

THE WOODS AND FLORA OF THE FLORIDA KEYS: CAPPARACEAE

By WILLIAM L. STERN,¹ GEORGE K. BRIZICKY, AND
FRANCISCO N. TAMOLANG²

Introduction

Capparaceae³ A. L. de Jussieu, are primarily a tropical and subtropical family of xerophilous and heliophilous trees, shrubs, vines, and herbs characterized by acrid juice. The family comprises about 45 genera with approximately 700 species which are widely distributed in the New and Old Worlds. Almost half the genera are monotypic. Representatives of two pantropical genera occur on the Florida Keys: the native *Capparis* L., and *Cleome* L., which is probably naturalized. The present study deals only with the woody *Capparis*. (An excellent discussion of the taxonomic status of Capparaceae, ecology, morphology, pollination mechanisms, and distribution, is given in Jacobs, 1960.)

Capparis is a pantropical genus of about 250 species, best represented in America and Africa. Pax and Hoffmann (1936) subdivided *Capparis* into 14 sections. These appear to be fairly natural, although they are based almost exclusively on exomorphic, and perhaps not always unquestionable, characters. Chromosome numbers are known for a few species ($2n=18, 30, 38, 40, 84$; Darlington and Wylie, 1956) and can hardly be of any assistance at the present time. The genus as a whole appears to be insufficiently known; more comprehensive investigations based on adequate material, and a revision would be desirable. The two species of *Capparis* which occur on the Florida Keys probably represent two sections of the genus, as noted below.

Capparaceae, usually placed in the order Rhoadales near Papaveraceae and Fumariaceae, are presently assumed to be most closely

¹ Previous numbers in this series appeared in the journal *Tropical Woods* (Yale University, School of Forestry) under the running title, "The Woods and Flora of the Florida Keys": "Introduction" by W. L. Stern and G. K. Brizicky, vol. 107, pp. 36-65, 1957; "Compositae" by S. Carlquist, vol. 109, pp. 1-37, 1958; "Goodeniaceae" by W. L. Stern and G. K. Brizicky, vol. 109, pp. 38-44, 1958; "Passifloraceae" by W. L. Stern and G. K. Brizicky, vol. 109, pp. 45-53, 1958; and "Wood Anatomy and Phylogeny of Batidaceae" by J. McLaughlin, vol. 110, pp. 1-15, 1959.

² Department of Botany, Smithsonian Institution, Washington, D.C.; Gray Herbarium, Harvard University, Cambridge, Massachusetts; and Forest Products Research Institute, University of the Philippines, College, Laguna, Philippines, respectively.

³ This taxon is more widely known as Capparidaceae. However, the authors have chosen to follow the recommendations in Appendix II, "Nomina familiarum conservanda," of the 1961 edition of the *International code of botanical nomenclature*, where the approved name is Capparaceae.

related to Cruciferae, with affinities to Moringaceae, Resedaceae, and Tovariaceae. Hutchinson's (1926) order Capparales ("Capparidales") has been considered by Takhtajan (1959) to comprise all the above-mentioned families and Koeberliniaceae. Papaveraceae and Fumariaceae are excluded. Data from the biochemistry of these families (Hegnauer, 1961) seem to be in favor of the Takhtajan delimitation of Capparales. However, conclusions based on these data should probably be considered preliminary, since the material investigated is inadequate.

This study is based in large part on the wood specimens listed in table 1; these are on deposit for reference in several institutions including the division of plant anatomy of the U.S. National Museum. Associated herbarium vouchers from the U.S. National Herbarium, and other institutions, have also been examined where necessary. Microscope slides of wood prepared expressly for this research are on deposit in the division of plant anatomy.

Capparis cynophallophora L. Sp. Pl. 504. 1753.

Capparis jamaicensis Jacq. Enum. Pl. Carib. 23. 1760.

The Jamaica caper, *Capparis cynophallophora*, is a shrub or small tree with lepidote branchlets. Leaves are elliptical, oblong-elliptical or narrowly elliptical, rounded or notched at apex, rounded at base, not conspicuously reticulate-veined, glabrous on the upper surface, rusty or silvery lepidote with peltate trichomes on the lower surface, and exstipulate. Flower buds are 4-angled. The opened flowers are about 3 cm. in diameter. Sepals are more or less equal (appearing 1-seriate), free, lanceolate to ovate-lanceolate, acute, and valvate in aestivation. The receptacular nectariferous glands are liguliform. Staminal filaments are purplish. The one-locular ovary develops a torulose fruit-body which is lepidote, and 20-30 cm. long. The seeds are more or less reniform, and the embryo is coiled (cochleate).

DISTRIBUTION.—*C. cynophallophora* occurs in exposed areas in the coastal hammocks on most of the Florida Keys. It can be found in similar habitats north to Pine Key, Boca Ciega Bay (Pinellas Co.) and Cape Canaveral (Brevard Co.) on peninsular Florida. The Jamaica caper probably occurs on all the West Indian Islands, southern Mexico, Central America, and northern South America. In Panama, specimens from both coasts have been seen.

Capparis flexuosa (L.) L. Sp. Pl. Ed. 2. 722. 1762.

Capparis cynophallophora L. Syst. Nat. Ed. 10. 2:1071. 1759.

Morisonia flexuosa L. Pl. Jamaic. Pug. 14. 1759; Amoen. Acad. 5:398. 1760.

The limber caper, *Capparis flexuosa*, is a glabrous shrub or small tree with leaves of similar shape to *C. cynophallophora* (fig. 1). However, in this species, they are conspicuously reticulate-veined and

glabrous, minutely stipulate, and each bears an oblong, axillary gland. Subglobular flower buds open into blooms about 5–7 cm. in diameter. The sepals are unequal (distinctly 2-seriate), the exterior ones smaller than the interior, somewhat connate at the base, subcircular, and distinctly imbricate in aestivation. Receptacular nectariferous glands are broad and low appearing as glandular spots or pits. The staminal filaments are white. The ovary is 2-locular in the material investigated by W. R. Ernst.⁴ Fruit-body (fig. 1) is continuous or somewhat torulose, glabrous, 10–20 cm. long; seeds are irregularly shaped, obliquely ellipsoidal, ovoid or obovoid, and slightly angular; the embryo is straight, and the cotyledons infold one another and cover the radicle with the lobes of their obliquely cordate bases.

DISTRIBUTION.—The range and habitat of *C. flexuosa* resemble those of the preceding, but this species appears to be more widespread. Specimens have been seen from as far north as Merritt Island (Brevard Co.) in Florida, from Mexican states on both coasts (north to Sinaloa on the west, and Tamaulipas on the east), from the West Indies, and from both coasts of Central America. The limber caper has been collected in Colombia, Ecuador, Venezuela, Paraguay, Trinidad and Tobago, and Brazil (Santa Catarina) in South America. Macbride (1938) thinks it probable that this species also occurs in Peru.

The nomenclatural confusion in which *Capparis cynophallophora* L. was usually known as *C. jamaicensis* Jacq., and *C. flexuosa* L. was known as *C. cynophallophora* L., was cleared up by Fawcett (1914). Although *C. cynophallophora* L. was placed into the section *Cynophalla* by Pax and Hoffmann (1936), the morphological characters⁵ of this species clearly show that it belongs to the section *Quadrella* where De Candolle (1824) had already placed it. Radlkofer (1884, 1887) confirmed the place of *C. cynophallophora* ("*C. jamaicensis*") in this section, the original description of which he emended by adding some anatomical characters of the leaves.

Xylem Anatomy

The transverse section of *Capparis cynophallophora* L. exhibits alternating concentric bands of cells which make up the groundmass of the wood. Cells in these bands are nonseptate fiber-tracheids. Bands with cells having conspicuously wider lumina and somewhat thinner walls alternate with bands comprising narrow-lumened fiber-tracheids with thicker walls. These bands vary considerably in width, and adjacent bands commonly merge to form irregular arcuate

⁴ Dr. Ernst has examined the Florida Keys capers in preparation for publishing "The genera of Capparaceae and Moringaceae in the southeastern United States" (1963).

⁵ Four-angled flower buds, lepidote pubescence, equal and valvate sepals, and the presence of sclerenchymatous idioblasts ("*spiculares*") in the mesophyll of leaves.

segments. That these are bands associated with growth is evident from their formation and arrangement, but whether they are reflective of climatic conditions is questionable.

Fiber-tracheids have obscurely bordered pits which average 1.6μ in diameter. The thickness of radial cell walls varies from thin to thick, and ranges from $0.62-4.20 \mu$ with an average of 2.07μ . The range in length of fiber-tracheids is from $292-661 \mu$ with an average of 487μ . Most cells fall between 415 and 523μ in length.

The wood is diffuse-porous and pores are moderately small ranging from $8-107 \mu$ in tangential diameter, averaging 62μ wide. Most are between 33 and 83μ in diameter. In transverse outline pores are circular to oval. There are normally 20 pores per square millimeter of which 24 percent are solitary. Mostly, however, pores are clustered and in radial multiples of 2-4 (5). Aggregations of pores present a complex picture appearing usually as somewhat irregular clusters of cells with one or two large central pores surrounded by several smaller, more or less wide-lumened cells. These aggregations, which shall be designated "pore complexes," consist of several cell types and modifications: "normal" vessels with regular elements, extremely narrow vessels, and axial parenchyma cells. Vessel element walls vary from thin to thick, from $1.7-5.0 \mu$, and average 3.8μ . Mostly they range between 3.3 and 8.3μ in thickness. Perforation plates are simple in even the very narrowest vessel elements, and are circular as viewed in the radial section. End walls of vessel elements (fig. 6) are mostly oblique and range from $0^\circ-55^\circ$ from the horizontal. Intervascular pitting is alternate, and the pits are crowded which sometimes produces angular pit borders. Pits are tiny, ranging from $2-3 \mu$ in diameter, and appear to be obscurely vested (cf. Bailey, 1933). However, this could not be determined with assurance on the sections available. Vessel elements average 192μ in length and range from $94-296 \mu$. Most vessel elements are between 139 and 235μ in length. Vessel-axial parenchyma pitting resembles the intervacular pitting in that it is alternate, but pits may be oblong in shape as well as circular.

Vascular rays (figs. 6, 7) as viewed on the tangential section are numerous and average 12 per mm. Most rays are uniseriate, but it is also common to see essentially uniseriate rays with short, bi- and triseriate central segments. Other rays are mostly bi- and triseriate throughout. Uniseriate rays are low and average 20 cells high (0.34 mm.). They vary from 4-30 cells ($0.29-0.46$ mm.) in height. The multiseriate rays are correspondingly low being roughly of the same dimensions as the uniseriate rays. Rays are essentially homocellular; that is, composed completely of procumbent cells (Kribs' homogeneous type I). Pitting between vascular ray cells and cells

of the axial parenchyma is alternate. Crystals occur more or less commonly in ray cells and fall within Chattaway's (1955) category 6, "rhomboidal, square or diamond-shaped."

Axial parenchyma is vasicentric consisting of a uniseriate sheath around pores or pore complexes, and sometimes it is also mixed among the cells in the complex. Crystals were not noted in axial parenchyma cells.

In *Capparis flexuosa* (L.) L., the banded nature of the imperforate tracheary elements of the groundmass (figs. 2, 3) as seen on the transverse section is not as sharply defined here as in the *C. cynophallophora* specimen described in the foregoing. The areas of narrow and wide-lumened cells are highly irregular, and the distinction between the areas is not sharp.

Imperforate tracheary elements of the groundmass are nonseptate fiber-tracheids characterized by small, minutely bordered pits (average 1.8μ in diameter). Radial thickness of cell walls varies from very thin to thick, and ranges from 0.62 – 6.14μ with an average of 2.25μ . Fiber-tracheids range from 292 – 584μ in length, averaging 418μ . The most frequent range is between 385 and 492μ .

The wood is diffuse-porous, the pores are circular to oval, and are moderately small varying from 21 – 96μ with an average of 56μ in tangential diameter (figs. 2, 3). Most are between 24 and 90μ in width. There are about 35 pores per square millimeter of which 6 percent are solitary and the remainder in radial groups of 2–10 (mostly 2–5) with many irregular clusters. Pore complexes (figs. 2, 3) consist of a few large pores surrounded by other cells as noted above under the description of *C. cynophallophora*. Walls of vessel elements range from thin to thick, from 1.5 – 7.5μ , and average 5.1μ . Perforation plates are simple in all vessel elements and circular to oval. Vessel elements have oblique end walls which vary from 0° – 70° from the horizontal. Intervascular pitting is alternate and crowded; the pits seem to be vested and are very small (2 – 4μ , average 3.2μ) with circular to somewhat angular borders. Vessel elements range in length from 63 – 261μ and average 175μ . The most frequent range is between 156 and 210μ . Vessel-axial parenchyma pitting is alternate and pits usually have circular borders.

Vascular rays as seen on the tangential section are numerous and average 10 per mm. Most rays are bi- and triseriate, uniseriate rays being of less frequent occurrence. Both uniseriate and multiseriate rays are low, the former ranging from 3–26 cells high (0.06 – 0.26 mm.), the latter ranging from 5–60 cells high (0.09 – 1.1 mm.). Rays are homocellular composed essentially of procumbent cells (Kribs' homogeneous type I). Multiseriate rays commonly have several-celled uniseriate wings. Pitting between ray and axial parenchyma

cells is alternate. Ray cells often contain crystals designated by Chattaway (1955) as "rhomboidal, square or diamond-shaped."

Axial parenchyma (figs. 2, 3) consists of a vasicentric sheath surrounding pores or pore groups. Strands may also occur among the vessels in the group. No crystals were seen in the cells of axial parenchyma.

Anatomical distinctions between the two species of *Capparis* collected from the Florida Keys, as described here, are slight. Minor variations in cell size occur, especially in the extreme ranges, but these are of little or no consequence considering the great coincidence of average figures and those for most frequent range. Most noticeable of the differences between the two species is the width of vascular rays. In *C. cynophallophora*, rays are largely uniseriate (figs. 6, 7), whereas in *C. flexuosa* bi- and triseriate rays predominate. Regardless, rays with bi- and triseriate segments occur in the former, and uniseriate rays appear in the latter. We may expect that this distinction then, is one of degree rather than the two conditions being mutually exclusive. A statistical analysis of many specimens of each species would doubtlessly determine the taxonomic validity of this potential anatomical distinction.

Analyses of Cells and Tissues

The descriptions above would seem to belie the complex nature of the wood, and especially the difficulties in interpretation of certain of the cellular components. In order best to interpret and evaluate the constituent elements of the wood in the Florida Keys capers, and for purposes of comparison, prepared slides of all species of *Capparis* were borrowed from the Samuel James Record Memorial Collection at Yale University; wood specimens of *Capparis* from the National Collections of wood were examined; and fluid-preserved specimens of the Keys species of *Capparis* were specially gathered for this study. All wood samples employed in these studies were associated with corresponding herbarium vouchers except as noted in table 1.⁶ Furthermore, wherever possible vouchers were examined to substantiate the authenticity of identification; in some doubtful cases twigs from vouchers were examined microscopically and compared with the wood samples to assure concurrence.

⁶ The authors are deeply indebted to Dr. Graeme Berlyn and Mr. Richard A. Mark of Yale University for the privilege of examining *Capparis* slides and some herbarium vouchers from the Record Memorial Collection, and to Mr. John R. Millar of the Chicago Natural History Museum for allowing us to see and compare herbarium vouchers of *Capparis* with wood specimens used for comparative studies. Dr. James A. Duke of the Missouri Botanical Garden aided in verifying the identification of some herbarium vouchers on deposit in St. Louis and for sending us bits of twigs for comparison. For his help in preparing slides, and for other kindnesses, the authors are grateful to Mr. Edward S. Ayensu, research assistant at the Smithsonian Institution. Particular gratitude is due Mr. George Stevenson of Plantation Key, Florida, and Dr. P. B. Tomlinson of the Fairchild Tropical Garden in Miami, Florida, for their most kind assistance in collecting fluid-preserved stems of *C. flexuosa* and *C. cynophallophora* together with herbarium vouchers.

GROUNDMASS.—After a preliminary study of the material on hand, we found that a convincing interpretation of the cells and tissues of the wood of *Capparis* would require fluid-preserved specimens. But nowhere was this need more strongly felt than in the correct identification of the cells comprising the tissues surrounding the pore complexes to be described below. Bands are more or less obvious on the transverse section of all woods examined (figs. 2, 3), except for *C. nitida* (fig. 4) and *C. schunkei*. At first it seems obvious that these bands are merely rings of growth demarcated by alternating layers of thick- and thin-walled imperforate tracheary elements. But, in *C. pulcherrima* and *C. angulata* (figs. 10, 11), it seems equally apparent that at least some of the bands are truly and purely parenchymatous. In certain species, e.g., *C. decidua*, a confounding of bands occurs; some seem to be totally prosenchymatous and others at least partly parenchymatous. One is tempted here to call this arrangement boundary parenchyma after the definition of Jane (1956). In *C. nitida* (fig. 4) and a few other species pore complexes are much simplified and seem to consist of a solitary pore, a short radial multiple, or a small cluster surrounded by a several- to many-seriate sheath of vasicentric parenchyma. In the slides prepared from previously dried wood, certain groundmass cells which look like imperforate tracheary elements (fibers) take on some of the characteristics of parenchyma (compare fig. 2 with fig. 3), i.e., cytoplasmic remains are present within the lumina. This was indicated by the strong affinity for haematoxylin shown by the cell contents. Walls are thinner in these cells than in adjacent prosenchymatous elements, and the compound middle lamella seems thicker and possesses a great affinity for haematoxylin and little for safranin. The foregoing observations raised questions in the minds of the authors which seemed solvable only after the examination of fluid-preserved rather than dried tissues.

For purposes of cytological examination, the fluid-preserved collections of Stevenson (Newcomer's fixative) and Tomlinson (F. A. A.) were utilized. In all, five specimens were available: two of *C. flexuosa*, two of *C. cynophallophora*, and a single, unnamed specimen from the Fairchild Tropical Garden. Our observations indicate that in the specimens of *Capparis* investigated a well-formed fusiform nucleus is present in every imperforate tracheary element, from bark to the inner edge of the radial section (i.e., for a distance of 6–10 mm.), in all but the Stevenson collection of *C. cynophallophora* (fig. 13). Here, the innermost elements lack a nucleus. Furthermore, starch grains occlude the cell cavity completely, except for the narrowed tips, of practically all imperforate tracheary elements in the specimens of *C. flexuosa* (fig. 13). In *C. cynophallophora* starch occurs mostly in the thick-walled imperforate tracheary elements at the margins of "growth

rings," but not in every cell. As in *C. flexuosa*, starch grains totally occlude the cell cavity. In the unnamed Tomlinson specimen starch occurs in bands corresponding to the alternating layers of thick- and thin-walled imperforate tracheary elements—it is present only in the thick-walled cells.

We may assume from the above that the imperforate tracheary elements of the groundmass in the five *Capparis* specimens under analysis, partake of the nature of parenchymatous cells. It is probable that they continue to perform vital as well as mechanical functions long after formation by the vascular cambium. In this connection it is interesting to consider Carlquist's (1961) remarks, which point out the possibility of axial parenchyma cells arising from libriform wood fibers through the mechanism of "fiber dimorphism."

These findings contrast strongly with the widely held characterization of imperforate tracheary elements as being dead at ontogenetic maturity. The living nature of these cells is indicated by the presence of a presumably functioning protoplast which, among other activities, stores starch. The cell wall pitting in these elements, however, consists of tiny vestigially bordered or simple pit-pairs, whereas in vascentric parenchyma cells in the same specimen the pit-pairs are as large as intervascular pits, simple, half-bordered, or even fully bordered.

Fahn and Leshem (1963), in a study of xylem anatomy of woody desert plants from Israel and other woody plants native to Switzerland, reported living fibers in 70 percent of 60 species in 24 plant families. Furthermore, they state that fibers over the entire sapwood contained living protoplasts. Included in their study was *Capparis spinosa* L. which showed living fibers in the xylem. Esau (1953) mentions that "In contrast to other wood fibers, the septate forms long retain their protoplasts and serve for storage of starch, oils" Cumbie (1960) also mentions the presence of nucleated fibers in certain transitional herbaceous-woody legumes, and Carlquist has remarked on the presence of these in Compositae in correspondence with the authors. Harrar (1946) examined the wood of over two thousand species of plants from the Yale collections and recorded the presence of starch in the septate fiber-tracheids of many hundreds of these. It is reasonable to assume that these starch-containing cells, especially in sapwood, are living, and Harrar also believes they may function in a manner similar to axial parenchyma.

It is likely that further cytological studies based on fluid-preserved material of the stem will force us to revise, or at least to broaden, our currently held notions as to the physiological condition of the imperforate tracheary element. Our observations here, and those of Fahn, indicate relatively long-lived protoplasts in imperforate trache-

ary elements; furthermore, it is not only the septate fiber-tracheids which retain their vital functions for more or less long periods after formation; the phenomenon may also occur in nonseptate elements. The universality of this phenomenon still remains to be tested.

Interesting physiological questions concern the ultimate fate of this stored starch. If it is dissolved and subsequently transported, must a still-living cell be postulated? How does the dissolved starch pass from the storage cells to where it is "needed" elsewhere in the plant? The tiny pits in libriform fibers and fiber-tracheids would certainly present a significant barrier to free passage. Even then, through what cells would the dissolved starch be conducted?

These observations on fluid-preserved wood, coupled with those on previously dried wood, helped us considerably to interpret with a degree of assurance, the nature of the groundmass cells in *Capparis*. By and large, the cells of the groundmass are imperforate tracheary elements, either libriform wood fibers or fiber-tracheids.

AXIAL PARENCHYMA.—The growth rings are not to any extent dependent for distinction upon the occurrence of boundary parenchyma, and are visible because of alternating layers of thick- and thin-walled fibers (figs. 2, 3). The situation in *C. decidua*, where axial parenchyma cells are involved in growth-ring margins, is of sporadic occurrence on the transverse section, and is dependent on the presence of closely adjacent, tangential rows of pore complexes next to the growth-ring margin. The seemingly apotracheal parenchyma cells are in reality vasicentric parenchyma cells mixed among the cells of the groundmass at the growth-ring boundary.

All species have narrow sheaths of vasicentric parenchyma surrounding the pore complexes (figs. 2-4, 10, 11). Cells adjacent to these narrow sheaths which appear parenchymatous, as in *C. nitida* (fig. 4), are merely thin-walled, wide-lumened, imperforate tracheary elements as described above. In two species, *C. pulcherrima* and *C. angulata* (figs. 10, 11), true banded axial parenchyma occurs, as well as the vasicentric, and sometimes aliform and confluent configurations. These bands are composed of several uniform cell layers which contrast strikingly with the parenchymatous-appearing, thin-walled, prosenchymatous cells that mark the boundaries of growth rings in other species.

PORE COMPLEXES.—All species of *Capparis* investigated were characterized by the presence of more or less complicated groupings of pores and associated cells as observed on the transverse section (figs. 2, 3, 10, 11). These pore complexes consist of a few large vessels, a variable number of small vessels, sometimes imperforate tracheary elements, and always associated axial parenchyma. As indicated previously the latter is always paratracheal, forming a complete

sheath around the pore complex, and sometimes strands are intermixed among other elements within the complex. Parenchyma cells are relatively thick-walled and lignified. The tiny vessel elements which occur in association with the large vessel elements are interesting in that they always possess simple perforations (figs. 2, 3, 11, 12). They may be narrower than adjacent imperforate tracheary elements; sometimes they are imperfect and contain only a single perforation; and occasionally perforations appear on the axial walls.

To interpret these complexes solely on the transverse section is impossible. It is hardly possible to distinguish tiny pores from transverse sections of associated imperforate tracheary elements (figs. 2, 3, 10, 11). Without doubt then, our analyses of pore groupings are in error—an error difficult to overcome, for if there is a single feature of the wood which might be said to characterize *Capparis*, it is the pore complex described above.

VASCULAR RAYS.—Vascular rays in *Capparis* are essentially homocellular and are composed of procumbent cells (figs. 5–9). However, in a number of species—*C. decidua*, *crotonantha*, *linearis*, *oxysepala*, *quina*, *schunkei*, *tenuisiliqua*, *verrucosa*, and *angulata*—rows of squarish marginal cells are of sporadic occurrence, and it is possible that this phenomenon occurs in all species of *Capparis* to a certain extent. In some of the species examined other peculiarities are present to a more limited extent. Thus, inflated ray cells which resemble secretory cells of some lauraceous woods occur in *C. ferruginea*, *nobilis*, *quina*, and *tenuisiliqua*; and sheath cells are of infrequent occurrence in the rays of *C. nobilis*, *schunkei*, *verrucosa*, and *angulata*. Seriation of rays varies from 1–7 cells wide. Height of uniseriate rays is from 1–22 cells, of the multiseriate rays, from 3–55 cells (figs. 6–9).

OTHER FEATURES.—Storied structure occurs in only one of the species studied, *C. angulata* (fig. 9). The cells which comprise bands of parenchyma, and the vessel elements, are in marked seriation as viewed on the tangential section. Cozzo (1944, 1946) and Cozzo and Cristiani (1950) record partial storying in *C. salicifolia* Gris. and *C. tweediana* Eichl. Rhomboidal crystals were observed in most of the species under investigation, and it is probable that all species of *Capparis* possess the genetic potential to form crystals under conducive environmental circumstances. Most commonly, crystals were found in the ray cells, but sometimes they were also observed in the cells of the axial parenchyma.

Phylogenetic Specialization in the Wood

The structure of the wood of *Capparis* is indicative of a high level of evolutionary specialization, as shown by the presence of simple perforation plates in vessels and alternate intervascular pitting (figs.



FIG. 1. *Capparis flexuosa* (L.) L., Crawl Key, Florida; upper portion of shrub showing mature fruits, $\times 1/4$ (W. L. Stern 1519, US).

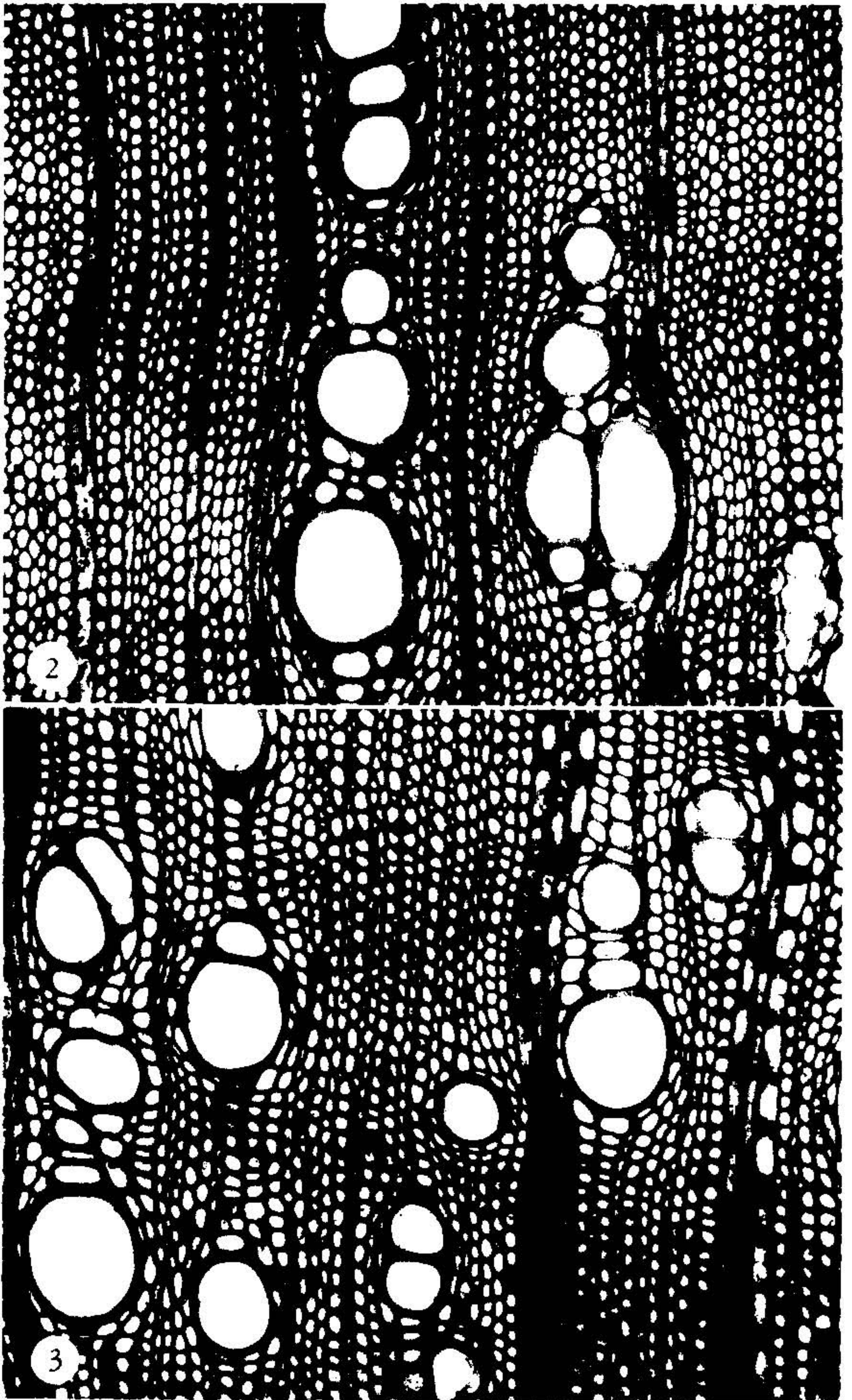


FIG. 2. *Capparis flexuosa* (L.) L., transverse section of wood illustrating pore complexes, and uniseriate sheath of vasicentric axial parenchyma which is discernible in this material prepared from fluid preserved tissues, $\times 160$ (*G. Steyermark*, n. U.Sw. 30300). FIG. 3. *C. flexuosa* (L.) L., transverse section for comparison with figure 2. Notice that on this section, prepared from dried tissues, it is not possible to distinguish the uniseriate sheath (axial parenchyma) from the surrounding imperforate cells, $\times 160$ (*J. G. Jack*, 5033,

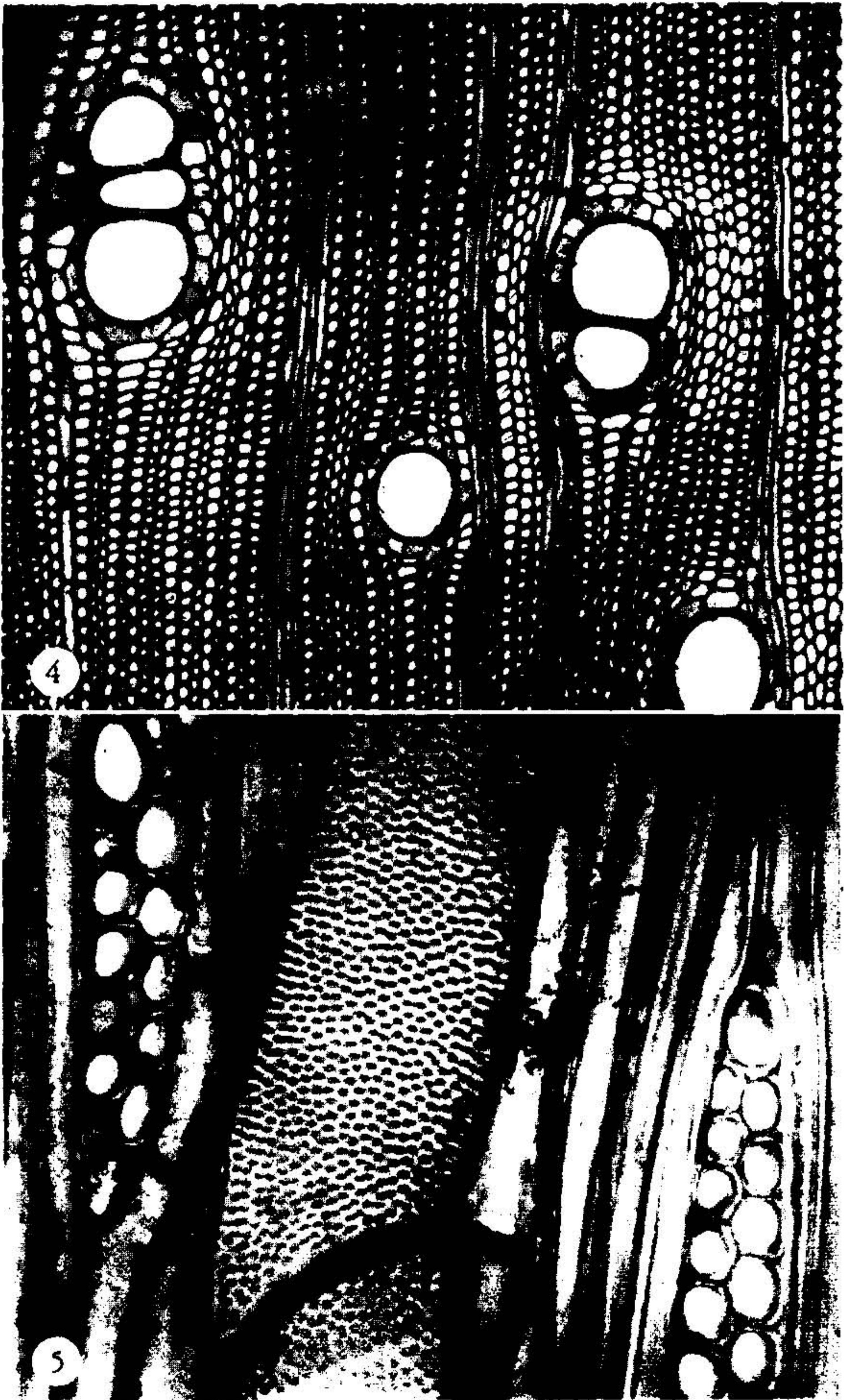


FIG. 4. *Capparis nitida* Ruiz & Pav., transverse section of wood illustrating easily visible sheath of uniseriate vascentric axial parenchyma, and uncomplicated arrangement of pores, $\times 160$ (*Ll. Williams 5725*, Yw 18819). FIG. 5. *C. tarapotensis* Fisch., tangential section of wood showing alternate intervacular pitting, and homocellular vascular rays composed solely of procumbent cells, $\times 645$ (*Ll. Williams 6051*, Yw 19028).

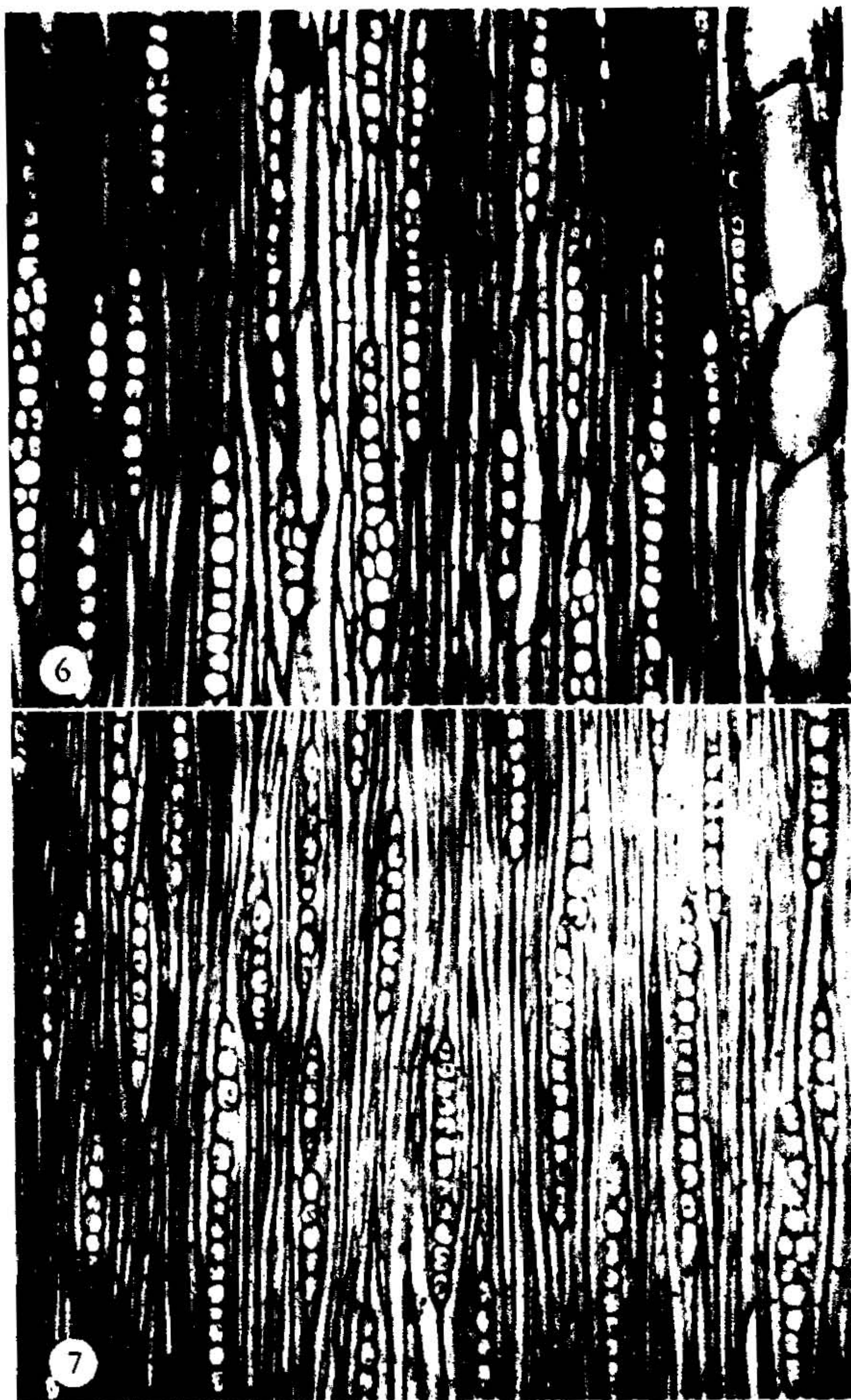


FIG. 6. *Capparis cynophallophora* L., tangential section of wood, $\times 200$ (G. Stevenson s.n., USw 30299). FIG. 7. *C. cynophallophora* L., tangential section of wood, $\times 200$ (P. B. Tomlinson 19.111.62.1). Vascular rays in these sections are illustrative of Group I type; mostly uniseriate with occasional biseriates bearing uniseriate extensions.



FIG. 8. *Capparis vitida* Ruiz & Pav., tangential section of wood showing Group II vascular rays; multiseriate and fusiform. $\times 160$ (*L. Williams*, 5725, Yw 18819). FIG. 9. *C. angulata* Ruiz & Pav., tangential section of wood showing Group II vascular rays, stored fusiform axial parenchyma cells, and stored vessel elements. $\times 160$ (*F. Wojtkowski*, 5672, USw 16017).

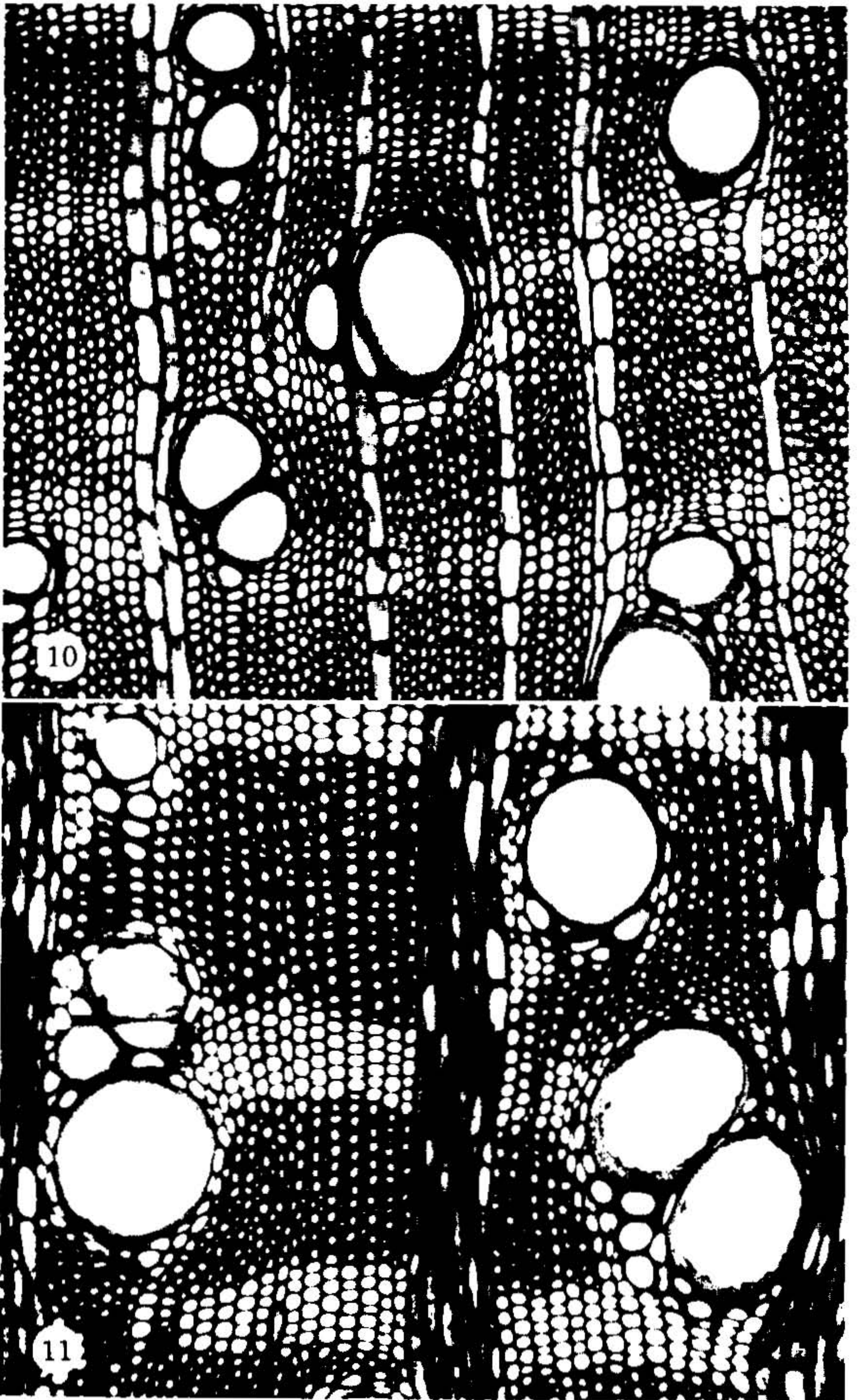


FIG. 10. *Capparis puberula* Jacq., transverse section of wood to illustrate banded axial parenchyma. $\times 100$ (*J. Dugand 195: 159, Yw 23936*). FIG. 11. *C. annulata* Ruiz & Pav., transverse section of wood to illustrate banded axial parenchyma. $\times 100$ (*F. H. S. 19672, USw 14017*).

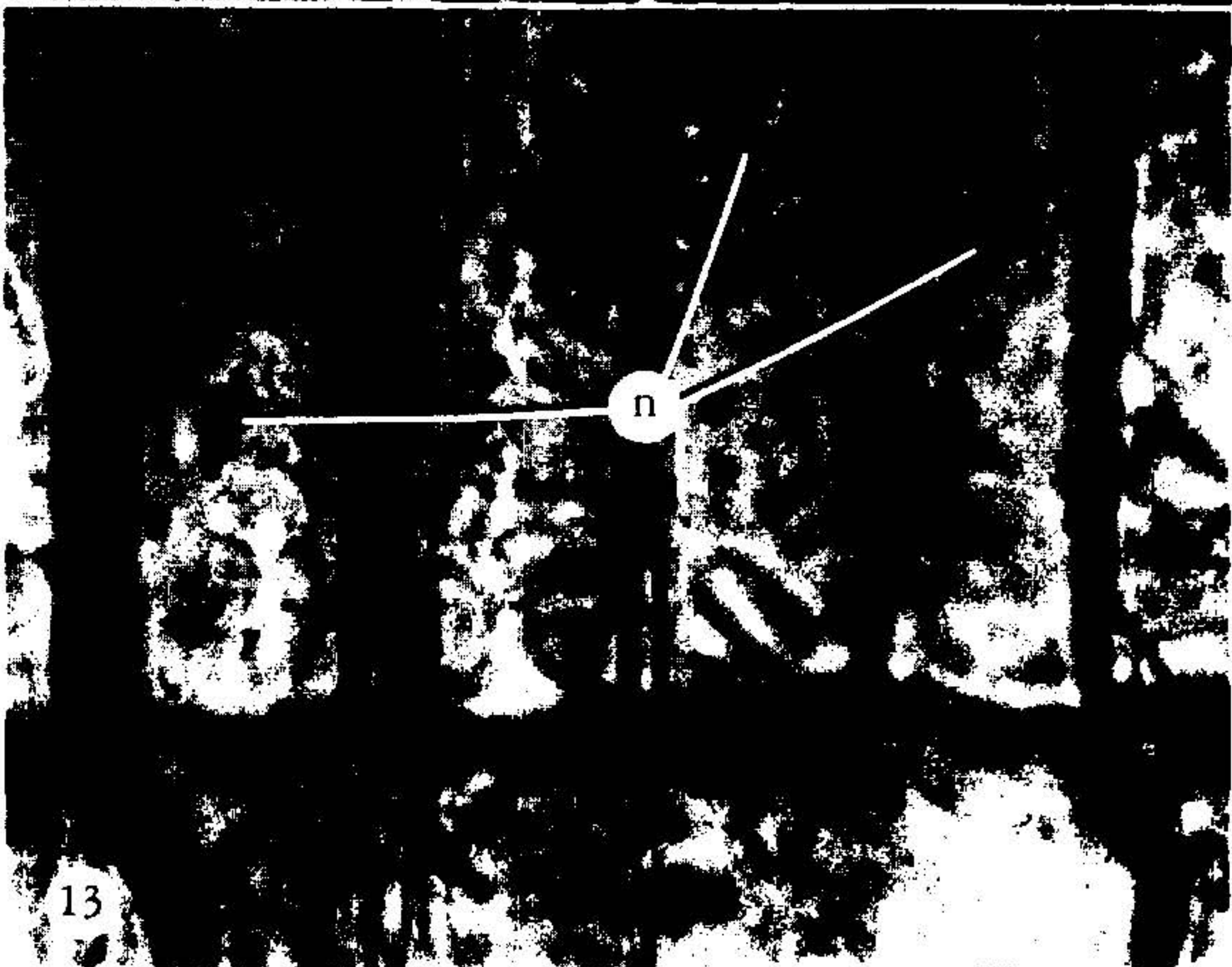
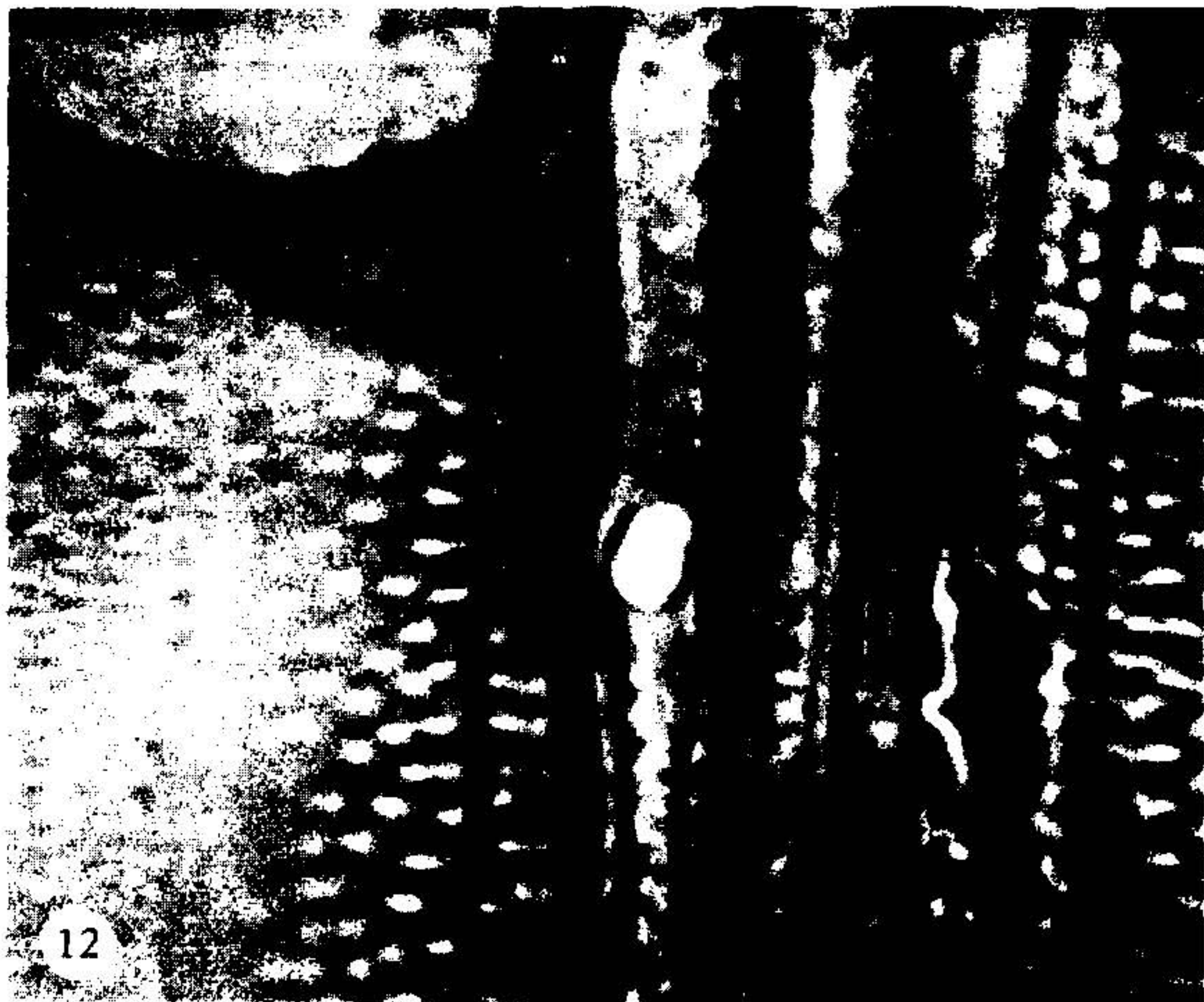


FIG. 12. *Capparis tenuisiliqua* Jacq., radial section of wood to show simple perforation in tiny vessel element (center) associated in complex with vessel of normal diameter (left). - 1800 (S. J. Record 80, Yw 16479). FIG. 13. *C. flexuata* (L.) Lam., radial section of wood to demonstrate presence of fusiform crystals in fiber tracheids at 1 cm. distance from vascular cambium; starch grains are also visible in the lamina of the fiber tracheids. - 1875 (G. Steud. ex Gr., USw 30300).

5, 9, 12), the highly peculiar pore complexes (figs. 2, 3, 10, 11), paratracheal parenchyma and other parenchyma modifications (figs. 2-4, 10, 11), homocellular vascular rays (figs. 5-9), and imperforate tracheary elements with simple or vestigially bordered pits. This fact causes us to wonder at the relatively low taxonomic placement of Capparaceae and the comparative primitiveness of the families with which it is ordinarily associated in some schemes of plant classification.

The authors appreciate that the phylogenetic position of a family containing 45 genera cannot be established through a brief study of one genus using a single criterion, i.e., xylem anatomy. It is suggested, however, that Capparaceae, with almost 50 percent monotypic genera, may be a highly derived taxon in which the evolutionary links among the genera have passed out of existence over the ages. What remains today are the end-products of evolution; the connecting stages, in the form of transitional taxa, are extinct.

Bessey (1914) derives the Rhocadales (containing Capparaceae) directly from Ranales; Engler and Diels (1936) also place Rhocadales in close association with Ranales; and in the Bentham and Hooker (1862) system, Capparaceae are placed in the Parietales next to Ranales. Wettstein (1935) treats Capparaceae in Rhocadales and mentions that they are related to both Cruciferae and Papaveraceae. Furthermore, he states that Capparaceae contain the types from which the Cruciferae could have arisen. Pax and Hoffman (1936) say that without doubt Capparaceae belong in Rhocadales and are most closely allied to Cruciferae.

In light of the above, it is rather interesting to examine the position of Capparaceae in Hutchinson's (1959) treatment. Here they occur quite high in the Lignosae as the type of Capparales. He derives this order from the Dilleniales via Bixales and Pittosporales. Hutchinson regards the similarity in flower and fruit structure between Cruciferae and Capparales as parallel evolution. Furthermore, in addition to Capparaceae, Hutchinson includes Moringaceae and Tovariaceae (*Tovaria* is included in Capparaceae by Bentham and Hooker) in Capparales. Takhtajan (1954), like Hutchinson, gives Capparales a more derived placement in his scheme. He shows the order emanating from Cistales, along with Cucurbitales, Salicales, and Tamaricales. However, Takhtajan (1959) retains Cruciferae in Capparales, whereas Hutchinson includes it in Cruciales, a separate order.

Capparis wood differs markedly from that in some families ordinarily associated with Capparaceae (i.e., Papaveraceae, Cruciferae, and Resedaceae), in having homocellular rays consisting solely of procumbent cells. The pore complexes described above for *Capparis* have not been recorded in the woods of the Papaveraceae, Cruciferae,

or Resedaceae which are anatomically specialized along other lines (cf. Metcalfe and Chalk, 1950). In certain respects, the wood of *Moringa* resembles *Capparis* in that rays are homocellular and storied axial parenchyma is present. Metcalfe and Chalk (1950) place some emphasis on the presence of myrosin cells in parietalean taxa as a significant indicator of relationship. All the taxa mentioned above possess myrosin cells except Papaveraceae (Hegnauer, 1961). It is noteworthy in this regard that Moringaceae, which Hutchinson considers in his taxonomically elevated Capparales, is placed by Bentham and Hooker in Sapindales. Without the benefit of detailed anatomical and associated studies in the other genera of Capparaceae, and comparative investigations into the anatomy of Papaveraceae, Cruciferae, Resedaceae, and Moringaceae, a brief survey such as this of the anatomy of families reputedly related to Capparaceae can only lead to wild speculation. It is sufficient to say that our study lends some anatomical support to Takhtajan's and Hutchinson's placement of Capparaceae in a separate order, more highly placed than the parietalean families with which it is usually associated.

Anatomically, the most highly advanced species among those investigated appears to be *C. angulata*. That this is so is indicated by the combination of pronounced storying among the cells of the axial parenchyma and vessels, coupled with the highly modified banded, vasicentric, aliform, and confluent parenchyma distribution (figs. 9, 11). *C. pulcherrima* is also more highly specialized than the other species; it lacks the storied structure of *C. angulata*, but exhibits the same kind of parenchyma specialization (fig. 10).

Intragenetic Alignment

The species of *Capparis* can be divided into two groups based upon the seriation of rays. At first it seemed desirable to make a separation into three groups: (1) species with uniseriate rays, (2) species with rays having short multiseriate segments supporting several- to many-celled uniseriate wings, and (3) species with multiseriate rays and only a single apical cell, i.e., fusiform as viewed in the tangential section. However, closer scrutiny caused us to alter our course and to unite the first two groups. We found that woods with predominantly uniseriate rays always had some rays which fell into the second group, and woods in the second group often had many uniseriate rays (figs. 6, 7), so that apparently no consistent separation between groups 1 and 2 could be made (cf. remarks on anatomical distinction between *C. flexuosa* and *C. cynophallophora*). Therefore, only two groupings, based on ray width, were devised: (I) species with predominantly uniseriate rays, or with rays composed of short bi- (or tri-) seriate segments having conspicuous several- to many-

celled, uniseriate extensions (figs. 6, 7), and (II) species with predominantly multiseriate rays which appear fusiform on the tangential section and possess only one or two cells at their apices (figs. 8, 9). Further studies involving more species might show transitions between these two groups, but on the basis of this investigation they appear sufficiently exclusive of each other.

The species studied in our investigation were dispersed into the sections of *Capparis* recognized in the treatment of Pax and Hoffmann (1936). The appropriate ray classification was placed next to each binomial and the results are outlined in table 2. Although representation of species in the various sections is in some cases meager, it is noteworthy, excepting section *Cynophalla*, that the sections are homogeneous with respect to the ray type shown. Whether this taxonomic-anatomic device would stand up if further species were introduced, remains to be shown. Or, as may be the case in *Cynophalla*, the anatomical evidence may indicate a lack of taxonomic homogeneity within the section. Substantiation for the latter was mentioned previously. Recent work of W. R. Ernst has shown that *C. cynophallophora* belongs in section *Quadrella*, rather than *Cynophalla*.

Summary

Although *Capparis flexuosa* and *C. cynophallophora* are easily separated, even by their gross foliar morphology, the anatomical distinctions are more subtle, and possibly less reliable. In *C. cynophallophora*, vascular rays are largely uniseriate, whereas in *C. flexuosa*, bi- and triseriate rays predominate.

Observations made on sections cut from fluid-preserved material, showed that the banding in the wood of the two capers from the Florida Keys, and in other species, is caused solely by alternating layers of thick- and thin-walled prosenchymatous cells. Axial parenchyma is strictly paratracheal and is not normally a part of these bands. The groundmass is purely prosenchymatous. Fiber-tracheids in *C. flexuosa* and *C. cynophallophora* may remain living for longer or shorter periods after formation by the vascular cambium and ontogenetic maturity takes place in these cells. This phenomenon is probably more widespread than heretofore realized.

The wood anatomy of *Capparis* can be characterized by the presence of pore complexes, alternate intervascular pitting and simple perforation plates, paratracheal parenchyma, homocellular vascular rays, and imperforate tracheary elements with simple or vestigially bordered pits. Also, certain species exhibit storied structure. These features are all associated with phylogenetic advancement and indicate that

Capparis, and possibly Capparaceae, occupies a more derived position than it is usually afforded.

Using the seriation of vascular rays, the species of *Capparis* can be separated into two groups. These groups follow the Pax and Hoffmann sectional delimitations of the genus except for the section *Cynophalla*, which appears anatomically heterogeneous. Floral studies of the two Keys species of *Capparis*, both placed in *Cynophalla* by Pax and Hoffmann, give taxonomic support to this suggestion. More intensive studies on a broader sampling of species will probably produce at least two more anatomical features useful in separating the species of *Capparis*: configuration of the axial parenchyma, and presence or absence of storying. Application of these features will serve to test the proposed separation of *Capparis* by ray seriation, and may enable us further to refine our anatomical system.

TABLE 1.—*Specimens of Capparis wood examined*

[Citation of specimens follows the recommendations of Stern and Chambers (1960). WOOD COLLECTIONS: (USw) Smithsonian Institution, (Yw) Yale University School of Forestry. HERBARIA: (MO) Missouri Botanical Garden, (NY) New York Botanical Garden, (US) Smithsonian Institution, (Y) Yale University School of Forestry, (A) Harvard University Arnold Arboretum, (GH) Harvard University Gray Herbarium, (F) Chicago Natural History Museum, (Ilanoth) National and University Institute of Agriculture, Lev Hasharon, Israel.]

<i>Species and Authority</i>	<i>Collector and No.</i>	<i>Country of Origin</i>	<i>Wood Collection Catalog No.</i>	<i>Location of Vouchers</i>
angulata Ruiz & Pav.	F. Woytkowski 5672	Peru	USw 16017	MO
baducca L.	B. A. Krukoff 4665	Brazil	USw 9145	NY, US
baducca L.	B. A. Krukoff 4889	Brazil	USw 9248	NY, US
cynophallophora L.	J. G. Jack 5715	Cuba	Yw 16674	Y, A
cynophallophora L.	J. G. Jack 5809	Cuba	Yw 16695	?
cynophallophora L.	J. G. Jack 6742	Cuba	Yw 16746	?
cynophallophora L.	W. L. Stern & G. K. Brizicky 262	U.S.A. (Fla. Keys)	Yw 51100	Y, US
cynophallophora L.	G. Stevenson <i>s.n.</i>	U.S.A. (Fla. Keys)	USw 30299	US
cynophallophora L.	P. B. Tomlinson 19.III.62A	U.S.A. (Fla.)	USw 30301	US
crotonantha Standl.	G. P. Cooper 660	Panama	Yw 12293	Y
decidua (Forsk.) Edgew.	Conserv. Forests Punjab <i>s.n.</i>	India	Yw 844	
ferruginea L.	G. C. Bucher 4	Cuba	Yw 15999	Y
flexuosa (L.) L.	J. G. Jack 5633	Cuba	Yw 16629	Y, A
flexuosa (L.) L.	W. L. Stern & G. K. Brizicky 236	U.S.A. (Fla. Keys)	Yw 51079	Y, US
flexuosa (L.) L.	G. Stevenson <i>s.n.</i>	U.S.A. (Fla. Keys)	USw 30300	US
flexuosa (L.) L.	P. B. Tomlinson 18.III.62A	U.S.A. (Fla.)	USw 30302	US
galeata Fresew.	M. Chudnoff <i>s.n.</i>	Israel	USw 18238	Ilanoth 85
linearis Jacq.	H. M. Curran & M. Haman 424	Venezuela	Yw 2797	US, GH
magnifica Gilg ex Ule	B. A. Krukoff 5788	Brazil	USw 9803	NY
nitida Ruiz & Pav.	Ll. Williams 5725	Peru	Yw 18819	US, F
nobilis F. Muell.	"Commercial sample"	Australia	Yw 19327	
odoratissima Jacq.	H. M. Curran & M. Haman 500	Venezuela	Yw 2814	US

TABLE 1.—*Specimens of Capparis wood examined*—Continued

<i>Species and Authority</i>	<i>Collector and No.</i>	<i>Country of Origin</i>	<i>Wood Collection Catalog No.</i>	<i>Location of Vouchers</i>
odoratissima Jacq.	Espina & Giacometto B9-A	Colombia	Yw 20991	Y
odoratissima Jacq.	G. Newhall & H. Pittier 11	Venezuela	Yw 19929	Y
oxysepala C. Wright ex Radlk.	R. S. Flores (FM 613234)	Mexico	Yw 21317	F
portoricensis Urban	N. L. Britton & W. Kramer XVII	Puerto Rico	Yw 3090	Y
pulcherrima Jacq.	A. Dugand 495; 159	Colombia	Yw 23936	Y
quina Macbr.	Ll. Williams 5753	Peru	Yw 18826	F, US
schunkei Macbr.	Ll. Williams 4118	Peru	Yw 18378	F, US
schunkei Macbr.	Ll. Williams 4820	Peru	Yw 18588	F, US
schunkei Macbr.	Ll. Williams 6692	Peru	Yw 19045	F
sola Macbr.	F. Woytkowski 5826	Peru	USw 18268	MO
tarapotensis Eichl.	Ll. Williams 6654	Peru	Yw 19028	F, US
tenuisiliqua Jacq.	S. J. Record 80	Colombia	Yw 16479	Y, GH
tenuisiliqua Jacq.	S. J. Record 69	Colombia	Yw 16468	Y, GH
verrucosa Jacq.	S. J. Record 44	Colombia	Yw 16443	Y, A
verrucosa Jacq.	S. J. Record 68	Colombia	Yw 16467	Y
verrucosa Jacq.	S. J. Record 82	Colombia	Yw 16481	Y, A, GH
sp.	B. A. Krukoff 6184	Brazil	USw 7539	NY
sp.	P. B. Tomlinson 19.III.62B	U.S.A. (Fla.)	USw 30303	US

TABLE 2.—Anatomical subdivision of *Capparis* based on ray structure

<i>Par & Hoffmann Section</i>	<i>Species</i>	<i>Ray Type</i>
Capparis ("Eucapparis")	<i>galeata</i>	II
Cynophalla	<i>cynophallophora</i>	I
	<i>flexuosa</i>	I
	<i>tarapotensis</i>	II
	<i>nitida</i>	II
	<i>verrucosa</i>	I
	<i>portoricensis</i>	II
	<i>linearis</i>	I
Mesocapparis	<i>crotonantha</i>	II
Homback	<i>decidua</i>	II
Capparidastrum	<i>tenuisiliqua</i>	I
	<i>oxysepala</i>	I
	<i>badueca</i>	I
	<i>quina</i>	I
	<i>sola</i>	I
Quadrella	<i>odoratissima</i>	I
Colicodendron	<i>schunkei</i>	II
	<i>angulata</i>	II
Calanthea	<i>ferruginea</i>	I
	<i>pulcherrima</i>	I
Busbeckia	<i>nobilis</i>	II

Literature Cited

- BAILEY, I. W.
1933. The cambium and its derivative tissues. No. VIII. Structure, distribution and diagnostic significance of vestured pits in dicotyledons. *Journ. Arnold Arb.*, vol. 14, pp. 259-273.
- BENTHAM, G., and HOOKER, J. D.
1862. *Capparideae*. *Genera plantarum*, vol. 1, part 1, pp. 103-110.
- BESSEY, C. E.
1915. The phylogenetic taxonomy of flowering plants. *Ann. Missouri Bot. Garden*, vol. 2, pp. 109-164.
- CARLQUIST, S.
1961. *Comparative plant anatomy*. Pp. i-ix + 146.
- CHATTAWAY, M. M.
1955. Crystals in woody tissues; Part I. *Tropical Woods*, vol. 102, pp. 55-74.
- Cozzo, D.
1944. La estructura estratificada del leño de *Capparis salicifolia* Gris. *Revista Ingen. Agron.*, vol. 6, pp. 151-153.
1946. Relación anatómica entre la estructura del leño de las especies argentinas de "Capparis" y "Atamisquea." *Lilloa*, vol. 12, pp. 29-37.
- Cozzo, D., and CRISTIANI, L. Q.
1950. Los generos de fanerogamas argentinas con estructura leñosa estratificada. *Revista Inst. Invest. Cienc. Nat. Buenos Aires Bot.*, vol. 1, pp. 363-405.

CUMBIE, B. G.

1960. Anatomical studies in the Leguminosae. *Tropical Woods*, vol. 113, pp. 1-47.

DARLINGTON, C. D., and WYLIE, A. P.

1956. Chromosome atlas of flowering plants. Pp. i-xix+519.

DE CANDOLLE, A. P.

1824. Capparideae. *Prodromus systematis naturalis regni vegetabilis*, vol. 1, pp. 237-254.

ENGLER, A., and DIELS, L.

1936. *Syllabus der Pflanzenfamilien*. Ed. 11, pp. i-xlii+419.

ERNST, W. R.

1963. The genera of Capparaceae and Moringaceae in the southeastern United States. *Journ. Arnold Arb.*, vol. 44, pp. 81-95.

ESAU, K.

1953. *Plant anatomy*. Pp. i-xii+735.

FAHN, A., and LESHEM, B.

1963. Wood fibers with living protoplasts. *New Phytol.*, vol. 62, pp. 91-98.

FAWCETT, W.

1914. Notes on Jamaican species of *Capparis*. *Journ. Bot.*, vol. 52, pp. 142-144.

HARRAR, E. S.

1946. Note on starch grains in septate fiber-tracheids. *Tropical Woods*, vol. 85, pp. 1-9.

HEGNAUER, R.

1961. Die Gliederung der Rhocadales sensu Wettstein im Lichte der Inhaltstoffe. *Planta Medica*, vol. 9, pp. 37-46.

HUTCHINSON, J.

1926. The families of flowering plants. Vol. 1. Dicotyledons. Pp. i-xii+328.

1959. The families of flowering plants. Vol. 1. Dicotyledons. Ed. 2, pp. i-xi+510.

JACOBS, M.

1960. Capparidaceae. *Flora Malesiana*, ser. 1, vol. 6, part 1, pp. 61-105.

JANE, F. W.

1956. The structure of wood. Pp. i-vii+427.

MACBRIDE, J. F.

1938. Capparidaceae. *Flora of Peru*. *Publ. Field Mus. Bot.*, vol. 13, part 2, no. 3, pp. 984-1006.

METCALFE, C. R., and CHALK, I.

1950. Anatomy of the dicotyledons. Vol. 1, pp. i-lxiv+1-724; vol. 2, pp. 725-1500.

PAX, F., and HOFFMANN, K.

1936. Capparidaceae. In Engler and Prantl, *Die natürlichen Pflanzenfamilien*, ed. 2, vol. 17b, pp. 146-233.

RADIKOFER, L.

1884. Ueber einige *Capparis*-Arten. *Sitz-ber. Akad. München II*, vol. 14, pp. 101-182.

1887. Ueber einige *Capparis*-Arten. *Sitz-ber. Akad. München II*, vol. 17, pp. 365-422.

STERN, W. L., and CHAMBERS, K. L.

1960. The citation of wood specimens and herbarium vouchers in anatomical research. *Taxon*, vol. 9, pp. 7-13.

TAKHTAJ(1)AN, A. L.

1954. Origins of angiospermous plants. Pp. 68 [Translated from the Russian by Olga H. Gankin, 1958].

1959. Die Evolution der Angiospermen. Pp. i-viii+344.

WETTSTEIN, R.

1935. Handbuch der systematischen Botanik. Pp. i-x+1152.