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FORCHHAMMERIA AND STIXIS (BRASSICALES): STEM AND WOOD ANATOMICAL DIVERSITY,
ECOLOGICAL AND PHYLOGENETIC SIGNIFICANCE

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ABSTRACT

Qualitative and quantitative data are given for wood anatomy of six of the 11 recognized species of *Forchhammeria* (Mexico, Central America, West Indies), a genus formerly placed in Capparaceae. Though still in Brassicales, the genus has been excluded, along with several other genera, from the major recognized families of that order on the basis of molecular data. Liquid-preserved material of several species permitted detailed histological accounts of the successive cambia and their development in the stems of *Forchhammeria*. Successive cambia have a curious distribution in Brassicales that may represent homoplasies. Most wood features of the genus do not appear highly xeromorphic, but presence of tracheids as a wood background tissue and abundance of starch and perhaps water storage in ray parenchyma and conjunctive tissue can be cited as mechanisms likely to resist embolism formation. *Forchhammeria* retains green leaves throughout the dry season. *Forchhammeria tamaulipana*, known only from Tamaulipas State, Mexico, the single species of a new subgenus, **Pauciflora**, is newly described. Its embryos have nearly equal cotyledons and germinate epigeously, whereas all remaining species of the genus are pseudomonocotylous and hypogeous. These and other distinctive features of *F. tamaulipana* may prove significant in providing links to other brassicalean genera. The family name Stixaceae Doweld is now appropriate for *Forchhammeria*, *Neothorelia*, *Stixis*, and *Tirania*.

Key words: *Borthwickia*, Capparaceae, ecological wood anatomy, Stixaceae, successive cambia.

INTRODUCTION

Forchhammeria Liebm. is a distinctive woody genus of Brassicales, native to moderately dry to dry areas of Mexico, Central America, and the West Indies. Formerly included within Capparaceae (e.g., Pax and Hoffmann 1936), *Forchhammeria* has many distinctive features that pose interesting phylogenetic, biogeographical, systematic, and structural questions. Although molecular work shows that *Forchhammeria* is securely placed within Brassicales (=Capparales), as currently recognized (Hall et al. 2004; Su et al. 2012), topology of the clade to which it belongs is not yet at hand because no group of workers has had access to all relevant genera and species. *Forchhammeria* has been placed close to several genera (*Neothorelia* Gagnep., *Stixis* Lour., and *Tirania* Pierre, from southeast Asia) and the family Borthwickiaceae (monospecific, Yunnan and adjacent Myanmar) as well as the families Gyrostemonaceae, Pentadiplandraceae, and Resedaceae (Hall et al. 2004; Su et al. 2012). Although polytomies appear in their molecular constructions, the families and genera in this list appear to form a clade. In addition, a series of smaller families (e.g., Cleomaceae, Emblingiaceae, Tovariaceae, etc.) group in a second clade within Brassicales (Hall et al. 2002, 2004; Su et al. 2012), which may be termed core Brassicales. Capparaceae in the older, more inclusive sense, proves to be paraphyletic, and the segregation of these families is warranted. Brassicaceae is not a sister group of Capparaceae in these constructions, and both families should be recognized.

Hall et al. (2004) recognized a provisional polytomous “GRFT” clade, to include Gyrostemonaceae, Resedaceae, *Forchhammeria* and *Tirania*. Su et al. (2012) expanded the GRFT clade to include *Borthwickia*, formerly of Capparaceae, as well as Pentadiplandraceae. *Tirania* was tentatively assigned to Capparaceae tribe Stixaceae by Pax and Hoffmann (1936). *Stixis* consists of 15 species from southeast Asia (Pax and Hoffmann 1936). Other members of Stixaceae according to Pax and Hoffmann include *Forchhammeria* and *Physena* Noronha. *Physena* is now considered as the sole genus of Physenaceae, a sister family of the similarly monogeneric family Asteropeiaceae (both from Madagascar), the two families shown by molecular evidence to be located within Caryophyllales (Cuénoud et al. 2002). *Forchhammeria* was the third genus of Stixaceae in the Pax and Hoffmann treatment. The monotypic genera *Tirania* (*T. purpurea* Gagnep. from Vietnam) and *Neothorelia* (*N. laotica* Gagnep. from Laos and Thailand; Williams and Chayamarit 2005) were considered as possible members of Stixaceae by Pax and Hoffmann (1936). *Forchhammeria* is thus a geographical outlier of the remaining genera, although recent molecular data (Su et al. 2012) suggest it is close to the “GRFT” clade of genera that should be excluded from Capparaceae (Hall et al. 2004), as is *Borthwickia* (Su et al. 2012).

Gyrostemonaceae and Resedaceae do not have successive cambia (Carlquist 1978, 1998). All species of *Forchhammeria* do have successive cambia, but so does *Stixis* (Metcalf and Chalk 1950; original data). Successive cambia have been

reported in *Boscia* Lam. by Adamson (1935) and in *Cadaba* Forssk., *Maerua* Forssk. and *Niebuhria* DC. (as *Boscia variabilis* Collett & Hemsl., by Hansen 1977), but some species of *Boscia* and *Maerua* as presently sampled do not have successive cambia (Metcalfé and Chalk 1950; original observations). The occurrence of successive cambia in both *Forchhammeria* and in the African genera *Boscia*, *Cadaba*, and *Maerua* was thought to be noteworthy by Hansen (1977), but the presence of successive cambia in *Stixis* and elsewhere in Brassicales (*Cleome droserifolia* (Forssk.) Delile of Cleomaceae: Fahn et al. 1986) and the capability for transoceanic dispersal of capparids (e.g., *Capparis sandwichiana* DC. in the Hawaiian Islands) and Resedaceae (Martin-Bravo et al. 2009) suggest that perhaps we should not consider geographic closeness of the genera when weighing the systematic affinities of *Forchhammeria*.

Regardless of the genetic basis for occurrence of successive cambia in Brassicales, Caryophyllales, or other orders, this secondary thickening phenomenon (formerly termed "included phloem," a confusing umbrella term) has significance that we are just beginning to appreciate (Carlquist 2007). The examination of various examples in recent years has led to new realizations about the ontogenetic nature of successive cambia (Carlquist 2007). The successive cambia of *Forchhammeria* are of potential interest because they may be related to survival in the habitats of Mexico and the West Indies that have a prolonged dry season. The functional significance of successive cambia has not been addressed by wood physiologists because they are much more difficult as experimental material than are single-cambium stems. The successive cambia reported in *Boscia*, *Cadaba*, and *Maerua* (Metcalfé and Chalk 1950; Hansen 1977) have late onset, and thus are different from the successive cambia in *Forchhammeria*, which are initiated in relatively young stems.

The present study builds on an earlier essay (Hansen 1977) and endeavors to make quantitative wood data assembled in that work more widely available. In addition, new qualitative data, based mostly on liquid-preserved materials, have been added to the xylarium materials studied by Hansen. These new materials have been studied by means of light microscopy and scanning electron microscopy (SEM). The latter method has permitted a detailed understanding of some anatomical features that have not been investigated previously. *Forchhammeria* consists of 10 species plus six subspecies (Hansen 1977). Three subgenera (*Forchhammeria*, *Helandra*, and *Pauciflora*) are recognized here (the latter new), and species of all three are represented in anatomical studies of the present paper. Six of the 10 species are used to consider issues of ecological anatomy, and some possible correlations between structure, habit, and habitat.

Note should be taken that phloem and conjunctive tissue within the stems of *Forchhammeria* (as well as those of other genera of angiosperms with successive cambia) are not part of secondary xylem (Carlquist 2007). Because the conjunctive tissue and secondary phloem are not embedded within secondary xylem, the term "included phloem" is inappropriate and must be discontinued. These features have been explained recently (Carlquist 2012a,b). Conjunctive tissue separates vascular increments (=bands of secondary phloem + secondary xylem). Hansen (1977) did not include *Stixis* in his studies, but *Stixis* has successive cambia, the details of which are

remarkably like those in *Forchhammeria*, and so that genus has been included in the present essay. This new information has prompted consideration of relationships of both *Forchhammeria* and *Stixis* in a wider phylogenetic context.

A species of *Forchhammeria* that has the most distinctive features for the genus has lain undescribed since its discovery about 70 years ago. It is described in a terminal section of this paper, and it becomes the sole species of a new subgenus. It is distinctive because of features that are unusual in the genus and of phylogenetic significance. It also is important because it occurs in small numbers in a limited area.

MATERIALS AND METHODS

The collections studied are as follows: *Forchhammeria* subgenus *Forchhammeria*.—*Forchhammeria macrocarpa* Standl.: Hansen 1751 (MAD). *Forchhammeria pallida* Liebm.: Hansen 1425 (MAD); Hansen 1453 (MAD); Hansen 1591 (MAD); Olson 873 (MEXU); Olson 699 (MEXU); Olson 925 (MEXU). *Forchhammeria watsonii* Rose: Hansen 1373 (MAD); Olson s.n., Dec 2004, Sonora, Mexico; J. F. Wiens, 20 Feb 2002, cult. Arizona Sonora Desert Museum, Tucson AZ, from material collected at San Carlos, Sonora, Mexico. *Forchhammeria* subgenus *Helandra* Standl.—*Forchhammeria hintonii* Paul G. Wilson: Hansen 1493 (MAD). *Forchhammeria trifoliata* Radlk.: H. H. Bartlett 11493, USW-29650; Hansen 1701 (MAD); Hansen 3002 (MAD).—*Forchhammeria* subgenus *Pauciflora*. *Forchhammeria tamaulipana* B.F.Hansen, H.H.Iltis & Carlquist: Hansen 3786 (MAD); H. H. Iltis & B. Simon 30785, 14 August 1991 (MAD, RSA). Species in other genera: *Boscia albitrunca* (Burch.) Gilg & Benedict, *B. hildebrandii* Gilg, coll. J. H. Ferreira, USW-21795, *Cadaba rotundifolia* Forssk., Kw 630, *Stixis parviflora* (Griff.) Pierre, R. S. Boecca 7349, USW-28950, Sumatra.

Materials studied by Hansen and presented in Table 1 were dried specimens studied by means of the usual sliding microtome methods; measurements of cell length were derived from macerations. Materials collected by Olson were liquid-preserved. These stems were sectioned by means of a sliding microtome and either stained with safranin and fast green and processed into permanent (Canada balsam) slides, or else dried and studied with SEM. The procedure for the latter involves drying sections between pairs of glass slides on a warming table, and then mounting them on aluminum stubs, sputter-coating them with gold, and observing then with a Hitachi S2600 SEM at the Santa Barbara Botanic Garden. A Zeiss EVO SEM at the Santa Barbara Museum of Natural History was used for images of crystal-bearing tissues in *Stixis*.

RESULTS: QUALITATIVE FEATURES

Forchhammeria Subgenus *Forchhammeria*

Forchhammeria watsonii (Fig. 1–8). Cortex consists of parenchyma cells that are rich in starch or bear one crystal or else contain any of several types of crystals plus some starch grains. Interspersed among the cortical parenchyma are thick-walled sclereids, in nests of various sizes. These sclereids contain a single large crystal each (occasionally more).

Portions of vascular increments are seen in the transection micrograph (Fig. 1). The increments are separated by conjunctive tissue that is composed of cells with thin secondary

Table 1. Quantitative wood features of *Forchhammeria*.

Collection	VEL	VD	V/mm ²	TL	RW	RH
Subgenus <i>Forchhammeria</i>						
<i>F. pallida</i>						
<i>Hansen 1425</i>	202	82	12	1240	90	1966
<i>Hansen 1453</i>	208	95	7	1406	77	1838
<i>Hansen 1591</i>	191	76	14	1028	127	1289
<i>F. macrocarpa</i>						
<i>Hansen 1751</i>	172	94	8	876	167	1724
<i>F. watsonii</i>						
<i>Hansen 1373</i>	151	66	10	711	152	2960
Subgenus <i>Helandra</i>						
<i>F. hintonii</i>						
<i>Hansen 1493</i>	281	49	11	1888	207	4205
<i>F. trifoliata</i>						
<i>Hansen 1701</i>	222	77	5	1686	271	4999
<i>Hansen 3002</i>	248	55	7	1812	232	5385
Subgenus <i>Pauciflora</i>						
<i>F. tamaulipana</i>						
<i>Hansen 3786</i>	182	47	67	866	108	2054
All collections, averaged	206	71	16	1279	159	2936

Key: VD = mean vessel diameter, μm ; VEL = mean vessel element length, μm ; V/mm² = mean number of vessels per mm² of transection; TL = mean tracheid length; RW = mean width of multiseriate rays, μm ; RH = mean height of multiseriate rays, μm .

walls. Occasional thick-walled crystalliferous sclereids are present in the conjunctive tissue. These sclereids tend to occur opposite strands of secondary phloem. Phloem strands contain one or more bands of crushed secondary phloem (Fig. 2, 3), indicative of continual production of phloem by the vascular cambium in each vascular increment. Starch grains are abundant in phloem rays (Fig. 3, right) and in conjunctive tissue. Sieve tube elements and companion cells are scattered throughout the secondary phloem (Fig. 2); phloem parenchyma may predominate in some zones of the secondary phloem (Fig. 3, left). Octahedral crystals were observed in secondary phloem parenchyma (Fig. 4).

Secondary xylem (Fig. 5–8) features solitary vessels, circular in outline (Fig. 5). Axial parenchyma is commonly paratracheal (Fig. 5), but diffuse and diffuse-in-aggregates patterns are also present. Axial parenchyma as seen in longitudinal sections occurs in strands of 2–4 cells. Rays (Fig. 6) are both narrow multiseriate and uniseriate, the Heterogeneous Type II of Kribs (1935). Ray cells are lignified and commonly contain starch. Vessels have narrow slit-like pit apertures (Fig. 7) that are somewhat irregular in outline, suggestive of a minor degree of vesturing. Pit cavity diameter is about 2 μm . Tracheids are present as the imperforate tracheary element type (Fig. 1–8). Pits on tracheids are prominently bordered (Fig. 8) but without obvious vesturing.

Forchhammeria pallida (Fig. 9–16) has wood that is similar to that of *F. watsonii*, so that the illustrations selected are to present features in which *F. pallida* tends to differ from *F. watsonii*, or features that were seen to better advantage in preparations of *F. pallida*. Axial parenchyma is diffuse, with a moderate tendency toward a vasicentric scanty arrangement (Fig. 9). Axial parenchyma strands consist of two to five cells. Prominent slit-like pit apertures (grooves interconnecting pit apertures) are present on vessel walls. Pit apertures are clearly, if inconspicuously, vested (Fig. 10). Pit cavities are 2 μm in diameter. Tracheids are the imperforate tracheary element type (Fig. 13, bottom). Rays are multiseriate only and are

composed of somewhat procumbent cells as well as some square cells; they approach Kribs's (1935) Homogeneous Type II. Ray cells have bordered pits on tangential walls (Fig. 11). Ray cells are filled with starch grains (Fig. 12).

In *F. pallida*, there are prominent bands of thick-walled sclereids in conjunctive tissue, mostly opposite the phloem poles of the preceding vascular increment (Fig. 9). These sclereids are isodiametric in shape, closely packed, and polyhedral (Fig. 13). The sclereid walls are thick and the lumen of each is filled with a single polyhedral crystal (Fig. 14, 15), so that there is very little lumen space. Numerous narrow simple pits traverse the sclereid walls. Conjunctive tissue cells that are not crystal-containing sclereids have moderately thick secondary walls and are filled with starch (Fig. 16).

Forchhammeria Subgenus *Helandra*

Forchhammeria trifoliata (Fig. 17–21). The stem cortex consists of starch-rich parenchyma cells, thick-walled sclereids, each containing a large polyhedral crystal, in small nests and also occasional strands of thick-walled narrow fibers with occluded lumina. Conjunctive tissue consists of cells with secondary walls. Although small crystals or starch grains are common in conjunctive tissue cells, no thick-walled sclereids were observed in the material studied. A small number of thin-walled sclereids were noted.

Secondary xylem consists of solitary vessels in a background of thick-walled tracheids (Fig. 17). Axial parenchyma is mostly diffuse-in-aggregates, with some diffuse and some vasicentric scanty (Fig. 17). Axial parenchyma strands consist of 2–5 cells in length. Rays are exclusively wide multiseriate (Fig. 18) and consist of procumbent cells plus square cells, a close approach to Kribs's Homogeneous Type II, differing only in having less procumbency of ray cells as seen in radial sections than Kribs (1935) specified for this type. The rays are thus intermediate to Paedomorphic Type II (see Carlquist 2001). The pits on vessel

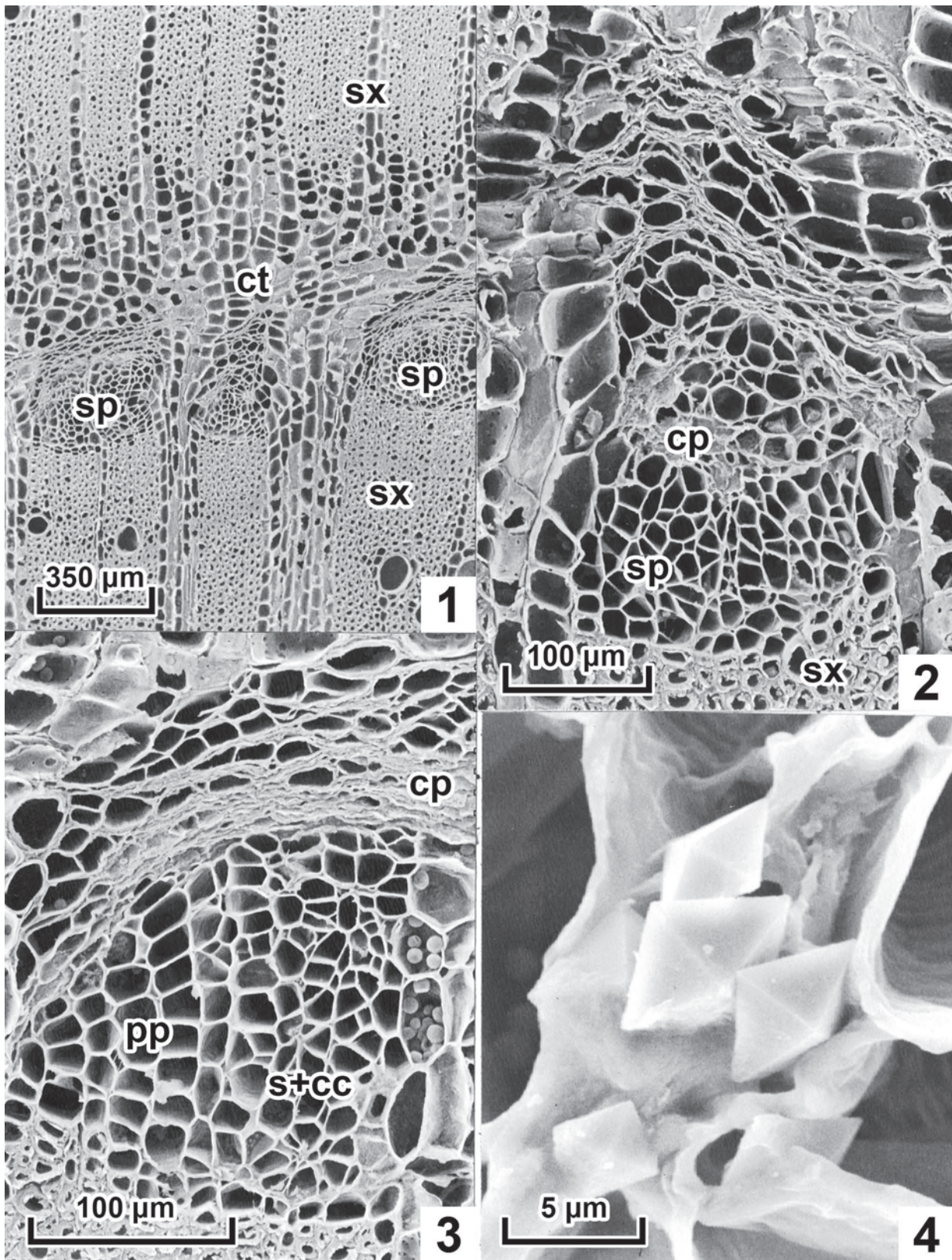


Fig. 1–4. Scanning electron microscopy (SEM) micrographs of transections of stem transections of *Forchhammeria watsonii*, Olson *s.n.*, Dec 2004.—1. Transection of adjacent vascular increment portions to show ground plan of the successive cambial pattern.—2. Secondary phloem strand shows several years of phloem accumulation; crushed sieve tube elements take on a laminar appearance; some phloem parenchyma cells survive the crushing process. Some conjunctive tissue (radial rows of cells) is shown at upper right.—3. Secondary phloem strand; crushed phloem above; portion of phloem at left consists wholly of phloem parenchyma, that at right contains mostly sieve tube elements and companion cells; phloem ray at right edge.—4. Octahedral crystals from phloem ray parenchyma. Key: cp = crushed phloem; ct = conjunctive tissue; pp = phloem parenchyma; s + cc = sieve tube elements plus companion cells; sp = secondary phloem; sx = secondary xylem.

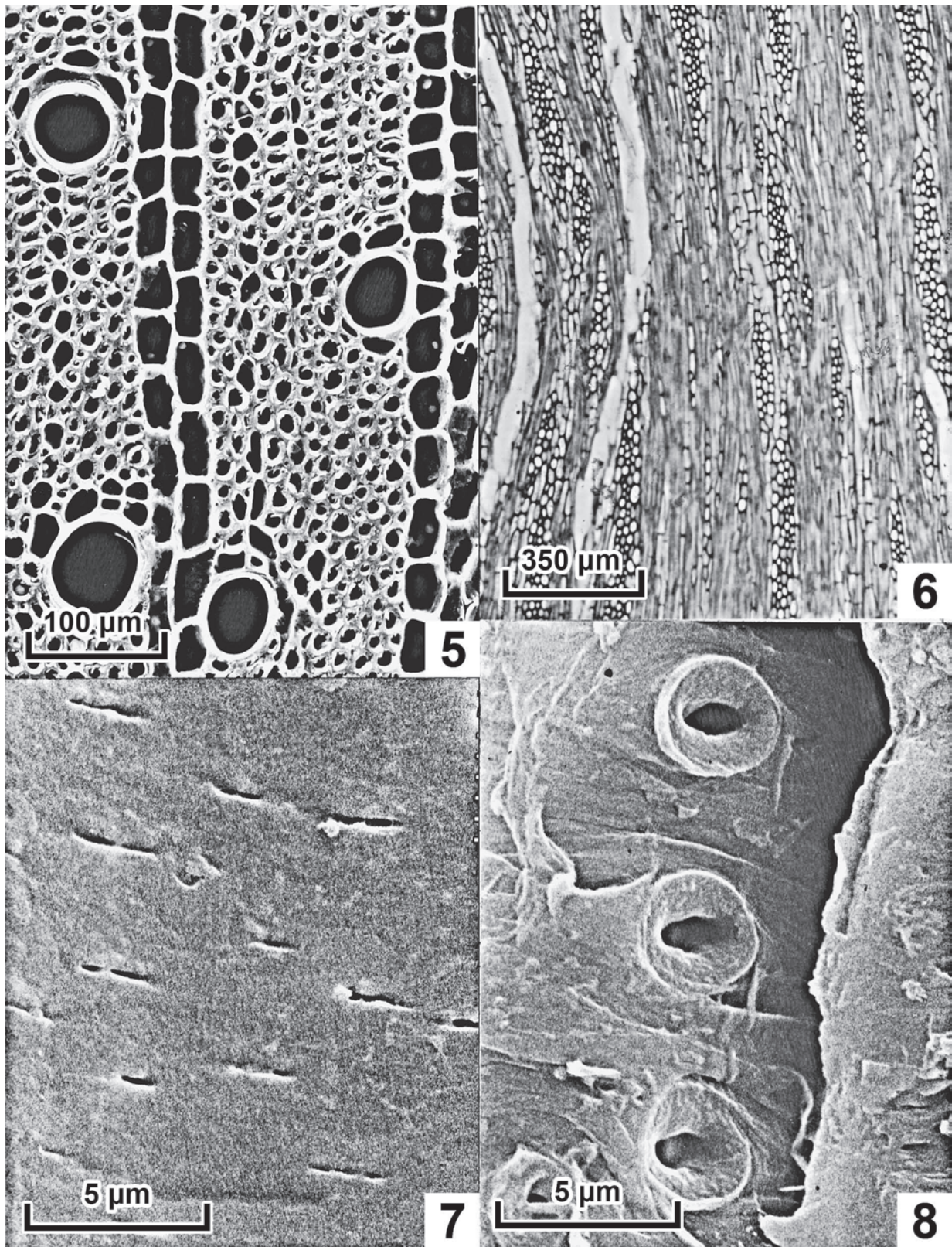


Fig. 5–8. SEM micrographs (5, 7, 8) and a light photomicrograph (6) of secondary xylem sections of *Forchhammeria watsonii*, Olson s.n., Dec 2004.—5. Transection; vessels are solitary, thick-walled; axial parenchyma is mostly vasicentric.—6. Tangential section. Rays range from tall and wide to uniseriate.—7. Inner surface of vessel; pit apertures are slit-like, with irregularities indicating inconspicuous vesturing.—8. Outer surface of tracheid, showing three bordered pits.

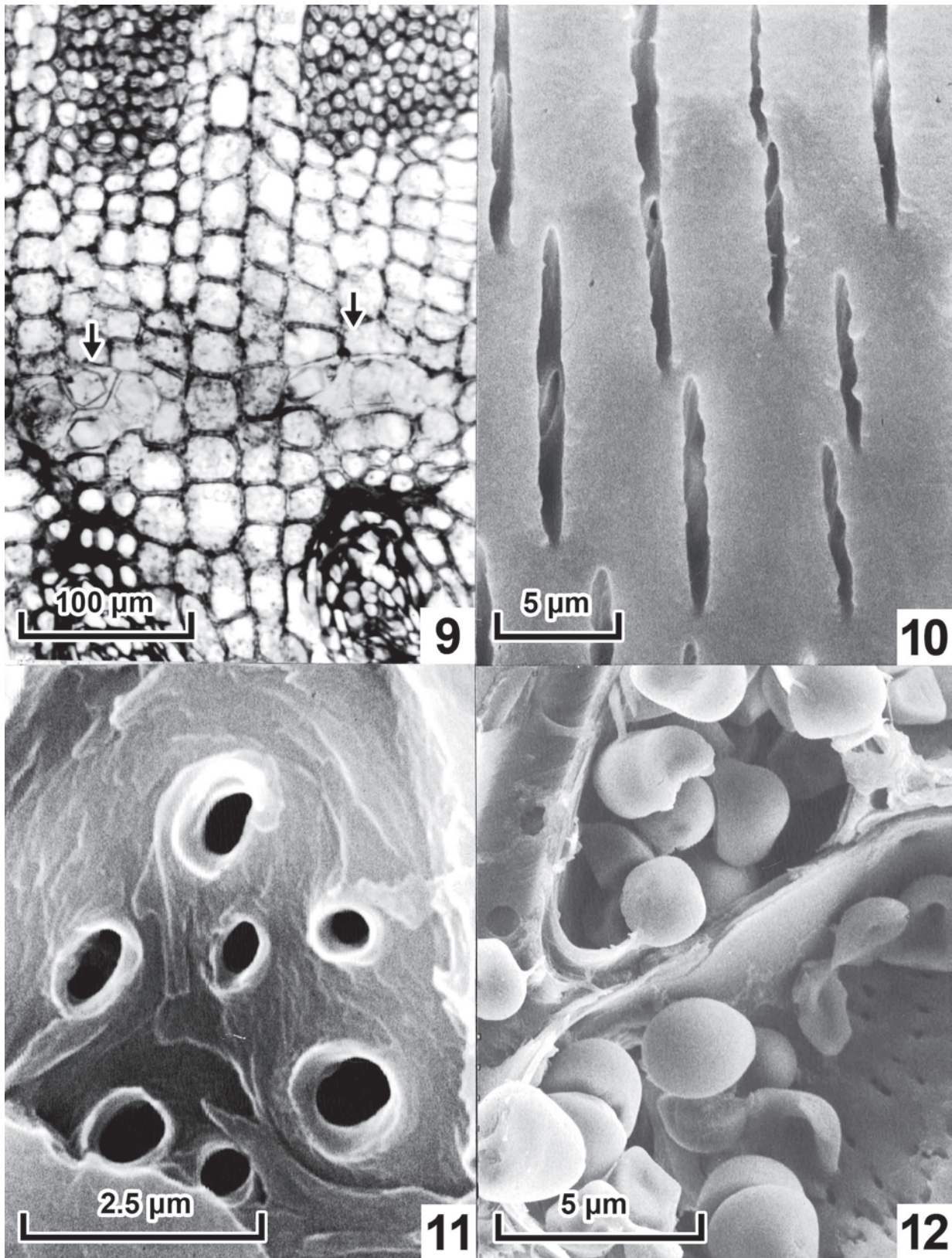


Fig. 9–12. Light photomicrographs (9) and SEM micrographs (10–12) of stem sections of *Forchhammeria pallida*, Olson 873.—9. Portions of two adjacent vascular increments, separated by conjunctive tissue. Arrows indicate thick-walled sclereids that contain a large crystal each; axial parenchyma in secondary xylem (above) is diffuse.—10. View of inside of vessel wall. Pits are slit-like, with a tendency towards elongation as grooves. Pit aperture margins are vestured (bumps on edges of the slit-like apertures).—11. Outer surface of ray cell from tangential section, to show borders on the pits of the ray cell tangential wall.—12. Portions of two ray cells containing starch grains, from tangential section.

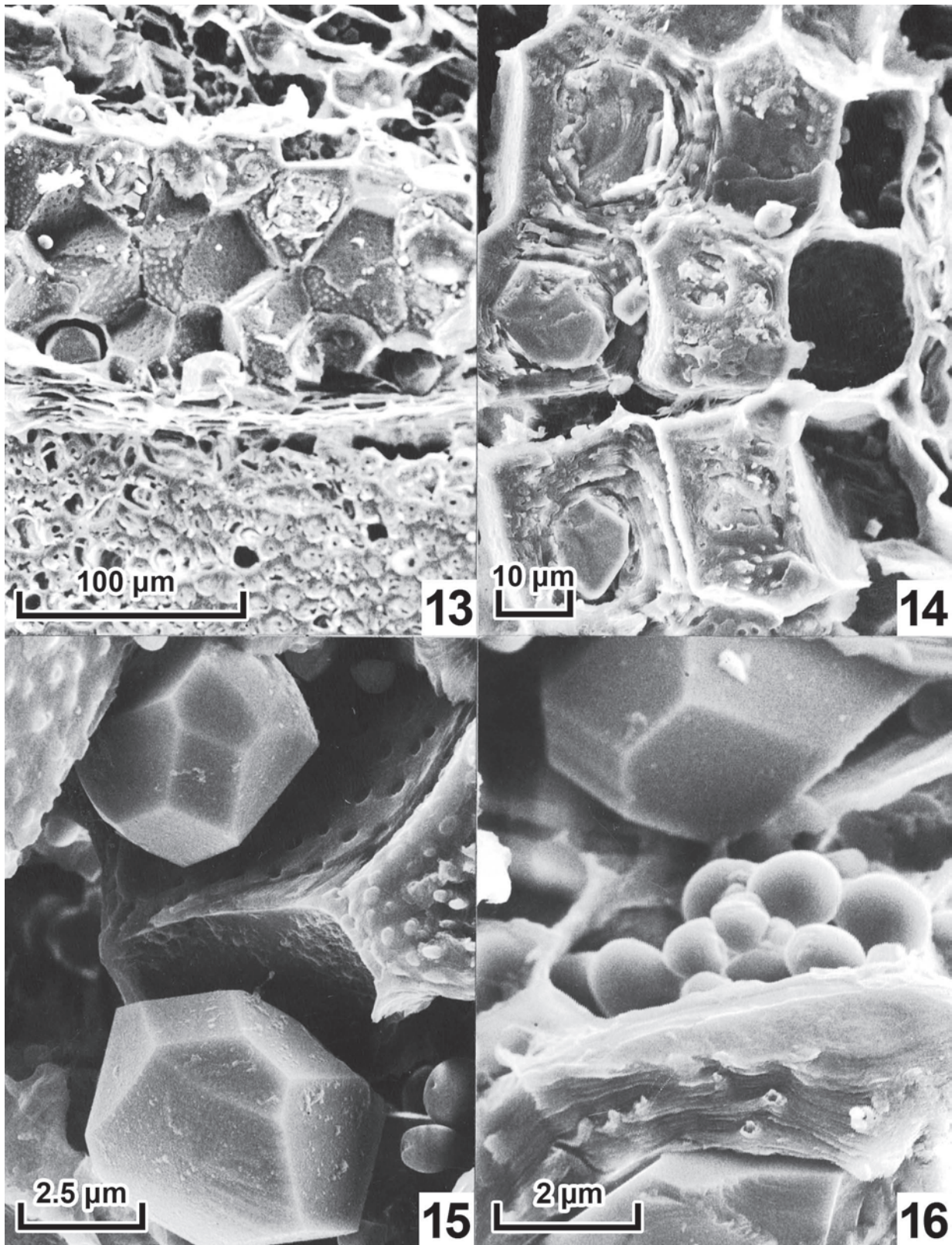


Fig. 13–16. SEM micrographs of sclereids from transections of conjunctive tissue of stem of *Forchhammeria pallida*, Olson 873.—13. Low power section, to show band of sclereids with parenchymatous conjunctive tissue above, and below, secondary xylem and crushed phloem.—14. Higher-power photograph, to show that crystals fill the lumen of each of the thick-walled sclereids; thin-walled conjunctive tissue cells at right.—15. Crystals from two adjacent sclereids, to show the irregularly polyhedral crystals.—16. From top to bottom, a polyhedral crystal; a portion of a starch-containing cell; thick sclereid wall containing pits, and a slice of a polyhedral crystal.

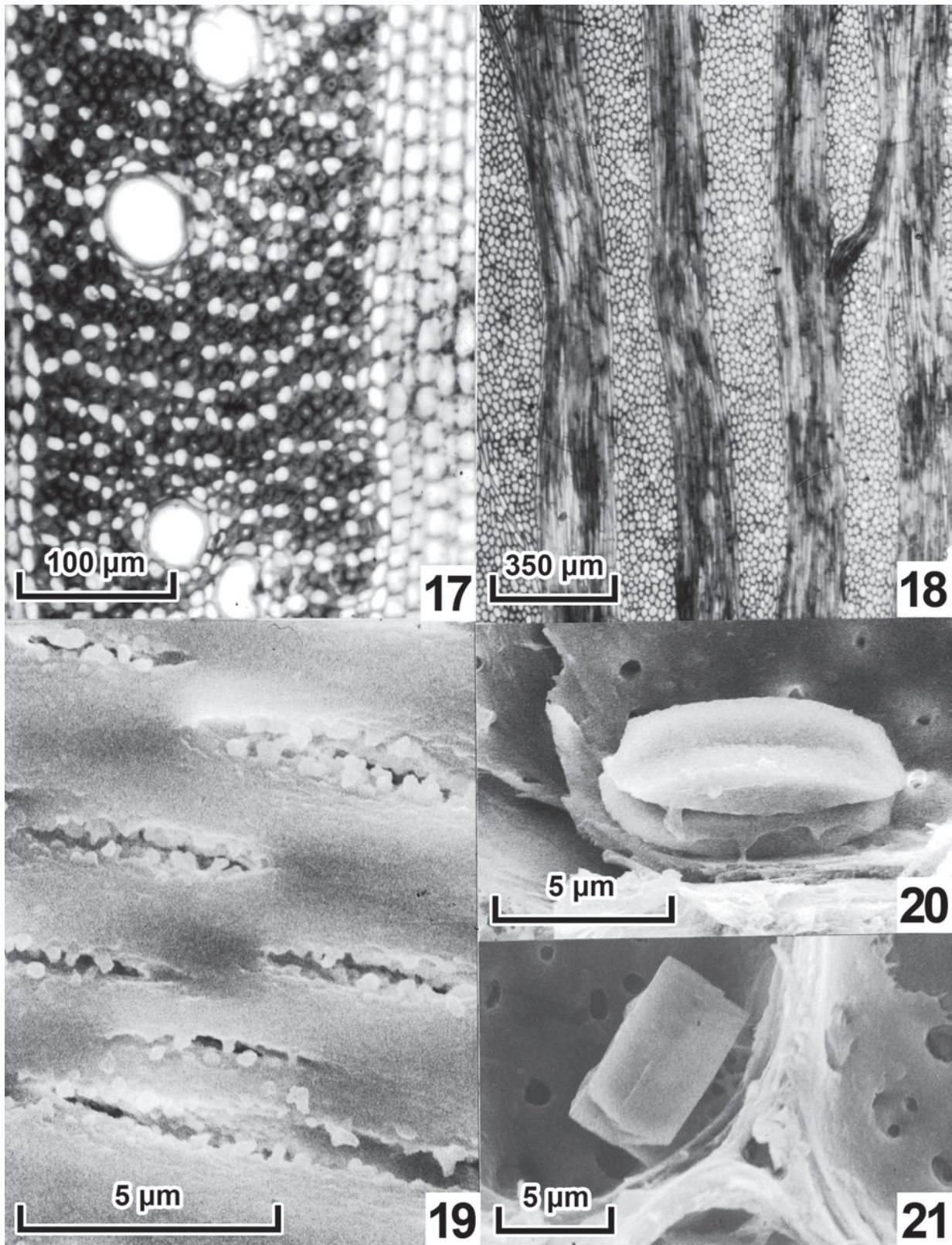


Fig. 17–21. Light photomicrographs (17, 18) and SEM micrographs (19–21) of wood of *Forchhammeria trifoliata* stem, USw-29650.—17. Transection, vessels are solitary, axial parenchyma is diffuse plus diffuse-in-aggregates.—18. Tangential section, rays are all wide, multiseriate, and tall.—19. View of inner surface of vessel wall, showing prominently vestured narrow pit apertures.—20. Elongate quadrangular crystal with tapered ends from ray cell tangential section.—21. Elongate quadrangular crystal with blunt ends from ray cell tangential section.

walls are small, with pit cavity diameter averaging about 2 μm . The pit apertures are slit-like, and prominently vested (Fig. 19). Quadrangular crystals, either with tapered ends (Fig. 20) or blunt ends (Fig. 21) are common in phloem parenchyma, ray cells, and conjunctive tissue, but other crystal shapes are encountered also.

Forchhammeria *Subgenus* Pauciflora

Forchhammeria tamaulipana. The stem has a conspicuous phelloderm, up to 20 cells in thickness. Cortical parenchyma cells have primary walls only. Nests of thick-walled lignified sclereids are present in cortex. Many of the sclereids contain a single polyhedral crystal each. Cortex, ray, and conjunctive tissue contain massive quantities of starch. The ontogeny of a vascular increment is illustrated in Fig. 22. The master cambium (wide triangular pointer) is in an active state of division. The vascular cambium (arrows) of the most recent increment has already produced considerable secondary phloem, which appears crushed except for some phloem parenchyma (perhaps as a result of drying, since a dried wood sample was studied). Conjunctive tissue and rays are composed of cells with lignified walls, and contain numerous starch grains. A few of the crystal-bearing sclereids, like those figured for *F. watsonii*, occur in conjunctive tissue, opposite the phloem strands of the preceding vascular increment.

Rays are Heterogeneous Type II of Kribs (1935). Uniseriate rays are relatively few, and wide multiseriate rays are common. Vessels occur in a background of tracheids. Although many vessels are solitary, some are in contact and form groups of two, occasionally more. Vessel grouping may relate to the fact that vessel density is greater than in other species, and therefore packing may account for the contacts among vessels as compared to the preceding species, in which vessels are solitary. Axial parenchyma is diffuse (Fig. 23). Pits on vessel walls are clearly vested as seen from outer vessel surfaces (Fig. 24). Pit cavities of both vessels and tracheids are 2–3 μm in diameter, mostly about 2.5 μm . Pits on tracheids (Fig. 25) have vestures around pit apertures. A few ray cells contain small rhomboidal crystals.

Stixis

Of the genera of tribe Stixeeae of Pax and Hoffmann (1936) other than *Forchhammeria*, material of only one species of *Stixis*, *S. parviflora* (Fig. 26–33), was available.

Cortex was not present in the sample studied. Vascular increments (Fig. 26) lack perceptible growth rings, although change in diameter of vessels may signal seasonal fluctuation. Vessels are solitary (Fig. 26–28). Axial parenchyma is diffuse, differing in abundance according to position within a vascular increment (Fig. 26: denser-appearing zones of secondary xylem contain less axial parenchyma). Axial parenchyma is mostly in strands of two cells. Vascular rays are close to Homogeneous Type II of Kribs (1935), but some square cells as seen in radial sections are present also (to the extent that upright and square cells are found, the rays would be transitional to/from Heterogeneous Type II). Rays are predominantly quite wide (Fig. 27, 28). Ray cells have secondary walls (Fig. 28). A layer of thin-walled sclereids, each containing one or more crystals, is adjacent to the innermost secondary xylem of each vascular increment (Fig. 29). Secondary phloem contains crystals in phloem parenchyma (Fig. 30). Imperforate tracheary elements are all

tracheids with vested bordered pits (Fig. 31), with bordered pits the same size as those on vessels (Fig. 32, 33). Pits on vessel walls are clearly vested (Fig. 32, 33). The conjunctive tissue sclereids contain one to a few rhomboidal crystals each, and have moderately thick lignified walls.

RESULTS: QUANTITATIVE WOOD FEATURES

The quantitative data on wood features assembled by Hansen (1977) are reproduced here as Table 1. All figures given are means, except for those on ray seriation. The significance of quantitative wood features is considered in a section, below, concerning the ecological significance of wood features within the genus. Some simple analyses of differences among species with respect to quantitative wood features can, however, be offered at this point. The comparatively long vessel elements and tracheids of the two species of subgenus *Helandra* are notable, as can be seen by their departure from the means for the genus as a whole (last line of table). The narrow vessels and greater vessel density (number of vessels per mm^2) in *F. tamaulipana* stand out.

With respect to vessel density, one must keep in mind that we cannot readily compare vessel density in *Forchhammeria* to that in genera of Brassicales that have a single vascular cambium. Vessel density is low in species with successive cambia (Carlquist 1975). In part, this can be an artifact of including conjunctive tissue into areas surveyed. However, in most species with successive cambia, conjunctive tissue occupies only a fraction of the transectional area of the stem, so its inclusion does not lower the vessel density figure by much. In addition, species with successive cambia may characteristically have low vessel density, even when conjunctive tissue is excluded from the transectional areas surveyed. This may be a result of the probability that more numerous vessels are functional in a species with successive cambia, a conclusion suggested by the presence of living phloem accumulation in older vascular increments, a result of the continued action of the vascular cambia. Crushed phloem becomes more abundant as one follows vascular increments inward in a stem, but a large number of the vascular increments have viable phloem. This suggests that vessels in conductive condition are being maintained in vascular increments from previous years (Carlquist 2007). (Note should be taken that vascular increments are not initiated on an annual basis, and one can find growth ring margins at various points within a vascular increment as seen in transection).

SYSTEMATIC CONCLUSIONS

Perhaps one should not draw conclusions from a single sample of a stem of *Stixis*, because many variations may be shown by anatomy of species of *Stixis* not studied here, as well as anatomy of the genera *Neothorelia* and *Tirania* (both monospecific). Comparative anatomy deals in terms of character presence, however (absence is difficult to prove), and assemblages of characters. In these terms, the similarities between vascular increment design and secondary xylem anatomy of *Forchhammeria* and *Stixis* is astonishing. These similarities include occurrence of successive cambia, occurrence of diffuse parenchyma in secondary xylem, presence of tracheids as the imperforate tracheary element type, presence of pits on vessels with small (compared with most families of

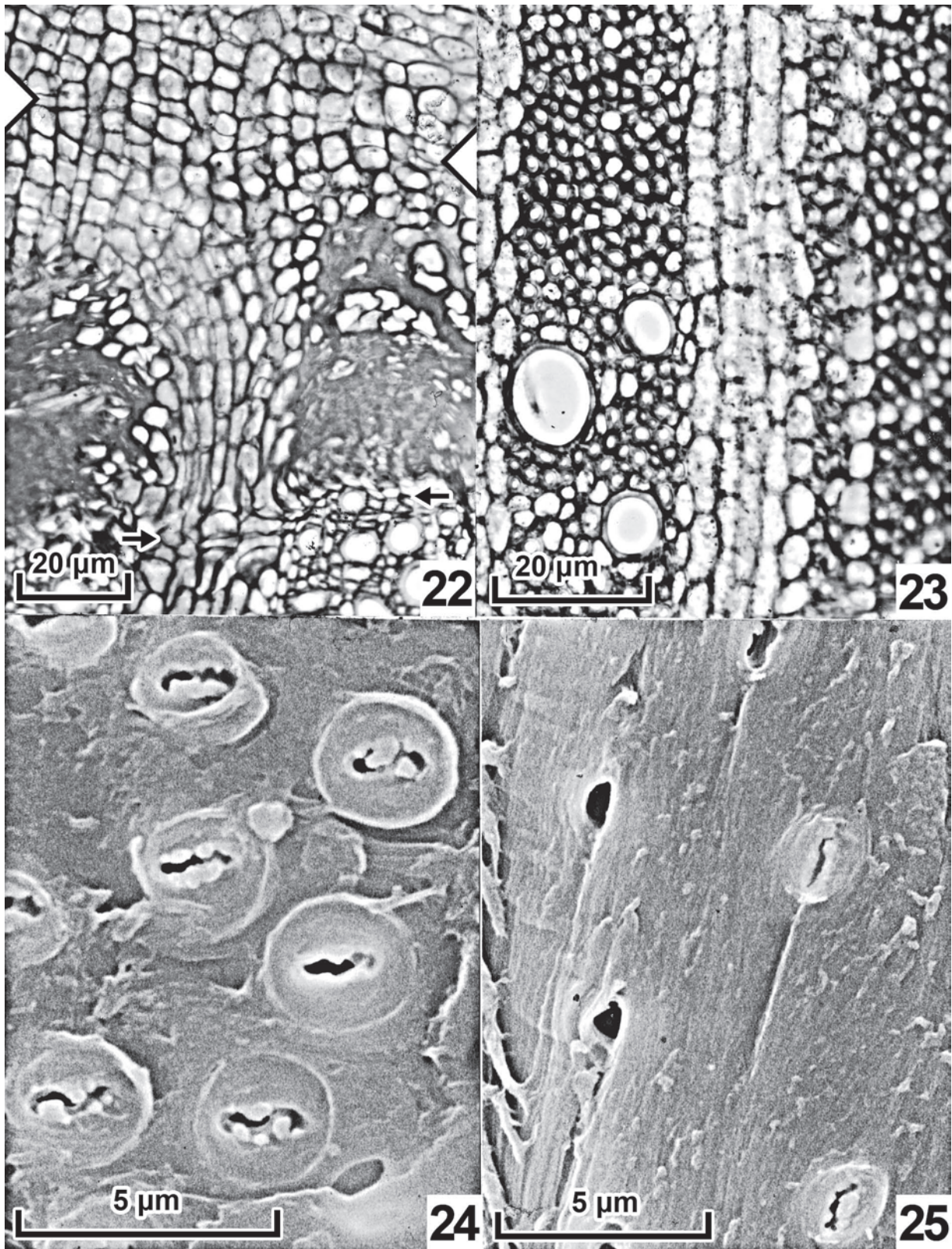


Fig. 22–25. Light photomicrographs (22, 23) and SEM micrographs (24, 25) of stem of *Forchhammeria tamaulipana*, Iltis & Simon 30785.—22. Transection showing cortex (top) and portions of the outermost vascular increment. Pointers indicate the orientation of the master cambium, and the arrows show the vascular cambium.—23. Portion of secondary xylem seen in transection. Vessels are solitary. Axial parenchyma is diffuse, diffuse-in-aggregates, and vasicentric scanty.—24. Outer surface of vessel from radial section; pit cavities are circular, pit apertures are clearly vestured.—25. Outer surface of tracheids from radial section; vesturing is present in pit apertures (top center, lower right).

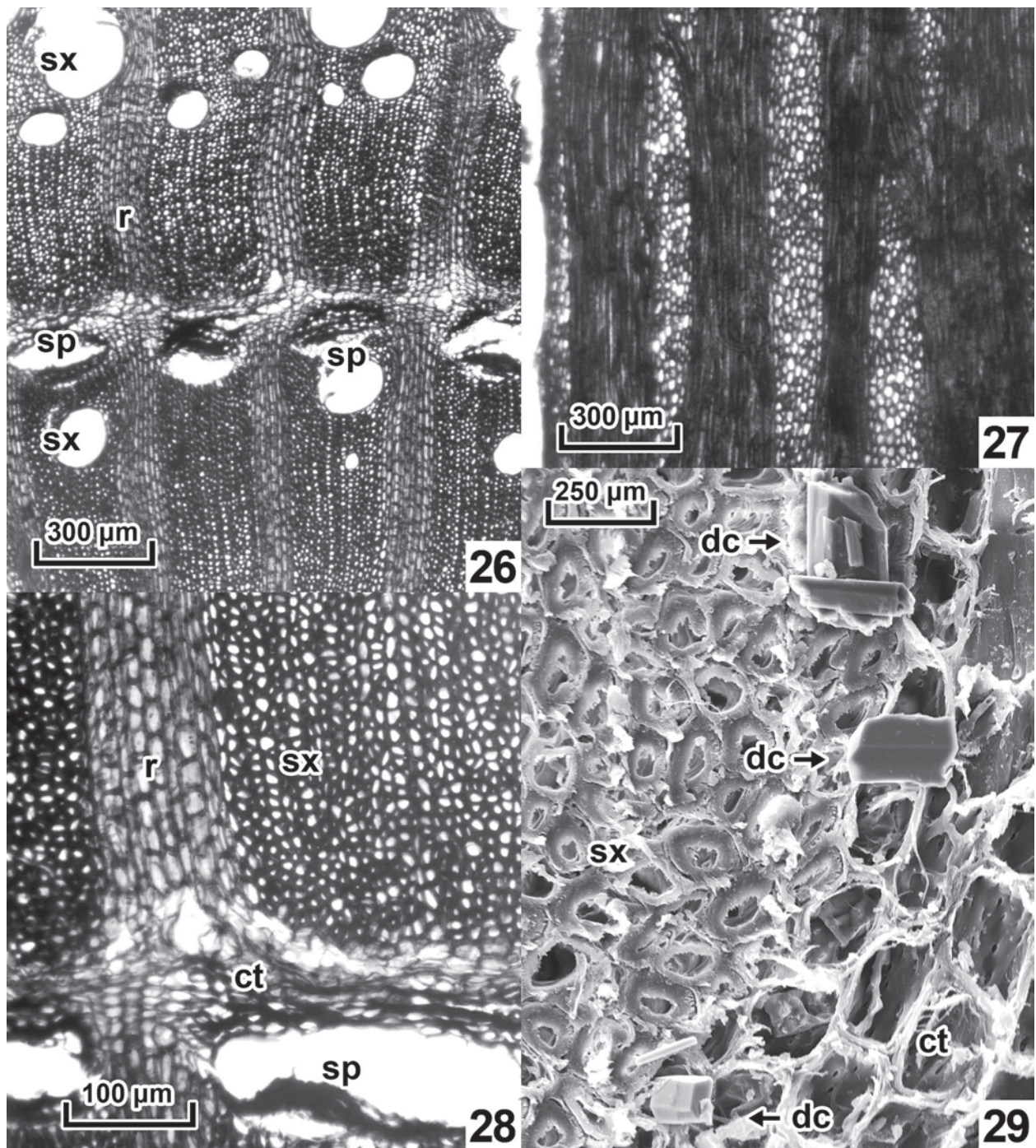


Fig. 26–29. Light photomicrographs (26–28) and SEM micrograph (29) of stem of *Stixis parviflora* (USw-28950).—26. Transection, showing portions of two vascular increments.—27. Tangential section: rays are wide, tall.—28. Portion of transection; from top to bottom: secondary xylem, conjunctive tissue, and secondary phloem.—29. Portion of secondary xylem from transection, and conjunctive tissue with sclereid layer internal to the secondary xylem. Key: ct = conjunctive tissue; dc = dislodged crystals, r = ray; sp = secondary phloem; sx = secondary xylem.

Brassicales) diameter pit cavities, presence of slit-like apertures and vestures on pits of vessels, presence of wide multiseriate rays (combined with a paucity of uniseriate rays), and presence of a layer of sclereids, each containing a crystal, opposite phloem strands, in the conjunctive tissue. Successive cambia have been reported for Brassicales as a characteristic formation only in *Forchhammeria* and *Stixis* (Metcalf and Chalk 1950). They have been reported occasionally within the

genera *Boscia*, *Cadaba*, and *Maerua* (Adamson 1935; Metcalfe and Chalk 1950; Hansen 1977), but most wood samples in those genera lack them because they are late-onset successive cambia. The cell layers of crystalliferous sclereids in conjunctive tissue have not been reported in genera other than *Forchhammeria* and *Stixis*. Wide multiseriate rays do not characterize woody Brassicales, but there are some exceptions in the case of Gyrostemonaceae (Carlquist 1978) and

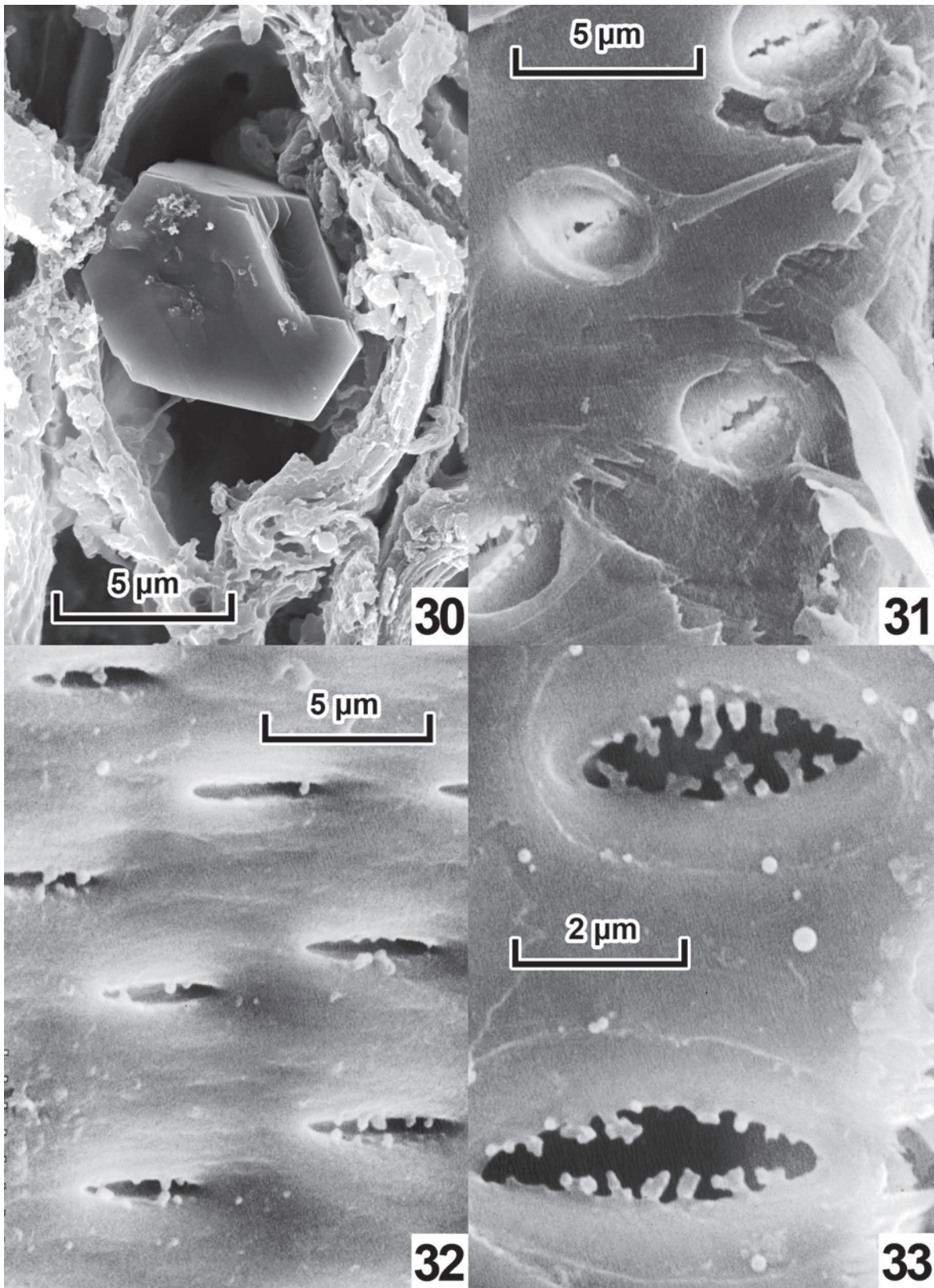


Fig. 30–33. SEM micrographs of details from stem of *Stixis parviflora* (USw-28950).—30. Crystal with irregular outline and laminate fine structure, from secondary phloem parenchyma cell in stem transection.—31–33. Details of tracheary elements from secondary xylem of tangential section of stem.—31. Outer surface of tracheid, showing vestured bordered pits.—32. Inner surface of vessel; pit apertures are vestured.—33. Outer surface of vessel; pit apertures are prominently vestured.

Resedaceae (Carlquist 1998), which form, together with *Forchhammeria* and another stixoid (*Tirania*), the “GRFT” clade as recognized by Hall et al. (2004). This clade was modified by Su et al. (2012) to include Borthwickiaceae and Pentadiplandraceae. The “GRFT” clade expanded to include Borthwickiaceae, Gyrostemonaceae, Resedaceae, Pentadiplandraceae, and the stixoids may be provisionally termed the “stixoid” clade. The other features cited in the listing in the above paragraph do occur in some other Brassicales, but uncommonly so (e.g., libriform fibers or, less commonly, fiber-tracheids, characterize most Brassicales); vestured pits have been reported in a minority of the genera of the order (Jansen et al. 2000). The GRFT clade formed a polytomy, not resolved, due to lack of material of some genera, in the Hall et al. (2004) molecular-based cladogram. Su et al. (2012) also show a polytomy involving *Forchhammeria*, *Stixis*, and the Gyrostemonaceae. Gyrostemonaceae and Resedaceae lack vestured pits, as far as is known (Carlquist, unpubl. data); they also lack successive cambia (Carlquist 1978, 1998). *Stixis* and *Forchhammeria* share successive cambia, diffuse axial parenchyma, wide, high multiseriate rays (with few or no uniseriate rays), presence of tracheids, presence of vestured pits in tracheids and vessels, a peculiar crystal-bearing layer of sclereids internal to the secondary xylem of each vascular increment, and crystals in phloem parenchyma. In addition, *Forchhammeria* and *Stixis* both have camptodromous secondary venation in leaves and fruits with a fleshy mesocarp and a hard, sclerenchymatous endocarp. Although we do not know whether *Borthwickia*, *Neothorelia*, and *Tirania* have successive cambia, nor do we know any xylary details, we do know that the stixoids share palynological similarities (Su et al. 2012): the pollens of *Neothorelia* and *Tirania* are essentially identical (Mitra 1975). The genera of the stixoid clade all have axile placentation (Su et al. 2012). Should one wish provisionally to recognize the stixoids in the Pax and Hoffmann (1936) sense, minus *Physena* (now Caryophyllales), at the familial level for *Forchhammeria*, *Neothorelia*, *Stixis*, and *Tirania*, the name Stixaceae Doweld (*Phytologia* 90: 417 [2008]) is available. The Angiosperm Phylogeny Group (2009) noted this as a possibility but stopped short of recommending recognition of Stixaceae pending acquisition of further data. The important thing to note here is that if one were examining the wood of *Stixis* without knowing its identity, one could easily say that it falls within the diversity presented here for *Forchhammeria*. Although wood anatomy is not decisive in phylogenetic placement, this concatenation of unusual character states that create a resemblance between the woods of the two genera is indeed amazing, and we may provisionally recognize Stixaceae with four component genera. Gyrostemonaceae, Resedaceae, Borthwickiaceae, and Pentadiplandraceae would remain separate from Stixaceae, as proposed by Su et al. (2012). Su et al. (2012) recognized a “core Brassicales” clade that contains Brassicaceae, as well as Capparaceae, Cleomaceae, and Tovariaceae, as a clade that branches from Brassicales jointly with the stixoid clade, with Emblingiaceae as sister. Earlier branchings of the brassicalean tree include Bataceae, Caricaceae, Koerberliniaceae, and Tropaeolaceae. Although recognition of a series of rather small families in Brassicales may seem unusual, this procedure is endorsed by The Angiosperm Phylogeny Group (2009). The alternative is to recognize two large and heterogeneous clades as perhaps two large families

which would be indefinable on any perceptible morphological basis, submerging distinctive families that have been universally recognized, such as Gyrostemonaceae and Resedaceae.

Within genus *Forchhammeria*, sampling of the species is not inclusive enough to claim any features as “diagnostic species characters.” Rather, what is revealed here is diversity in character expressions, so that the stem and wood anatomy of *Forchhammeria* is not uniform. This diversity is expressed, where qualitative features are involved, in such things as the varied axial parenchyma arrangements. The prominence of the sclereid band in conjunctive tissue of *F. watsonii* contrasts with the paucity of the sclereids in other species, such as *F. tamaulipana*. Rays in the species studied show differences in proportion of upright versus procumbent cells, and in whether uniseriate rays are present or absent. Further sampling will undoubtedly offer more dimensions. One can state axiomatically that in comparative anatomy of angiosperms, one never has enough materials nor does one sample the available materials sufficiently to make statements about exclusivity in character presence or absence (Carlquist 2010).

ECOLOGICAL INTERPRETATIONS

Those who have seen *Forchhammeria* in the dry regions of Mexico, such as the Sonoran thorn scrub, often note the fact that during the dry (winter) season, *Forchhammeria* shrubs and trees are leafy and green, in contrast with associated vegetation, much of which is drought-deciduous. This phenomenon forces us to examine what mechanisms might relate to the evergreen nature of *Forchhammeria*. *Forchhammeria* tends to occupy coastal thorn forests and interior depressions in Mexico. *Forchhammeria pallida* even drops its leaves during the wet season. *Forchhammeria* often coexists with genera that have successive cambia, such as *Guapira*, *Ipomoea*, *Iresine*, *Lagrezia*, *Pisonia*, *Simmondsia*, and *Stegnosperma*. The accompaniment of the secondary xylem bands with secondary phloem bands in these genera may aid in preventing embolisms during times of water stress; we have little knowledge of the physiology of stems with successive cambia at present. Dryland monocot vascular bundles may work in a similar fashion.

Leaf anatomy and physiology, which are not considered here, are very likely of prime importance, and should be included in obtaining the total picture of water management and life strategies of *Forchhammeria*. Wood features, especially those related to vessels, are almost always indicators of how a plant deals with water economy, however (Carlquist 1966, 2012a). *Forchhammeria* habitats all experience periods of prolonged drought.

Three vessel dimensions are sensitively related to ecological wood anatomy: vessel diameter, vessels per mm² (vessel density), and vessel element length. Vessel length is related to water economy, and has been much cited by wood physiologists, but is not a feature available from isolated wood samples. Are these features indicative of the adaptations of *Forchhammeria*?

Vessel diameter.—Vessel diameter tends to be narrower in more xeromorphic woods (Carlquist 1966, 1975), and one could say that any species with mean vessel diameter less than 100 μm represents a xeromorphic condition (note the data in Carlquist and Hoekman 1985). The mean vessel diameter of *Forchhammeria* as a whole (71 μm) does not seem strongly

xeromorphic. In Asteraceae (Carlquist 1966), the mean vessel diameter for all collections ($N = 353$) is $51 \mu\text{m}$, and the mean diameter for desert Asteraceae is $39 \mu\text{m}$, both figures significantly below that for *Forchhammeria*. Vessel diameter for a sampling of desert eudicots is $29 \mu\text{m}$ (Carlquist 1975: 206), whereas a sampling of species with successive cambia yields the figure $69 \mu\text{m}$ (ibid.). Thus, *Forchhammeria* does not look, with respect to vessel diameter, like a desert shrub, but it is in line with other genera and species that have successive cambia. The special significance of successive cambia with respect to vessel diameter is discussed below.

Vessel element length.—With respect to vessel element length, the mean figure for *Forchhammeria*, $206 \mu\text{m}$, seems close to that of a sampling of desert eudicots, $218 \mu\text{m}$ (Carlquist 1975: 206), but it is even closer to the figure for dryland Asteraceae ($198 \mu\text{m}$, Carlquist 1966), but above that for eudicot species with successive cambia, $146 \mu\text{m}$ (Carlquist 1975: 205). Vessel element length is short in species with successive cambia, a fact probably related not so much to ecology but to the origin of vascular cambia from cortical cells (via the master cambium) rather than procambium in species with successive cambia (Carlquist 2013). In species with a single vascular cambium, and cambial origin from undifferentiated procambium, the length of the fusiform cambial initials changes continually over time, whereas in species with successive cambia, the length of initials is set early by the master cambium and then replicated during initiation of each vascular cambium from the master cambium (Carlquist 2007, 2013). Short vessel element length does correlate with wood xeromorphy (Carlquist 1966; Carlquist and Hoekman 1985). The shortness of vessel elements of *Forchhammeria* should be assumed to be adaptive, whatever its mode of origin.

Vessel density.—Vessel density (number of vessels per mm^2 of transection) is low in *Forchhammeria* as a whole, but that is also true in all species with successive cambia (Carlquist 1975: 206). The figure in *F. tamaulipana* is higher than in the remaining species, but if we omit *F. tamaulipana*, the vessel density figure for the genus is 9. The narrowest vessels for the genus (as a mean) are in *F. tamaulipana*, which correlates with the higher vessel density in that species. While vessel element quantitative data in species with successive cambia cannot be directly compared to those in species with single cambia, within the genus, *F. tamaulipana* does have the most xeromorphic wood in terms of the three quantitative features of vessels discussed here.

Successive cambia.—Why should woods with successive cambia have such low vessel density? Without an understanding of how successive cambia work, interpretation of this feature would be difficult. One should remember that each vascular cambium in a species with successive cambia produces secondary phloem, perhaps most actively during the growing season (Fig. 2, 3), with older phloem crushed and deactivated. The net effect is to keep the three-dimensionally disposed system of secondary phloem in a stem with successive cambia alive and functioning. Inferentially (we need experimental data on this point), the longevity of these strands of secondary phloem scattered throughout the stem suggests that vessels and associated parenchyma are functional also. Thus, in such a species, functional conductive tissue is not limited to the most

recent secondary xylem. We therefore have to judge the ecological wood anatomy of a species with successive cambia differently from that of a species that produces only a single cylinder of secondary xylem (and secondary phloem). We do not know, for any given species with successive cambia, how many vascular increments are actively functioning in the conductive process. The three-dimensional character of the conductive process and of parenchyma tissue afforded by successive cambia could potentially increase water, photosynthate, and mineral input and retrieval. We need experimental work to verify such possibilities.

Tracheids.—The relative paucity (low density per mm^2 of transection) of vessels in *Forchhammeria* may be related to the presence of successive cambia, as noted above, but it may also be related to the fact that imperforate tracheary elements of *Forchhammeria* are tracheids, and thus are an ideal background tissue in a wood design that promotes high safety combined with low flow rate characteristics. The pits on *Forchhammeria* tracheids are small in pit cavity diameter (about $2.5 \mu\text{m}$), but they are densely placed, and have the same diameter as those on vessel walls. This is also true in *Stixis* (Fig. 31–33). The conductive function of tracheids is important in a genus such as *Forchhammeria*, because tracheids do not embolize readily and are conductively safe (Carlquist 2001). The presence of tracheids is correlated with lack of vessel grouping in many angiosperm woods (Carlquist 1984) and is a kind of visual statement that tracheids are more important than vessel grouping in promoting conductive safety (minimal disruption of the conductive process by air embolisms).

Vesturing.—All species of *Forchhammeria* have vesturing of vessel pits (as does *Stixis*), although to various degrees. Some vestures may even be seen on pit apertures of tracheids in some *Forchhammeria* species. Vestures, like helical thickenings, serve to deter formation of air embolisms, or to reverse them, in conductive cells of angiosperm woods (Jansen et al. 2000; Kohonen and Helland 2009).

Rays.—The rays of *Forchhammeria* (which are true vascular rays, produced by successive vascular cambia) are surprisingly large in width and height (Table 1). Notably tall rays occur in *F. hintonii* and *F. trifoliata*, which also have notably long tracheids and vessel elements. Are wide rays related to xeromorphy? They are in some succulents such as cacti (Mauseth 1993). *Forchhammeria* does not qualify as a succulent, but its wide rays, as well as its conjunctive tissue, do store massive amounts of starch, which when converted to sugar could help remove embolisms. Conjunctive tissue and rays would be capable of storing some water. A comparison of fresh and dry weights for stem woods would be informative in this regard. Perhaps more significantly, we know nothing about the roots of *Forchhammeria* (or related genera).

Sclereids, crystals, phelloderm.—The significance of sclereid nests in cortex and, to a lesser extent, in conjunctive tissue seems clearly related to herbivore deterrence. The sclereid walls and crystals represent a significant energy investment, correlative to the massive starch storage in the stem. The significance of the unusually thick phelloderm needs to be elucidated.



Fig. 34. Portion of isotype specimen of *Forchhammeria tamaulipana* (Iltis & Simon 30785). The fruit (stigmas visible), dislodged from a calyx, is shown. The inflorescence bearing the calyx is incomplete—a portion bearing one or two flowers is absent.

A DISTINCTIVE NEW SPECIES

Although first noticed about 1960 (Hansen 1977), a new species from Tamaulipas, Mexico, has lain undescribed until now. The information presented here is derived from study of the isotype specimen and its label information as well as from the data of Hansen (1977).

Forchhammeria tamaulipana B.F.Hansen, H.H.Iltis & Carlquist, sp. nov. (Fig. 34–39).—**TYPE:** Mexico. Tamaulipas: on open, gravelly bare soil (heavily overgrazed), a clay terrace near river and highway (101), east end of bridge and just south of the bridge, 39 km southwest of Ciudad Victoria on road to Jaumave, alt. 600–700 m, shrubby desert, with *Prosopis*, *Yucca*, *Agave*, *Opuntia*, and barrel cacti, 14 August 1991, Hugh H. Iltis & Brian Simon 30785 (holotype MAD; isotype RSA).

Shrub 2–4 m tall, with numerous stiff virgate branches, the stems 3–6 cm thick at the bases, brittle. Leaves simple, dark green, elliptical, acute to briefly acuminate at tip, secondary veins camptodromous. Lamina 10–60 mm long (mostly about 45 mm), 8–13 mm (mostly about 10 mm) wide, entire, flat, midvein evident on lower surface, glabrous (Fig. 34). Petiole 9–12 mm (mostly about 10) mm long. Inflorescences axillary, 1–5 fruits per branch. Female flowers about 3 mm long, the calyx lobes (Fig. 35) broadly triangular (some rotundate), apetalous. Male flowers about 3 mm long (Fig. 36), petals about 2 mm long, elliptical (Fig. 36, 37). Fruits about 7 mm in diameter. Embryo with two subequal convolute cotyledons

(Fig. 38). Ovaries (Fig. 35) and fruits (Fig. 34, 35–39) with two sessile stigmas. Exocarp rugose; mesocarp composed of parenchyma containing sclereid nests (Fig. 34, 35–38), endocarp woody (Fig. 38).

The Jaumave Valley, where *F. tamaulipana* is endemic, is a small rain shadow lowland depression, bordered to the east by the peaks of the Sierra Madre Oriental, which wring moisture from air coming in from the Gulf of Mexico. Endemism is high in the Jaumave Valley, the flora of which includes the cycad *Dioön*, the cactus genus *Obregonia*, and a number of species of *Mammillaria*.

The characteristics of *F. tamaulipana* are sufficiently distinct to include it into a new subgenus; summaries of the other subgenera (descriptions derived in part from Pax and Hoffmann 1936) follow description of the new subgenus. Pax and Hoffmann (1936) offer a key to species other than *F. tamaulipana*.

FORCHHAMMERIA Liebm. subgenus **Pauciflora** B.F.Hansen, H.H.Iltis & Carlquist, subgen. nov.—**TYPE:** *Forchhammeria tamaulipana* B.F.Hansen, H.H.Iltis & Carlquist.

Flowers in inflorescences of 5 or fewer flowers. Female flowers apetalous, but male flowers with 5 elliptical petals. Sepals 4–5. Ovary biloculate, stigmas 2. One locule remains small and is not evident in fruit. Fruits spherical. Cotyledons 2, subequal, convolute, germination probably epigeous. Shrub with 5–10 virgate stems, branching at or near ground level. Leaves simple, glabrous. Characters of the sole species, *F. tamaulipana*.

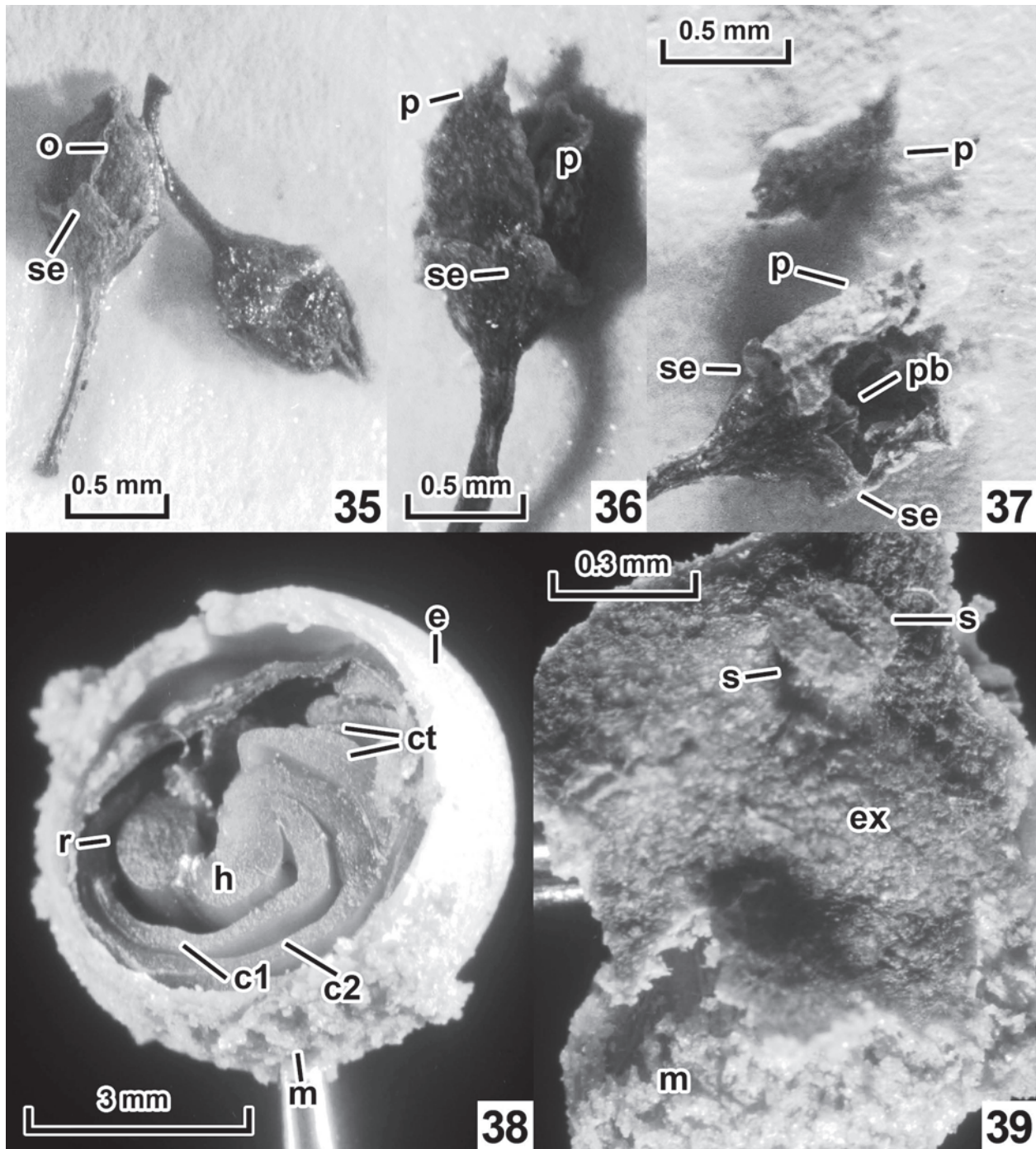


Fig. 35–39. Details from the isotype specimen of *Forchhammeria tamaulipana* (Iltis & Simon 30785).—35. Two female flowers; ridge on flower at left caused by drying; pair of stigmas visible on flower at right.—36. Male flower, intact.—37. Male flower, with one petal dissected away and placed above the flower.—38. Section through fruit, showing the embryo and its cotyledons.—39. Surface and subsurface layers of fruit. Key: c1, c2 = the two cotyledons in sectional view; ct = cotyledon tips in sectional view; e = endocarp; ex = exocarp; h = hypocotyl; m = mesocarp; o = ridge on ovary; p = petal; pb = base of petal (upper portion broken off); r = radicle in near-transsectional view; s = stigma; se = sepal. The fruit, which is shown also in Fig. 34, was boiled in water prior to dissection; the flowers (Fig. 35–37) have not been rehydrated.

FORCHHAMMERIA subgenus FORCHHAMMERIA Standl. in *J. Washington Acad. Sci.* **14**: 270 (1934). Flowers typically in panicles of more than 10 flowers. Female and male flowers apetalous. Sepals 4–6. Ovary biloculate, but one locule remains small and is not evident in fruit. Fruits oval. Cotyledon one, the radicle rudimentary, germination hypogeous. Shrubs or small trees, branched above rather than at ground level. Leaves glabrous (*F. pallida*) or hairy (*F. macrocarpa*, *F. watsonii*), simple.

FORCHHAMMERIA subgenus HELANDRA Standl., *ibid.* Flowers in racemes or panicles, typically of more than 10 flowers. Female and male flowers apetalous. Sepals 6–8. Ovary biloculate; of the two locules, one aborts and forms an outgrowth at the base of an almost globose fruit. Cotyledon 1, the radicle rudimentary, germination hypogeous. Shrubs or small trees, branched above rather than at ground level. Leaves glabrous, simple (*F. brevipes* Urb., *F. hintonii*, *F. longifolia* Standl., *F. sessilifolia* Standl., *F. sphaerocarpa* Urb.) or trifoliolate (*F. trifoliata*).

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