

THE MORPHOLOGY AND RELATIONSHIPS OF
IDENBURGIA AND NOUHUYSIA

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With two plates

INTRODUCTION

IN A PREVIOUS PAPER (5), we excluded *Idenburgia* and *Scyphostegia* from the Monimiaceae. Since doing so, we have devoted considerable attention to additional investigation of the morphological characteristics of these peculiar genera, and to the problem of determining their relationships. It soon became evident that *Idenburgia* is closely related to, if not actually congeneric with, *Nouhuysia*. In writing to Professor van Steenis for additional material, we learned that he had a paper in press (7), in which he concludes that the two genera are identical and places the combination in a new tribe, the Nouhuysieae of the Guttiferae. He recognizes three distinct species of *Nouhuysia*, *N. papuana* Lauterbach, *N. arfakensis* (Gibbs) van Steenis and *N. pauciflora* (A. C. Sm.) van Steenis; *Idenburgia novoguineensis* Gibbs, *I. pachyphylla* Gilg & Schlechter, and *I. elaeocarpoides* Gilg & Schlechter being reduced to synonymy with *N. papuana* Lauterbach.¹

Upon the basis of our detailed study of the exomorphic and endomorphic characters of the vegetative and reproductive parts of *Idenburgia* and *Nouhuysia*, we are in agreement with van Steenis regarding the identity of the two genera, but we question whether *Nouhuysia* actually belongs in the Guttiferae. Furthermore, there are questions regarding speciation within the genus that appear to need extensive investigation. It seems desirable accordingly to summarize salient features of the morphological and anatomical data that we have accumulated during the last few years.

MATERIAL

Our observations are based upon the examination of material from the following 25 collections of *Nouhuysia* and *Idenburgia*:

Versteegh 1668 (type of *N. papuana* Lauterbach); *Clemens* 3828 (type of *I. pauciflora* A. C. Sm.), *Kostermans* 2217 [*N. arfakensis* (Gibbs) v. Steenis], 2198; *Clemens* 2240, 2422, 3122, 3978, 3978A, 4194A, 5122, 5499b, 7023, 8754, 8835, 11134, 12353; *Brass* 11078, 12661; *Brass & Versteegh* 10472; *Gibbs* 5654; *Neth. Ind. For. Serv.* bb 24085, bb 25014; *Pulle* 647; *Rutten* 2240.

¹ Since our manuscript went to press, we have learned through Dr. A. C. Smith of a paper by S. Hatusima (*Bot. Mag. Tokyo* 65: 107-111, 1952.) in which he likewise reduces *Idenburgia* to *Nouhuysia*. This paper is not available as yet in the libraries of Greater Boston.

STYLOIDS

A significant criterion in all of the collections that we have examined is the occurrence of visible calcium oxalate dominantly in the form of styloids. Although the styloids vary markedly in size, attaining at times a length of 350 microns and a breadth of 30 microns, their characteristic crystallographic form is that illustrated in *Fig. 6*. They are square or rectangular in sectional view, and are formed more or less abundantly in the lamina of the leaves and tepals and in the cortex and secondary phloem of the stem and petiole. Furthermore, they may occur, at least in certain cases, in the pith of the stem, in the connective of the stamens and in the pericarp of the fruit. In leaves and tepals, aberrations of form due to twining or the development of more than one crystal in a single cell are statistically of relatively infrequent occurrence. Transitions to raphides, such as may be observed for example in certain of the Parietales and Rubiales, do not occur. Nor have we been able to detect the presence of mucilage in the crystal-bearing cells. Transitions to aggregates of smaller crystals or to druses do occur, however, at times in the phloem and pith of the stem, e.g. *Brass 11078*.

In the lamina of the leaves and tepals — where the styloids commonly are large and have their major axis oriented parallel to the surfaces of the lamina — they are contained within cells that are markedly different from the surrounding cells and therefore appear to be idioblasts. Their outlines are visible in surface view of herbarium specimens when boiled leaves and tepals are examined under an ordinary binocular microscope with adequately controlled surface illumination. It is significant in this connection that, in clearing dried leaves for detailed study of their internal structure in transmitted light, the styloids tend to disintegrate and may disappear under prolonged treatment in 3% sodium hydroxide at 52°C. Therefore, it is essential to verify observations based on cleared material by the examination of thin sections of tissues that have not been subjected to the action of either acids or alkali.

LEAVES

Although the simple, extipulate leaves with glandular-serrate margins vary considerably in size, in the form of their apex and in hairiness, they are characterized in all collections by having a fundamentally similar pattern of vasculature. Three independent and relatively widely separated vascular strands or traces at the trilacunar nodes of the stem, *Fig. 10*, enter the base of the petiole, where they aggregate in the characteristic vascular configuration illustrated in *Fig. 12*. Thus, throughout most of the petiole and the midrib of the lamina the vascular tissues are distributed in the form of a trough with acutely inturned margins. The venation of the lamina is fundamentally pinnate and arcuate-reticulate in all cases. The veins and veinlets are more or less heavily jacketed with thick-walled fibers, and therefore tend to be embossed and conspicuous in dried specimens. The

stomata are of relatively constant size, form and structure, and are surrounded by ordinary epidermal cells, *Figs. 8 and 9*, no special subsidiary cells being formed in relation to them. The cell walls of the lower epidermis, as seen in surface view of the lamina, commonly tend to be conspicuously undulate, *Fig. 9*, but this character is less constant than the preceding ones, *Fig. 8*. A much wider range of variability occurs, however, in the cells of the mesophyll. The upper epidermis is subtended by palisade tissue, no hypodermal layer being formed in any of the leaves that we have examined. The palisade tissue is subtended by a small-celled, relatively compact form of spongy parenchyma, the rest of the mesophyll being composed of larger cells with more extensive intercellular lacunae. The cells of the palisade commonly are distributed in a single layer, but more than one such layer is encountered in certain cases, viz. *Brass 11078* and *Brass & Versteegh 10472*. The cells may be slender and typically elongated (*Kostermans 2198, Brass 12661*) or they may be short and poorly differentiated from the subtending compact form of spongy mesophyll (*Clemens 3828, 3978*). The cells of the spongy mesophyll in comparable parts of the lamina vary in size and form from one collection to another. They may be thin-walled throughout the lamina, thin-walled with occasional sclerotic modification, *Fig. 2*, a mixture of thin-walled and thick-walled, or prevailing thick-walled, *Figs. 1 and 7*. Similarly, the cells that jacket the veins and veinlets may be either thin-walled or thick-walled. The intercellular lacunae also vary markedly in size, compare *Figs. 1 and 7*.

STEMS

The fundamental structures of the stem, viz. pith, xylem, phloem and cortex, are remarkably similar in all collections that we have examined, such minor differences as occur being of a quantitative, rather than of a qualitative, nature. The most significant diagnostic criteria, other than the occurrence of styloids particularly in the phloem, are the primitive structure of the xylem and the character and distribution of the sclerenchymatous cells in the cortex.

The secondary xylem is formed by a primitive type of cambium having long fusiform initials with extensively overlapping ends. The vessels are slender, thin-walled and angular, *Fig. 13*, and are distributed either singly or in occasional radial clusters. The vessel members are long with extensively overlapping ends and with unusually numerous scalariform perforations, *Fig. 14*. The pitting between vessels in lateral contact is scalariform and transitional to opposite, as is that between vessels and parenchymatous cells. The more slender vessel members closely resemble scalariformly pitted tracheids and exhibit transitions between imperforate and perforate scalariform bordered pits. The fiber tracheids have numerous pits with conspicuous borders in both their radial and their tangential walls. The orifice of these pits may be included, slightly extended, or much extended by cracking of the secondary wall. The distribution of the wood parenchyma is apotracheal-diffuse. The rays are conspicuously heterogeneous,

the uniseriate ones being composed of very tall erect cells, and the biseriate and triseriate ones of lower cells which tend to become procumbent in the outer wood of older stems, *Fig. 13*.

There is a more or less compact zone of thick-walled fibers in the so-called pericyclic layer of the stem. This is jacketed by a broad zone of cortical sclerenchyma, composed of large cells of somewhat irregular form and orientation. These cells, although of a sclerenchymatous nature, are characterized by having relatively thin, lignified walls and unusually large lumina.

FLOWERS AND FRUITS

The floral morphology of the various species of *Idenburgia* as well as of *Nouhuysia papuana* conforms to a similar plan with little variation. The exomorphic characters of the tepals, stamens, pistil and fruit have been described and adequately illustrated by Gibbs (2), Gilg and Schlechter (3), and van Steenis (7). The chief variable factor appears to be in the number of stamens present in a flower, *I. arfakensis* with six standing at one extreme and *I. elaeocarpoides* with 10–13 representing the other extreme. *Idenburgia pauciflora* has flowers decidedly of smaller size in relation to other species of the genus and is distinctive in the possession of profuse dense tomentum on both its vegetative and reproductive parts.

The vasculature of the flowers also presents a rather stabilized pattern in the two genera. The median vascular strands, *Text-fig. 3, md*, of the two pairs of decussately arranged tepals are derived directly from the axial cylinder; the marginal veins, *mr*, of the adjacent tepals, however, are formed by four commissural strands, *com*. Stamens, *st*, receive a single strand each of which broadens slightly while traversing the connective. The remainder of the vascular tissue of the axis, consisting generally of eight to 12 strands, supplies the gynoecium, *g*. Two of these strands fuse together to form the "ventral" vein which runs vertically in the tissue separating the two locules, *v* in *Text-figs. 2 and 3*, and finally bifurcates, each branch supplying one ovule. The other strands of the gynoecium traverse the ovary wall and in the region of the stigma undergo considerable proliferation and anastomosis, *Text-fig. 2*.

The gynoecium in all the species of *Idenburgia* and in *Nouhuysia* examined by us is bilocular, lodging a single anatropous ovule in each locule, *Text-fig. 1*. The funicle is rather massive and characteristically papillose externally. Generally both ovules develop to produce two-seeded fruits. In certain collections, however, single-seeded fruits have been described (3,6). An examination of such specimens has revealed that this condition is due to a failure of one of the ovules to develop to maturity. The seed structure of the two genera under consideration are remarkably alike, the most noteworthy feature being the pronounced centripetal ruminations of the stony layer of the seed, *Fig. 11*.

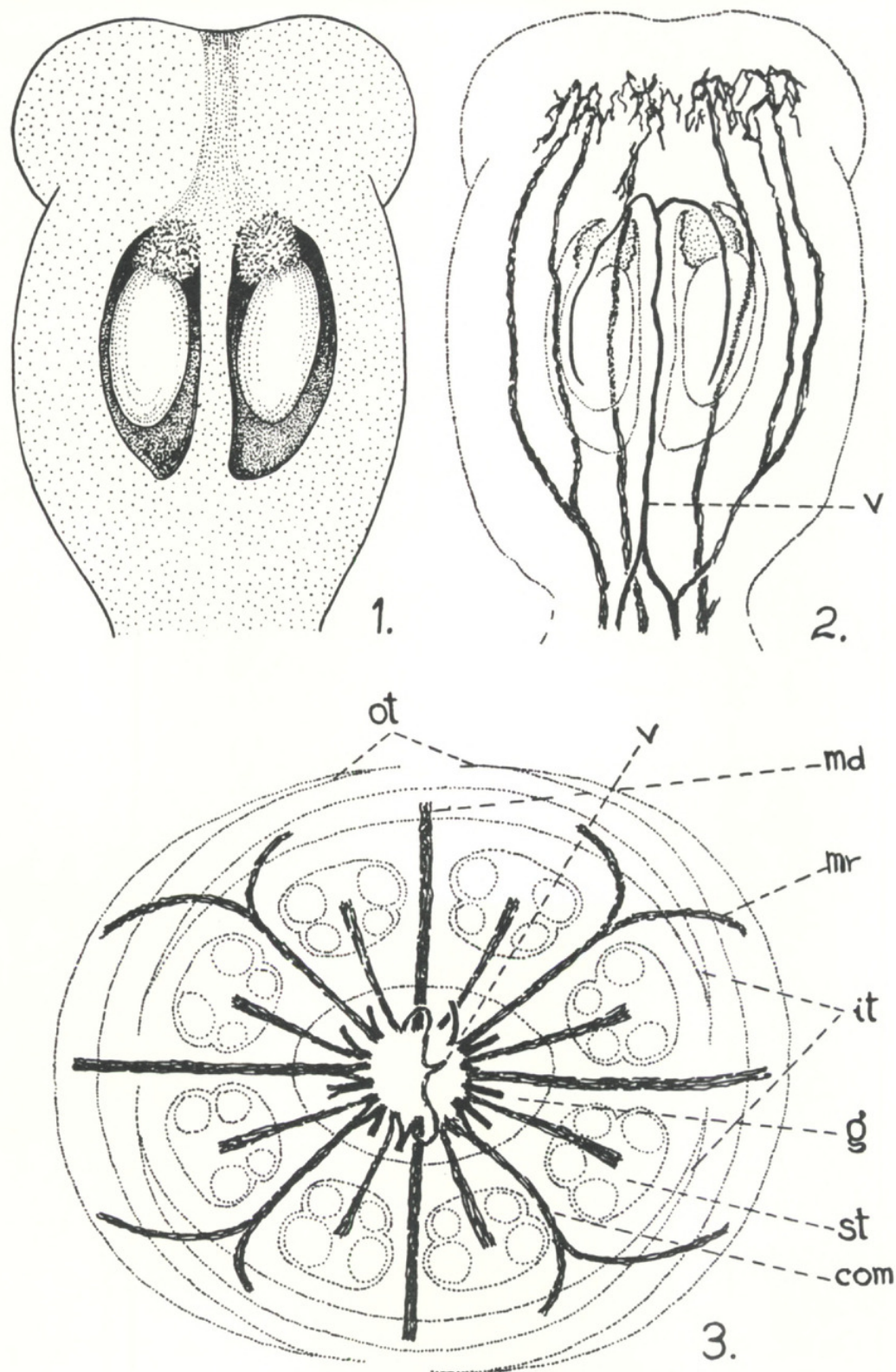


FIG. 1. Gynoecium of *Idenburgia* cut longitudinally to expose the ovules. FIG. 2. Longitudinally cut half of the gynoecium of *Idenburgia* showing the pattern of vasculature. *v* = ventral vein. FIG. 3. A generalized vascular diagram of the flower of *Idenburgia*. *com*: = commissural strand; *g* = gynoecium; *it* = inner tepal; *md* = median strand; *mr* = marginal strand; *ot* = outer tepal; *st* = stamen; *v* = ventral vein.

POLLEN

Erdtman is quoted by van Steenis as stating that the pollen of *Kostermans 2198* is 3-porate, oblate ($14.5 \times 20.5\mu$), with an exine 1.5μ in thickness, pattern \pm obscure. We have examined the pollen from eight different collections. *Gibbs 5654* and *Kostermans 2198* are characterized by dominantly oblate, 3-porate pollen, *Fig. 3*, with a minor admixture of 4-porate grains. The inner exine is greenish and highly refractive in lactic acid and the outer exine exhibits a barely detectable sculpture in surface view. The pollen of *Rutten 2240* is similar but differs in being dominantly 4-porate with a minor admixture of 5-porate grains. *Clemens 3828* (type of *I. pauciflora* A. C. Sm.) is dominantly 3-porate but differs in its conspicuously smaller size. *Kostermans 2217* (*I. arjakensis* Gibbs) and *Clemens 2422* have a conspicuously granular-reticulate outer exine in surface view, the former being prevailingly 3-porate, and the latter 4-porate and conspicuously smaller, *Fig. 5*. In marked contrast to the pollen of these collections, is that from *Brass 12661* and *Clemens 5499b* which is inaperturate, spherical and much larger, *Fig. 4*. It is significant, however, that all of the various forms of pollen are characterized by having a relatively thick, conspicuously hyaline inner exine.

DISCUSSION

The combination of exomorphic and endomorphic characters of both the reproductive and vegetative parts is closely similar in all collections, and there can be no doubt that *Idenburgia* and *Nouhuysia* are congeneric. Such morphological variations as occur tend to intergrade more or less extensively, *N. pauciflora* (A. C. Sm.) van Steenis being at one extreme of variability, for example in hairiness, and *N. arjakensis* (Gibbs) van Steenis in leaf form. When these specimens are excluded as easily recognizable species, the remaining collections of *Nouhuysia* present a problem of considerable taxonomic difficulty. Should all of them be assigned to one variable species, *N. papuana* Lauterbach, as concluded by van Steenis, or should additional species be segregated as attempted by Gibbs and by Gilg and Schlechter?

Unfortunately, such conspicuous differences in the internal structure of leaves as those illustrated in *Figs. 1, 2* and *7* are at present of questionable utility. The structural differences between sun-leaves and shade-leaves of the same plant and between leaves of plants growing in moist, as contrasted with arid, environments are known to be considerable. Therefore extensive additional collections must be made in order to determine whether such foliar structural differences are due to genetic factors or merely to the effects of varying environmental factors. It is significant in this connection, however, that the differences in pollen morphology, illustrated in *Figs. 3* and *4*, exceed the limits of variability that may be anticipated in a single species. Unfortunately, owing to the limited number of available collections with mature pollen, it is not possible at present to

establish valid correlations between differences in pollen morphology and other diagnostic criteria.

Although the available material is inadequate for a satisfactory solution of the problem of speciation within *Nouhuysia*, it provides a summation of evidence that is significant in any discussion of the relationships of the genus. That the genus does not belong in, or in close relationship to, the Trimeniaceae or Monimiaceae is indicated by fundamentally significant morphological and anatomical differences in all of its organs. "Ethereal oil cells," which occur so characteristically throughout the Monimiaceae and the Trimeniaceae, are absent, as are large mucilage cells of the type which are a significant diagnostic criterion in *Trimenia* and *Piptocalyx*. Crystallization of calcium oxalate in the form of styloids, which is so typical of *Nouhuysia*, is alien to the Monimiaceae and allied families. Furthermore, the genus has a dominantly trilacunar nodal anatomy in contrast to the unilacunar structure which occurs throughout the Monimiaceae, Lauraceae, Gomortegaceae, Trimeniaceae, Amborellaceae and Austrobaileyaceae. In addition, the pollen morphology of *Nouhuysia* is fundamentally unlike that of these families. Although *Trimenia*, *Piptocalyx* and many genera of the Monimiaceae have retained a relatively primitive form of secondary xylem, they exhibit a tendency for the elimination of wood parenchyma and for the formation of septate fibers that is absent in *Nouhuysia*. The similarities in the flowers are superficial. The form and particularly the vasculature and other internal structures of the tepals, stamens and pistil of *Nouhuysia* prove upon detailed examination to be fundamentally different from those of *Trimenia* and *Piptocalyx*.

Similarly a summation of available evidence appears to exclude *Nouhuysia* from close relationship to the Guttiferae. The genus lacks the schizogenous secretory receptacles and the subsidiary cells oriented parallel to the guard cells of the stomata that are such characteristic diagnostic features of that family. The xylem is at a conspicuously more primitive level of structural specialization. Furthermore, the trilacunar nodal structure is alien to the Guttiferae which are dominantly unilacunar. In addition, styloids are not known to occur in the Guttiferae whose form of crystallization is of a different type. Nor have outstanding similarities in the reproductive parts been described which might be interpreted as neutralizing such significant differences.

As in the case of *Calyptosepalum*, discussed in another paper (1), *Nouhuysia* exhibits a combination of reproductive and vegetative characters that negates its inclusion at present in any existing family. It appears to be another of the numerous relics of an ancient woody dicotyledonous flora that have survived in New Guinea, New Caledonia, Fiji and adjacent regions. What to do with such genera as they successively come to light is a problem of major taxonomic importance. When thoroughly investigated, they promise to reveal much new evidence regarding the morphological characteristics of primitive angiosperms, and, therefore, should not be relegated to a position where they become lost from view. To refer them at once to existing families not only tends to conceal them, but also is

extremely misleading in many cases. Lauterbach's (4) brief description and premature reference of *Nouhuysia* to the Guttiferae is undoubtedly responsible in part for the genus being overlooked and for the description of subsequent collections as species of a new genus, viz. *Idenburgia*.

Past experience with relic genera, e.g. *Casuarina*, *Degeneria*, *Himantandra*, *Amborella*, *Trochodendron*, *Tetracentron*, *Euptelea*, *Illicium*, *Cercidiphyllum*, etc., indicates that many, if not most, of them will have to be placed eventually in separate families, regardless of the results of such a procedure in multiplying the number of small families. This should not be attempted, however, until adequate collections of material are available for detailed and comprehensive investigations of all parts of the plant or until there is a summation of evidence which justifies the exclusion of a genus from existing families and the establishment of a new one. In the meantime, it appears wiser to place such relic genera in a special category of plants of uncertain or undetermined affinities comparable to the Fungi Imperfecti of mycologists rather than to continue to toss them about from one existing family to another as is commonly done at present.

Certain relic genera, when thoroughly studied, prove to be related to existing families, e.g. *Degeneria* and *Himantandra* to the Magnoliaceae or *Amborella*, *Trimenia*, *Gomortega* and *Austrobaileya* to the Monimiaceae and Lauraceae, and therefore may justifiably be placed in independent families in close proximity to them. Others, e.g. *Casuarina*, *Cercidiphyllum*, *Euptelea*, *Trochodendron* and *Tetracentron*, appear to be relics of more remotely related plants having no close surviving relatives and had best be retained in a general category of uncertain affinities, at least until their true relationships are revealed by paleobotanical evidence.

The genus *Nouhuysia* belongs for the time being at least in such a category of plants of uncertain or undetermined affinities.

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We are indebted to the Arnold Arboretum for the loan of all of its collections of *Idenburgia* and *Nouhuysia*, and to Professor van Steenis for his kindness in sending us pollen-bearing flowers of *Gibbs* 5654, *Rutten* 2240 and *Kostermans* 2217. The junior author wishes to express his keen appreciation of helpful privileges extended to him by the Director and the staff of the herbarium at Kew.

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EXPLANATION OF PLATES

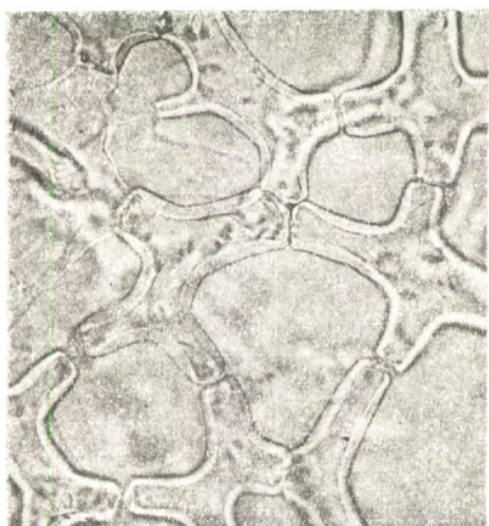
PLATE I

FIG. 1. *Clemens 5499b*. Cleared leaf, showing large intercellular spaces in the mesophyll and heavy thickening of the walls of its constituent cells, $\times 150$. FIG. 2. *Clemens 12353*. Cleared leaf, showing thin-walled mesophyll and scattered sclereids, $\times 150$. FIG. 3. *Kostermans 2198*. Oblate, triporate pollen, $\times 440$. FIG. 4. *Brass 12661*. Spheroidal, inaperturate pollen, $\times 440$. FIG. 5. *Clemens 2422*. Oblate, tetraporate pollen, $\times 440$. FIG. 6. *N.I.F.S. bb. 25014*. Cleared leaf, showing styloid, $\times 150$. FIG. 7. *Kostermans 2198*. Cleared leaf, showing thick-walled mesophyll and relatively small intercellular spaces, $\times 150$.

PLATE II

FIG. 8. *Kostermans 2198*. Cleared leaf, showing stomata and form of the surrounding epidermal cells, $\times 310$. FIG. 9. *Brass 12661*. Cleared leaf, showing stomata and form of the surrounding epidermal cells, $\times 310$. FIG. 10. *Clemens 3978*. Transverse section of the stem at the level of a trilacunar node, $\times 11$. FIG. 11. *Clemens 2240*. Transverse section of a fruit with two seeds, $\times 5$. FIG. 12. *Clemens 3978*. Transverse section of the mid-vein of the leaf, showing form of vascular tissues, $\times 19$. FIG. 13. *Clemens 2422*. Transverse section of the secondary xylem, $\times 40$. FIG. 14. *Clemens 2422*. Radial longitudinal section of the xylem, showing the scalariform perforations, $\times 150$.

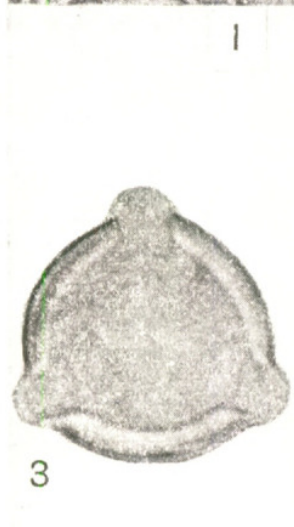
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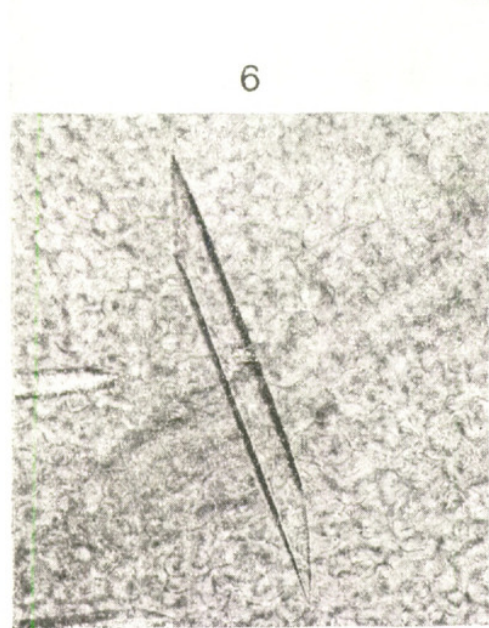
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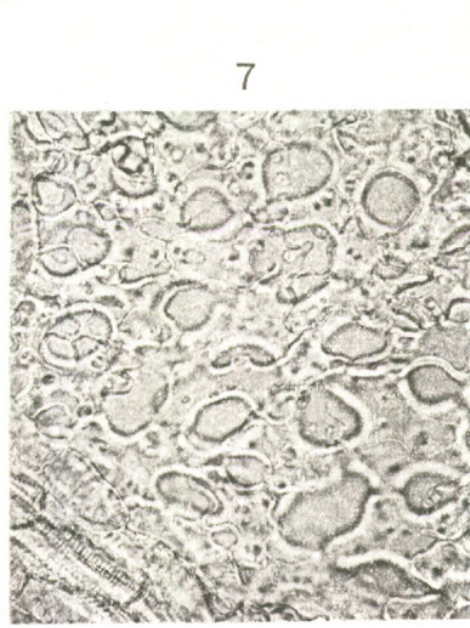
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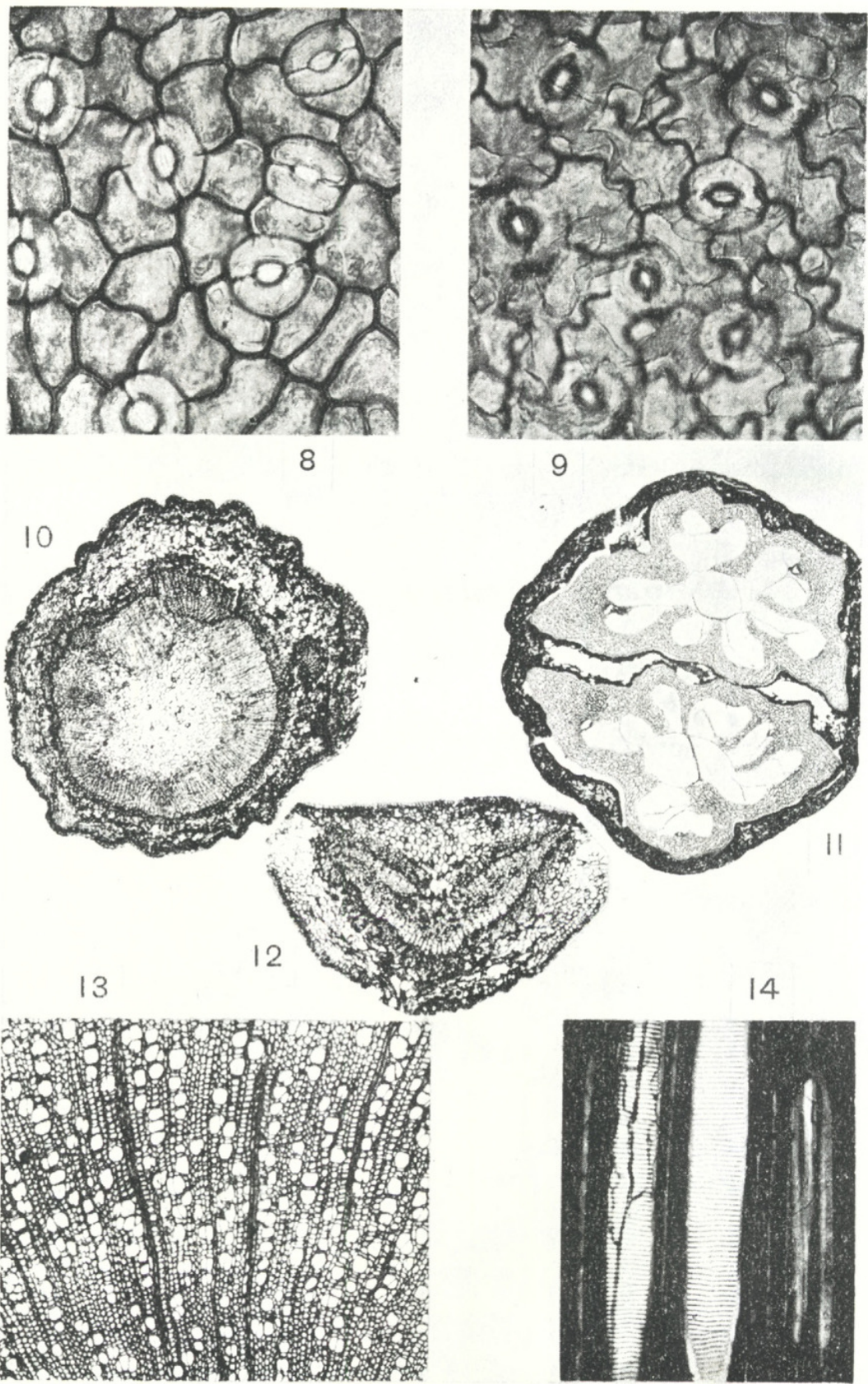
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