

## SYSTEMATIC ANATOMY AND ONTOGENY OF THE STEM IN PASSIFLORACEAE

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Although the taxonomy of the passionflower family, Passifloraceae, has been studied extensively, especially that of the genus *Passiflora* (Killip 1938), the anatomy and ontogeny of the woody stem have been little explored. This was clearly pointed out by the studies of Stern and Brizicky (1958), who recorded for the first time in the family the presence of anomalous stem growth and storied structure in the xylem of *Passiflora multiflora* L. Interestingly, the occurrence of these two phenomena seemed to accord with Killip's suggestion that *P. multiflora*, the single member of his subgenus *Apodogyne*, ought to be segregated as a separate genus on the basis of its sessile ovary. Obaton (1960) encountered anomalous stems in *Adenia cissampeloides* Harms (included phloem; i.e., phloem strands surrounded by xylem), and *Crossostemma laurifolium* Planch. (intruded phloem; i.e., ribs or flanges of phloem extending into the xylem cylinder from the bark side of the stem) of the Passifloraceae. Her observations indicate that certain other species of *Adenia* (e.g., *Adenia lobata* Engl.) have normal stem structure, even in the thickest portions. She felt compelled, therefore, to segregate as a distinct species a specimen of *Adenia lobata*, obtained from Bingerville, Ivory Coast, which showed abnormal stem structure. Furthermore, she asserts that *Adenia kontiensis* A. Chev., which has long been confused with *Adenia lobata*, is distinguished from it by the less numerous, thicker, and more rounded tubercles on the stem. Because Obaton's study of stem structure in Passifloraceae lacks detailed anatomical descriptions and specimens are not documented by herbarium voucher citation, it is of little use taxonomically.

Except for the works of Stern and Brizicky, and Obaton, there is no record in the anatomical literature that anomalous stem growth occurs in the Passifloraceae. Schenck (1893) states that growth in the stem of Passifloraceae is normal; Solereder (1908) emphasizes that even the climbing forms of Passifloraceae have normal structure. Solereder, furthermore, repudiates Schwendener's (1874) assertion that *Passiflora*

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*trifasciata* has 6 medullary vascular bundles which are provided on the inside and the outside with small bast-coverings (bicollateral) for the protection of the conducting cells. Dr. L. Chalk of Oxford University, in an informal communication, suggested that Schwendener's remarks at least imply that he suspected the occurrence of anomalous structure in this particular species of *Passiflora*. Neither Metcalfe and Chalk (1950) nor Boureau (1957) make mention of this feature in Passifloraceae.

In the taxonomic studies of Passifloraceae by Harms (1925), Masters (1871), and Killip (1938), no mention of atypical stem development in this family has been noted. Ordinarily, development of the anomalous configuration commences in the thicker portions of the stem, not regularly collected for herbarium specimens. Because of this condition, taxonomists have perhaps overlooked these strange stems.

Owing to certain similarities in the anatomy and morphology of Passifloraceae and Flacourtiaceae, taxonomists have found it difficult to decide to which the genus *Paropsia* should be assigned. Bentham and Hooker (1867) included under Passifloreae, the genera *Passiflora*, *Tacsonia*, *Deidamia*, *Basanthe*, *Tryphostemma*, *Paropsia*, *Smeathmannia*, *Barteria*, and *Crossostemma*. Harms (1893) later transferred *Paropsia* to Flacourtiaceae, and Gilg (1925) included the genera *Paropsia*, *Soyauxia*, *Hounea*, *Smeathmannia*, *Paropsiopsis*, and *Barteria* under the tribe *Paropsieae* of this same family. Fernandes and Fernandes (1958a, 1958b) disagree with Harms and Gilg and assert that *Paropsia* should be placed in Passifloraceae. Brizicky (1961) pointed out that the present delimitations of the family seem to be fairly natural. However, he remarked that a taxonomic re-evaluation of Passifloraceae and their closest allies, such as Flacourtiaceae—*Paropsieae*, based on comparative anatomy and other botanical disciplines, is needed.

In a preliminary report on the woods of Flacourtiaceae, Tupper (1934) indicated that axial parenchyma is generally lacking. However, he encountered abundant axial wood parenchyma in the genus *Paropsia* in support of den Berger's (1928) observation that this genus has abundant, diffuse wood parenchyma. Metcalfe and Chalk (1950) mention that although there are certain anatomical differences between *Paropsia* and the genera of Passifloraceae, there are also anatomical similarities, and, for example, the occurrence of fibriform vessel members in some species may support its affinity with Passifloraceae.

Palynological studies by Erdtman (1952) have shown that pollen grains of *Paropsia* are more similar to those of Passifloraceae than to those of Flacourtiaceae. The pollen grains of *Paropsia brazzeana*, for instance, are usually 6-colporate and subprolate; the sexine is as thick



as the nexine, and reticulate. Erdtman suggests that the tribe *Paropsieae* (Flacourtiaceae) should, at least in part, be referred to Passifloraceae.

In general, our investigations uphold the anatomical findings of Tupper and den Berger, and support Bentham and Hooker (1867), and Fernandes and Fernandes (1958a, 1958b) in their assertions that the genus *Paropsia* belongs with Passifloraceae.

Passifloraceae consists of 12 genera with over 500 species distributed throughout the tropics. Eight of the genera are confined to the Old World, three are exclusively American and one, *Passiflora*, is predominantly New World. Most of the Old World genera have few species; more than two-thirds of all species in the family belong to *Passiflora*.

Members of the Passifloraceae (figs. 1, 2) are herbaceous or woody, tendril bearing lianas, or erect shrubs and trees. Leaves are alternate, simple or compound, and have entire, toothed, or deeply cleft margins, with predominantly 3–5 nerved blades. Petioles are often glanduliferous; stipules are setaceous or broadly ovate, but sometimes foliaceous.

Flowers may be brilliantly colored or greenish, many centimeters in diameter or less than one. They may be axillary or in cymes, but are usually reduced to solitary or paired peduncles. Bracts are ordinarily present. Five (4), rarely 3, basally connate sepals are present. The petals 5(4), or wanting, are distinct or briefly basally connate, often smaller than the sepals. Sepals and petals are imbricate. The floral tube is usually associated with a corona. The androecium consists of 5 stamens, rarely 10, usually opposite the petals; anthers are versatile, 2-locular at anthesis, and dehisce longitudinally. The gynoecium consists of 3–5 carpels; stigmatic branches are capitate, clavate, or discoid; the styles number as many as the carpels; the ovary is stipitate, rarely sessile, 1-locular with numerous anatropous ovules on 3–5 parietal placentae. The fruit is a berry or a loculicidal capsule; the seed has a straight embryo and fleshy endosperm. Both Killip (1938) and Masters (1871) have excellent descriptions of these highly modified flowers, accompanied by drawings and explanations.

#### Materials and Methods

Table 1 lists the 60 stem and wood specimens (44 species of 9 genera) examined. The citation of specimens follows the recommendations of Stern and Chambers (1960), and herbarium vouchers are listed as well as the names and numbers of the collectors. Names of species are in accordance with those stated in Killip (1938) for American Passifloraceae.



Microtechnical procedures followed were modified from those outlined by Wetmore (1932) and are standard for the preparation of sections of stem and wood. Microscope slides of wood specimens prepared for this investigation have been deposited in the Division of Plant Anatomy of the Smithsonian Institution (USw).

Diagnostic characters for descriptions of passifloraceous woods were selected from Tippo's (1941) list. For the most part, terms used in the anatomical descriptions comply with those approved by the Committee on Nomenclature of the International Association of Wood Anatomists (1957). In a few instances, however, certain liberties were taken with the definitions.

Lack of sufficient wood material in a number of cases made the preparation of macerations impracticable, hence, length measurements of fibers and vessel elements were taken from sections. Therefore, our method of making measurements cannot conform exactly to the recommendations of Chalk and Chattaway (1934, 1935) that total lengths of cells be used. Tangential vessel diameters and lengths of fibers and vessel elements were recorded from 30 cells in each specimen.

Because of the conflicting and ambiguous results brought on by employing only names to categorize vascular rays (Kribs 1935), it was thought best to employ the suggestions of the Committee on Nomenclature (1957). These direct the anatomist to describe rays using brief sentences or phrases to point out the width, height, frequency of occurrence, and cellular composition. Classification of axial wood parenchyma used here is in most part that presented by Metcalfe and Chalk (1950). The various types of parenchyma distribution fall into two main categories: apotracheal, in which parenchyma strands show no regular relation to vessels; and paratracheal, in which parenchyma strands show a close and regular association with vessels.

Four descriptive terms have been chosen to characterize the appearance on the transverse surface of the mature vascular cylinder of stems in Passifloraceae: (1) **NORMAL TYPE**—a stem in which xylem and phloem cylinders are roughly circular and concentric with little or no distortion of pith and cortex; (2) **INCLUDED PHLOEM TYPE**—similar to (1), but with patches of phloem embedded in the xylem cylinder; (3) **INTERRUPTED TYPE**—wedge-shaped sections of xylem, alternating around the stem with similarly shaped sections of phloem, characterized by marginal series of steps; (4) **DISPERSED TYPE**—irregularly shaped, disoriented strands of xylem and phloem associated with fragments of vascular cambium spread throughout a parenchymatous matrix.



TABLE 1.—*Specimens of Passifloraceae stems examined*

Citation of specimens follows the recommendations of Stern and Chambers (1960). WOOD COLLECTIONS: (Yw) The Samuel James Record Memorial Collection, Yale University, New Haven; (USw) Division of Plant Anatomy, Smithsonian Institution, Washington; (Aw) The Arnold Arboretum, Cambridge; (Uw) Botanical Museum and Herbarium, Utrecht. HERBARIA: (TEF) Inspection Générale des Eaux et Forêts, Tananarive; (FHO) The Imperial Forestry Institute, Oxford; (Y) Yale School of Forestry, New Haven; (A) The Arnold Arboretum, Cambridge; (US) U.S. National Herbarium, Smithsonian Institution, Washington; (NY) New York Botanical Garden, New York; (U) Botanical Museum and Herbarium, Utrecht; (K) Royal Botanic Gardens, Kew.]

<i>Species</i>	<i>Collector and Number</i>	<i>Geographical Origin</i>	<i>Herbarium Voucher</i>	<i>Location and Catalog Number</i>
<i>Adenia lobata</i> (Jacq.) Engl.	E. S. Ayensu <i>s.n.</i>	Ghana	US	
<i>Androsiphonia adenostegia</i> Stapf	G. P. Cooper 276	Liberia	Y	Yw 15191
<i>Barteria nigritiana</i> Hook. f.	E. S. Ayensu <i>s.n.</i>	Ghana	US	
<i>Crossostemma laurifolium</i> Planch.	C. Vigne 3503	Ghana	FHO	Yw 29724
<i>Dilkea johannesii</i> Rodr.	A. Ducke 329	Brazil	Y	Yw 34093
<i>Mitostemma glaziovii</i> Mast.	A. C. Smith 3117	British Guiana	Y	Yw 35812
<i>Paropsia adenostegia</i> (Stapf) Engl.	G. P. Cooper 211	Liberia	Y	Yw 15140
<i>Paropsia madagascariensis</i> (Baill.) H. Perrier	—	Madagascar	TEF	USw 27402
<i>Paropsia schliebenii</i> Sleumer	H. J. Schlieben 429 (5442)	Tanganyika	Y	Yw 30003
<i>Paropsia vareciformis</i> Mast.	H. E. Desch 2003 (32695)	Malaya	—	Yw 29187
<i>Passiflora arborea</i> Spreng.	J. Cuatrecasas 22014	Colombia	Y	Yw 44493
<i>Passiflora auriculata</i> H.B.K.	R. H. Woodworth & P. A. Vestal 362	Panama Canal Zone	A	Aw 362
<i>Passiflora auriculata</i> H.B.K.	W. L. Stern 1585A	Trinidad	US	USw 30687
<i>Passiflora coccinea</i> Aubl.	B. Maguire 24179	Suriname	NY	Yw 44096
<i>Passiflora caerulea</i> L.	—	—	—	Aw 5323
<i>Passiflora coriacea</i> A. Rich.	R. H. Woodworth & P.A. Vestal 501	Panama Canal Zone	A	Aw 501
<i>Passiflora edulis</i> Sims	—	Cuba (cult. Soledad)	—	Aw 5283
<i>Passiflora edulis</i> Sims	E. S. Ayensu <i>s.n.</i>	Ghana	US	
<i>Passiflora edulis</i> Sims	W. L. Stern & S. Carlquist 1287	Kauai, Hawaii	US	USw 25985



TABLE 1.—*Specimens of Passifloraceae stems examined*—Continued

<i>Species</i>	<i>Collector and Number</i>	<i>Geographical Origin</i>	<i>Herbarium Voucher</i>	<i>Location and Catalog Number</i>
<i>Passiflora elliptica</i> Gardn.	H. S. Irwin 2222	Brazil	Y	Yw 53094
<i>Passiflora fuchsiiflora</i> Hemsl.	F. P. Jonker & Daniels 817	Suriname	U	USw 30677
<i>Passiflora fuchsiiflora</i> Hemsl.	F. P. Jonker & Daniels 1098	Suriname	U	USw 30678
<i>Passiflora fuchsiiflora</i> Hemsl.	J. Lanjouw & J. C. Lindeman 2639	Suriname	U	Uw 1859, USw 30686
<i>Passiflora fuchsiiflora</i> Hemsl.	B. Maguire & D. B. Fanshawe 22807	British Guiana	NY	Yw 43907
<i>Passiflora gigantifolia</i> Harms (?)	A. Rimbach 50	Ecuador	Y	Yw 20743
<i>Passiflora glandulosa</i> Cav.	A. C. Smith 2822	British Guiana	Y	Yw 35711
<i>Passiflora glandulosa</i> Cav.	BAFOG 4033	French Guiana	U	USw 30679
<i>Passiflora glandulosa</i> Cav.	F. P. Jonker & Daniels 788	Suriname	U	USw 30680
<i>Passiflora glandulosa</i> Cav.	F. P. Jonker & Daniels 830	Suriname	U	USw 30681
<i>Passiflora glandulosa</i> Cav.	J. Lanjouw & C. J. Lindeman 1820	Suriname	U	Uw 1559, USw 30685
<i>Passiflora glandulosa</i> Cav.	J. Lanjouw & J. C. Lindeman 2765	Suriname	U	USw 30682
<i>Passiflora glandulosa</i> Cav.	J. C. Lindman 4530	Suriname	U	Uw 3142
<i>Passiflora glandulosa</i> Cav.	A. A. Pulle 353	Suriname	U	USw 30683
<i>Passiflora laurifolia</i> L.	—	Cuba	A	Aw 25273
<i>Passiflora maguirei</i> Killip	B. Maguire & D. B. Fanshawe 23285	British Guiana	US	Yw 44006
<i>Passiflora maliformis</i> Vell.	—	Cuba (cult. Soledad)	—	Aw 5284
<i>Passiflora menispermifolia</i> H. B. K.	R. H. Woodworth & P. A. Vestal 637	Panama Canal Zone	A	Aw 637



TABLE 1.—*Specimens of Passifloraceae stems examined*—Continued

<i>Species</i>	<i>Collector and Number</i>	<i>Geographical Origin</i>	<i>Herbarium Voucher</i>	<i>Location and Catalog Number</i>
<i>Passiflora misera</i> H.B.K.	R. H. Woodworth & P. A. Vestal 456	Panama Canal Zone	A	Aw 456
<i>Passiflora mollissima</i> (H.B.K.) Bailey = <i>Tacsonia mollissima</i> H.B.K.	A. Rimbach 19	Ecuador	Y	Yw 19485
<i>Passiflora multiflora</i> L.	W. L. Stern & G. K. Brizicky 522	Plantation Key, Florida	Y	Yw 51303
<i>Passiflora nitida</i> H.B.K.	J. J. Wurdack & L. S. Adderley 43025	Venezuela	NY	USw 17808
<i>Passiflora punctata</i> L.	R. H. Wetmore & E. Abbe 26	Panama Canal Zone	A	Aw 26
<i>Passiflora quadrangularis</i> L.	M. Grant 2617	Tahiti	Y	Yw 26455
<i>Passiflora quadriglandulosa</i> Radscheid	G. H. M. Lawrence 607	Colombia	A	Aw 21303
<i>Passiflora riparia</i> Mart. ex Mast.	A. C. Smith 3157	British Guiana	Y	Yw 35837
<i>Passiflora rubra</i> L.	—	—	—	Aw 5286
<i>Passiflora securiclata</i> Mast.	A. C. Smith 3116	British Guiana	Y	Yw 35811
<i>Passiflora seemannii</i> Griseb.	R. H. Wetmore & E. Abbe 147	Panama Canal Zone	A	Aw 147
<i>Passiflora spinosa</i> (Poepp. & Endl.) Mast.	J. J. Wurdack & L. S. Adderley 43009	Venezuela	NY	USw 17798
<i>Passiflora variolata</i> Poepp. & Endl.	J. J. Wurdack & L. S. Adderley 43230	Venezuela	NY	USw 17923
<i>Passiflora vitifolia</i> H.B.K.	R. H. Wetmore & R. H. Woodworth <i>s.n.</i>	Panama Canal Zone	—	Aw 854A
<i>Passiflora vitifolia</i> H.B.K.	J. J. Wurdack & L. S. Adderley 43026	Venezuela	NY	USw 17809
<i>Passiflora vitifolia</i> H.B.K.	F. Woytkowski 509	Peru	Y	Yw 52812



TABLE 1.—*Specimens of Passifloraceae stems examined*—Continued

<i>Species</i>	<i>Collector and Number</i>	<i>Geographical Origin</i>	<i>Herbarium Voucher</i>	<i>Location and Catalog Number</i>
<i>Passiflora</i> sp. nov.	J. J. Wurdack & L. S. Adderley 43154	Venezuela	NY	USw 17874
<i>Passiflora</i> sp.	B. Maguire 28327	Venezuela	NY	USw 24782
<i>Passiflora</i> sp.	J. J. Wurdack & L. S. Adderley 43055	Venezuela	NY	USw 17834
<i>Passiflora</i> sp.	F. P. Jonker & Daniels 1227	Suriname	U	USw 30684
<i>Smeathmannia laevigata</i> Sol. ex R. Br.	J. Espirito-Santo <i>s.n.</i>	Portuguese Guinea	US	USw 30675
<i>Smeathmannia pubescens</i> Sol. ex R. Br.	G. P. Cooper 442	Liberia	Y	USw 5792
<i>Smeathmannia pubescens</i> Sol. ex R. Br.	G. P. Cooper 51	Liberia	K	Yw 13701

### Anatomy of the Family

Growth rings are absent in most of the species investigated except for *Paropsia schliebenii* and *Smeathmannia pubescens*. All of the woods are diffuse-porous, the randomly distributed pores ranging in size from very small to moderately large. The occurrence of solitary pores (figs. 3–6) characterizes the wood of Passifloraceae, although radial (figs. 7–9) and tangential multiples (fig. 4), as well as pore clusters, are found in some species. Pores in all species are rounded; however, “flattened” pores (fig. 3) sometimes appear. Pores are variable in size even in different species of the same genus. In some species of *Passiflora*, for example, vessel diameter is less than 100  $\mu$ , while in other species the vessel diameter is over 300  $\mu$ . Vessel element lengths are extremely short in *Adenia* and *Passiflora* to moderately short in *Crossostemma* and *Smeathmannia*.

Slope of the end walls in the vessel elements varies from oblique (fig. 14) to transverse. Oblique end walls are regularly associated with wood from arboreal species. Perforation plates are almost exclusively simple (fig. 11); in *Paropsia adenostegia*, both simple and scalariform perforation plates (fig. 12) may occur in the same section. The scalariform plates here have few bars, and at times show a tendency toward the reticulate configuration. Metcalfe and Chalk (1950) observed a few scalariform plates in *Androsiphonia* and *Mitostemma glaziovii*, but none was observed in *M. glaziovii* during this investigation.



The imperforate tracheary elements generally consist of fiber-tracheids (fig. 13) bearing pits with very distinct borders. However, tracheids (fig. 13) occur in some species, and very thick-walled libriform wood fibers (fig. 10) are commonly found in the arboreal members of the family. The fiber lengths range from moderately short to medium-sized.

Intervascular pitting is mostly alternate (fig. 21), and the pit apertures are generally elliptical or flattened, and tend to be limited by the border. In *Passiflora fuchsiflora* coalesced apertures were observed.

Fibriform vessel members (fig. 13) of Woodworth (1935) were observed in most species of *Passiflora* and in *Paropsia schliebenii*. These cells are longer than vessel elements in the same species, and bear simple perforation plates that occur about one-fourth the distance from each end of the element. Fibriform vessel members are fusiform cells more or less randomly distributed within the groundmass, and show fewer axial connections among conspecific elements than occur among elements making up typical vessels. Lateral wall pitting of these cells is similar to that of the fiber-tracheids.

Vascular ray tissue (figs. 10, 17) is composed of both uniseriate and multiseriate rays. Some species have typically high multiseriate rays; in others, only biseriate rays with long uniseriate wings occur. The tendency for rays to widen centrifugally, as seen in transverse sections, is common in *Passiflora*. In most species of *Passiflora* storied uniseriate rays (fig. 17) are found among higher, nonstoried multiseriate rays. Vascular rays may be heterocellular or homocellular. In *Paropsia vareciformis* rays consist of procumbent cells associated with uniseriate margins of square cells. Rays consist exclusively of upright cells in *Passiflora maguirei* and *Passiflora mollissima*. Ontogenetic splitting of multiseriate rays into uniseriate and biseriate rays was observed in many species. Chalk and Chattaway (1933) reported on the presence of perforated ray cells in *Androsiphonia adenostegia*. Similarly perforated ray cells were observed in *Passiflora vitifolia* and *Passiflora elliptica* (fig. 15).

Axial wood parenchyma is generally moderately abundant to very abundant. The usual arrangement is apotracheal (figs. 7, 8, 20); however, paratracheal parenchyma (figs. 3-6, 9) does occur, and in some species it is vasicentric and aliform. Combinations of diffuse and diffuse-in-aggregates, with a tendency toward banded, and even vasicentric arrangements are found in the same species (fig. 9); narrow bands occur in others. In *Paropsia*, the bands are wavy; banded and aliform arrangements are both observed in *Dilkea johannesii*; in *Crossostemma laurifolium*, only vasicentric parenchyma arrangement occurs.



Pith flecks (fig. 16) occur in the wood of about 70 percent of the *Passiflora* species studied. Three types of anomalous stem development (see pp. 48, 60, 61) were observed in the species investigated: included phloem type, interrupted type (figs. 24, 25), and dispersed type (fig. 23). Tyloses and gummy deposits were present in ray cells and vessels (fig. 8) of a few species. Rhomboidal crystals, and occasionally druses, were observed in most species investigated, particularly in ray cells.

#### Anatomy of the Species

*Crossostemma laurifolium*: Growth rings absent; pores mainly solitary, rounded, average diameter 198  $\mu$ , range 140  $\mu$ –210  $\mu$ ; average vessel element length 424  $\mu$ , range 311  $\mu$ –442  $\mu$ ; vessel wall thickness 2  $\mu$ –5  $\mu$ ; perforation plates simple; vessel element end wall inclination almost transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 614  $\mu$ , range 497  $\mu$ –756  $\mu$ ; fibriform vessel members absent; vascular rays mostly multiseriate without any uniseriate extensions, 2–5 cells wide, 8–12 cells high, few uniseriate, 5–14 cells high, mainly homocellular consisting of procumbent cells, uniseriates sometimes showing upright cells; axial parenchyma vasicentric; crystals present in ray cells; uniseriate rays vaguely storied; stem anomalous (interrupted); pith flecks absent.

*Dilkea johannesii*: Growth rings absent; pores mostly solitary, rounded, average diameter 205  $\mu$ , range 104  $\mu$ –211  $\mu$ ; average vessel element length 378  $\mu$ , range 335  $\mu$ –401  $\mu$ ; vessel wall thickness 4  $\mu$ –8  $\mu$ ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 560  $\mu$ , range 433  $\mu$ –741  $\mu$ ; fibriform vessel members absent; vascular rays mostly multiseriate without any uniseriate extensions, 2–6 cells wide, 5–13 cells high, some uniseriate, 4–15 cells high, mainly heterocellular; axial parenchyma diffuse, abundant; crystals present in ray cells; uniseriate rays vaguely storied; stem normal; pith flecks absent.

*Mitostemma glaziovii*: Growth rings absent; pores mostly solitary, rounded, average diameter 112  $\mu$ , range 92  $\mu$ –130  $\mu$ ; average vessel element length 416  $\mu$ , range 392  $\mu$ –478  $\mu$ ; vessel wall thickness 3  $\mu$ –5  $\mu$ ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 550  $\mu$ , range 520  $\mu$ –719  $\mu$ ; fibriform vessel members absent; vascular rays mostly multiseriate without any uniseriate extensions, 2–4 cells wide, 7–12 cells high, few uniseriate, 8–13 cells high, heterocellular; axial parenchyma diffuse; crystals present in ray cells; storying absent; stem normal; pith flecks absent.



*Paropsia adenostegia*: Growth rings inconspicuous; pores mainly solitary, few radial multiples, angular to rounded, average diameter  $50\ \mu$ , range  $35\ \mu$ – $56\ \mu$ ; average vessel element length  $450\ \mu$ , range  $420\ \mu$ – $773\ \mu$ ; vessel wall thickness  $2\ \mu$ – $3\ \mu$ ; perforation plates scalariform and simple; vessel element end wall inclination oblique; intervascular pitting alternate; imperforate tracheary elements libriform wood fibers, average length  $668\ \mu$ , range  $574\ \mu$ – $968\ \mu$ ; fibriform vessel members absent; vascular rays mainly uniseriate, 5–12 cells high, and biseriate, 5–12 cells high, heterocellular; axial parenchyma diffuse, banded in places; crystals absent; storying absent; stem normal; pith flecks absent.

*Paropsia madagascariensis*: Growth rings absent; pores mainly in radial multiples, rounded, average diameter  $85\ \mu$ , range  $64\ \mu$ – $127\ \mu$ ; average vessel element length  $468\ \mu$ , range  $420\ \mu$ – $780\ \mu$ ; vessel wall thickness  $2\ \mu$ – $3\ \mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements libriform wood fibers, average length  $580\ \mu$ , range  $394\ \mu$ – $803\ \mu$ ; fibriform vessel members absent; vascular rays multiseriate without any uniseriate extensions, 2–3 cells wide, 5–11 cells high, heterocellular; axial parenchyma diffuse; crystals present in ray cells; storying absent; stem normal; pith flecks absent.

*Paropsia schliebenii*: Growth rings present; pores mainly in radial multiples, rounded, average diameter  $45\ \mu$ , range  $27\ \mu$ – $62\ \mu$ ; average vessel element length  $590\ \mu$ , range  $398\ \mu$ – $772\ \mu$ ; vessel wall thickness  $2\ \mu$ – $3\ \mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements libriform wood fibers, average length  $775\ \mu$ , range  $424\ \mu$ – $907\ \mu$ ; fibriform vessel members present; vascular rays multiseriate, 2–3 cells wide, 13–28 cells high, few with uniseriate wings 4–8 cells high, largely homocellular, cells mainly procumbent but with a few upright cells; axial parenchyma diffuse; crystals absent; uniseriate rays vaguely storied; stem normal; pith flecks absent.

*Paropsia vareciformis*: Growth rings inconspicuous; pores mainly in radial multiples, rounded, average diameter  $70\ \mu$ , range  $62\ \mu$ – $110\ \mu$ ; average vessel element length  $480\ \mu$ , range  $382\ \mu$ – $697\ \mu$ ; vessel wall thickness  $2\ \mu$ – $3\ \mu$ ; perforation plates simple; vessel element end wall inclination almost transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids and libriform wood fibers, average length  $668\ \mu$ , range  $511\ \mu$ – $939\ \mu$ ; fibriform vessel members absent; vascular rays multiseriate 2–3 cells wide, 18–34 cells high, few with uniseriate wings 4–8 cells high, mainly homocellular, consisting solely of procumbent cells, other rays with some upright cells; axial parenchyma diffuse; crystals present in ray cells; uniseriate rays storied in places; stem normal; pith flecks absent.



*Passiflora arborea*: Growth rings present; pores 50 percent solitary, 30 percent radial multiples, 20 percent clusters, rounded, average diameter 130  $\mu$ , range 98  $\mu$ -152  $\mu$ ; average vessel element length 343  $\mu$ , range 295  $\mu$ -587  $\mu$ ; vessel wall thickness 2  $\mu$ -3  $\mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids and libriform wood fibers, average length 481  $\mu$ , range 394  $\mu$ -647  $\mu$ ; fibriform vessel members absent; vascular rays biseriate with long uniseriate wings 9-22 cells high, heterocellular; axial parenchyma mostly diffuse, diffuse-in-aggregates to banded and vasicentric; storying absent; stem normal; pith flecks present.

*Passiflora auriculata*: Growth rings absent; pores mainly solitary, rounded, average diameter 210  $\mu$ , range 198  $\mu$ -230  $\mu$ ; average vessel element length 362  $\mu$ , range 303  $\mu$ -479  $\mu$ ; vessel wall thickness 2  $\mu$ -5  $\mu$ ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 472  $\mu$ , range 403  $\mu$ -723  $\mu$ ; fibriform vessel members present; vascular rays mainly multiseriate 2-8 cells wide, 7-30 cells high, few with uniseriate wings 4-9 cells high, some uniseriate rays 5-12 cells high, heterocellular; axial parenchyma diffuse; crystals present in ray cells; uniseriate rays storied; stem anomalous (included phloem); pith flecks absent; tyloses present.

*Passiflora coccinea*: Growth rings absent; pores mainly solitary, rounded, average diameter 210  $\mu$ , range 182  $\mu$ -231  $\mu$ ; average vessel element length 385  $\mu$ , range 307  $\mu$ -478  $\mu$ ; vessel wall thickness 2  $\mu$ -7  $\mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements tracheids and fiber-tracheids, average length 437  $\mu$ , range 410  $\mu$ -629  $\mu$ ; fibriform vessel members present; vascular rays mainly uniseriate 1-18 cells high, some multiseriate without any uniseriate extensions, 2-8 cells wide, 6-13 cells high, heterocellular; axial parenchyma diffuse with local banding; crystals absent; uniseriate rays storied; stem anomalous (interrupted); pith flecks present; tyloses present.

*Passiflora edulis*: Growth rings absent; pores mainly solitary, rounded, average diameter 131  $\mu$ , range 101  $\mu$ -168  $\mu$ ; average vessel element length 185  $\mu$ , range 143  $\mu$ -208  $\mu$ ; vessel wall thickness 2  $\mu$ -7  $\mu$ ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 315  $\mu$ , range 298  $\mu$ -472  $\mu$ ; fibriform vessel members present; vascular rays mainly uniseriate 1-14 cells high, mostly 6-12 cells high, some multiseriate 2-3 cells wide, 8-12 cells high, uniseriate wings 4-8 cells high, few very high multiseriate rays, heterocellular; axial parenchyma mainly diffuse with some



banding; crystals present in ray cells; uniseriate rays storied; stem anomalous (interrupted); pith flecks absent.

*Passiflora elliptica*: Growth rings absent; pores 30 percent solitary, 62 percent radial multiples, 8 percent clusters, rounded, average diameter  $117\ \mu$ , range  $96\ \mu$ – $184\ \mu$ ; average vessel element length  $316\ \mu$ , range  $299\ \mu$ – $437\ \mu$ ; vessel wall thickness  $2\ \mu$ – $5\ \mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length  $420\ \mu$ , range  $413\ \mu$ – $489\ \mu$ ; fibriform vessel members present; vascular rays mainly multiseriate without any uniseriate extensions, 2–8 cells wide, 7–12 cells high, few uniseriate 4–9 cells high, heterocellular; axial parenchyma diffuse; crystals absent; uniseriate rays vaguely storied; stem normal; pith flecks present; tyloses present.

*Passiflora fuchsiiflora*: Growth rings absent; pores mainly solitary, rounded, average diameter  $135\ \mu$ , range  $97\ \mu$ – $154\ \mu$ ; average vessel element length  $396\ \mu$ , range  $284\ \mu$ – $473\ \mu$ ; vessel wall thickness  $2\ \mu$ – $5\ \mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length  $471\ \mu$ , range  $435\ \mu$ – $622\ \mu$ ; fibriform vessel members present; vascular rays mainly multiseriate 2–8 cells wide, 6–13 cells high, uniseriate wings 4–6 cells high, few very high multiseriate rays, some uniseriate 4–8 cells high, heterocellular; axial parenchyma diffuse and diffuse-in-aggregates with a few narrow bands; crystals present in ray cells; uniseriate rays and parenchyma strands vaguely storied; stem normal; pith flecks present.

*Passiflora glandulosa*: Growth rings vague; pores 60 percent solitary, 40 percent radial multiples, rounded, average diameter  $200\ \mu$ , range  $142\ \mu$ – $254\ \mu$ ; average vessel element length  $341\ \mu$ , range  $311\ \mu$ – $441\ \mu$ ; vessel wall thickness  $2\ \mu$ – $7\ \mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length  $403\ \mu$ , range  $361\ \mu$ – $547\ \mu$ ; fibriform vessel members present; vascular rays mainly uniseriate 1–7 cells high, some multiseriate 2–8 cells wide, 4–9 cells high, few very high multiseriate rays, heterocellular; axial parenchyma diffuse and in narrow bands; few crystals present in ray cells; uniseriate rays storied; stem anomalous (interrupted); pith flecks present.

*Passiflora laurifolia*: Growth rings absent; pores mainly solitary, rounded, average diameter  $124\ \mu$ , range  $98\ \mu$ – $155\ \mu$ ; average vessel element length  $318\ \mu$ , range  $264\ \mu$ – $410\ \mu$ ; vessel wall thickness  $2\ \mu$ – $5\ \mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length  $474\ \mu$ , range



401  $\mu$ –498  $\mu$ ; fibriform vessel members present; vascular rays mainly multiseriate 2–5 cells wide, 4–13 cells high, few uniseriate 1–15 cells high, few very high multiseriate rays, homocellular, consisting entirely of upright cells; axial parenchyma diffuse; crystals present in ray cells; uniseriate rays vaguely storied; stem normal; pith flecks present.

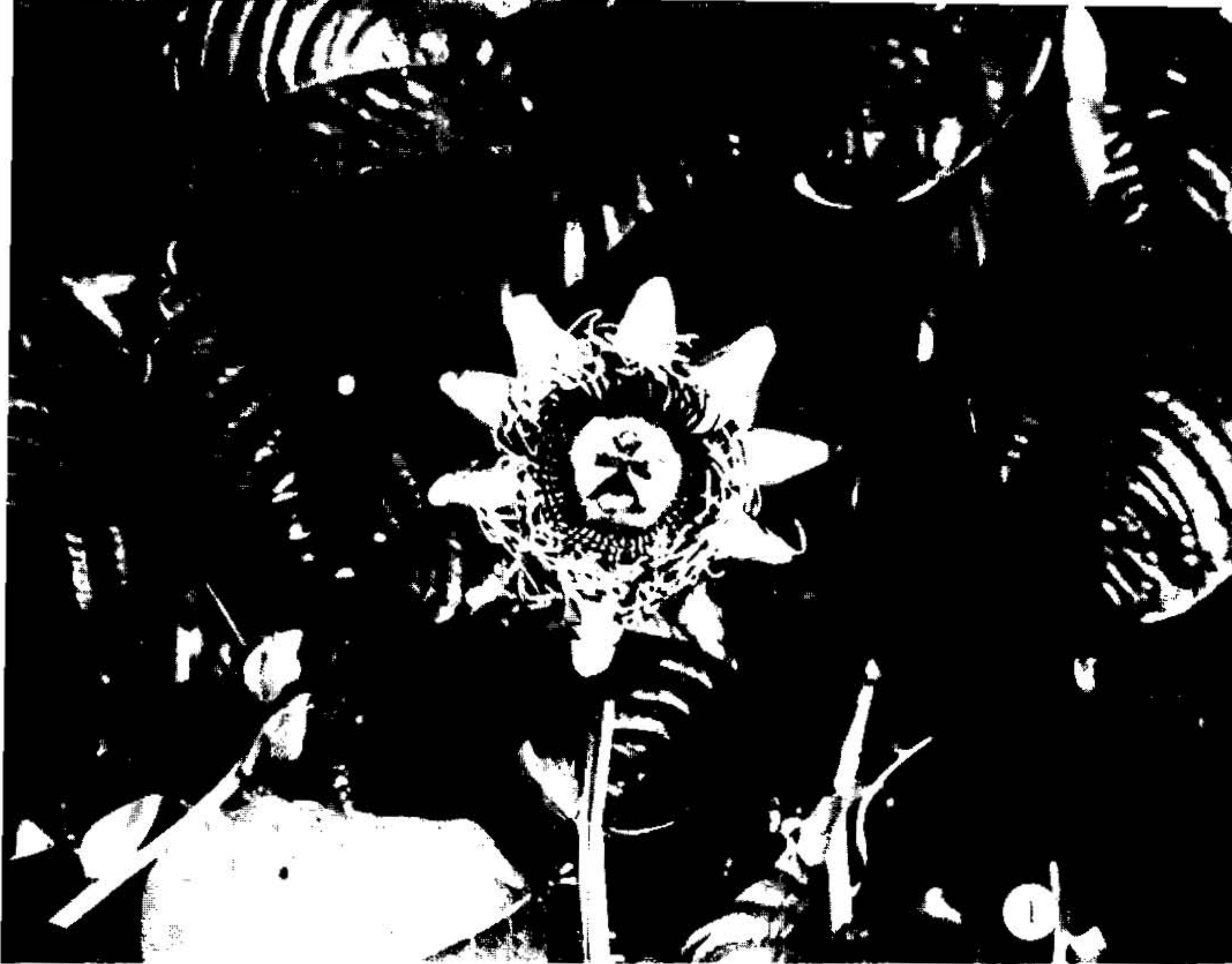
*Passiflora maguirei*: Growth rings absent; pores 85 percent solitary, radial multiples 10 percent, clusters 5 percent, rounded, average diameter 75  $\mu$ , range 42  $\mu$ –114  $\mu$ ; average vessel element length 211  $\mu$ , range 160  $\mu$ –351  $\mu$ ; vessel wall thickness 2  $\mu$ –4  $\mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids and libriform wood fibers, average length 488  $\mu$ , range 408  $\mu$ –730  $\mu$ ; fibriform vessel members absent; vascular rays mainly uniseriate 1–12 cells high, some multiseriate without uniseriate extensions, 2–8 cells wide, 6–12 cells high, homocellular, composed solely of upright cells; axial parenchyma diffuse, diffuse-in-aggregates, and in narrow bands; crystals absent; uniseriate rays vaguely storied; stem normal; pith flecks absent.

*Passiflora mollissima*: Growth rings absent; pores 90 percent solitary, 10 percent radial multiples, rounded, average diameter 111  $\mu$ , range 92  $\mu$ –170  $\mu$ ; average vessel element length 368  $\mu$ , range 284  $\mu$ –433  $\mu$ ; vessel wall thickness 2  $\mu$ –5  $\mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 432  $\mu$ , range 401  $\mu$ –520  $\mu$ ; fibriform vessel members present; vascular rays mainly multiseriate without uniseriate extensions, 2–5 cells wide, 6–14 cells high, few uniseriate 1–10 cells high, homocellular, comprising only square cells; ray cells with simple perforations; axial parenchyma diffuse; crystals present in ray cells; uniseriate rays vaguely storied; stem normal; pith flecks absent.

*Passiflora multiflora*: Growth rings absent; pores mainly solitary, rounded, average diameter 128  $\mu$ , range 102  $\mu$ –233  $\mu$ ; average vessel element length 345  $\mu$ , range 210  $\mu$ –445  $\mu$ , vessel wall thickness 2  $\mu$ –5  $\mu$ ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 422  $\mu$ , range 354  $\mu$ –591  $\mu$ ; fibriform vessel members present; vascular rays mainly uniseriate 2–15 cells high, some biseriate 25 or more cells high, homocellular, entirely of procumbent cells; axial parenchyma apotracheal and paratracheal; crystals present in ray cells; uniseriate rays storied, fibrous elements somewhat storied; stem anomalous (dispersed); pith flecks absent.

*Passiflora nitida*: Growth rings absent; pores solitary, rounded, average diameter 138  $\mu$ , range 104  $\mu$ –157  $\mu$ ; average vessel element length 234  $\mu$ , range 219  $\mu$ –447  $\mu$ ; vessel wall thickness 2  $\mu$ –4  $\mu$ ; vessel





CONTRIBUTION TO THE NATIONAL HERBARIUM VOL. III

PART 3 PLATE 1

FIG. 1. *Passiflora guianensis* (L.) P. & A. Flower with 11 stamens, the base of the  
 pedicel, and pistil. The pedicel is 1/2 inch long, 1/8 inch thick. FIG. 2. *P.  
 guianensis* (L.) P. & A. Unopened flower. Pedicel 1/2 inch long, 1/8 inch  
 thick. FIG. 3.





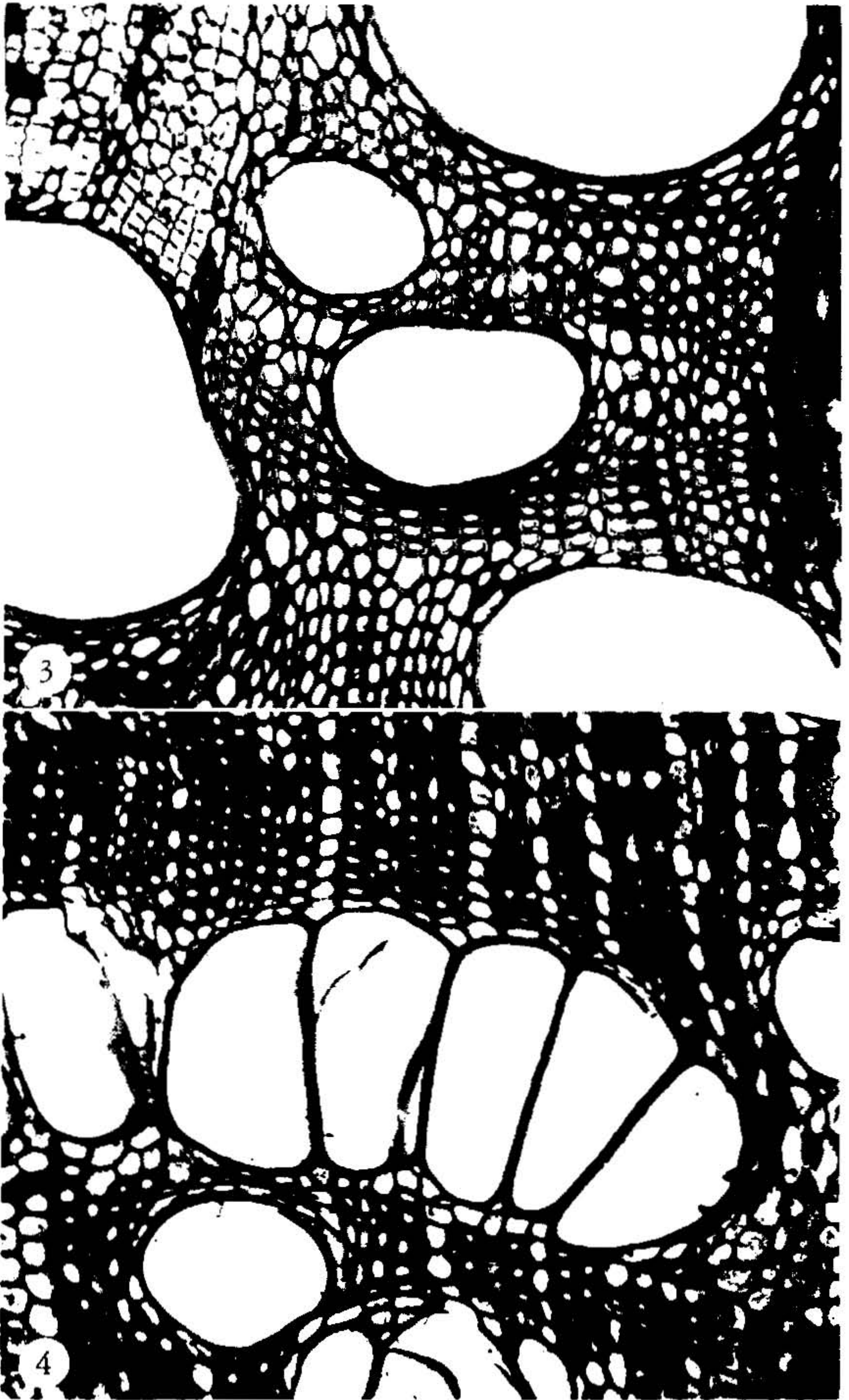


FIG. 3. *Passiflora coccinea* Aubl. Transverse section of wood showing solitary pores characteristic of lianous stems in Passifloraceae,  $\times 150$ . FIG. 4. *Passiflora* sp. Jonker & Daniels 1227. Transverse section of wood showing tangential pore disposition and vasicentric parenchyma,  $\times 150$ .



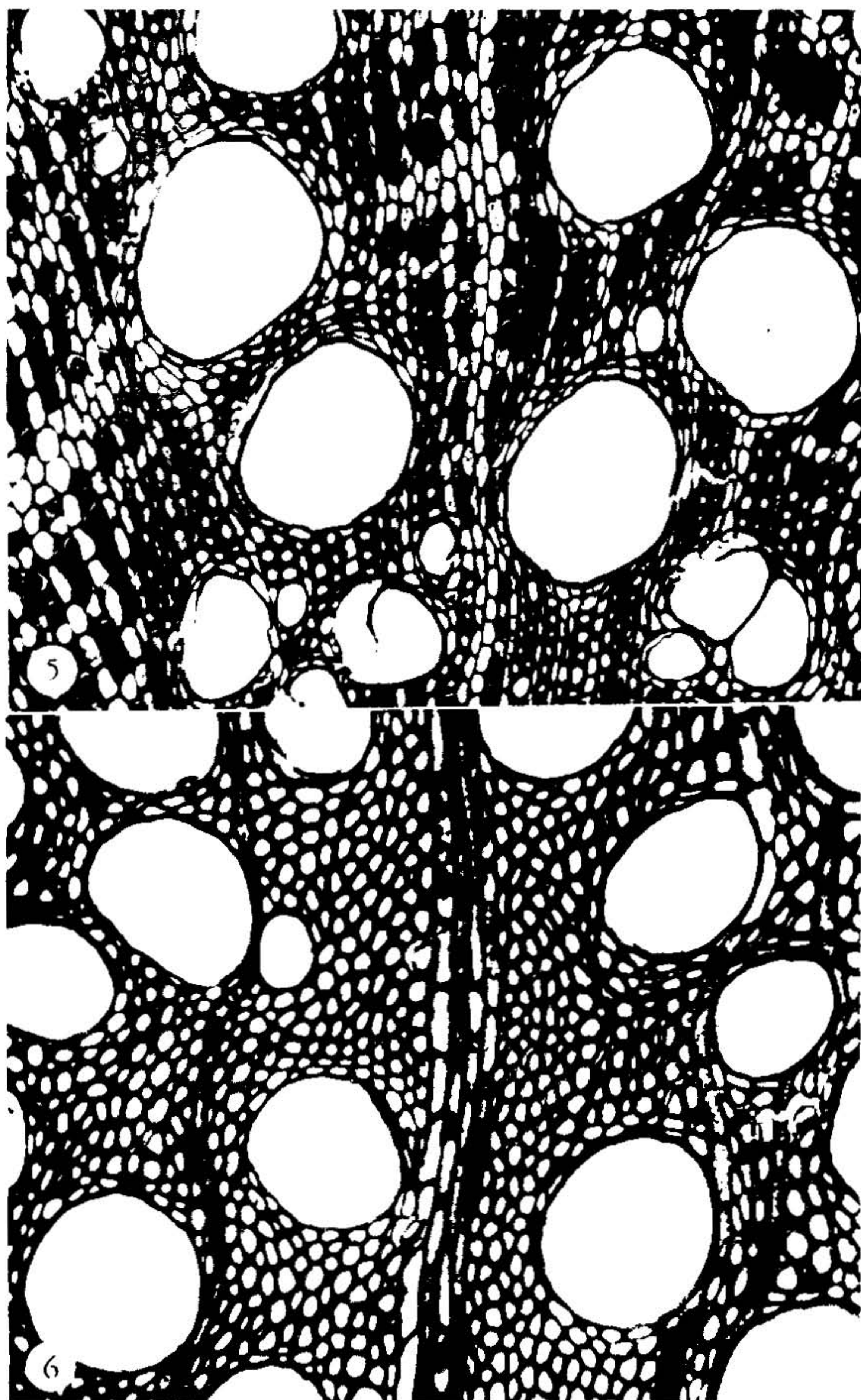


FIG. 5. *Passiflora* sp. *J. Kier & Daniels 1227*. Transverse section of wood showing mainly solitary pores, short apotracheal bands and vasicentric axial parenchyma,  $\times 150$ . FIG. 6. *Grostostemma laurifolium* Planch. Transverse section of wood with vasicentric parenchyma arrangement, and solitary, rounded pores,  $\times 150$ .



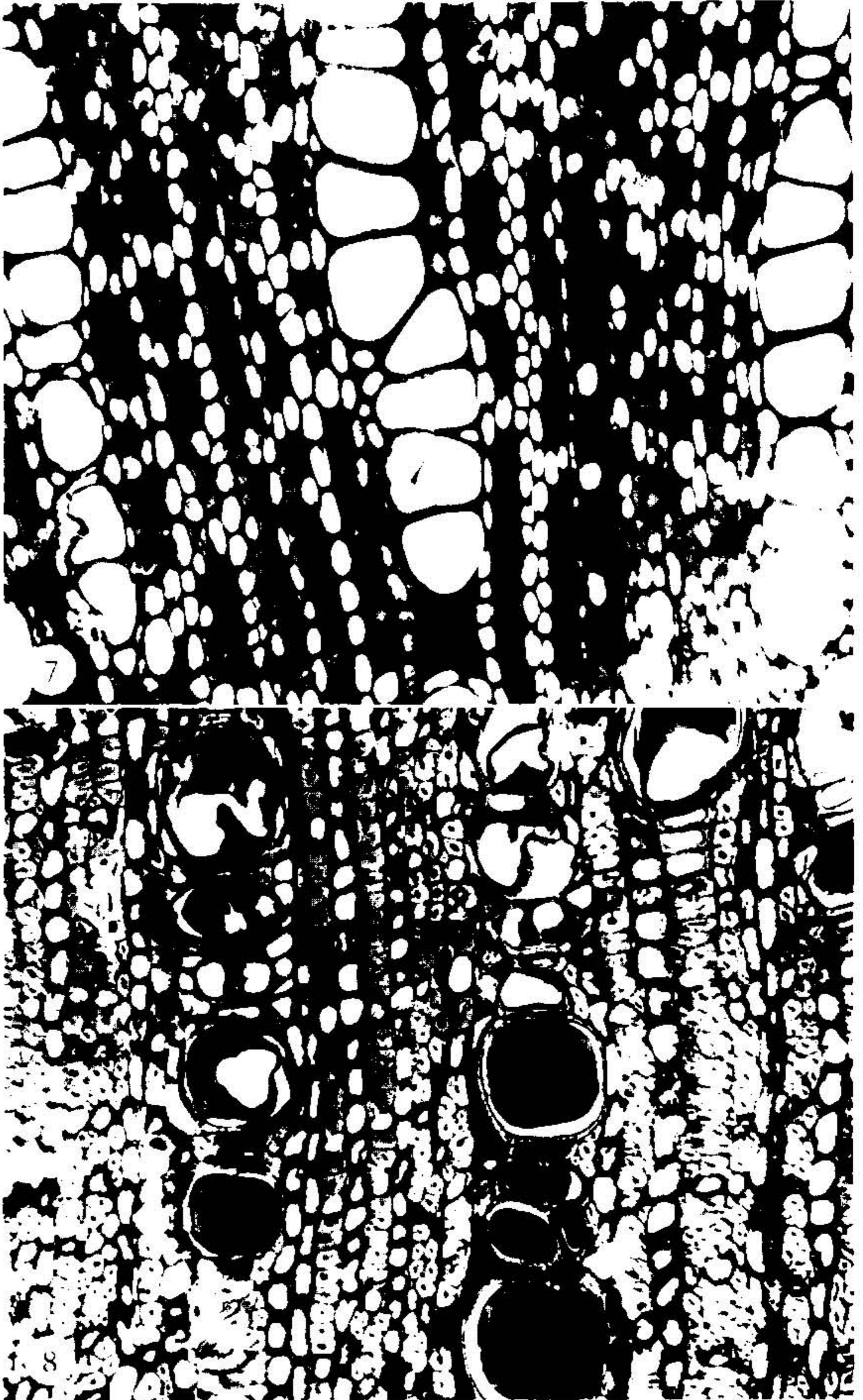


FIG. 7. *Socrathm ovata laevigata* Sol. ex R. Br. Transverse section of wood showing long radial pore multiples characteristic of arborescent stems, in Passifloraceae, and dilated axial parenchyma attachments.  $\times 150$ . FIG. 8. *Socrathm ovata pubescens* Sol. ex R. Br. Transverse section of xylem showing radial pores, thickened vessel walls, and gum deposits in vessels, axial and ray parenchyma cells.  $\times 100$ .



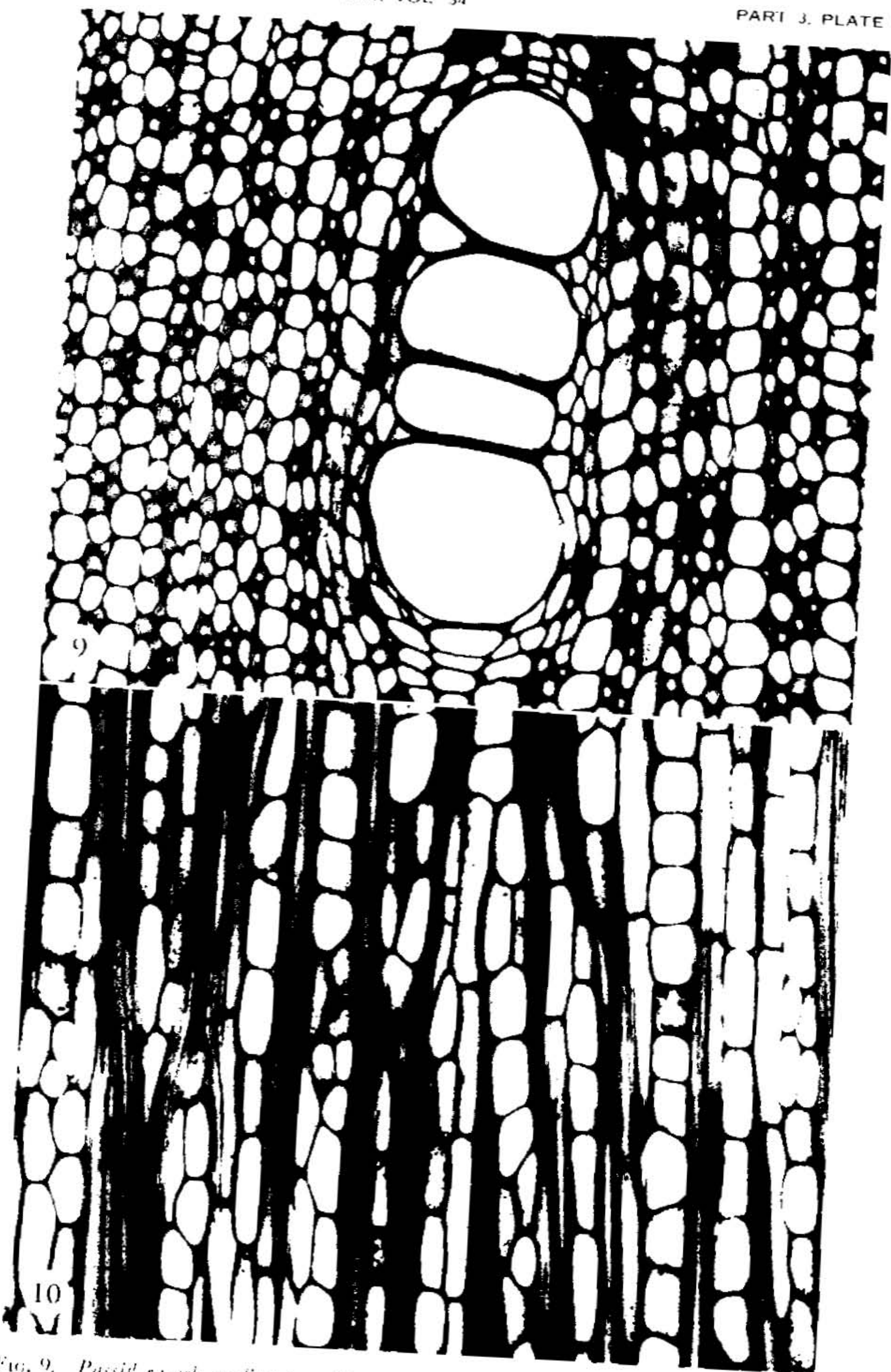


FIG. 9. *Passiflora arborea* Spreng. Transverse section of wood with radial pore multiple and several kinds of axial parenchyma arrangements: diffuse, diffuse-in-aggregates with a tendency toward banded, and vasicentric,  $\times 140$ . FIG. 10.—*Passiflora arborea* Spreng. Tangential section of wood showing biseriate heterocellular vascular rays with long uniseriate wings. Libriform wood fibers have thick walls,  $\times 200$ .



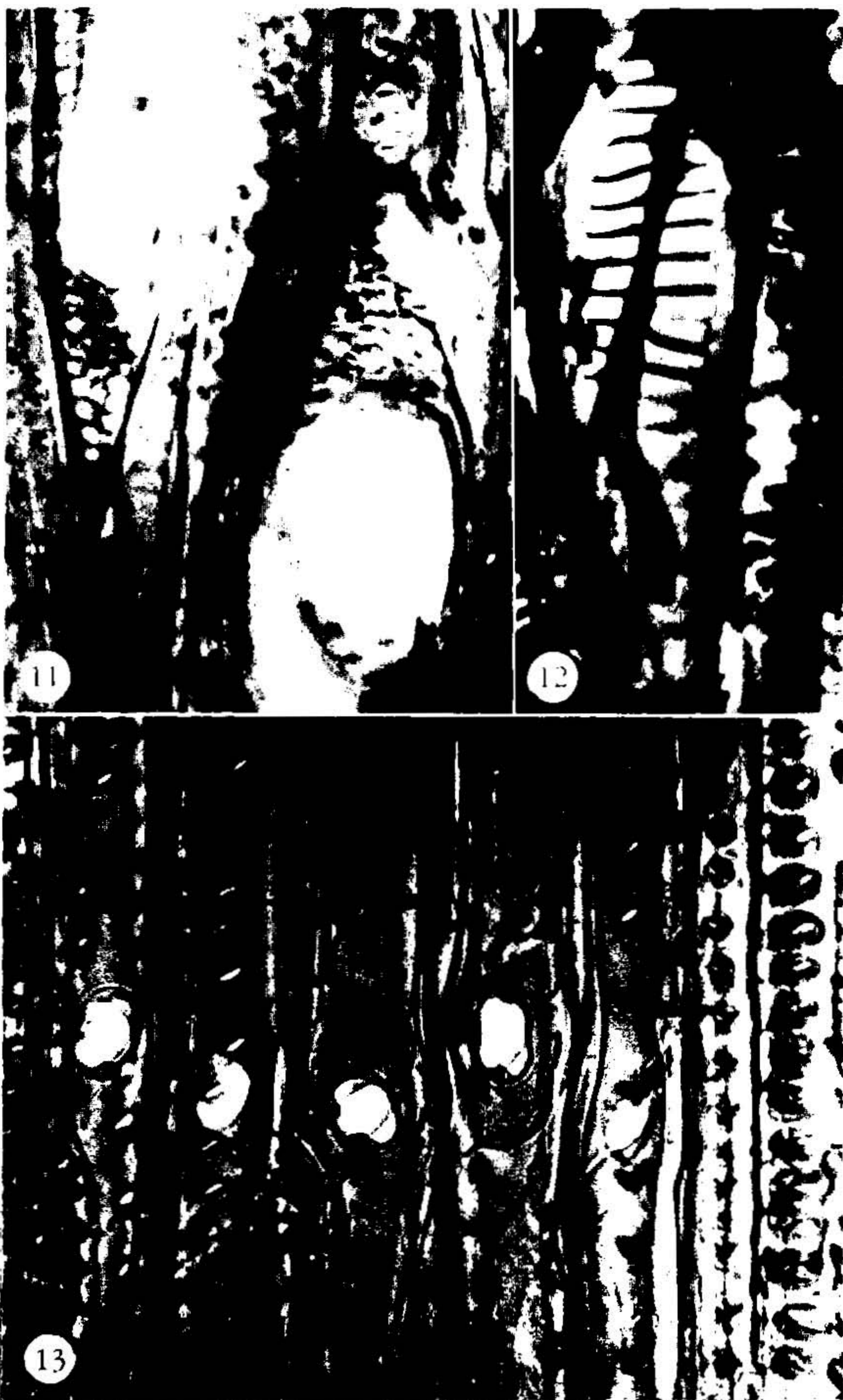


FIG. 11. *Passyia solidiorum* Steiner. Tangential section of xylem with large perforation plates.  $\times 850$ . FIG. 12. *Passyia alienata* (Stapf) Engelm. Tangential section of xylem showing secondary perforation plates. Inset in foreground is a fungus hypha.  $\times 850$ . FIG. 13. *P. stricta* (A. DC.) A. DC. Tangential section of xylem showing perforations in "fibers" (in vessel members) adjacent tracheids and fiber tracheids.  $\times 900$ .





FIG. 14. *Passiflora mollissima* (H. B. K.) Bailey. Tangential section of wood illustrating oblique vessel element end walls,  $\times 180$ . FIG. 15.—*Passiflora elliptica* Gardn. Radial section of wood showing perforated ray cell,  $\times 900$ . FIG. 16. *Passiflora arborea* Spreng. Transverse section of xylem showing a large pith fleck,  $\times 150$ .





FIG. 17. *Passiflora phyllanthifolia* (Cav.). Tangential section of wood depicting striated multiseriate rays, and light, wide, non-striated multiseriate rays.  $\times 400$ . FIG. 18. *Passiflora glandulifera* Cav. Transverse section of stem at base of furrow showing a xylem-pith interface as seen in the interrupted type of an analogous development: x = xylem, p = pith.  $\times 150$ .



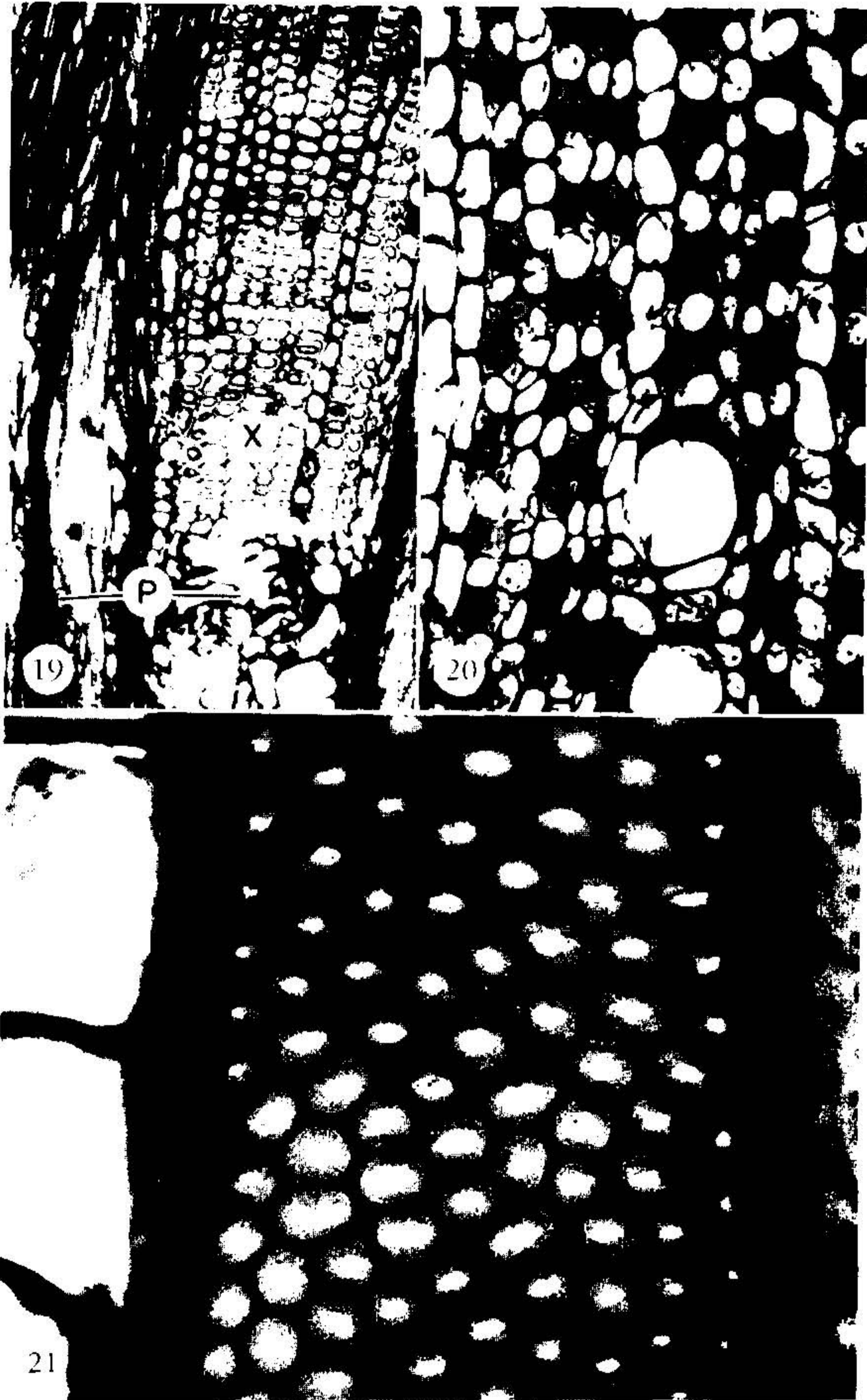
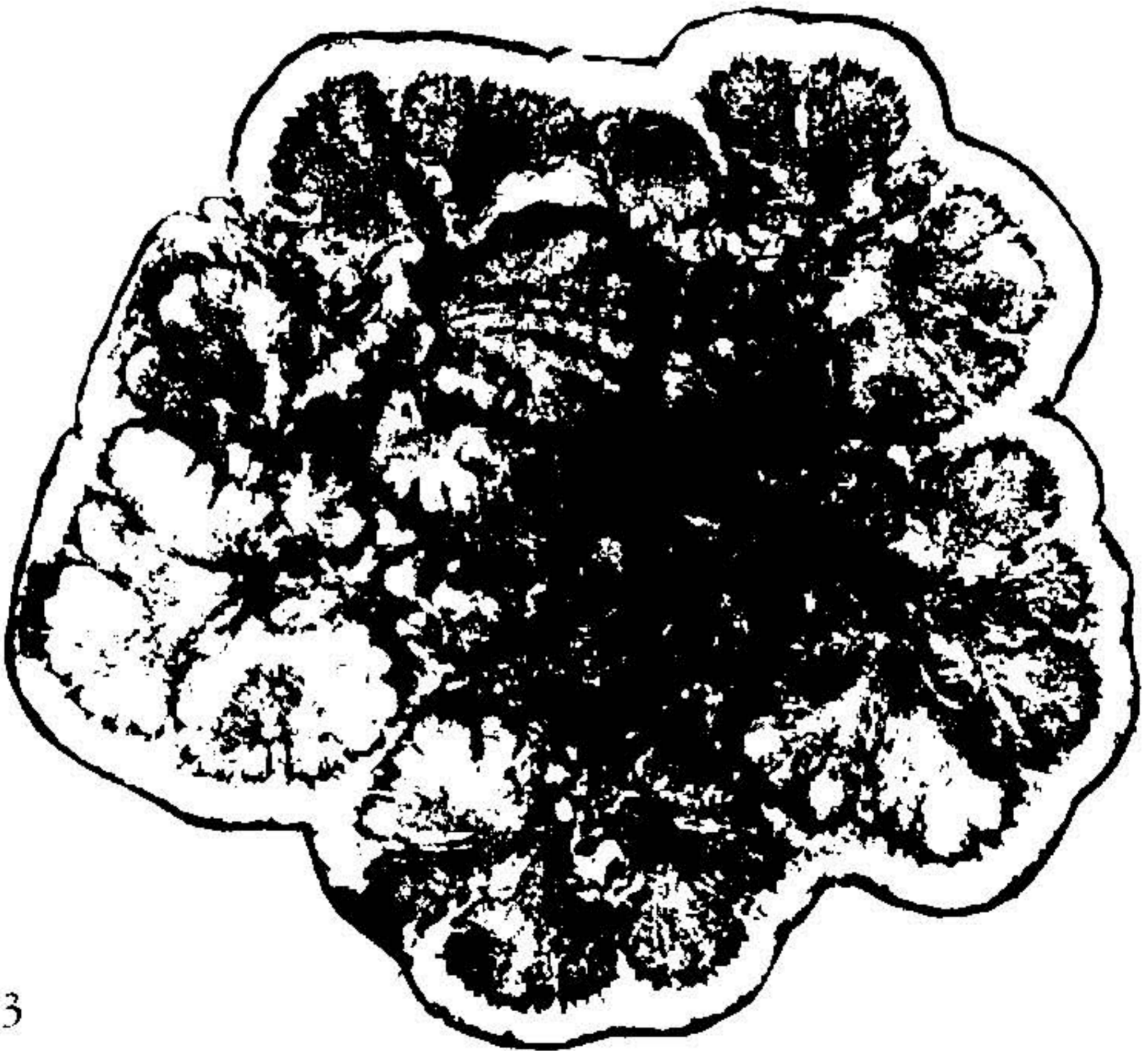


FIG. 19.—*Passiflora coccinea* Aubl. Transverse section of stem along xylem pith interface as seen in the interrupted type of anomalous development; x = xylem, p = pith,  $\times 150$ . FIG. 20. *Passiflora malagascariensis* (Baill.) H. Perrier. Transverse section of xylem illustrating the occurrence of abundant axial parenchyma in diffuse aggregate arrangement,  $\times 150$ . FIG. 21. *Passiflora arborea* Spreng. Tangential section of wood showing alternate intervacular pitting,  $\times 900$ .





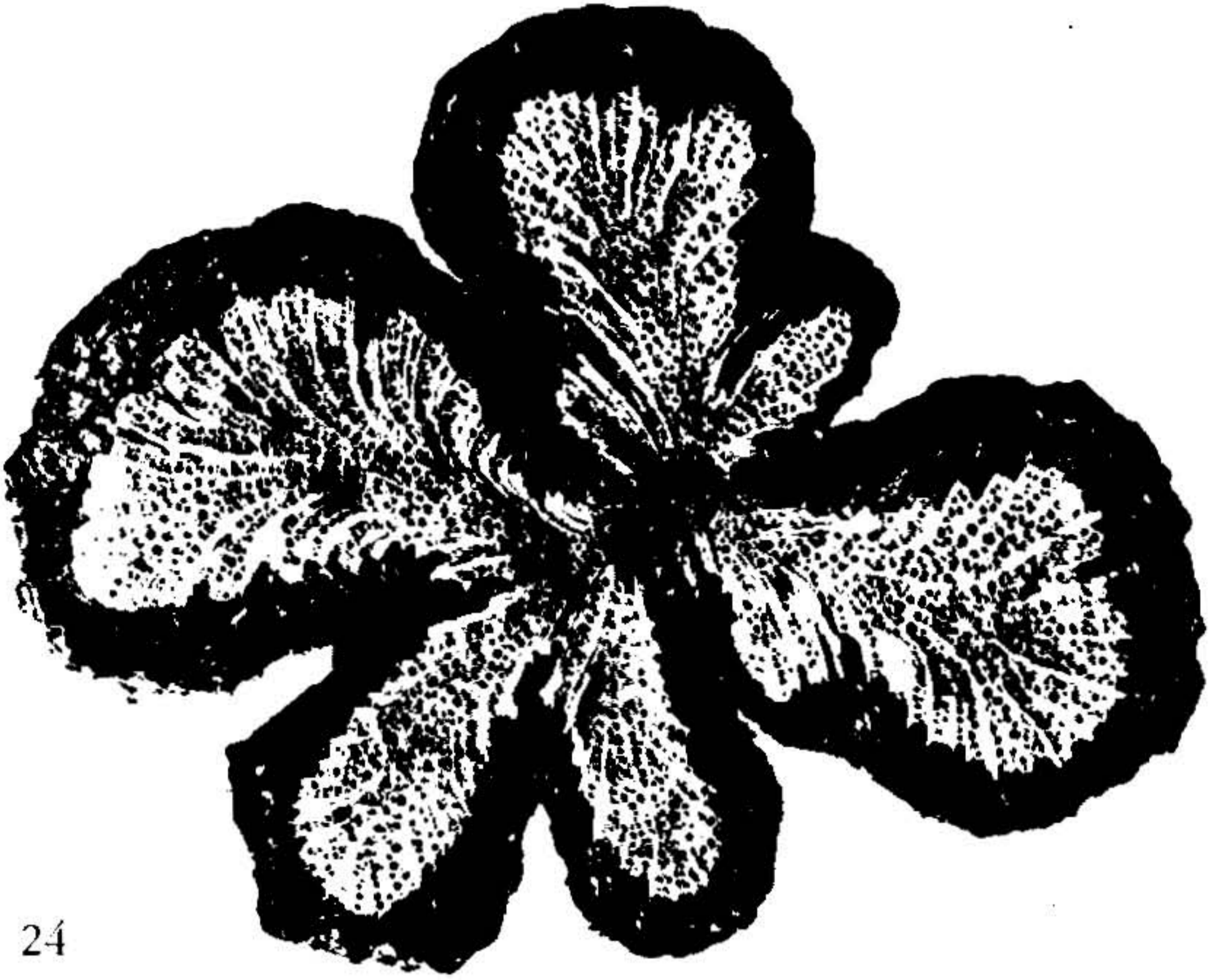
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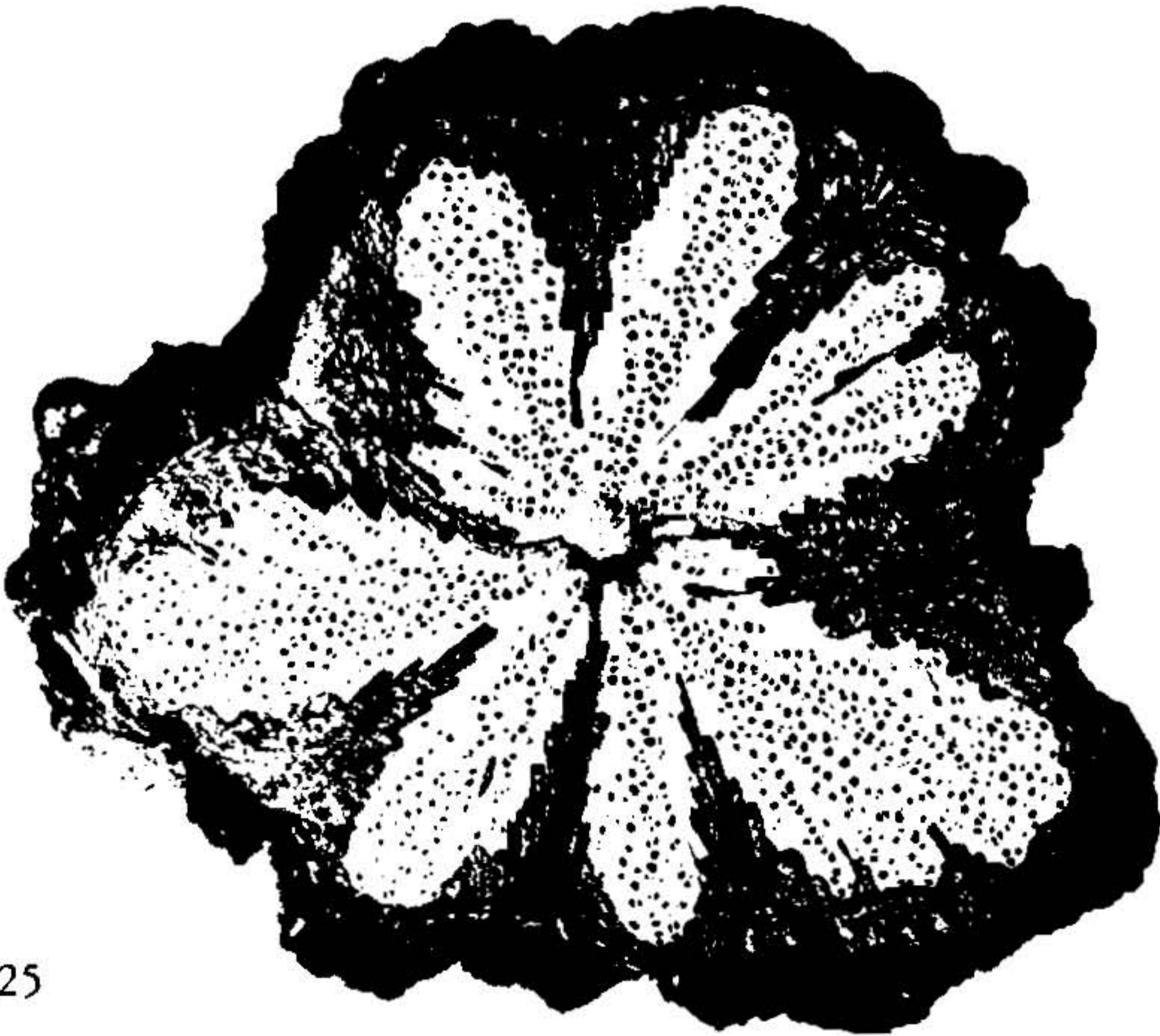
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FIG. 22. *Passiflora fuchsiiflora* Hemsl. Transverse section of stem showing normal type of development,  $\times 28$ . FIG. 23. *Passiflora multiiflora* L. Transverse section of stem illustrating dispersed type of anomalous structure.  $\times 2$ .





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FIG. 24.—*Passiflora glandulosa* Cav. Transverse section of stem showing interrupted type of anomalous structure; stem shape follows xylem outline,  $\times 2.8$ . FIG. 25.—*Passiflora* sp. B. Maguire 28327. Transverse section of stem illustrating interrupted type of anomalous structure; stem outline hardly reflects xylem configuration,  $\times 3.5$ .



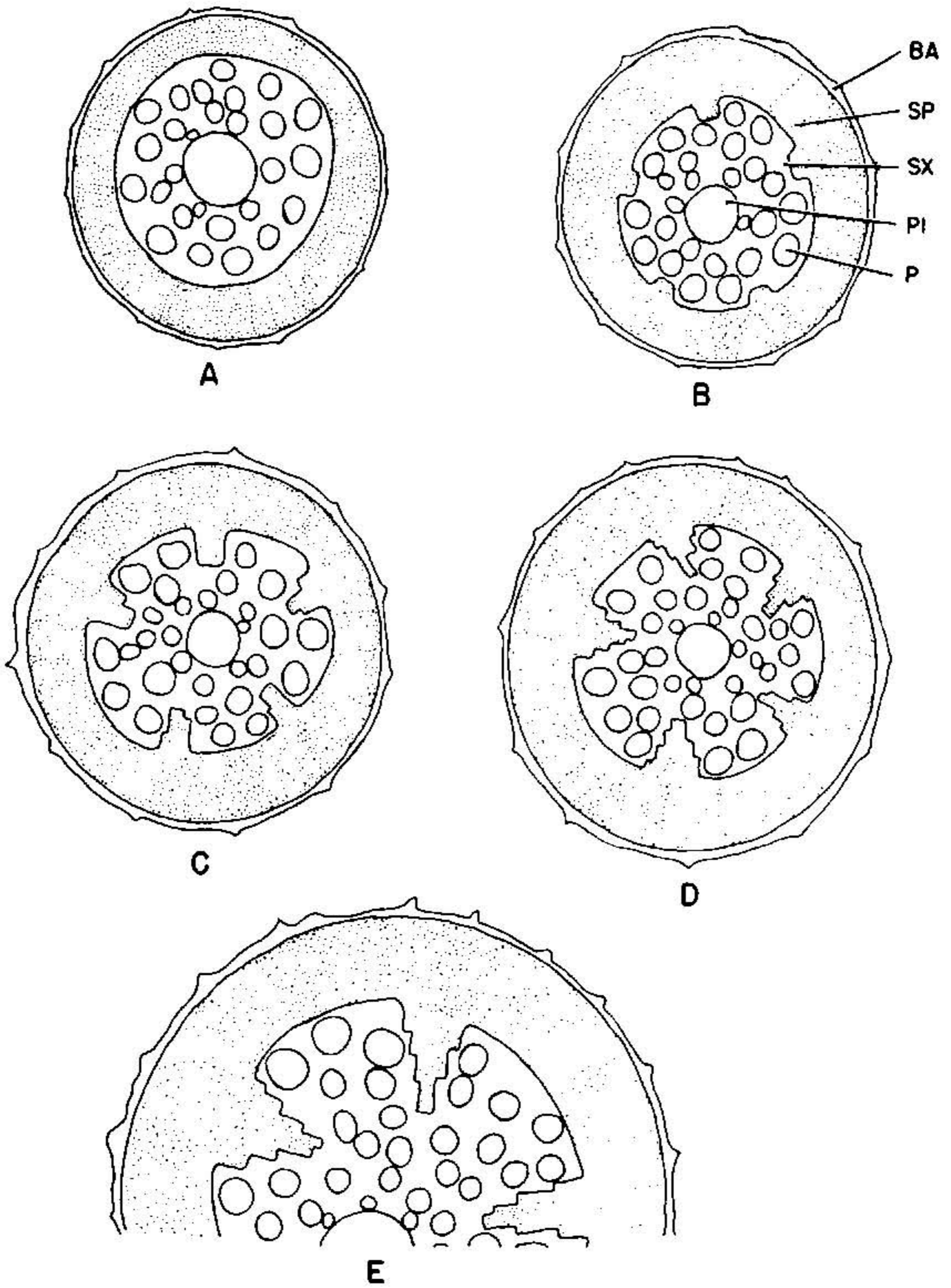


FIG. 26.—*Passiflora glandulosa* Cav. Ontogeny of the stem in serial transverse sections: A, an early internode depicting normal development at this stage; B, a later internode illustrating incipient formation of furrows in the vascular cylinder; C, D, E, phases leading to development of steplike configuration which results from unequal production of secondary xylem and phloem. BA=bark, SP=secondary phloem, SX= secondary xylem, PI=pith, P=pore.



element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 388  $\mu$ , range 208  $\mu$ –482  $\mu$ ; fibriform vessel members present; vascular rays mainly uniseriate 1–15 cells high, few multiseriate 2–4 cells wide, few very high multiseriate rays, heterocellular; axial parenchyma diffuse; crystals present in ray cells; uniseriate rays vaguely storied; stem anomalous (interrupted); pith flecks present.

*Passiflora quadriglandulosa*: Growth rings absent; pores mainly solitary, rounded, average diameter 161  $\mu$ , range 73  $\mu$ –207  $\mu$ ; average vessel element length 283  $\mu$ , range 203  $\mu$ –417  $\mu$ ; vessel wall thickness 2  $\mu$ –5  $\mu$ ; perforation plates simple; vessel element end wall inclination oblique to transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 420  $\mu$ , range 374  $\mu$ –513  $\mu$ ; fibriform vessel members present; vascular rays uniseriate 1–15 cells high, and multiseriate 2–many cells wide and 2–many cells high, heterocellular; axial parenchyma diffuse; crystals absent; uniseriate rays storied; stem anomalous (interrupted); pith flecks present.

*Passiflora securiclata*: Growth rings absent; pores 80 percent solitary, 20 percent radial multiples, rounded, average diameter 125  $\mu$ , range 101  $\mu$ –150  $\mu$ ; average vessel element length 268  $\mu$ , range 217  $\mu$ –301  $\mu$ ; vessel wall thickness 6  $\mu$ –7  $\mu$ ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting opposite; imperforate tracheary elements fiber-tracheids, average length 461  $\mu$ , range 328  $\mu$ –424  $\mu$ ; fibriform vessel members present; vascular rays mainly multiseriate without uniseriate extensions, 2–14 cells wide, 8–16 cells high, few uniseriate 1–8 cells high, mostly 3–6 cells high, heterocellular; ray cells with simple perforations; axial parenchyma diffuse, and with a few narrow bands; crystals present in ray cells; storying absent; stem normal; pith flecks present.

*Passiflora vitifolia*: Growth rings absent; pores mainly solitary, rounded, average diameter 160  $\mu$ , range 104  $\mu$ –196  $\mu$ ; average vessel element length 372  $\mu$ , range 214  $\mu$ –472  $\mu$ ; vessel wall thickness 3  $\mu$ –5  $\mu$ ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids, average length 455  $\mu$ , range 411  $\mu$ –549  $\mu$ ; fibriform vessel members present; vascular rays multiseriate, 2–many cells wide and few uniseriate 1–8 cells high, few very high multiseriate rays, heterocellular; ray cells with simple perforations; axial parenchyma diffuse; few crystals present in ray cells; storying absent; stem anomalous (interrupted); pith flecks present.

*Passiflora* sp. *Jonker & Daniels 1227*: Growth rings absent; pores 50 percent solitary, 30 percent radial multiples, 20 percent clusters, rounded, average diameter 125  $\mu$ , range 94  $\mu$ –178  $\mu$ ; average vessel



element length 344  $\mu$ , range 311  $\mu$ –433  $\mu$ ; vessel wall thickness 2  $\mu$ –4  $\mu$ ; perforation plates simple; vessel element end wall inclination transverse; intervascular pitting opposite to alternate; imperforate tracheary elements fiber-tracheids, average length 487  $\mu$ , range 431  $\mu$ –571  $\mu$ ; fibriform vessel members present; vascular rays mainly multiseriate 2–4 cells wide, few uniseriate 1–9 cells high, some very high multiseriate rays, homocellular, consisting solely of upright cells; axial parenchyma diffuse with a few narrow bands; crystals absent; uniseriate rays storied; stem apparently anomalous (included phloem); pith flecks present.

*Smeathmannia laevigata*: Growth rings absent; pores mainly in radial multiples, rounded, average diameter 84  $\mu$ , range 56  $\mu$ –101  $\mu$ ; average vessel element length 570  $\mu$ , range 466  $\mu$ –691  $\mu$ ; vessel wall thickness 2  $\mu$ –3  $\mu$ , perforation plates simple; vessel element end wall inclination oblique; intervascular pitting alternate; imperforate tracheary elements fiber-tracheids and libriform wood fibers, average length 472  $\mu$ , range 422  $\mu$ –801  $\mu$ ; fibriform vessel members absent; vascular rays mainly uniseriate 1–9 cells high, few biseriate 4–8 cells high, heterocellular; axial parenchyma diffuse; crystals absent; storying absent; stem normal; pith flecks absent.

*Smeathmannia pubescens*: Growth rings vague; pores mainly in radial multiples, rounded, average diameter 87  $\mu$ , range 62  $\mu$ –113  $\mu$ ; average vessel element length 590  $\mu$ , range 520  $\mu$ –674  $\mu$ ; vessel wall thickness 2  $\mu$ –3  $\mu$ ; perforation plates simple; vessel element end wall inclination oblique; intervascular pitting alternate; imperforate tracheary elements mostly libriform wood fibers, few fiber-tracheids, average length 431  $\mu$ , range 410  $\mu$ –792  $\mu$ ; fibriform vessel members absent; vascular rays mainly multiseriate without uniseriate extensions, 2–3 cells wide, 3–8 cells high, some uniseriate 8–13 cells high, heterocellular; axial parenchyma diffuse, and in narrow bands; crystals present in ray cells; storying absent; stem normal; pith flecks absent; gummy deposits present in ray cells and vessel elements.

### Ontogeny of the Stem

Ontogenetic investigations are based on series of transverse sections from the stems of four species of *Passiflora*: *P. auriculata*, *P. fuchsiflora*, *P. glandulosa*, and *P. multiflora*. Prepared slides of the last species were utilized from the earlier study by Stern and Brizicky.

*Passiflora fuchsiflora*: Ontogenetic series in this species illustrate only NORMAL (fig. 22) stem development, even in the very mature portions.

*Passiflora glandulosa*: Transverse sections of the youngest portions of the stem are quite normal and consist of concentric cylinders of



secondary xylem, vascular cambium, and secondary phloem around a central pith (fig. 26A). The vascular cambium, in these early stages, produces xylem and phloem in the usual fashion. At the fifth or sixth node from the tip of the stem, the vascular cylinder becomes furrowed; four, five, or six such furrows occur around the stem as a result of unequal production of xylem and phloem by the vascular cambium, more phloem than xylem being produced in the furrows (fig. 26B). As the stem ages and expands, tangential fragments of the vascular cambium remain behind to form steps at the margins of the furrows between the xylem and phloem (figs. 26C-E). These fragments of cambium along the margins of the furrows continue to produce secondary xylem and phloem in such a manner that a steplike configuration (fig. 26E) is produced as in some species of *Bignonia* (Schenck 1893). An interface between xylem and phloem as it occurs along the margin of a furrow is illustrated in figures 18 and 19. This stem configuration (figs. 24, 25) is designated the INTERRUPTED type, after Pfeiffer (1926, 1927).

*Passiflora multiflora*: A detailed ontogenetic study of the stem of this species was made by Stern and Brizicky. Essentially, the xylem cylinder is quite normal when young, as is the case in the other species studied. However, as growth of the stem parenchyma cells proceeds, the tracheary elements of xylem and phloem become separated into irregular masses by the dilation of the thin-walled pith and cortical cells, and cells of axial and radial xylem parenchyma. Each tracheary mass appears to be associated with a fragment of vascular cambium, and as a result of this irregularity the production of xylem and phloem proceeds in different directions and at different rates. The resultant anomalous developmental pattern (fig. 23) resembles that which occurs in some species of *Bauhinia* (Schenck 1893). The DISPERSED nature of xylem and phloem strands results from the rupturing of the vascular cambium by parenchyma cells, and the subsequent action of the disoriented bits of vascular cambium (Pfeiffer 1926, 1927; Stern and Brizicky 1958).

*Passiflora auriculata*: This species is generally normal in its ontogeny. In the mature portions of the stem, however, isolated phloem strands are formed in the secondary xylem which appear as patches on the transverse section. The production of INCLUDED phloem is quite erratic and phloem islands often appear radially oriented within the xylem mass. Phloem islands occur when the cambium, sporadically and briefly, produces phloem centripetally, followed by longer periods of normal xylem production. This type of anomalous development corresponds to the "foraminate type" of Pfeiffer (1926, 1927).



### Discussion

Any interpretation of xylem anatomy and taxonomy in Passifloraceae must take into consideration the interrelationships between microscopic structure and plant form. That anatomical structure may be especially modified in response to habit has been clearly pointed out by Bailey (1957) and described in certain tribes of Compositae by Carlquist (1959, 1960). Habit-related anatomical modifications may be superimposed upon specializations related to phylogeny, and the separation of these two facets of structural change is not always clear cut.

The Passifloraceae under study are either lianas or trees. Lianas are specialized plants among dicotyledons and have developed certain easily seen external modifications in response to this habit, such as tendrils and recurved hooks. The stem is attenuated; that is, narrow in transverse section in relation to the extreme length of the plant. In their study of the water-conducting system in climbers, Westermaier and Ambronn (1881) asserted that this feature represented an effective impediment to the flow of water in the stem. They argued that the relatively small cross section of stem available for the ontogenetic deposition of conducting elements and the great length of the conducting region were related to the anatomical peculiarities often evident in lianous stems. To counteract these morphological obstacles, anatomical development has been modified accordingly. Thus, in the case of vessels, a serious hindrance to rapid flow is the adhesion of water to the vessel walls. Broadening of vessels and elimination of scalariform perforation plates are two anatomical modifications which would tend to offset this limitation. A groundmass of thin-walled, conductive tracheids, as opposed to thick-walled, supportive libriform wood fibers, would also act to increase the area available for water transport.

Table 2 contains data from which a number of interesting correlations between anatomical structure and habit may be drawn. Without exception, all trees have libriform wood fibers as well as fiber-tracheids; none of the lianous species possesses libriform wood fibers, and the groundmass of the xylem consists of fiber-tracheids and tracheids. Fibriform vessel members occur in the lianous species of *Passiflora* and in *Paropsia schliebenii*, a tree. Noteworthy in this instance, is that these peculiarly modified cells have not been seen in the rare *Passiflora maguirei*, a vine, nor do they occur in the lianous species of *Crossostemma*, *Dilkea*, or *Mitostemma* which were available to us. All lianous species are characterized by predominantly solitary pores; only among certain tree species are the pores mostly in groups. An exception is *Passiflora elliptica*. The mean diameter of pores in



TABLE 2—Salient anatomical characteristics in the stems of Passifloraceae

[+ = present; - = absent; ± = more or less]

Species							Vessels						Storied structure	Perforated ray cells	Opposite intervascular pitting		
	Tree	Liana	Stem anomalous	Fiber-tracheids, or fiber-tracheids and tracheids	Libriform wood fibers, or libriform wood fibers and fiber-tracheids	Fibriform vessel members	Pores			Average vessel element length in $\mu$	End wall angle						
							Average diameter in $\mu$	Distribution			Predominantly transverse	Transverse and oblique				Predominantly oblique	
								Predominantly solitary	Solitary and grouped								Predominantly grouped
<i>Crossostemma laurifolium</i>		+	+	+		-	198	+			424	+		±	-	+	
<i>Dilkea johannesii</i>		+	-	+		-	205	+			378	+		±	-	-	
<i>Mitostemma glaziovii</i>		+	-	+		-	112	+			416	+		-	-	-	
<i>Paropsia adenostegia</i>	+		-		+	-	50	+			450			+	-	-	
<i>Paropsia madagascariensis</i>	+		-		+	-	85			+	468			+	-	-	
<i>Paropsia schliebenii</i>	+		-		+	+	45			+	590			+	-	-	
<i>Paropsia vareciformis</i>	+		-		+	-	70			+	480	+		±	-	-	
<i>Passiflora arborea</i>	+		-		+	-	130		+		343	+		±	-	-	
<i>Passiflora auriculata</i>		+	+	+		+	210	+			362	+		+	-	+	
<i>Passiflora coccinea</i>		+	+	+		+	210	+			385	+		+	-	-	
<i>Passiflora edulis</i>		+	+	+		+	131	+			185	+		+	-	+	
<i>Passiflora elliptica</i>		+	-	+		+	117			+	316			±	-	+	
<i>Passiflora fuchsiflora</i>		+	-	+		+	135	+			396			±	-	+	
<i>Passiflora glandulosa</i>		+	+	+		+	200	+			341			+	-	-	
<i>Passiflora laurifolia</i>		+	-	+		+	124	+			318			±	-	+	
<i>Passiflora maguirei</i>		+	-		+	-	75	+			211			±	-	-	
<i>Passiflora mollissima</i>		+	-	+		+	111	+			368			±	+	+	
<i>Passiflora multiflora</i>		+	+	+		+	128	+			345	+		+	-	-	
<i>Passiflora nitida</i>		+	+	+		+	138	+			234			±	-	-	
<i>Passiflora quadriglandulosa</i>		+	+	+		+	161	+			283			+	-	-	
<i>Passiflora securielata</i>		+	-	+		+	125	+			268	+		-	+	+	
<i>Passiflora vitifolia</i>		+	+	+		+	160	+			372	+		-	+	-	
<i>Passiflora</i> sp. ( <i>Jonker Daniels 1927</i> )		+	+	+		+	125		+		344	+		+	-	+	
<i>Smeathmannia laevigata</i>	+		-		+	-	84			+	570			+	-	-	
<i>Smeathmannia pubescens</i>	+		-		+	-	87			+	590			+	-	-	

the lianous species of Passifloraceae is 148  $\mu$ , species averages ranging from 75  $\mu$ -210  $\mu$ . On the other hand, pores average 78  $\mu$  in diameter in the trees, the species averages ranging from 45  $\mu$ -130  $\mu$ . Two points should be raised in this connection: *Passiflora arborea*, an arboreal species, has an average pore diameter which exceeds that in some of the lianous species, and *Passiflora maguirei*, a lianous species, has an average pore diameter less than that in some of the arboreal species. Vessel element lengths also appear to be correlated with habit; that is, average vessel element length in tree species is longer (498  $\mu$ ; range 343  $\mu$ -590  $\mu$ ) than in lianous species (330  $\mu$ ; range 185  $\mu$ -424  $\mu$ ). Strictly transverse vessel element end walls occur only in



certain lianous species, and strictly oblique vessel element end walls are confined to certain arboreal species. Most Passifloraceae exhibit both types of end walls. The only case of scalariform perforation plates is found in *Paropsia adenostegia*, a tree. Two further correlations may be noted: Opposite intervacular pitting and anomalous stem structure have been seen only in lianous species.

Overlooking the few obvious exceptions mentioned above, some important generalizations can be stated concerning stem anatomy in Passifloraceae. Vines have shorter vessel elements and broader vessels which are solitary in distribution. Furthermore, they possess fiber-tracheids and tracheids, along with fibriform vessel members. Trees, on the other hand, have longer vessel elements and narrower vessels which are inclined to be grouped in distribution; fibriform vessel members are absent. These generalized correlations of anatomical structure with habit can be interpreted reasonably only on a physiological, rather than on a phylogenetic, basis. Considered in conjunction with previous statements on the water-conducting system in lianas, and the special anatomical problems associated with these attenuated stems, it is easy to see that the xylem anatomy of these vines is particularly modified to increase the flow of water. Besides the evident facilitation of this process by the broad vessels composed of short elements, it is altogether likely that the fiber-tracheids, tracheids, and fibriform vessel members play an active part in support of this function. These anatomical modifications, coupled with others mentioned above, are doubtlessly related to water conduction in the lianous species. It is in the wood structure of the trees, therefore, that a search must be made for those anatomical modifications related to phylogenetic specialization in Passifloraceae.

The most reliable indicators of evolutionary trends in the xylem of dicotyledons are the development and subsequent specialization of vessels (Bailey 1957). Long, attenuated, angular vessel elements with many-barred scalariform perforation plates and scalariform intervacular pitting most closely resemble tracheids, and on this basis are regarded as most primitive. Short, truncated, rounded vessel elements with simple perforation plates and alternate intervacular pitting are least like tracheids and are considered most advanced. Correlations between trends of vessel specialization and concurrent modification of associated tissues have been employed in reaching conclusions relative to the phylogenetic development of imperforate tracheary elements, and radial and axial parenchyma, for example.

The totality of evidence from the xylem of arborescent Passifloraceae points to attainment of a moderate stage of phylogenetic specialization by these plants. Vessel elements average about



500  $\mu$  in length, less than the 649  $\mu$  average for 600 dicotyledons.<sup>2</sup> Vessel diameters average 80  $\mu$ , somewhat less than the 94  $\mu$  average for 1500 dicotyledons. Imperforate tracheary elements are considerably shorter on the average (582  $\mu$ ) than the 1317  $\mu$  average for 534 dicotyledons. Vessels are rounded in transverse section and pores are either predominantly grouped, or comprise grouped and solitary distributions. Intervascular pitting is alternate, and perforations are simple in all species; however, scalariform perforations also occur in *Paropsia adenostegia* and perhaps in other species. Imperforate tracheary elements are libriform wood fibers and fiber-tracheids; some species possess libriform wood fibers exclusively, but none exhibits solely fiber-tracheids. Vascular rays are largely heterocellular, although in *Paropsia schliebenii* and *P. vareciformis* homocellular rays have been recorded. Axial parenchyma is generally diffuse in nature, but the vasicentric configuration occurs in *Passiflora arborea* in conjunction with the diffuse and diffuse-in-aggregates types. Storied structure is absent in most species. Interestingly, the two species which show homocellular vascular rays also exhibit a tendency for storying in the rays. Storying and homocellular rays are often considered as advanced characteristics. Among the arboreal Passifloraceae on hand for this study, there does not appear to be any trend in xylem specialization to indicate an evolutionary series of any kind. Because Metcalfe and Chalk mention the occurrence of scalariform intervascular pitting and scalariform perforation plates in species and genera of which we have no representation (e.g., *Androsiphonia* and *Barteria*), it is likely that with a broader range of material trends of specialization in the xylem of the arboreal Passifloraceae would become evident.

Three types of anomalous stem development have been observed from ontogenetic studies. Material for these studies was available only in the genus *Passiflora*, although *Crossostemma laurifolium* also exhibits an anomalous stem. The anomalous growth in *Passiflora multiflora* is quite distinct, and is caused by the dilation of the parenchymatous elements of the xylem which disrupts the cambium, subsequently to form irregular masses of tracheary tissue. Thin-walled xylem parenchyma is necessary for the accomplishment of such a process. Although this type of anomalous development also occurs in *Bauhinia*—Leguminosae and in other plants it would be ludicrous to assume any genetic relationship here. Bailey (1957) has cautioned, that because "... similarities due to parallel evolution are surprisingly common in the xylem of dicotyledons" they cannot be utilized in positive assertions of relationship or phylogenetic

<sup>2</sup> Data on general anatomical averages are from appendices in Metcalfe and Chalk (1950).



derivation without corroborative evidence from other parts of the plant.

The unique stem in *Passiflora multiflora* appears to lend credence to Killip's original suggestion that the species be segregated into a genus on the basis of its sessile ovary. Along these lines it might be well to point out here the occurrence of anomalous stems and storied rays among several subgenera of *Passiflora*. These two features, thus, probably have little taxonomic significance on the species level.

Stern and Brizicky noted that anomalous stem structure, somewhat similar to that in *Passiflora multiflora*, also occurs in *Passiflora coccinea* (subgenus *Distephana*). Present studies indicate, however, that the anomalous stem growth in *Passiflora coccinea* results from tangentially unequal production of secondary xylem and phloem by the vascular cambium (interrupted type) and not from disrupted and displaced layers of cambium (dispersed type).

Earlier investigators (Masters 1871, Schenck 1893, Solereder 1908, Killip 1938, Metcalfe and Chalk 1950, Boureau 1957) may have overlooked the anomalous stem condition in Passifloraceae because it ordinarily becomes apparent only in the older portions of the stem not normally included in herbarium specimens. However, in *Passiflora glandulosa*, the unequal development of xylem and phloem proceeds very early in ontogeny. The time of attainment of the mature ontogenetic pattern is not consistent among the species studied, and it may be strictly genetic, or influenced by edaphic or other environmental stimuli.

From the above descriptions of the ontogeny of the stem in Passifloraceae, it appears that the most specialized and highly modified is the dispersed type of configuration exemplified by *Passiflora multiflora*. It might be of interest to speculate on the phylogenetic development of this type of stem in Passifloraceae, and upon its relationship, if any, to the other types described here. Reference to figures of this paper, and to the developmental sequences depicted in the Stern and Brizicky paper, points to the possibility that the dispersed type of vascular cylinder may have developed phylogenetically from the interrupted type by continued distention of cells in the parenchymatous groundmass to rupture the vascular cambium completely. This phenomenon would have to be coupled with, and preceded by, unequal production of secondary xylem and phloem. The ontogeny of the stem of *P. multiflora* shows stages of development representative of the interrupted type of configuration as seen in *P. glandulosa*. On the other hand, the production of included phloem in Passifloraceae might be viewed as another offshoot of the unequal production of secondary xylem and phloem. In this case, the unequal production



never became associated with rupturing of the vascular cylinder brought on by distention of cells in the parenchymatous groundmass, and the basic integrity of the vascular cylinder was continually maintained.

In the course of this investigation we observed cells that Woodworth (1935) termed "fibriform vessel members." Originally (1934), he assigned the name "perforated fiber-tracheids" to these same structures, which perhaps best describes these elements. Woodworth explained later, however, that "for purposes of definition, this descriptive phrase is unfortunate," because in effect it means, perforated, imperforate cells. Basically, these are elongate elements, similar in most respects to fiber-tracheids, except for the presence of simple perforations. From the structural standpoint, fibriform vessel members resemble fiber-tracheids on the one hand, and vessel elements on the other. They incorporate within the same cell the greater length and fusiform shape of the fiber-tracheid with the perforation plates of vessel elements.

Such a combination of features calls for a reconsideration of the basic distinction between the two cell types; that is, imperforate element *vs.* vessel (perforate) element. According to the *International glossary of terms used in wood anatomy* (Committee on Nomenclature 1957), a vessel is an axial series of cells where the cells have coalesced to form an articulated, tubelike structure of indeterminate length. This designation implies that a vessel may consist of but two cells interconnected by perforations; by definition, therefore, two axially aligned fibriform vessel members must be considered a vessel.

Even though the occurrence of the fibriform vessel member is greatly restricted taxonomically, and use of the term is correspondingly limited on this account, the name is inadequately descriptive, and more importantly, it has misleading phylogenetic implications. Woodworth was aware of these factors, and considered them in justifying the use of his term. In every respect these cells resemble imperforate tracheary elements except for the presence of perforations; they bear little resemblance to normal vessel elements in the same wood. Furthermore, the perforation is ordinarily intercalated between the ends of the cells, and the terminations of these cells have little if any similarity to the ligulate ends of normal vessel elements where ligulae occur. The perforation itself is aberrant, usually small in size, poorly formed, and unlike those in normal vessel elements. These cells are twice as long as the fusiform cambial initials from which they have been derived, and differ strongly from normal vessel elements in this way. It is extremely dubious that these cells are allied in any way, ontogenetically or phylogenetically, with true vessel elements. Therefore, to call these cells vessel members of any kind



would be to relate them, even if in name only, with normal vessel elements upon whose phylogenetic modification rests our entire scheme of evolution in the xylem. Because of these factors, we strongly urge the disuse of fibriform vessel member and the re-assumption of Woodworth's original term—perforated fiber-tracheid—to describe these cells despite the obvious ambiguity, viz, a tracheid, by definition, is an imperforate cell.

Although no extensive series of interconnected cells of this type was seen in the species studied, there are interconnections involving two, occasionally three, or even five such cells. Axial continuity between fibriform vessel members and fiber-tracheids also occurs, although no continuity between fibriform vessel members and true vessel elements was noted. That there is actual conduction of fluid between contiguous cells of fibriform vessel members and between fibriform vessel members, fiber-tracheids, and tracheids, is probable in view of the peculiar water transport problems of lianas. Woodworth, on the other hand, remarked that it seems unlikely that the fibriform vessel members contribute significantly to water movement in such plants. Regardless, it does seem entirely reasonable to assume that lianous plants require additional anatomical modifications, such as perforations in fiber-tracheids, to ensure a more efficient water conducting system even if the contribution of these modifications to total water transport is comparatively small. Woodworth examined the xylem of other lianas for fibriform vessel members and located them only in some species of Celastraceae. Notwithstanding the apparent advantage to water conduction in lianas of anatomical modification which would tend to facilitate this phenomenon, it is obvious that the genetic potential for such modification must exist as a preliminary requisite.

The perforated ray cell, which occurs in some species of Passifloraceae, has also been observed by Chalk and Chattaway (1933) in 73 species of 16 unrelated plant families. Different specimens of the same species vary considerably in the number of these cells present. Perforated ray cells are produced when axially oriented vessels bend tangentially to pass through one or more cells of a ray. Perforations in the ray cells usually correspond in kind to the normal perforations in associated vessel elements. Chalk and Chattaway have suggested that from the position of the rays, these cells are developed from ray initials instead of fusiform initials. Since perforated ray cells have such a wide distribution, and are so variable in occurrence even within species, their taxonomic significance is limited.

Pith flecks occur commonly in the species of *Passiflora*; that is, more regularly than if the presence were merely in response to a chance trauma. Although the occurrence of pith flecks is commonly



attributed to outside agents, such as the larvae of cambium miners, their consistent occurrence within the genus *Passiflora* may have minor taxonomic significance. *Passiflora* bark may be especially attractive to certain organisms which seek it out in preference to other food sources. The mutualistic relationship between ant species and myrmecophytes is an example of this kind.

*Paropsia*, considered previously in this study, has been variously placed in Flacourtiaceae and Passifloraceae. The wood anatomy of *Paropsia* shows considerable similarity to some genera of Passifloraceae, especially *Smeathmannia*, a genus comprising mostly shrubs and trees. Pores mainly in radial multiples, rounded; perforation plates simple in some species; vessel element end wall inclination oblique; alternate intervascular pitting; libriform wood fibers; the occurrence of abundant axial parenchyma; and fibriform vessel members, indicate affinity of *Paropsia* with Passifloraceae. The occurrence of axial parenchyma in *Paropsia* is significant, for this tissue is generally lacking in woods of the Flacourtiaceae (Record and Hess 1943; Tupper 1934). Pollen grain analysis provides further substantiation for aligning *Paropsia* with Passifloraceae. Erdtman (1952) has shown that pollen of both *Passiflora maculifoli* and *Paropsia brazzeana* has a reticulate sexine and measurements of the subprolate grains are  $52 \mu \times 44 \mu$  and  $53 \mu \times 41 \mu$ , respectively. He further suggests that the tribe *Paropsieae* of Flacourtiaceae should, at least in part, be referred to Passifloraceae. Convincing resolution of this problem will depend upon further studies in other botanical disciplines.

### Summary

1. Growth rings are absent or inconspicuously developed; rounded pores are mainly solitary and in radial multiples; simple perforation plates and alternate intervascular pitting occur in all species; vessel element end walls vary from oblique to transverse. Imperforate tracheary elements are tracheids, fiber-tracheids, and libriform wood fibers; fibriform vessel members occur in some species. Perforated ray cells are found in a few species. Vascular rays are both heterocellular and homocellular, uniseriate and multiseriate; uniseriate rays are commonly storied. Axial parenchyma is diverse in form and includes a range of types in both apotracheal and paratracheal series.

2. Certain anatomical modifications are correlated with plant form; lianas have shorter vessel elements and broader, solitary vessels; fibriform vessel members are present. Trees show longer vessel elements and narrower, grouped vessels; fibriform vessel members are generally absent. The anatomical modifications in the xylem



of lianas are related to physiology and habit rather than to phylogenetic position.

3. Xylem anatomy of tree species indicates that Passifloraceae is only moderately advanced phylogenetically.

4. Anomalous stem development occurs in *Crossostemma* and *Passiflora*. Ontogenetic series show four types of mature stem configurations in the family: (1) normal type; (2) included phloem type; (3) interrupted type; and (4) dispersed type. It is postulated that the dispersed type of configuration is the most highly modified anomalous stem form in Passifloraceae. It is doubtful that the anomalous stem condition here constitutes a valid taxonomic feature in assuming genetic relationships between Passifloraceae and other families, or that its occurrence provides a basis for taxonomic arrangement within the family.

5. The presence of abundant axial parenchyma and of fibriform vessel members in *Paropsia schliebenii* supports the position that *Paropsia* belongs to Passifloraceae rather than Flacourtiaceae.

6. The substitution of "perforated fiber-tracheid" for "fibriform vessel member" is recommended to avoid possible phylogenetic misconceptions related to the use of the word vessel in this descriptive sense.

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