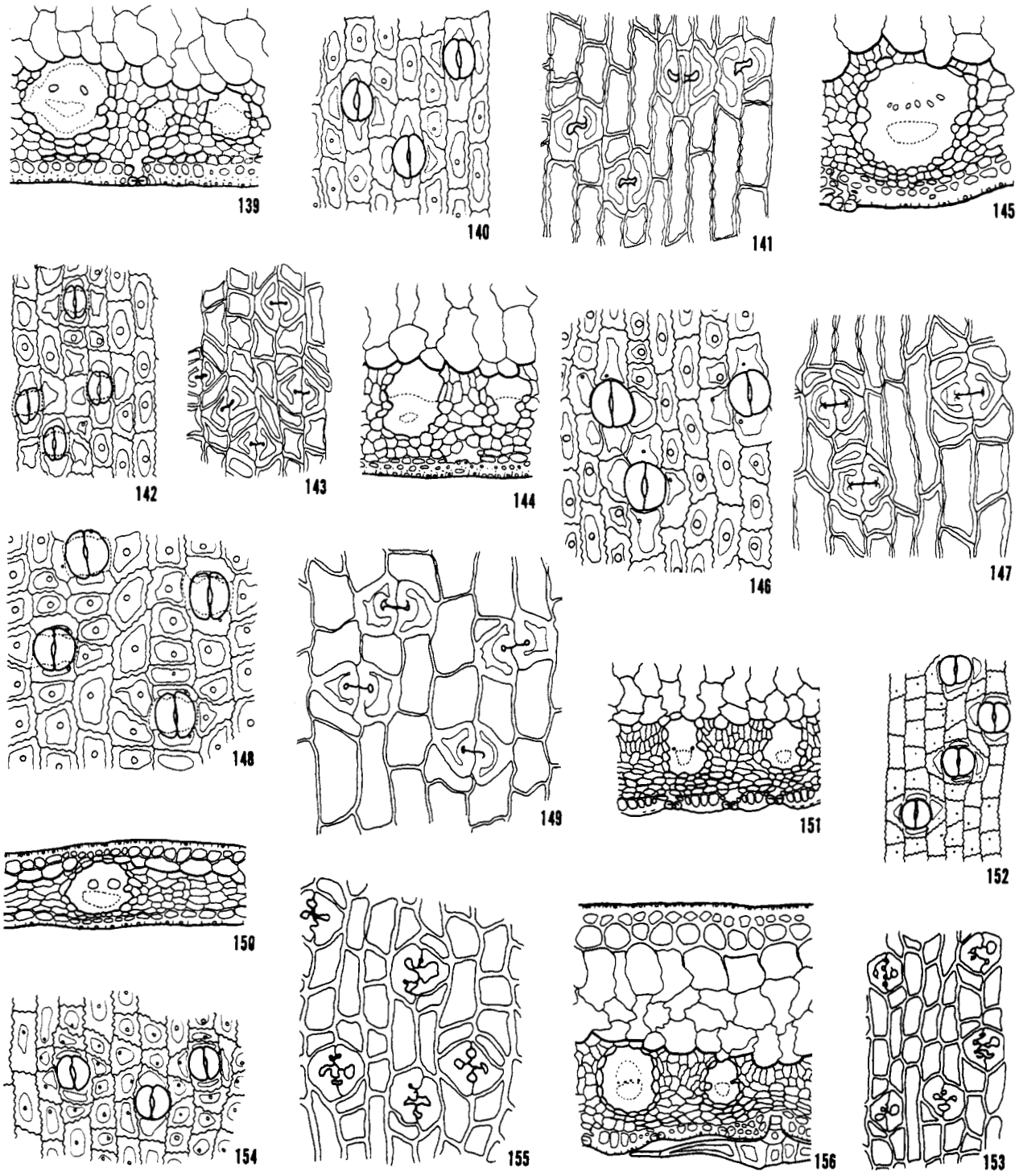
FIGURES 88–106.—*Navia,* leaf anatomy. *N. garcia-barrigae:* 88, cross section, × 133; 89, scale, × 133; 90, abaxial epidermis, × 267; 91, abaxial subepidermis, × 267. *N. rupestris:* 92, cross section, × 133; 93, abaxial epidermis, × 267; 94, abaxial subepidermis, × 267. *N. cataractarum:* 95, abaxial epidermis, × 267; 96, abaxial subepidermis, × 267. *N. lindmanioides:* 97, abaxial epidermis, × 267; 98, abaxial subepidermis, × 267; 99, cross section, × 133. *N. parvula:* 100, cross section, × 133; 101, abaxial epidermis, × 267; 102, abaxial subepidermis, × 267. *N. lepidota:* 103, abaxial epidermis, × 267; 104, abaxial subepidermis, × 267; 105, abaxial third cell layer, × 267; 106, cross section, × 133.



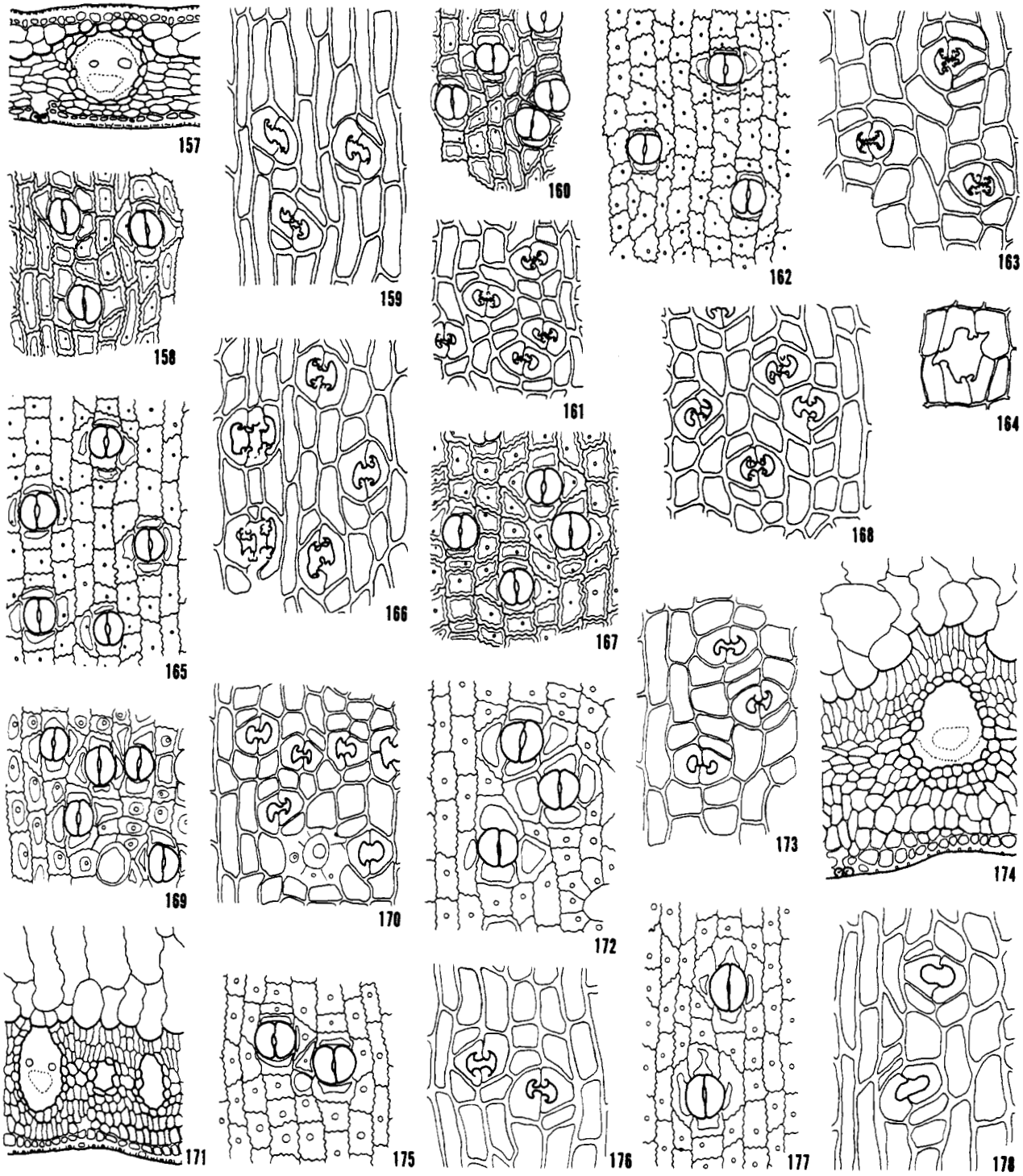
FIGURES 107–126.—*Navia,* leaf anatomy. *N. involucrata:* 107, abaxial epidermis, × 267; 108, abaxial subepidermis, × 267. *N. barbellata:* 109, cross section, × 133; 110, abaxial epidermis, × 267; 111, abaxial subepidermis, × 267. *N. splendens:* 112, abaxial epidermis, × 267; 113, abaxial subepidermis, × 267. *N. fontoides:* 114, abaxial epidermis, × 267; 115, abaxial subepidermis, × 267; 116, cross section, × 133. *N. cardonae:* 117, cross section, × 133; 118, abaxial epidermis, × 267; 119, abaxial subepidermis, × 267. *N. robinsonii:* 120, abaxial epidermis, × 267; 121, abaxial subepidermis, × 267, *N. aurea:* 122, abaxial epidermis, × 267; 123, abaxial subepidermis, × 167; 124, cross section, × 133. *N. lasiantha:* 125, abaxial epidermis, × 267; 126, abaxial subepidermis, × 267.



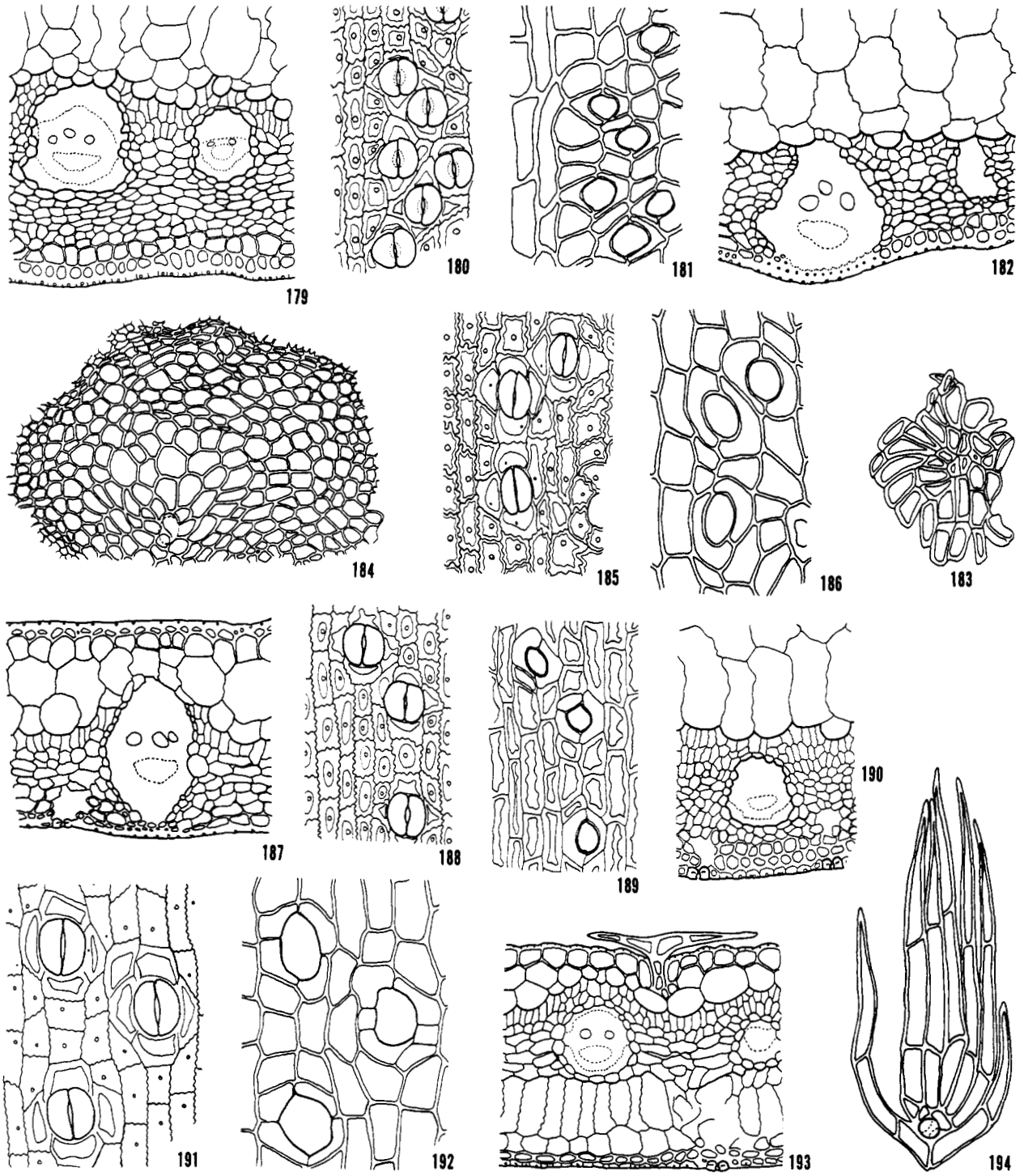
FIGURES 127–138.—*Navia,* leaf anatomy. *N. lasiantha:* 127, cross section, adaxial surface, × 133; 128, cross section, abaxial surface, × 133. *N. incrassata:* 129, abaxial epidermis, × 267; 130, abaxial subepidermis, × 167; 131, cross section, adaxial surface, × 133; 132, cross section, abaxial surface, × 133. *N. intermedia:* 133, cross section, × 133; 134, abaxial epidermis, × 267; 135, abaxial subepidermis, × 267. *N. immersa:* 136, cross section, × 133; 137, abaxial epidermis, × 267; 138, abaxial subepidermis, × 267.



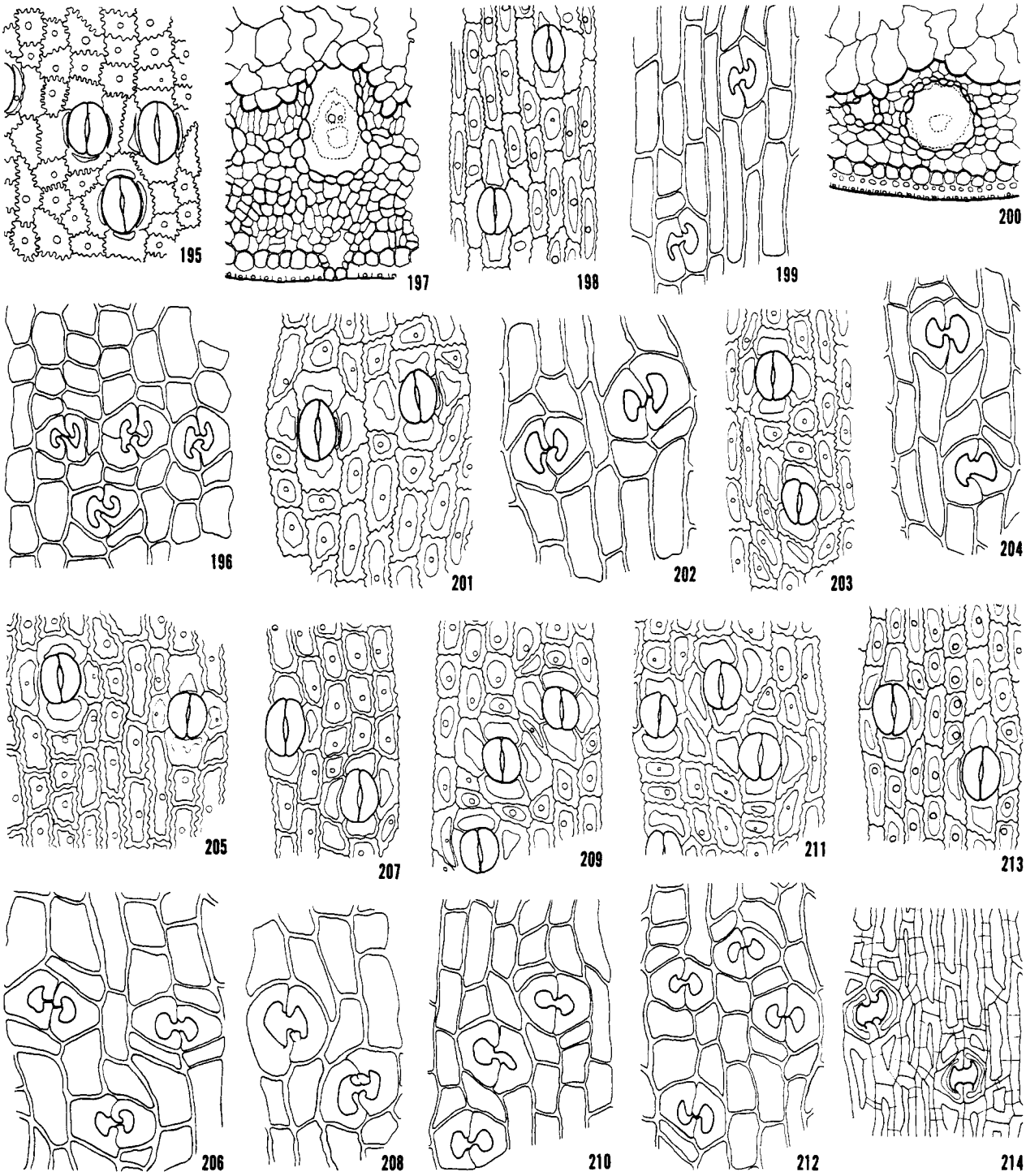
FIGURES 139–156.—*Navia,* leaf anatomy. *N. cucullata:* 139, cross section, × 133; 140, abaxial epidermis, × 267; 141, abaxial subepidermis, × 267. *N. pulvinata:* 142, abaxial epidermis, × 267; 143, abaxial subepidermis, × 267; 144, cross section, × 133. *N. scopulorum:* 145, cross section, × 133; 146, abaxial epidermis, × 267; 147, abaxial subepidermis, × 267. *N. angustifolia:* 148, abaxial epidermis, × 267; 149, abaxial subepidermis, × 267; 150, cross section, × 133. *N. abysmophila:* 151, cross section, × 133; 152, abaxial epidermis, × 267; 153, abaxial subepidermis, × 267. *N. duidae:* 154, abaxial epidermis, × 267; 155, abaxial subepidermis, × 267; 156, cross section, × 133.



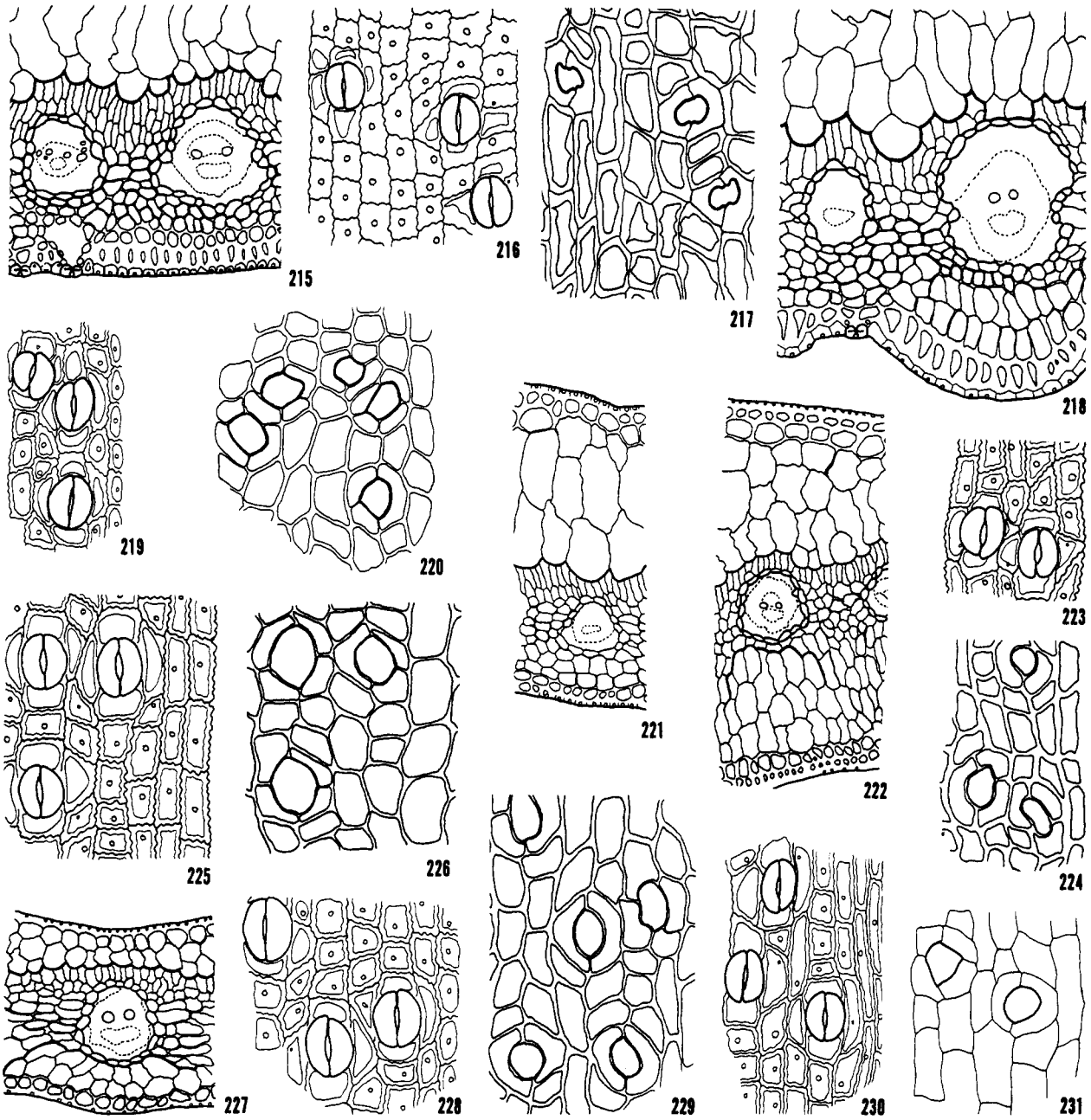
FIGURES 157–178.—*Navia,* leaf anatomy. *N. nubicola:* 157, cross section, × 133; 158, abaxial epidermis, × 267; 159, abaxial subepidermis, × 267. *N. cretacea:* 160, abaxial epidermis, × 267; 161, abaxial subepidermis, × 267. *N. latifolia:* 162, abaxial epidermis, × 267; 163, abaxial subepidermis, × 267; 164, abaxial third cell layer, × 267. *N. brachyphylla:* 165, abaxial epidermis, × 267; 166, abaxial subepidermis, × 267. *N. glauca:* 167, abaxial epidermis, × 267; 168, abaxial subepidermis, × 267. *N. semiserrata:* 169, abaxial epidermis, × 267; 170, abaxial subepidermis, × 267; 171, cross section, × 133. *N. caurensis:* 172, abaxial epidermis, × 267; 173, abaxial subepidermis, × 267; 174, cross section, × 133. *N. octopoides:* 175, abaxial epidermis, × 267; 176, abaxial subepidermis, × 267. *N. umbratilis:* 177, abaxial epidermis, × 267; 178, abaxial subepidermis, × 267.



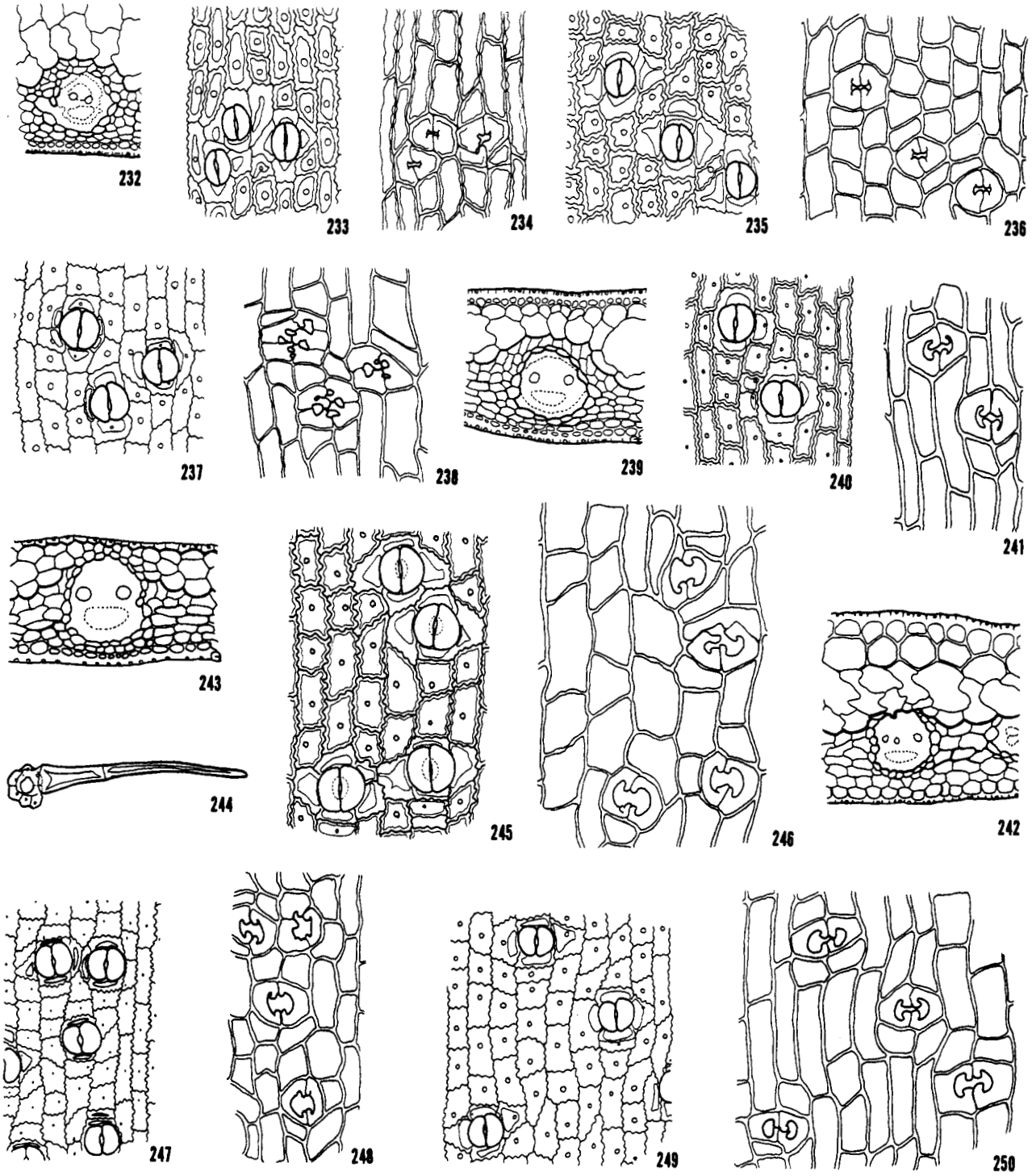
FIGURES 179–194.—*Navia,* leaf anatomy. *N. umbratilis:* 179, cross section, × 133. *N. serrulata:* 180, abaxial epidermis, × 267; 181, abaxial subepidermis, × 267; 182, cross section, × 133; 183, scale, × 133. *N. arida:* 184, scale, × 133; 185, abaxial epidermis, × 267; 186, abaxial subepidermis, × 267; 187, cross section, × 133. *N. saxicola:* 188, abaxial epidermis, × 267; 189, abaxial subepidermis, × 267; 190, cross section, × 133. *N. caulescens:* 191, abaxial epidermis, × 267; 192, abaxial subepidermis, × 267; 193, cross section, × 133; 194, scale, × 133.



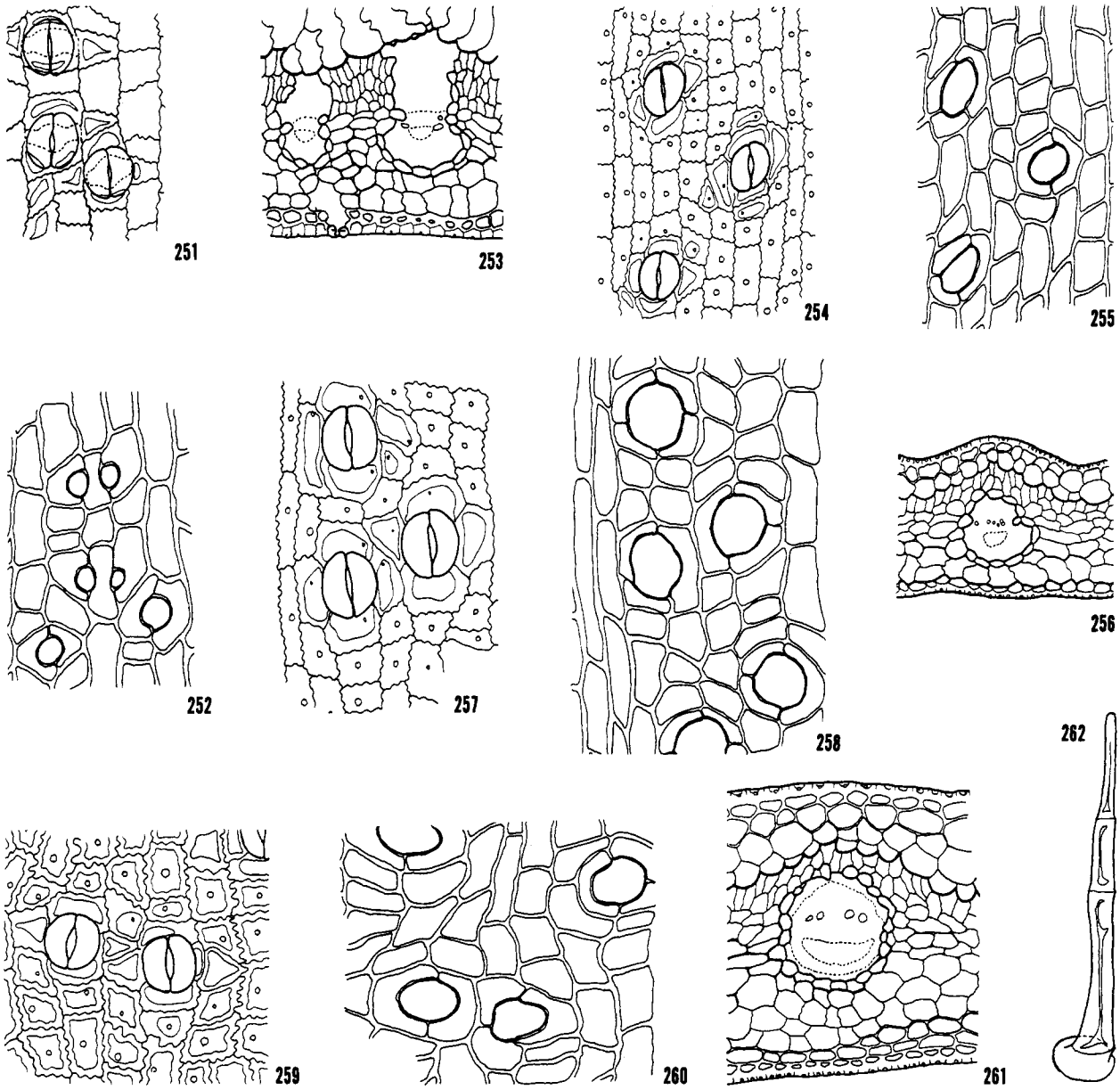
FIGURES 195–214.—*Navia*, leaf anatomy. *N. caricifolia:* 195, abaxial epidermis, × 267; 196, abaxial subepidermis, × 267; 197, cross section, × 133. *N. ocellata:* 198, abaxial epidermis, × 267; 199, abaxial subepidermis, × 267; 200, cross section, × 133. *N. maguirei:* 201, abaxial epidermis, × 267; 202, abaxial subepidermis, × 267. *N. subpetiolata:* 203, abaxial epidermis, × 267; 204, abaxial subepidermis, × 267. *N. gleasonii:* 205, abaxial epidermis, × 267; 206, abaxial subepidermis, × 267. *N. sandwithii:* 207, abaxial epidermis, × 267; 208, abaxial subepidermis, × 267. *N. connata:* 209, abaxial epidermis, × 267; 210, abaxial subepidermis, × 267. *N. affinis:* 211, abaxial epidermis, × 267; 212, abaxial subepidermis, × 267. *N. pungens:* 213, abaxial epidermis, × 267; 214, abaxial subepidermis, × 267.



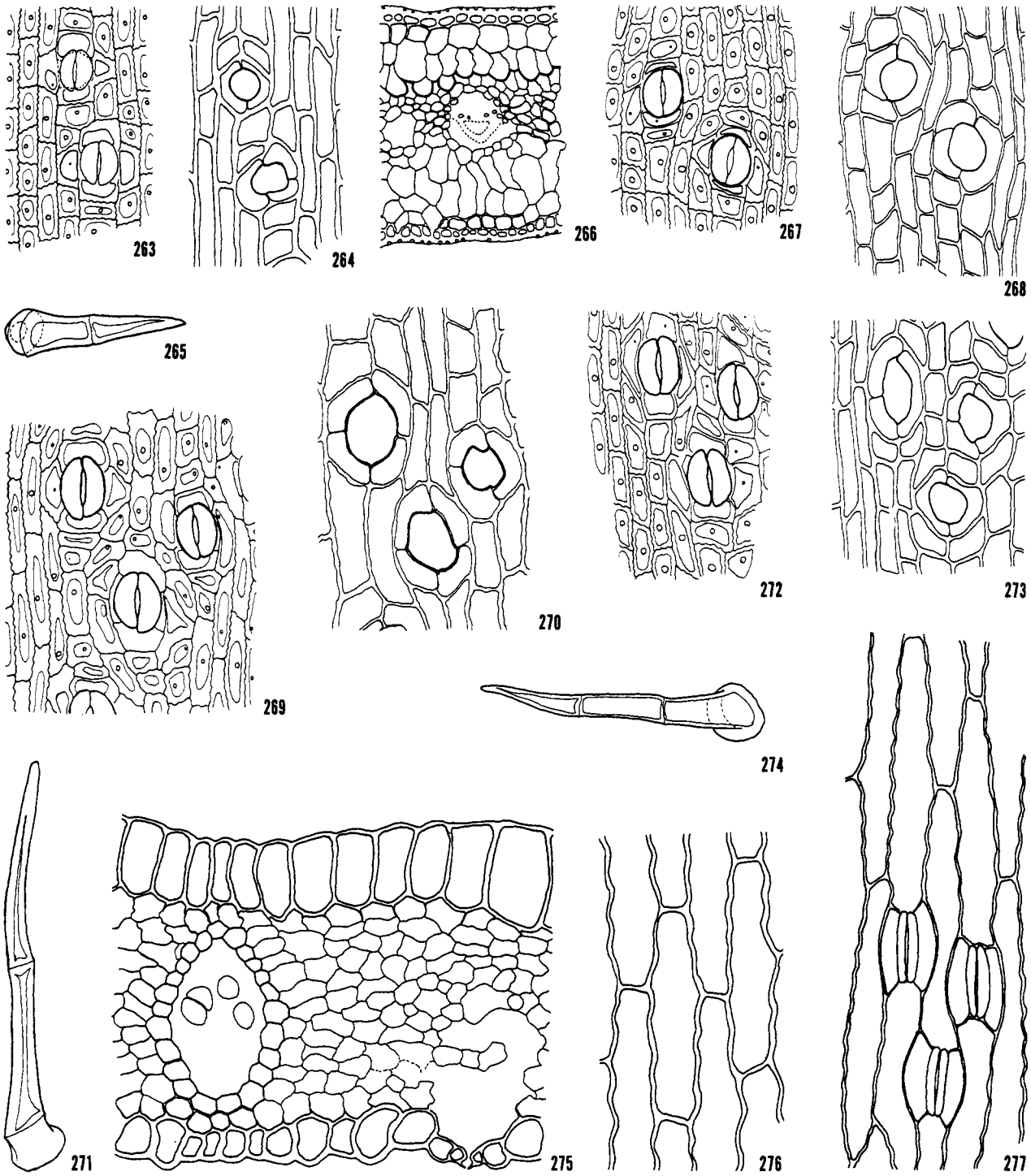
FIGURES 215–231.—*Navia*, leaf anatomy. *N. pungens:* 215, cross section, × 133. *N. mima:* 216, abaxial epidermis, × 267; 217, abaxial subepidermis, × 267; 218, cross section, × 133. *N. schultesiana:* 219, abaxial epidermis, × 267; 220, abaxial subepidermis, × 267; 221, cross section, × 133. *N. graminifolia:* 222, cross section, × 133; 223, abaxial epidermis, × 267; 224, abaxial subepidermis, × 267. *N. heliophila:* 225, abaxial epidermis, × 267; 226, abaxial subepidermis, × 267; 227, cross section, × 133. *N. bicolor:* 228, abaxial epidermis, × 267; 229, abaxial subepidermis, × 267. *N. acaulis:* 230, abaxial epidermis, × 267; 231, abaxial subepidermis, × 267.



FIGURES 232–250.—*Navia*, leaf anatomy. *N. navicularis:* 232, cross section, × 133; 233, abaxial epidermis, × 267; 234, abaxial subepidermis, × 267. *N. breweri:* 235, abaxial epidermis, × 267; 236, abaxial subepidermis, × 267. *N. colorata:* 237, abaxial epidermis, × 267; 238, abaxial subepidermis, × 267; 239, cross section, × 133. *N. xyridiflora:* 240, abaxial epidermis, × 267; 241, abaxial subepidermis, × 267; 242, cross section, × 133. *N. wurdackii:* 243, cross section, × 133; 244, trichome, × 133; 245, abaxial epidermis, × 267; 246, abaxial subepidermis, × 267. *N. pauciflora:* 247, abaxial epidermis, × 267; 248, abaxial subepidermis, × 267. *N. steyermarkii:* 249, abaxial epidermis, × 267; 250, abaxial subepidermis, × 267.



FIGURES 251–262.—*Navia,* leaf anatomy. *N. aloifolia:* 251, abaxial epidermis, × 267; 252, abaxial subepidermis, × 267; 253, cross section, × 133. *N. viridis:* 254, abaxial epidermis, × 267; 255, abaxial subepidermis, × 267; 256, cross section, × 133. *N. crispa:* 257, abaxial epidermis, × 267; 258, abaxial subepidermis, × 267. *N. stenodonta:* 259, abaxial epidermis, × 267; 260, abaxial subepidermis, × 267; 261 cross section, × 133; 262, trichome, × 133.



FIGURES 263–277.—*Navia,* leaf anatomy. *N. myriantha:* 263, abaxial epidermis, × 267; 264, abaxial subepidermis, × 267; 265, trichome, × 133; 266, cross section, × 133. *N. trichodonta:* 267, abaxial epidermis, × 267; 268, abaxial subepidermis, × 267. *N. lanigera:* 269, abaxial epidermis, × 267; 270, abaxial subepidermis, × 267; 271, trichome, × 133. *N. phelpsiae:* 272, abaxial epidermis, × 267; 273, abaxial subepidermis, × 267; 274, trichome, × 133. *N. lopezii:* 275, cross section, × 133; 276, abaxial epidermis, × 133; 277, abaxial epidermis, × 133.

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