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COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, I.

FOLIAR VASCULATURE OF PERESKIA, PERESKIOPSIS AND QUIABENTIA

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THE TRIBE PERESKIEAE Britt. & Rose of the subfamily Pereskioideae K. Schum. has long been considered to contain the less specialized representatives of the Cactaceae, i.e., as regards possessing normal leaves and a characteristic dicotyledonous woody habit of growth. Since the publication of Berger's (1926) "Die Entwicklungslinien der Kakteen," *Pereskia sacharosa* Griseb. and *P. aculeata* Mill. have been regarded, primarily upon the basis of floral evidence, as the most primitive members of the tribe and therefore of the Cactaceae as a whole (Buxbaum, 1953).

If the normal leaf-bearing cacti are to be utilized as an initial fundamental basis in studying salient trends of phylogenetic specialization within the Cactaceae, and in obtaining evidence of valid taxonomic, physiological and ecological significance, it is essential that both the exomorphic and the endomorphic structures of all organs and parts of *Pereskia* (including *Rhodocactus*), *Pereskioopsis* and *Quiabentia* be thoroughly investigated.

The simple, entire leaves of these genera vary markedly in size and form, not only in different putative species, but also at times in the same clone when grown under different environmental influences (e.g., wild *vs.* cultivated plants), and not infrequently in different parts of a single plant. The thickness of fully matured leaves appears to be somewhat more nearly stabilized at times within species, certain of the pereskias having relatively thin laminae in contrast to the more or less exaggerated succulence of others and particularly of various species of *Pereskioopsis* and *Quiabentia*. It is of interest to determine whether there are endomorphic structures within the leaves which are of reliable taxonomic utility in the differentiation of taxa, particularly genera and tribes. In clearing and sectioning leaves for microscopic examination, I have encountered differences in patterns of venation that appear to be of some significance in this connection.

Especially in the case of foliar succulence, critical details of vasculature are more or less obscure in superficial examination of leaves both from living plants and from herbarium specimens. Adequate clearing of such leaves involves more serious difficulties than I have encountered in dealing with the foliage of other families of the dicotyledons. Simple prolonged treatments with sodium hydroxide, lactic acid, chloral hydrate and other clearing reagents are unsatisfactory, maceration and disintegration of the lamina tending to occur before clearing is adequate. Successive, brief, carefully controlled treatments in 3% sodium hydroxide at 56° C., chloral hydrate, and, where essential, with hydrochloric acid or ferric chloride for the removal of superabundant crystals of calcium oxalate have yielded sufficiently clear preparations for the study of venation in most cases. However, the cleared leaves are so fragile that they must be handled with great care. All of the illustrations in PLATES IV–VI were made from unstained leaves mounted in diaphane.

In the leaves of 33 putative species from which I have succeeded in obtaining evidence, the foliar vasculature varies from dominantly pinnate (FIG. 25) to palmate or radiate (FIG. 26).

SPECIES WITH DOMINANTLY PINNATE VENATION

The leaves of *Pereskia aculeata* Mill., *P. bahiensis* Gürke, *P. bleo* DC., *P. corrugata* Cutak, *P. cubensis* Britt. & Rose, *P. portulacifolia* Haw., *P. grandifolia* Haw., *P. moorei* Britt. & Rose, *P. sacharosa* Griseb. (including *P. amapola* Web. and *P. argentina* Web.), *P. tampicana* Web. and *P. zinnifolia* DC. have a broad, conspicuous midvein which subtends an embossed costa on the abaxial or lower surface of the leaf.¹ In these leaves of typically pinnate vasculature, the comparatively tenuous principal lateral veins extend diagonally outward from contact with the midvein toward the margins of the lamina where they interconnect by curvatures of a “camptodrome” pattern. The details of the vasculature vary somewhat in leaves of different sizes and forms, the narrower and more extensively elongated leaves having more numerous lateral veins than do the proportionally broader and shorter forms. (Compare FIGS. 1 and 2.) The characteristically small leaves of *P. cubensis* (FIG. 4) and *P. portulacifolia* (FIG. 3) have a less conspicuously embossed costa in the upper part of the lamina.

In the case of *Pereskia colombiana* Britt. & Rose, *P. diaz-romeroana* Cárđ., *P. guamacho* Web., *P. humboldtii* Britt. & Rose, and *P. weberiana* K. Schum., the 4–6 lateral veins which diverge from the midvein in the basal half of the lamina commonly tend to be conspicuous and extensive in contrast to the tenuous shorter ones in the upper part of the leaf (FIGS. 5–9). These extensive basal lateral veins frequently tend to run more nearly parallel to the contour of the margins of the lamina rather

¹ Illustration (Britton & Rose, fig. 4, 1919) of the imperfectly known *P. lychnidiflora* DC. suggests that it may likewise belong in this category of putative species.

than abruptly and diagonally toward them. (Compare FIGS. 1 and 9.) The leaves of these putative species are quite variable in size and form. In the case of *P. guamacho*, where the general range of variability in size and form is quite similar to that in *P. colombiana*, some of the leaves, at least at times, have a pseudo-palmate venation as illustrated in FIG. 6.

SPECIES WITH PSEUDO-PALMATE TO PALMATE² VENATION

In available material of *Pereskiaopsis chapistle* Britt. & Rose, *P. kellermanii* (Rose) Britt. & Rose, *P. rotundifolia* (DC.) Britt. & Rose, *P. scandens* Britt. & Rose and *P. velutina* Rose, there are 3, 5, 7 or 9 conspicuous veins. The extensively arcuate lateral veins usually extend independently of the slender midvein from the base of the leaf toward its apex (FIGS. 17–21). Each of the lateral veins subtends a more or less conspicuously embossed costa on the abaxial or lower surface of the lamina, at least during certain stages of the maturation of the leaf. The lateral veins on each side of the midvein commonly tend to be aggregated slightly above the base of the leaf. In the case of *P. chapistle*, *P. porteri* and *P. velutina*, of which I have several collections both from wild and cultivated plants, the venation remains typically palmate regardless of variations in the size and form of the leaves (FIGS. 17, 18, 20, 21).

In available material of *P. aquosa* (Web.) Britt. & Rose, *P. blakeana* Ortega, *P. gatesii* Baxter, and *P. diguetii* Britt. & Rose, the lateral veins frequently, but not invariably, tend to diverge from contact with the midvein above the base of the leaf (FIGS. 14, 22) and therefore are pseudo-palmate rather than truly palmate. The thick, extremely succulent leaves of *Quiabentia pereziensis* Backbg. (FIG. 33) and *P. zehntneri* (Britt. & Rose) Britt. & Rose (FIG. 24) have a venation that varies from palmate to pseudo-palmate.

The leaves of *Pereskia pititache* Karw., *P. konzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, and *P. nicoyana* Web. are extraordinarily variable in form on shoots of the same plant (FIGS. 10–13, 15–16). The venation varies from pseudo-palmate to palmate. It is significant that the leaves of these putative pereskias differ from those of all other investigated species of *Pereskia* (with the exception of an occasional leaf of *P. guamacho* [FIG. 6]) in having a venation which resembles that of *Pereskiaopsis* and *Quiabentia* rather than a dominantly and characteristically pinnate one.

PRELIMINARY OBSERVATIONS UPON THE MICROSCOPIC STRUCTURE OF VEINS, VEINLETS AND LEAF TRACES

Although the patterns formed by the minor veins and veinlets vary considerably, as illustrated in FIGS. 27–32, fundamentally similar ones occur in the three genera *Pereskia*, *Pereskiaopsis* and *Quiabentia*. (Com-

² As defined by Asa Gray (1880) palmately or radiately veined leaves have "three, five, seven or nine ribs which spread from the top of the leaf-stalk and run through the blade like the toes of a web-footed bird."

pare Figs. 25, 26.) In these genera the veins, veinlets and the ends of the veinlets are composed of tracheary cells with helical and annular thickenings. The phloem fibers which cap the leaf traces in the stem do not extend outward into the lamina of the leaf (except in rare instances), but are replaced by elongated parenchymatous elements of a pseudo-collenchymatous nature. Nor are there sclereids, either free in the mesophyll or jacketing the veins or veinlets, such as occur at times in xerophytic species of other dicotyledonous families.

Where the veinlets are comparatively slender, as commonly in the large thin leaves of various pinnately veined pereskias (Fig. 27), they may be composed largely of a single linear series of tracheary cells which become shorter in the terminal parts of the veinlets (Fig. 33). Where the terminal parts are coarser (Figs. 28, 29) as commonly occurs in more succulent leaves, the tracheary cells tend to be more numerous and more nearly isodiametric (Fig. 34). In the case of the coarsest patterns of vasculature (Figs. 30, 31) the veinlets, as well as their terminal parts may be composed of, or jacketed by, short tracheary cells (Fig. 36).

Although patterns of veinlet vasculature may ultimately prove to be of some taxonomic significance in the differentiation of taxa (e.g., in the case of species of *Quiabentia*; compare Figs. 31, 32) much more extensive collections of the leaves of different species must be secured and studied than are available at present. This is due to there being considerable variation in the details of vasculature in different leaves of the same clone and at times in those of the same plant. Furthermore, it should be emphasized in this connection that it is essential to compare the vasculature of fully matured leaves, for more or less extensive changes in details of venation occur during the enlargement and expansion of the lamina of immature leaves.

The curious short, wide cells with broad, annular thickenings which have attracted so much attention in literature dealing with highly specialized representatives of the Cactaceae (e.g., Schleiden, 1845; van Tieghem, 1885; Darbishire, 1904) do not occur in any of the pereskias of which I have adequate material. On the contrary, they appear sporadically in the leaves and stems of various putative species of *Pereskiopsis*. Such cells and their possible precursors are of common and abundant occurrence in the basal parts of the leaves of *Quiabentia pereziensis* Backbg. and *Q. zehntneri* (Britt. & Rose) Britt. & Rose. In the leaves of these plants, the veins are composed of broader tracheary cells with coarser thickenings than are those of *Pereskia* and *Pereskiopsis*. (Compare Figs. 35 and 37.) The cells on the margins of the veins have very broad helical and annular thickenings which project deeply into the lumina of the cells. There are transitions between elongated forms of such tracheary cells and very short ones with a few annular thickenings. Such transitional forms suggest that the short, broad elements which occur in other cacti may have evolved by modification of ordinary tracheary cells with helical or annular thickenings.

The midvein of pereskias which have pinnate venation is not a simple structure, but is composed of discrete vascular strands aggregated in an arc, i.e., as seen in transverse sections of the lamina (FIGS. 45-47). The vascular arc varies considerably in form and size in leaves of different dimensions. In the base of some leaves close to their level of attachment to the stem, the arc is so extensive that it forms a nearly or completely closed cylinder (FIG. 48). The number of constituent vascular strands likewise varies, not only in leaves of different sizes, but also at different levels of the same lamina, i.e., tending to increase in number from the apex of the leaf toward its base (FIGS. 44-48). It is evident from cleared leaves and from serial transverse sections at successive levels of the lamina that such a midvein is constituted of *two* aggregations, the individual vascular strands of which extend diagonally outward into the longitudinal halves of the lamina.

The individual strands of the vascular aggregate in the midvein may fuse or divide in various parts of their longitudinal extension (FIGS. 44, 47). When such changes occur the behavior of the xylem and phloem frequently is not closely synchronized. During fission, the separation of strands of phloem usually precedes division of the xylem. Conversely during fusion concrescence of the xylem is precocious. The collenchymatous parenchyma commonly caps the strands of phloem (FIGS. 45-47) but may at times form a continuous layer over the entire abaxial surface of the arc of vascular strands.

The number of discrete strands at any particular level of the leaf may be an *even* or an *odd* one. It is significant in this connection, however, that in a majority of cases there is no conspicuous larger strand which occupies a median position in the arc of discrete bundles. Instead of this there commonly are two aggregates of strands on either side of a more or less conspicuous median parenchymatous gap (FIGS. 45-47). In the case of *Pereskia*, the slender midvein of palmately veined leaves not infrequently is composed of two discrete strands at least in parts of its extension (FIG. 43). Similarly the terminal part of the midvein in the apex of pinnately veined leaves may be composed at times of two more or less closely approximated strands (FIG. 44).

This evidence suggests from a phylogenetic point of view that, as in the case of Austrobaileyaceae, Trimeniaceae, Monimiaceae, Chloranthaceae and certain other families, the longitudinal halves of the lamina of *Pereskia*, *Pereskiaopsis* and *Quiabentia* are vascularized by branches of two independent systems of leaf traces rather than by dichotomies of a single trace (Bailey, 1956). According to this view, the simple midvein which occurs at times in *Pereskiaopsis* and *Quiabentia*, and the presence in some cases of a medianly placed strand in the arc of bundles of pinnately veined pereskias, is due phylogenetically to the fusion of branches of two independent systems or to asymmetries and the displacement of a single branch into a median position.

If such an interpretation is valid, additional evidence should be ob-

tainable from nodal and subnodal parts of the stem. The node of the leaf-bearing cacti is a consistently unilacunar one. In stems of *Pereskia aculeata*, and at least in parts of those of such species as *P. autumnalis*, *P. diaz-romeroana*, *P. guamacho* and *P. nicoyana* there commonly are two discrete leaf-traces at the nodal level (FIGS. 38, 39). These traces can be followed downward in serial transverse sections, or in adequately cleared stems, for considerable distances below the node. In the case of *Pereskia sacharosa*, *P. grandifolia*, *P. bleo* and in certain stems of *Pereskiaopsis*, there may be four (FIG. 40), six (FIG. 41), or more traces (FIG. 42) at the nodal level, such differences being correlated at least to a certain extent with variations in the size of the leaves, with variations in the diameter of stems to which the leaves are attached, or with combinations of such factors. The alternating phyllotaxy is so complex ($\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$) that it is difficult to follow these vascular strands downward in the same orthostiche. However, in favorable cleared stems of *Pereskiaopsis* it is possible to determine that the vascular strands frequently connect with two traces which may fuse for a varying distance and then diverge to *two* above the subtending leaf of the same orthostiche, where they connect with the traces of two separate adjacent orthostiches.

The totality of available evidence indicates that the vasculature of the leaf-bearing cacti presents varying phylogenetic modifications of a fundamentally two-trace unilacunar structure (Bailey, 1956). It is evident that apparent fission of vascular strands may occur at various levels of the stem, node and leaf. Furthermore, various asymmetries and aberrant fusion or division of vascular strands can lead at any given level to the appearance of an *odd* rather than an *even* number of vascular bundles.

More extensive investigation of nodal anatomy and of the form of the midvein in pinnately veined pereskias might eventually yield some evidence of taxonomic utility. But, as in the case of patterns formed by minor veins and veinlets, the range of structural variation in a single species, clone or plant is frequently so obvious that extensive collections must be studied before valid conclusions can be attained.

DISCUSSION

In the discussion of plant taxa and their relationships, evidence from similarities should be harmonized with that obtained from dissimilarities. In the case of the leaf-bearing cacti the similarities are so numerous in various organs and parts that it raises some question regarding the wisdom of placing putative genera in separate subfamilies or tribes. As regards leaves, the ranges of variability in a single clone (and not infrequently in a single plant) are so extensive that they necessitate a re-examination of putative species based in the past upon assumed differences in the size or external form of the foliar appendages. As I have shown, there are transitions in the leaf-bearing cacti between dominantly pinnate and typically palmate venation. Although the foliage of *Pereskiaopsis* and *Quiabentia* appears to be dominantly pseudo-palmate or palmate, it does

not differ consistently from that of *Pereskia* (including *Rhodocactus*), since similar venation occurs in *Pereskia autumnalis*, *P. conzattii*, *P. nicoyana* and *P. pititache*. Such species as *P. colombiana*, *P. diaz-romeroana*, *P. guamacho*, *P. humboldtii* and *P. weberiana* have a venation which appears to be transitional between that of the preceding species and those which have a dominantly pinnate venation. Pseudo-palmate and palmate venation is correlated with increasing succulence of the leaves. This suggests, but, by itself without corroborative evidence, does not conclusively prove, that the evolutionary transition is from pinnate to palmate.

It is evident thus far in my preliminary anatomical investigations that there are at least four categories of putative species of leaf-bearing cacti which differ more or less markedly in their foliar vasculature. It will be of interest in subsequent anatomical investigations to determine whether there are other anatomical differences in these categories of species which correlate with those of the foliar vasculature. In so doing, it will be desirable, if possible, to determine whether the similarities within each category are due solely to close genetic relationship or in part to parallel evolutionary changes.

The objection may be raised that it is difficult and uncertain to determine the identity of plants from which material is collected in gardens and in the wild. This is particularly the case at present in dealing with species. However, the possibility of misidentifications does not modify the conclusion that there are four categories of leaf-bearing cacti with differing foliar vasculature.

The two-trace unilacunar vasculature and its various modifications in leaf-bearing cacti is significant in any general discussion of the possible relationships of the Cactaceae to other families of the dicotyledons and particularly to those of the Centrospermae.

ACKNOWLEDGMENTS

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EXPLANATION OF PLATES

The source of the material figured for each species is given in brackets following the name. A complete listing of materials with all available documentary data will be given at the end of this series of papers.

PLATE I

FIGS. 1-9. LEAVES OF PERESKIA. All leaves drawn natural size. 1, *P. sacharosa* Griseb. [Mo. Bot. Gard.]; 2, *P. aculeata* Mill. [Moran 7272]; 3, *P. portulacifolia* (L.) Haw. [Jiménez 2578]; 4, *P. cubensis* Britt. & Rose [Atkins Gard.]; 5, *P. weberiana* Schum. [Cárdenas]; 6, *P. guamacho* Web. [Steyermark]; 7, *P. colombiana* Britt. & Rose [Record 16495]; 8, *P. diaz-romeroana* Cárdenas [Cárdenas]; 9, *P. guamacho* Web. [Steyermark].

PLATE II

FIGS. 10-16. LEAVES OF PERESKIA AND PERESKIOPSIS. All leaves drawn natural size. 10, *Pereskia konzattii* Britt. & Rose [Kimnach 172]; 11, *P. pititache* Karw. [Atkins Gard.]; 12, *P. autumnalis* (Eichlam) Rose [Moore]; 13, *P. nicoyana* Web. [Rodríguez 662]; 14, *Pereskiopsis blakeana* Ort. [Kimnach 81]; 15, *Pereskia pititache* Karw. [Atkins Gard.]; 16, *P. autumnalis* (Eichlam) Rose [Moore].

PLATE III

FIGS. 17-24. LEAVES OF PERESKIOPSIS AND QUIABENTIA. All leaves drawn natural size. 17, 18, *Pereskiopsis porteri* (T. S. Brandeg.) Britt. & Rose [17, N. Y. Bot. Gard.; 18, Moran 7349]; 19, *P. scandens* Britt. & Rose [N. Y. Bot. Gard.]; 20, 21, *P. chapistle* (Web.) Britt. & Rose [20, Hernandez; 21, N. Y. Bot. Gard.]; 22, *P. aquosa* (Web.) Britt. & Rose [N. Y. Bot. Gard.]; 23, *Quiabentia pereziensis* Backbg. [Cárdenas]; 24, *Q. zehntneri* (Britt. & Rose) Britt. & Rose [Boke].

PLATE IV

FIGS. 25, 26. CLEARED LEAVES OF PERESKIA AND PERESKIOPSIS. 25, *Pereskia cubensis* Britt. & Rose [Atkins Gard.], $\times 5.5$. 26, *Pereskiopsis velutina* Rose [Mo. Bot. Gard.], $\times 5.5$; two dark-colored tips of glochids are embedded in the cleared lamina.

PLATE V

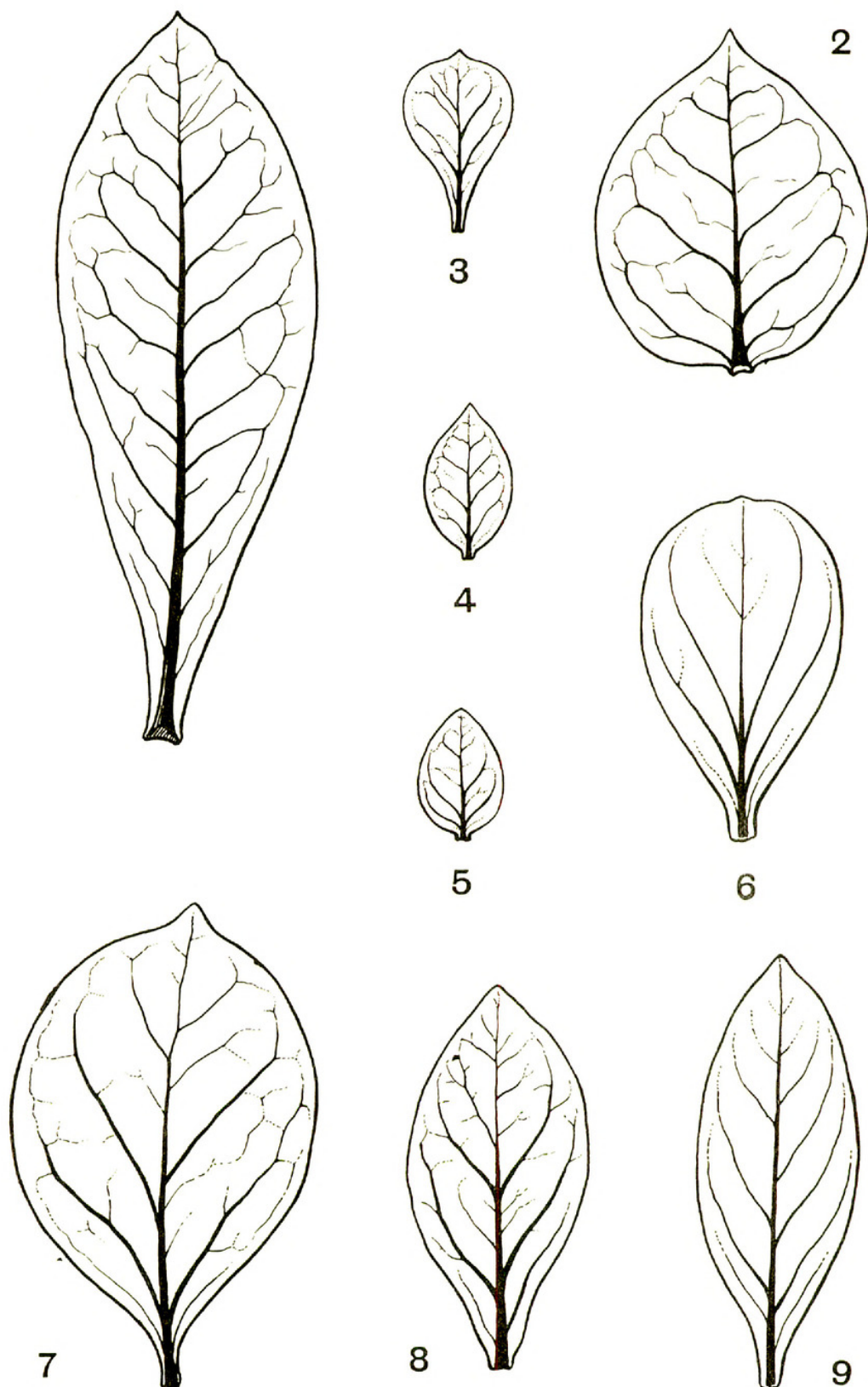
FIGS. 27-32. PORTIONS OF CLEARED LEAVES OF PERESKIA AND QUIABENTIA. All figures $\times 27$. 27, *P. aculeata* Mill. [Moran 7272]; 28, *P. weberiana* Schum. [Cárdenas]; 29, *P. nicoyana* Web. [Rodríguez 662]; 30, *P. pititache* Karw. [Atkins Gard.]; 31, *Q. pereziensis* Backbg. [Cárdenas]; 32, *Q. zehntneri* (Britt. & Rose) Britt. & Rose [Boke].

PLATE VI

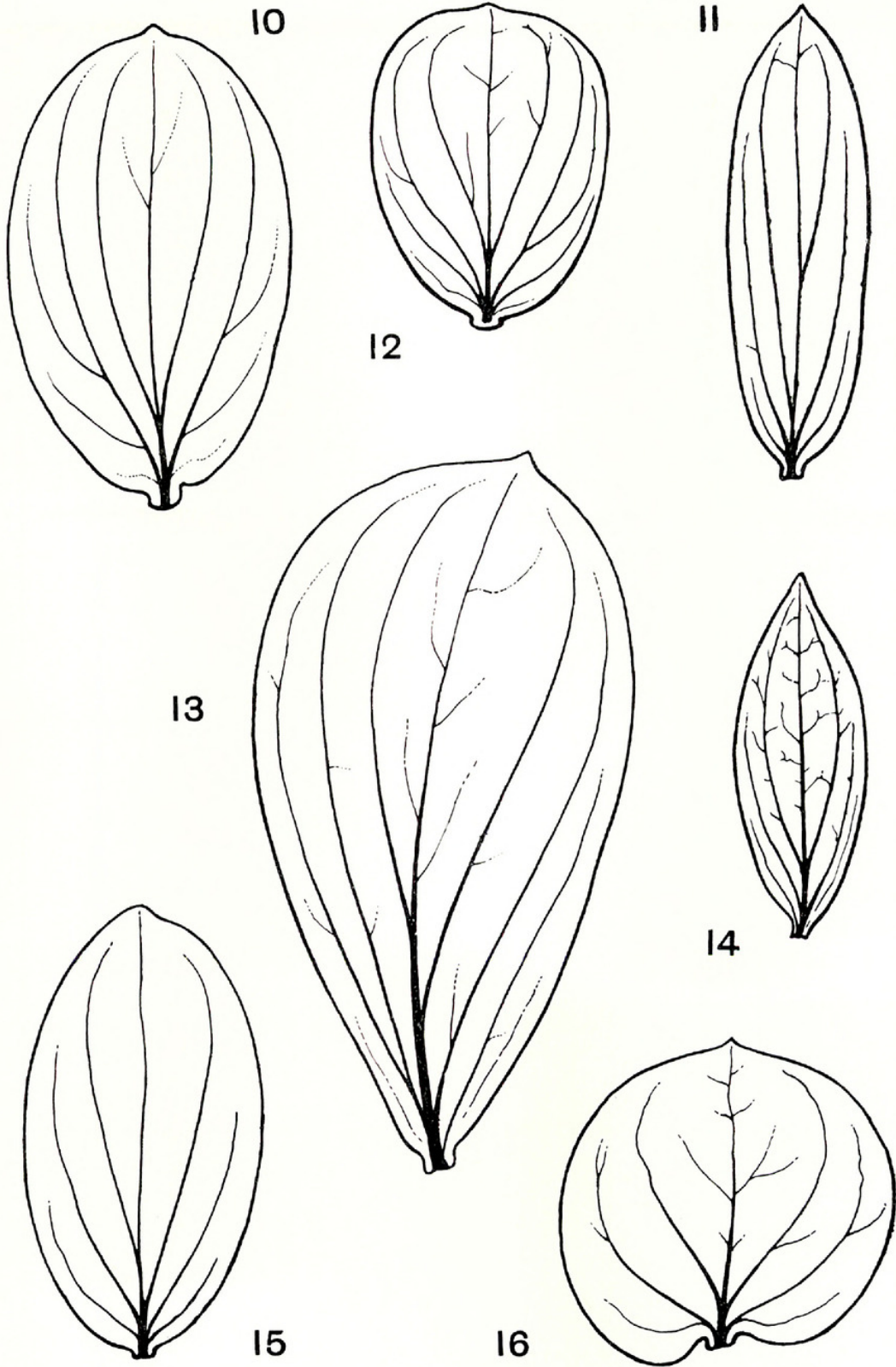
FIGS. 33-37. VASCULAR DETAILS OF VEINS AND VEINLETS IN LEAVES OF PERESKIA AND QUIABENTIA. All figures $\times 260$. 33, *Pereskia aculeata* Mill. [Moran 7272]; 34, *P. weberiana* Schum. [Cárdenas]; 35, *P. aculeata* Mill. [Moran 7272]; 36, *Quiabentia pereziensis* Backbg. [Cárdenas]; 37, *Q. zehntneri* (Britt. & Rose) Britt. & Rose [Boke].

PLATE VII

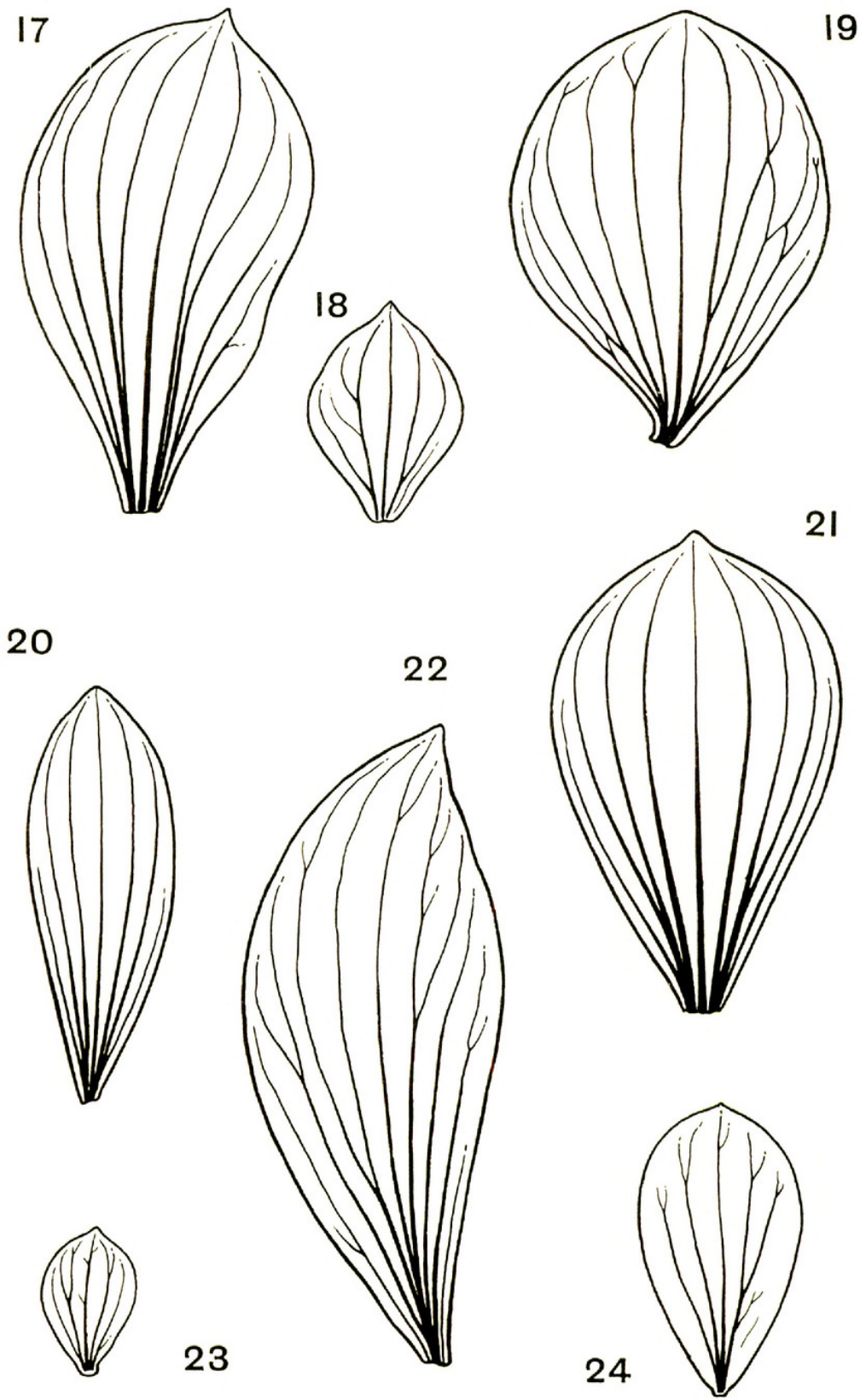
FIGS. 38-48. TRANSVERSE SECTIONS OF NODES AND OF MIDVEINS OF PERESKIA AND PERESKIOPSIS. All figures $\times 25$, except FIG. 44, $\times 72$. 38, *Pereskia aculeata* Mill. [Moran 7272], t.s. at 2-trace unilacunar node; 39, *Pereskia diaz-romeroana* Cárdenas [Cárdenas], t.s. at 2-trace unilacunar node; 40, *Pereskiopsis porteri* (T. S. Brandeg.) Britt. & Rose [N. Y. Bot. Gard.], t.s. at 4-trace unilacunar node; 41, *Pereskia sacharosa* Griseb. [Mo. Bot. Gard.], t.s. at 6-trace unilacunar node; 42, *Pereskia bleo* DC. [Rodríguez], t.s. at 10-trace unilacunar node; 43, *Pereskiopsis porteri* [N. Y. Bot. Gard.], t.s. of 2-strand midvein of leaf; 44, *Pereskia aculeata* [Moran 7272], t.s. of 2-strand midvein in apical part of leaf; 45, *Pereskia sacharosa* [Mo. Bot. Gard.], t.s. of 4-strand midvein some distance below apex of leaf; 46, *the same*, t.s. of 6-strand midvein in central part of leaf; 47, *the same*, t.s. of midvein in basal part of the lamina; 48, *Pereskia grandifolia* Haw. [Moran 7270], t.s. at base of petiole.



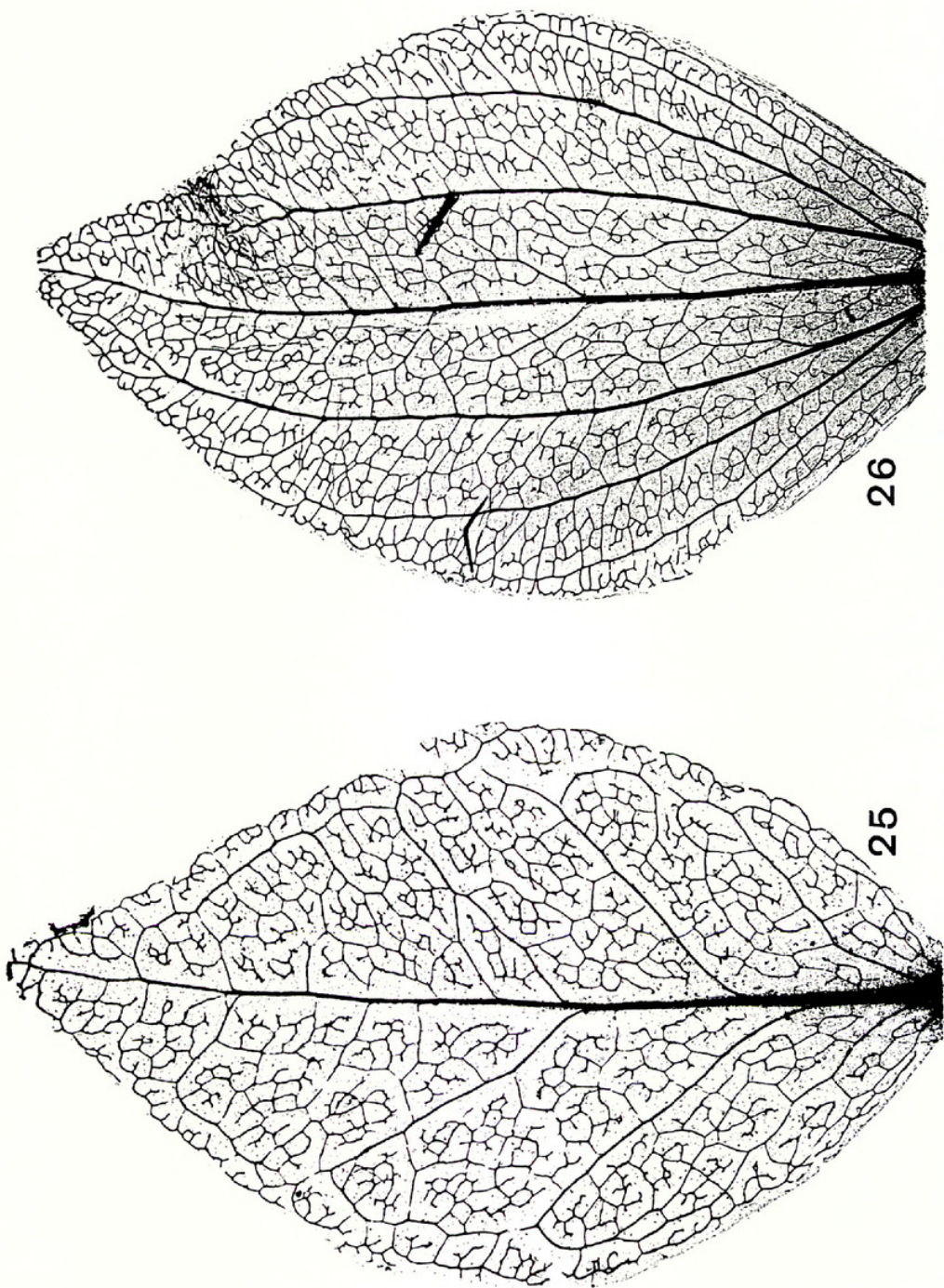
BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I



BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I



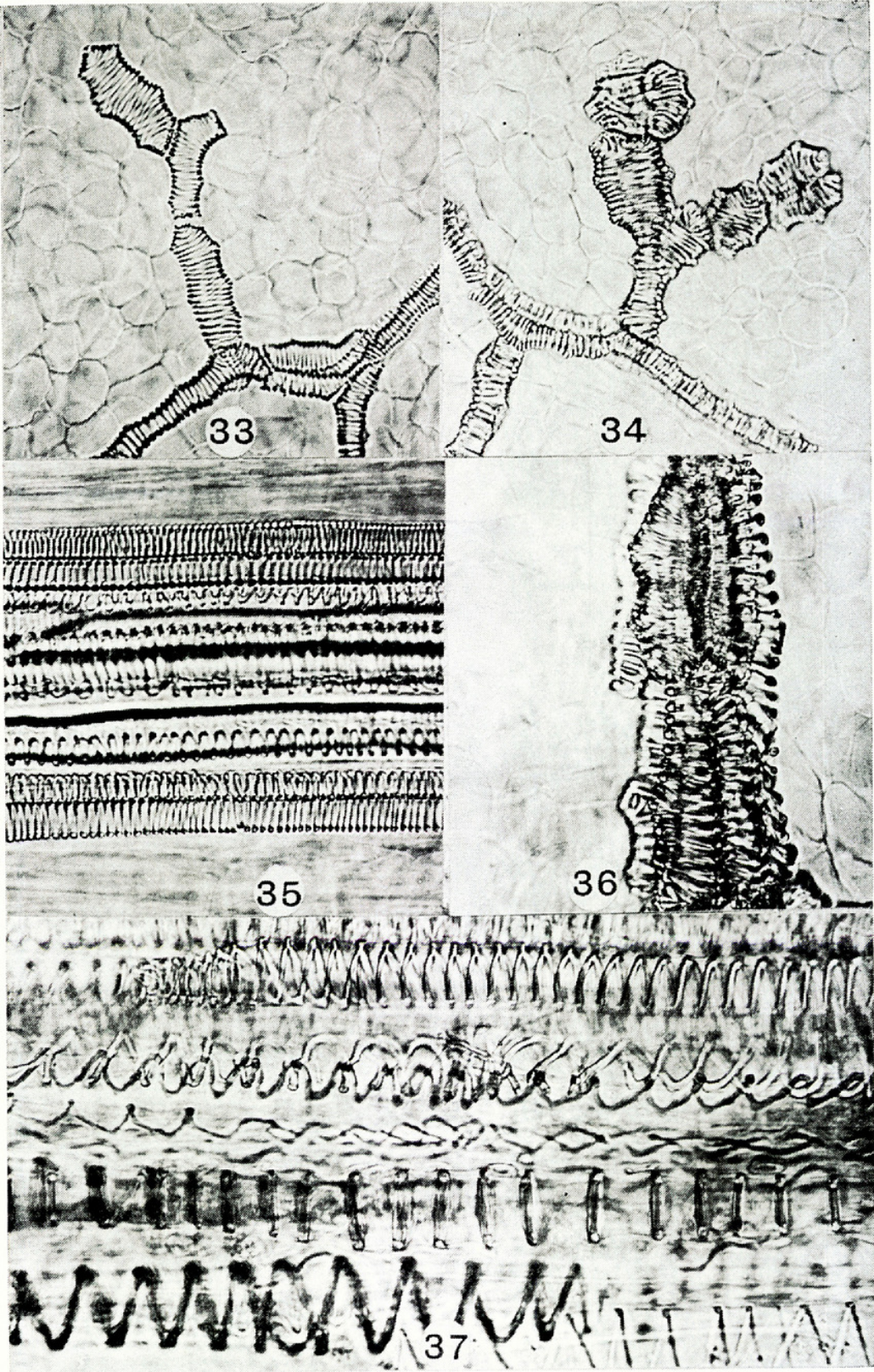
BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I



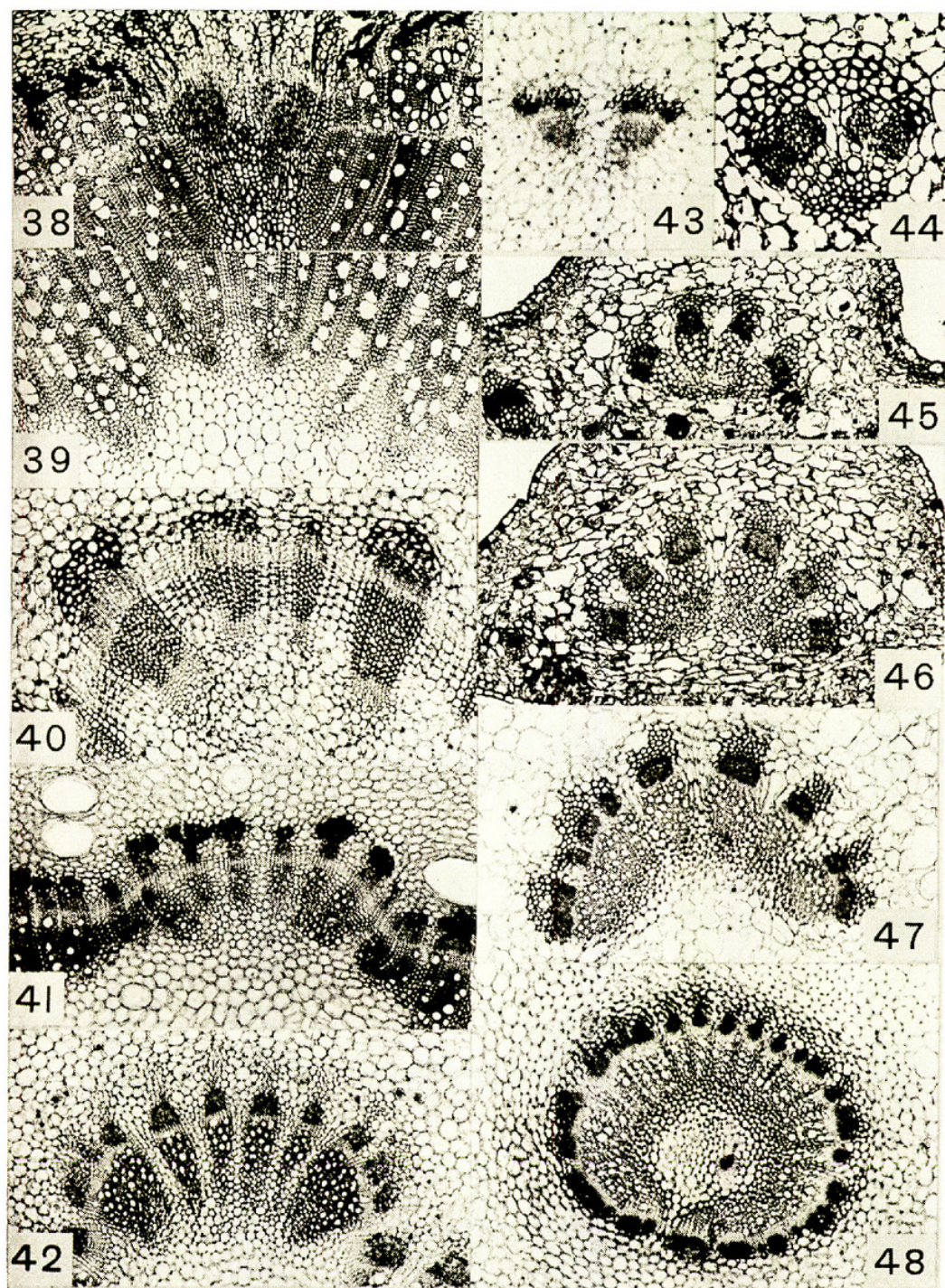
BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I



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BAILEY, ANATOMY OF LEAF-BEARING CACTACEAE, I



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