

Studies in *Fitchia* (Compositae): Novelties from the Society Islands; Anatomical Studies

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THE GENUS *Fitchia* has attracted interest because of its arborescent habit, its distribution in southeastern Polynesia, the endemism of its species, and its phylogenetic relationships. In a monograph of this genus, six species occurring on five islands were recognized (Carlquist, 1957). Following the appearance of that monograph, Grant notified Carlquist of his collection, while on a Bishop Museum Fellowship in 1931, of specimens of *Fitchia* from two additional islands (Bora Bora and Tahaa) in the Society Group. The genus had not been previously reported from these islands, and manuscript names, as a new species and subspecies, respectively, had been applied to the taxa. On Grant's invitation, Carlquist made the anatomical studies presented here which, it is felt, puts the recognition of the two new entities on a much firmer basis than gross morphology alone could have provided. In addition, descriptions are given of one additional specimen each of two previously known species of *Fitchia*, one from Tahiti, and one from Rapa. The occurrence of the two novelties is of more than ordinary interest because of the nature of this genus, and permits more extended remarks on the nature of speciation in *Fitchia*. Flowering material of *F. rapensis*, not available for the monograph, has been studied here. This paper, therefore, may be considered an addendum to the monograph. The taxonomic descriptions below have been prepared by Grant. The anatomical account which follows is the work of Carlquist, and has been prepared to conform with the types of data offered in the monograph.

TAXONOMIC DESCRIPTIONS

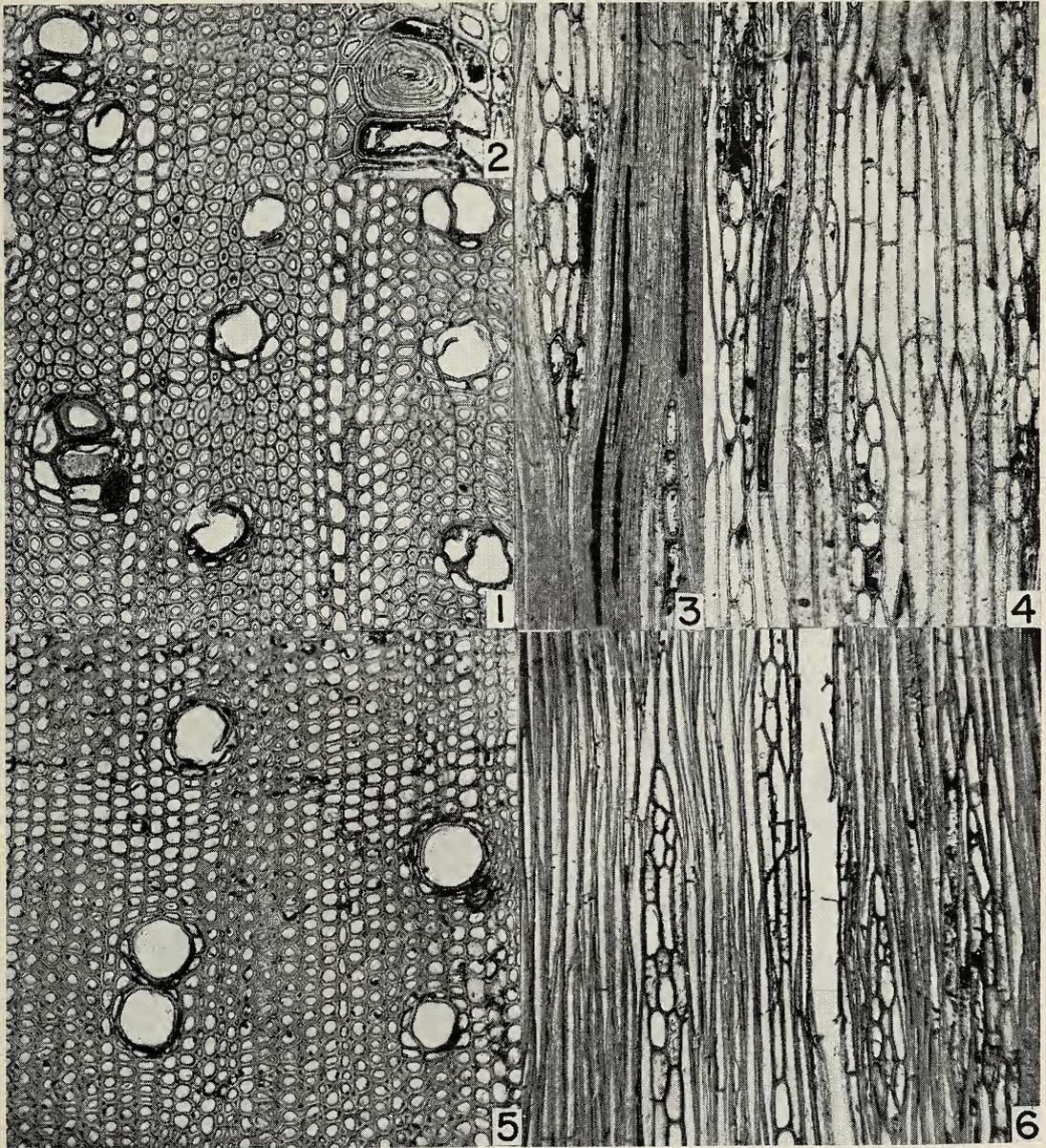
1. *Fitchia cordata* M. L. Grant et S. Carlquist, sp. nov.

Fig. 31

Frutex arboreus 2 m altus glaber, caule basi-liter 4 cm crasso. Folia simplicia petiolata petiolis 25–65 mm longis, longitudine media (N=42) 47 mm. Laminae late obovatae vel suborbiculares luteovirides 40–72 mm longae 36–65 mm latae, magnitudine media foliarum grandiorum circa 58 × 54 mm, basi cordata vel rotundata, apice obtuso acutove vel parum acuminato, margine crenulato vel subintegro, venulis lateralibus 5–10 (numero medio 8.5) pro unico latere. Pedunculi terminales 20–40 mm longi, longitudine media (N=7) 33 mm. Capitula solitaria circa 40-florata. Involucra 25 mm longa 25 mm lata, bracteis 3–4 seriatis viride-lutei coriaceis marginibus-scariosis, exterioribus late triangulatis 3 mm longis 9 mm latis, medi-oribus semiorbicularibus, interioribus lanceolatis 13–17 mm longis 5–7 mm latis. Bractee receptaculares 12–17 mm longae 2–3 (–5) mm latae. Corollae 15–20 mm longae, tubis circa 10 mm longis, sinibus subaequalis. Antherae saccis 5 mm longis, apicibus staminum cuneato-lanceolatis 1–1.5 mm longis. Ovaria ad anthesin 7–8 mm longa, stylis 20–22 mm longis. Achaenia matura 13–16 mm longa, aristas 8–10 mm longis plerumque triangulatis in sectione transversa subdeciduis.

Tree-like shrub, 2 m tall, 4 cm in diameter at the base, glabrous. Bark 1 mm thick, brown, almost smooth, with fine longitudinal ridges 0.5 mm deep. One-year twigs on flowering shoots greenish, 2.5–3 mm in diameter; two-

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FIGS. 1-6. Secondary xylem. Figs. 1-4, *Fitchia cuneata* ssp. *tabaaensis*. Figs. 5-6, *F. cordata*. Figs. 1, 2: Transverse sections; note tyloses in vessels; Fig. 2, a sclerified tylosis in which the lumen is nearly occluded. Figs. 3, 4: Tangential sections; Fig. 3 is a portion showing long, thick-walled fibers; Fig. 4 shows storied apotracheal parenchyma cells. Fig. 5: Transverse section; note band of apotracheal parenchyma above center of photograph. Fig. 6: Tangential section. Fig. 2, $\times 300$; others, $\times 117$.

year twigs pale brown, 4-5 mm in diameter; internodes 4-12 mm long, on vegetative shoots to 20 mm long. Leaves simple. Petioles 25-65 mm long, the average being 47 mm ($N=42$); the stipular sheaths 0.4-0.6 mm high. Blades

broadly ovate to suborbicular, yellowish-green, with a narrow (0.3 mm) stramineous margin, and with a dark callous at the apex; 40-72 mm long, 36-65 mm wide, the average ($N=8$) size of the largest blade on the flowering shoots

being 62×55 mm, the second largest 58×54 mm, and the smallest of the fully-developed leaves 64×43 mm; the base cordate to a depth of 1–2 (–3) mm or rounded; the apex obtuse to acute, with the margins near the tip slightly rounded to straight, or, if barely acuminate, departing at most 1 mm from a straight line; the margin crenulate, with 2–3 indentations (up to 0.5 mm deep) per cm, to subentire, the base entire for 20 mm adjacent to the petiole; with 5–10 (average 8.5) pairs of major lateral veins, usually curving somewhat towards the tip of the leaf. Peduncles terminal, 20–40 mm long, the average ($N=7$) 33 mm, often arcuate and reflexed. Head solitary, with about 40 flowers. Involucres 25 mm long and 25 mm wide; the bracts in 3–4 series, greenish-yellow, coriaceous, scarious-margined, the outermost broadly deltoid (3 mm long, 9 mm wide), the middle ones semicircular, and the inner ones lanceolate (13–17 mm long, 5–7 mm wide). Receptacular bracts 12–17 mm long, 2–3 (–5) mm wide. Corollas 15–20 mm long, the tube about 10 mm long, the shallower sinuses nearly equalling the ventral cleft, and the lobes with terminal hairs 0.1–0.6 mm long. Anther sacs 5 mm long, the stamen tips cuneate-lanceolate, 1–1.5 mm long. Ovary at anthesis 7–8 mm long; the styles 20–22 mm long. Ripe achenes 13–16 mm long, with awns 8–10 mm long; awns generally triangular in transection and somewhat deciduous.

DISTRIBUTION: Society Islands, endemic to Bora Bora.

SPECIMEN EXAMINED: Bora Bora, in dwarf rain-forest on the summit of Mt. Tarapaia, altitude 645 m, Jan. 3, 1931, *M. L. Grant* 4968 (BISH, type; RSA, ISTC, isotypes).

This species was found in several places on Mt. Tarapaia, none less than 25 m in altitude below the summit, but only four inflorescences were discovered, two in bud, one at anthesis, and one in fruit. Associated woody plants were *Alstonia*, *Metrosideros*, *Freycinetia*, and *Glochidion*. Native name: anei.

Mt. Tarapaia appears on U. S. Hydrographic maps as Mt. Pahia, elevation 2165 ft (= 660 m), the name and elevation being taken from French maps. It has been recorded as "Tarapaia." The only higher point on Bora Bora is

Otemanu (Mt. Temanu of the maps), elevation 725 m, a peak which apparently has never been climbed by anyone other than Polynesians.

2. *Fitchia cuneata* J. W. Moore, Bishop Mus. Bull. 102:48. 1933 ssp. *tabaaensis* M. L. Grant et S. Carlquist, subsp. nov.

Fig. 32

Frutex arboreus 2.5 m altus glaber, caule basaliter 2.5 cm crasso. Folia simplicia petiolata petiolis 10–37 mm longis, longitudine media ($N=30$) 20 mm. Laminae plerumque ellipticae vel parum ovatae obovataeque vel rhomboidales subatrovirides 40–110 mm longae 25–58 mm latae, magnitudine media foliarum grandiorum circa acuminato, margine crenulato serratove vel subintegro, venulis lateribus 5–10 (numero medio 7.5) pro unico latere. Pedunculi terminales 25–50 mm longi, longitudine media ($N=10$) 33 mm. Capitula solitaria circa 75-florata. Involucra 20–40 mm longa, 15–25 mm lata, bracteis 3–4 seriatis, viridulutei coriaceis marginibus chartaceis, exterioribus breviter ovatis reniformibusque 2–5 mm longis 6–15 mm latis, medioribus semiorbicularibus 8–12 mm longis 9–13 mm latis, interioribus cuneatis 12–20 mm longis, 4–8 mm latis. Bractee receptaculares lanceolatae 12–17 mm longae 2–4 mm latae. Corollae ad anthesin 15–22 mm longae, tubis 4–10 mm longis, dentibus 5–7 mm longis. Antherae saccis, 4.5–5 mm longis, apicibus staminum cuneato-lanceolatis 1.5 mm longis. Ovaria ad anthesin 8–10 mm longa, 3–4 mm lata, stylis 24–30 mm longis. Achaenia matura 10–20 mm longa, 4–6 mm lata, aristis 10–13 mm longis plerumque teretibus subpersistentibus.

Treelike shrub, 2.5 m tall, 2.5 cm in diameter at the base, glabrous. Bark 1 mm thick, brown, roughened with irregular scaly ridges. One-year-old twigs on flowering shoots greenish, 2 mm in diameter; two-year twigs pale brown, 3 mm in diameter; internodes 4–8 mm long, on vegetative shoots to 12 mm long. Leaves simple. Petioles 10–37 mm long, the average ($N=30$) 20 mm; the stipular sheaths 0.5–0.8 mm high. Blades mostly elliptical, varying to slightly ovate, obovate, or rhomboid, dull green, with a narrow stramineous margin, and with a dark

callous at the apex; 40–110 mm long, 25–58 mm wide, the average size ($N=10$) of the largest leaf on flowering shoots 84×45 mm, the second largest 75×42 mm, and the smallest of the fully developed leaves 59×30 mm; the base cuneate (usually) to barely rounded; the apex acute, occasionally slightly acuminate; the margin crenulate to toothed or subentire, with 2–4 indentations (up to 1 mm deep) per cm; with 5–10 (average 7.5) pairs of major lateral veins, mostly curving slightly toward the tip of the leaf. Peduncles terminal, 25–50 mm long, the average ($N=10$) 39 mm long, always reflexed and usually arcuate at anthesis. Heads solitary, with about 75 flowers. Involucres 15–25 mm long, 20–40 mm wide; the bracts in 3–4 series, greenish-yellow, coriaceous, chartaceous-margined, the outermost short ovate or reniform (2–5 mm long, 6–15 mm wide), the middle ones semi-circular (8–12 mm long, 9–13 mm wide), and the inner cuneate (12–20 mm long, 4–8 mm wide). Receptacular bracts lanceolate, 12–17 mm long, 2–4 mm wide. Corollas at anthesis 15–22 mm long, the tube 7–10 mm long, and the teeth 5–7 mm long, the shorter teeth about half the length of the limb, or eventually equalling it; lobes with hairs about 0.75–1 mm long. Anther sacs 4.5–5 mm long, the stamen tips cuneate-lanceolate, 1–1.5 mm long. Ovary at anthesis 8–10 mm long, 3–4 mm wide; styles 22–30 mm long, the stigmatic branches 0.8 mm long, barely separating at anthesis. Mature achenes 10–20 mm long, 4–6 mm wide; the awns 10–13 mm long, generally rounded in transection, subsistent.

DISTRIBUTION: Society Islands, endemic to Tahaa.

SPECIMEN EXAMINED: Tahaa, district of Ruutia, slopes of Mt. Ohiri, in rain-forest of *Crossostylis*, *Alstonia*, and *Morinda*, altitude 465 m, Jan. 25, 1931. *M. L. Grant 5161* (BISH, type; RSA, ISTC, isotypes).

This subspecies was observed in three other nearby localities, all within an altitudinal range of 15 m, and about 70 m below the top of Ohiri, the highest point on the island. Other associated woody plants were *Xylosma*, *Meryta*, *Metrosideros*, *Wikstroemia*, *Fagara*, *Astronia*, and *Hernandia*.

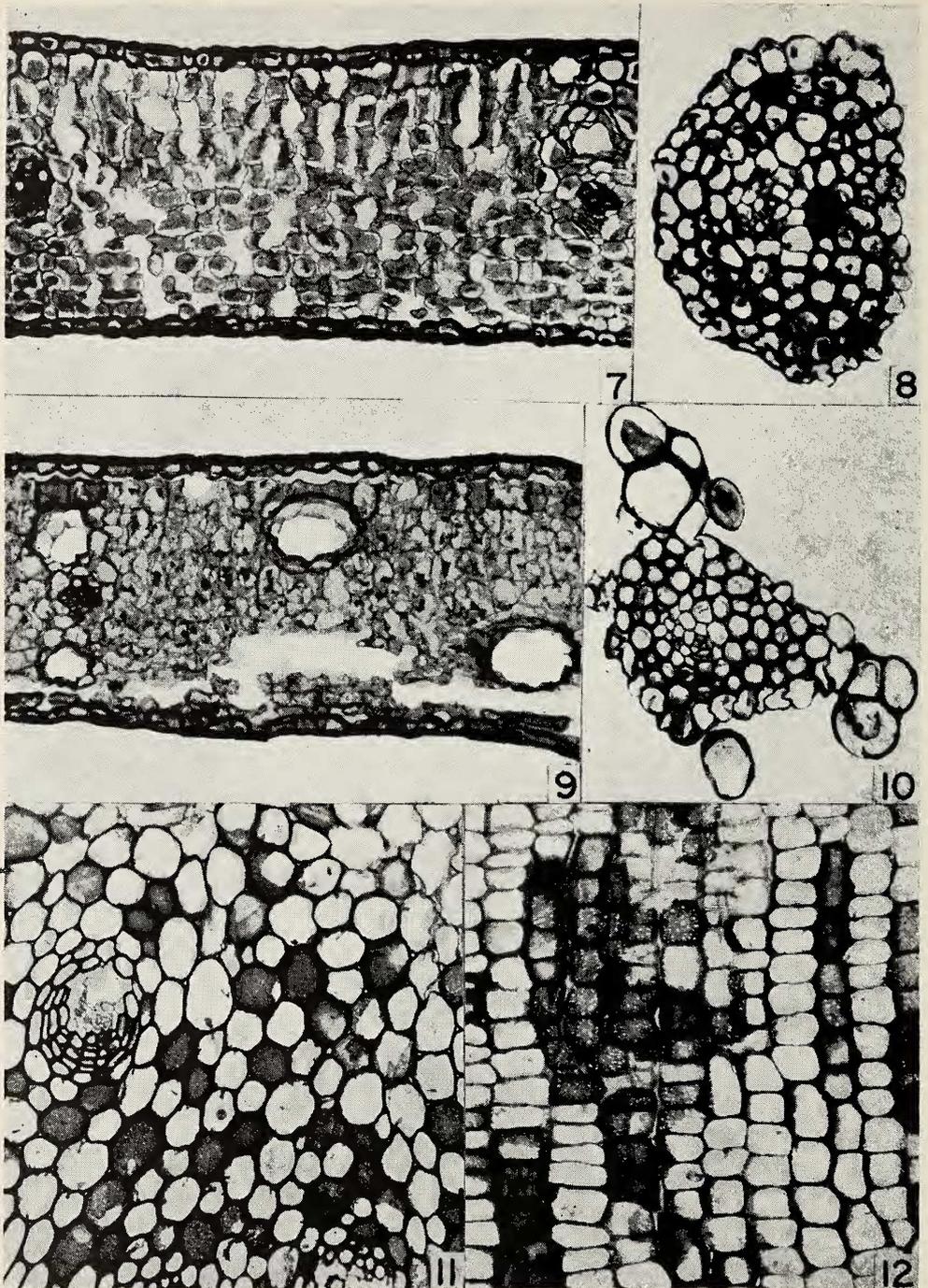
3. *Fitchia nutans* Hook f., London Jour. Bot. 4:640, t.23–24. 1845.

Since so few specimens of this species are available in the United States, and the several Kew and Paris sheets are without detailed habitat data, the citation of an additional collection may be of interest: Tahiti iti, district of Teahupoo, on Mt. Ronui, in *Metrosideros-Weinmannia* forest, altitude 890 m, July 2, 1930, *M. L. Grant 3925* (BISH, ISTC). The following description is from this collection alone.

Trees shaped glabrous shrub, 2.5 m tall, with a basal diameter of 5 cm; bark 2 mm thick, brown, with longitudinal ridges about 1 mm deep; the wood very sweet-smelling. One-year twigs 2–3 mm in diameter; two-year twigs 3.5–4.5 mm thick; internodes 7–10 mm long. Petioles 30–60 mm long; stipular sheaths 2–3 mm high. Blades ovate, yellowish-green, 60–130 mm long, 45–80 mm wide, the average of 12 leaves being 96×61 mm; truncate or cordate at the base, occasionally barely rounded, often somewhat oblique; the apex slightly acuminate; the margin irregularly and shallowly crenulate to entire; with 8–10 major lateral veins. Peduncles two in each of the four inflorescences present, 60–65 mm long, reflexed. Heads shattered with age, the involucral bracts and corollas having dropped. Receptacular bracts 13–14 mm long, 3–5 mm wide. Ripe achenes 9–10 mm long, 2–2.5 mm wide, with persistent awns 7–8 mm long.

This collection fits the general description of the species (Carlquist, 1957: 63), except as follows, with Carlquist's measurements and notes in parentheses: plant smaller (4.5–7.5 m tall), blades often crenulate (entire), maximum leaf size greater (115×70 mm), base often truncate to cordate (acute to obtuse), heads paired (solitary), receptacular bracts shorter (20–22 mm long), achenes much shorter (16–17 mm long at anthesis) and narrower (3–4 mm). These differences, however, do not seem significant enough to warrant separation, and the material matches Hooker's plate closely.

Although the type of the species was supposedly from "Elizabeth Island," all the evidence (Carlquist, 1957: 63) suggests that it is confined to Tahiti. The present specimen comes



FIGS. 7-12. Figs. 7, 8, 11, *Fitchia cordata*. Figs. 9, 10, 12, *F. cuneata* ssp. *tabaaensis*. Fig. 7: Leaf transection, adaxial face above. Secretory canal is above vein at right. Fig. 8: Transection of awn from an achene, adaxial face at right. Note lignification of hypodermal layers, presence of a single vascular bundle. Fig. 9: Leaf transection, adaxial face above. In addition to secretory canals adjacent to vein, left, secretory cavities may be seen, center and right. Fig. 10: Transection of awn from an achene, adaxial face upper right. Trichomes in section, above and below. Fig. 11: Transection of pith. Secretory canal with adjacent fibrosclereids, above; inner margins of vascular cylinder, below; note thin-walled cells at top of figure. Fig. 12: Longitudinal section of pith. All cells have secondary walls, some such are thicker walled. Figs. 7, 9, $\times 145$. Figs. 8, 10, $\times 255$. Figs. 11, 12, $\times 135$.

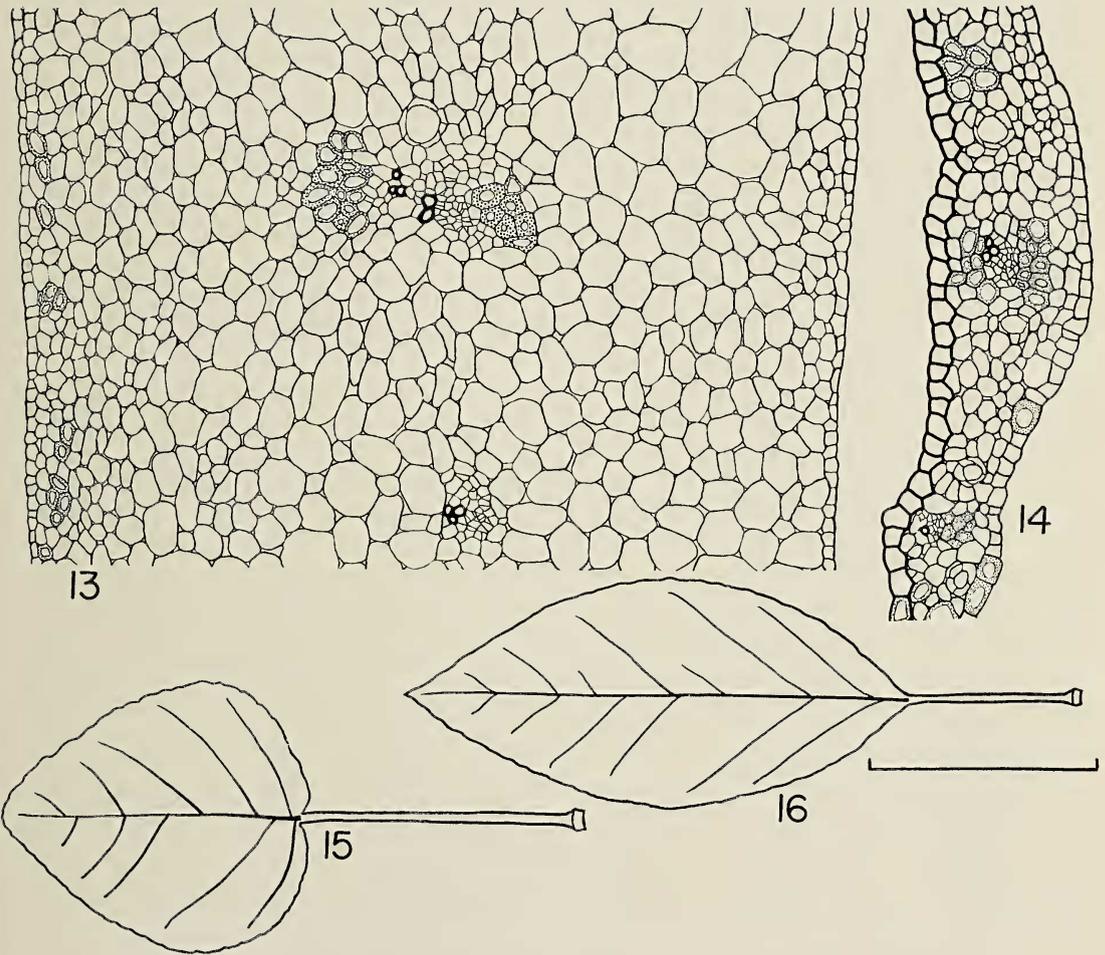
from the smaller mountain (Tahiti-iti) of the two which make up the island.

Hoffmann (1890: 353) reported *F. nutans* from Tabuai (= Tubuai), as well as from Tahiti and Elizabeth (now Henderson) I, but as Hemsley (1885: 20) had earlier shown, this supposed locality is based on the type sheet (Cuming 1424) which Hooker had earlier attributed to Elizabeth Island.

Erdtman (1952: 124) cites a specimen of *F. nutans* as "Fiji, Moseley, anno 1875." Carlquist (1957:63) suggested that this is in error,

because no other collections have been made of *Fitchia* in the Fiji group. Also, Hemsley (1885: 20) reports that there is at Kew a specimen collected by Moseley in Tahiti at an altitude of 4,000 ft, and this is probably the specimen cited by Erdtman.

Papy (1955: 325) mentions *F. nutans* as growing on "Tahiti, Moorea, Raiatea, Rapa." The record from Rapa is probably based on the report of Riley (1926: 55), which was made before *F. rapensis* had been described as a separate species (Brown, 1935: 366), although



FIGS. 13-16. Fig. 13: *Fitchia cordata*. Transection of involucral bract taken about midway along length of bract; adaxial face at left. Fig. 14: *F. cordata*. Transection receptacular bract, adaxial face at left. In Figs. 13, 14, tracheary elements shown in bold outline, fibers and sclereids stippled. Fig. 15: "Typical" leaf of *F. cordata*, showing main veins. Fig. 16: "Typical" leaf of *F. cuneata* ssp. *tabaaensis*. Figs. 13, 14, $\times 105$. Figs. 15, 16, $\times 2\frac{1}{2}$.

Papy was aware of this. Neither Moore nor Grant found *F. nutans* on Raiatea, and Papy was aware of the description of *F. cuneata* from that island. Moorea is certainly a likely locality for *F. nutans*, but for none of these localities does Papy cite specimens.

Thus, the geographic distribution offered by Carlquist (1957:2) must be broadened to include the occurrence of *F. nutans* on Tahiti-iti, *F. cordata* on Bora Bora, and *F. cuneata* ssp. *tabaaensis* on Tahaa.

4. *Fitchia rapensis* F. Brown, Bishop Mus. Bull. 130:366. 1935.

Since the ten previously recorded collections of this species are all without flowers (Carlquist, 1957: 62), the description of a flowering specimen should be of interest: Rapa, moist zone, altitude 520 m, Jan. 3, 1922, *W. B. Jones* 372 (Whitney Expedition) (BKL).

"Tree," glabrous. Petioles 40–75 mm long. Blades ovate, the larger ones averaging 90 mm long and 84 mm wide, rounded or scarcely cuneate at the base, the apex acute; entire; with about 12 pairs of major lateral veins. The single inflorescence is terminal, with two heads, the peduncles 50 and 60 mm long, reflexed. Heads 45 mm long and 45 mm wide. Bracts in about 4 series, those of the second layer semi-circular, 10 mm long and 22 mm wide, and those of the inner layer 20 mm long and 12 mm wide. Receptacular bracts cuneate, 16–17 mm long, 3–4 mm wide. Mature corollas 24–26 mm long, the ventral cleft reaching to 6–8 mm of the base, the segments eventually separating to within 10 mm of the base; the tips of the lobes often densely covered with sclerified cells, which are up to 0.75 mm long. Anther sacs 5.5–6 mm long, caudate, the tail 0.3–0.4 mm long; the stamen tips cuneate, 1.5 mm long. Mature style (broken off) at least 32 mm long. Achenes, at and just after anthesis, 10–12 mm long, 4 mm wide, the awns 12–15 mm long, strongly bent and twisted at the base.

ANATOMICAL DESCRIPTIONS

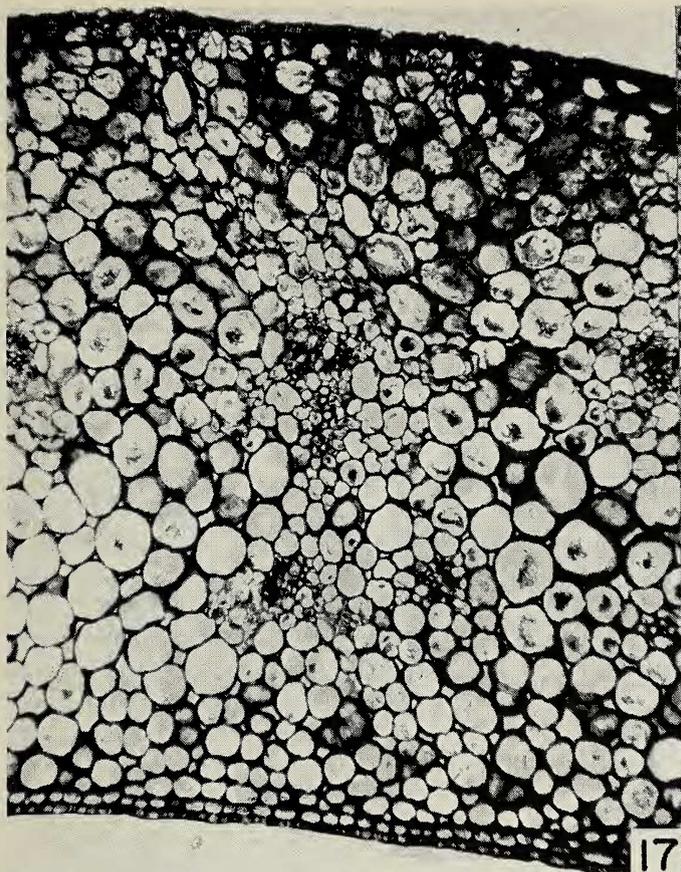
Anatomical studies were based on the herbarium specimens cited above. Liquid-preserved heads of *F. cuneata* ssp. *tabaaensis* and wood samples of both *F. cuneata* ssp. *tabaaensis* and *F. cordata*, for which the herbarium specimens serve as vouchers, were available. The methods of preparation of these materials are the same as those employed for such materials in the two papers (Carlquist, 1957, 1958) dealing with the anatomy of this genus.

SECONDARY XYLEM: With respect to qualitative features, the species of *Fitchia* other than *F. speciosa* are much alike in wood anatomy (Carlquist, 1958). *Fitchia cuneata* ssp. *tabaaensis* and *F. cordata* share the qualitative features of those species. The bands of apotracheal parenchyma are clearly shown by the two new taxa (Figs. 4, 5). Thick-walled fibers are readily apparent in *F. cuneata* ssp. *tabaaensis* (Figs. 1, 3); libriform fibers are less thick-walled in *F. cordata* (Figs. 5, 6). Sclerosed tyloses have been reported in *F. nutans* and *F. speciosa* (Carlquist, 1957, 1958); they are abundant in *F. cuneata* ssp. *tabaaensis* (Figs. 1, 2), although none were observed in *F. cordata*.

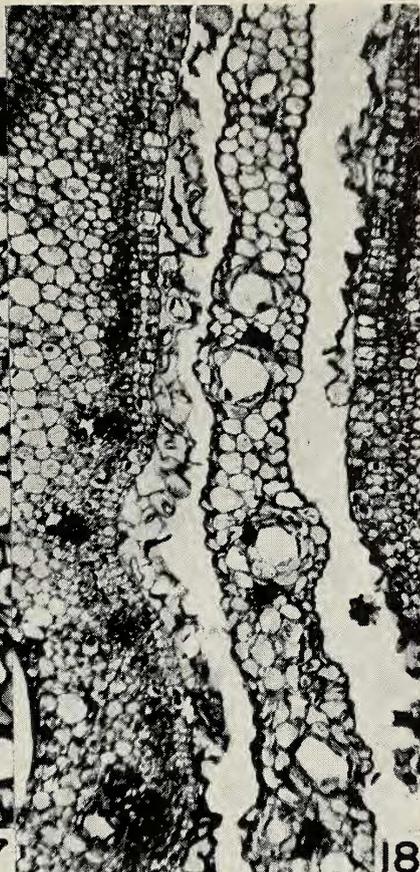
Quantitative features of the two new taxa are as follows: *F. cordata*: vessels per group: 1.37; average vessel diameter: 61.5 μ ; diameter of widest vessel: 88 μ ; average length vessel elements: 325 μ ; average length libriform fibers: 502 μ ; average length apotracheal parenchyma cells: 356 μ ; average height multiseriate rays: 1.17 mm. *Fitchia cuneata* ssp. *tabaaensis*: vessels per group: 1.66; average vessel diameter: 62.8 μ ; diameter of widest vessel: 92 μ ; average length vessel elements: 326 μ ; average length libriform fibers: 507 μ ; average length apotracheal parenchyma cells: 380 μ ; average height multiseriate rays: 1.51 mm.

Quantitative as well as qualitative data point up a close similarity between *F. cuneata* ssp. *tabaaensis* and the typical *F. cuneata*. Quantitative and qualitative data for *F. cordata* re-

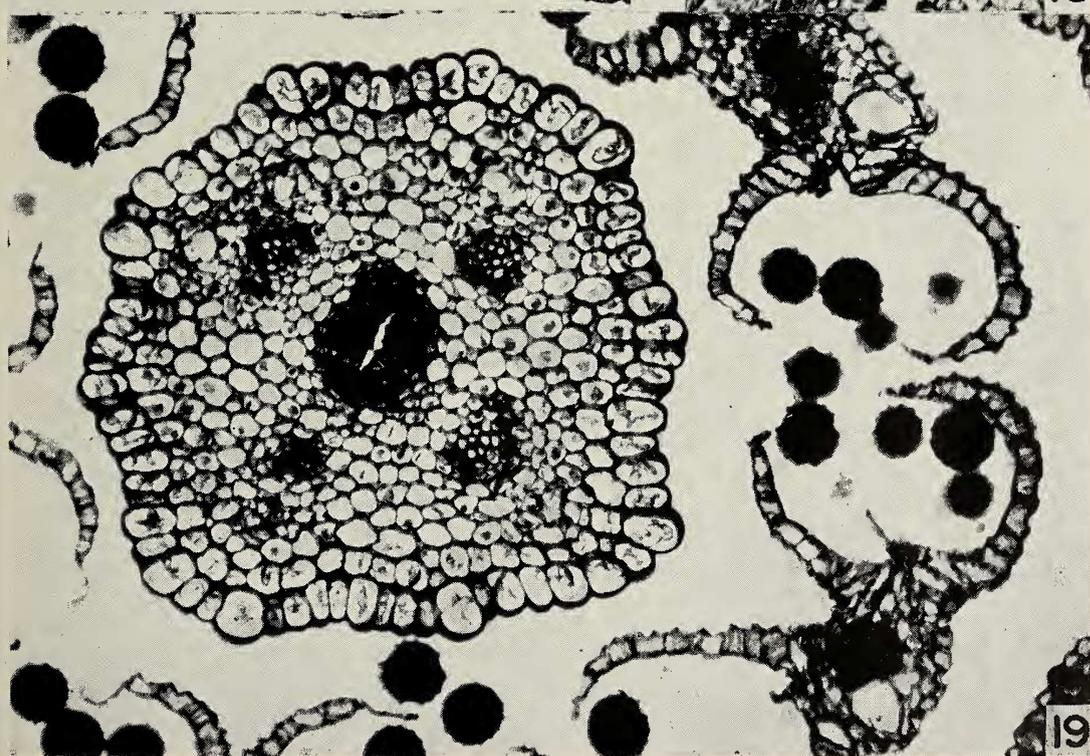
FIGS. 17–19. *Fitchia cuneata* ssp. *tabaaensis*. Fig. 17: Transection of involucral bract taken about midway along length; adaxial face below. Fig. 18: Transection of receptacular bract; adaxial face and adjacent achene at left. Fig. 19: Transection of style. At center of style, stigmatoid tissue. Exterior to each bundle is a secretory canal, except for bundle at upper left, which is flanked by a pair of canals. At right, anthers in transection. Note secretory canal in each of the two anthers. Fig. 17, $\times 100$; Fig. 18, $\times 80$; Fig. 19, $\times 120$.



17



18



19

semble the figures given (Carlquist, 1958: 6-7) for *F. cuneata* and *F. nutans*.

PITH: Pith anatomy proved important in distinguishing species of *Fitchia* (Carlquist, 1957). Likewise, the two new taxa possess characteristics useful for taxonomic purposes. Pith of *F. cordata* (Fig. 11) consists of both thick-walled, lignified, and thin-walled, non-lignified, cells. Secretory canals are present; each is surrounded by an eccentric zone of fibro-sclereids. Although secretory canals surrounded by small lignified thick-walled cells occur in *F. nutans* and *F. tabitensis*, the presence of these combined with occurrence of thin-walled non-lignified cells in pith is characteristic only of *F. cordata*. Pith of *F. cuneata* ssp. *tabaaensis* (Fig. 12) lacks secretory canals and consists of thin-walled and thick-walled lignified cells. The only pith pattern which matches this is that described in the monograph for typical *F. cuneata*.

LEAF: Leaf dimensions are mentioned in the taxonomic description above. However, averages of dimensions of leaves from a collection were used in the monograph, and these may be compared with those of the new taxa. Mature leaves of the collection of *F. cordata* (Fig. 15) show an average lamina width of 52.5 mm, an average lamina length of 53 mm, and a petiole length of 49.7 mm. The only *Fitchia* which resembles *F. cordata* both in form and dimensions is the extreme population of *F. rapensis* from the summit of Rapa. Leaves of *F. cordata* have longer petioles than that collection, and there is certainly no close relationship between *F. cordata* and *F. rapensis*. Leaves of *F. cuneata* ssp. *tabaaensis* (Fig. 16) which could be termed mature show the following average dimensions: lamina width, 48.0 mm; lamina length, 87.5 mm; petiole length, 26 mm. When compared with the chart in the monograph (Carlquist, 1957: 50) the lamina dimensions fall in the vicinity of *F. nutans* and some collections of *F. rapensis*. The leaves are wider than those of *F. tabitensis* but longer than those of the typical *F. cuneata*. Thus, leaf shape distinguishes both *F. cordata* and *F. cuneata* ssp. *tabaaensis*.

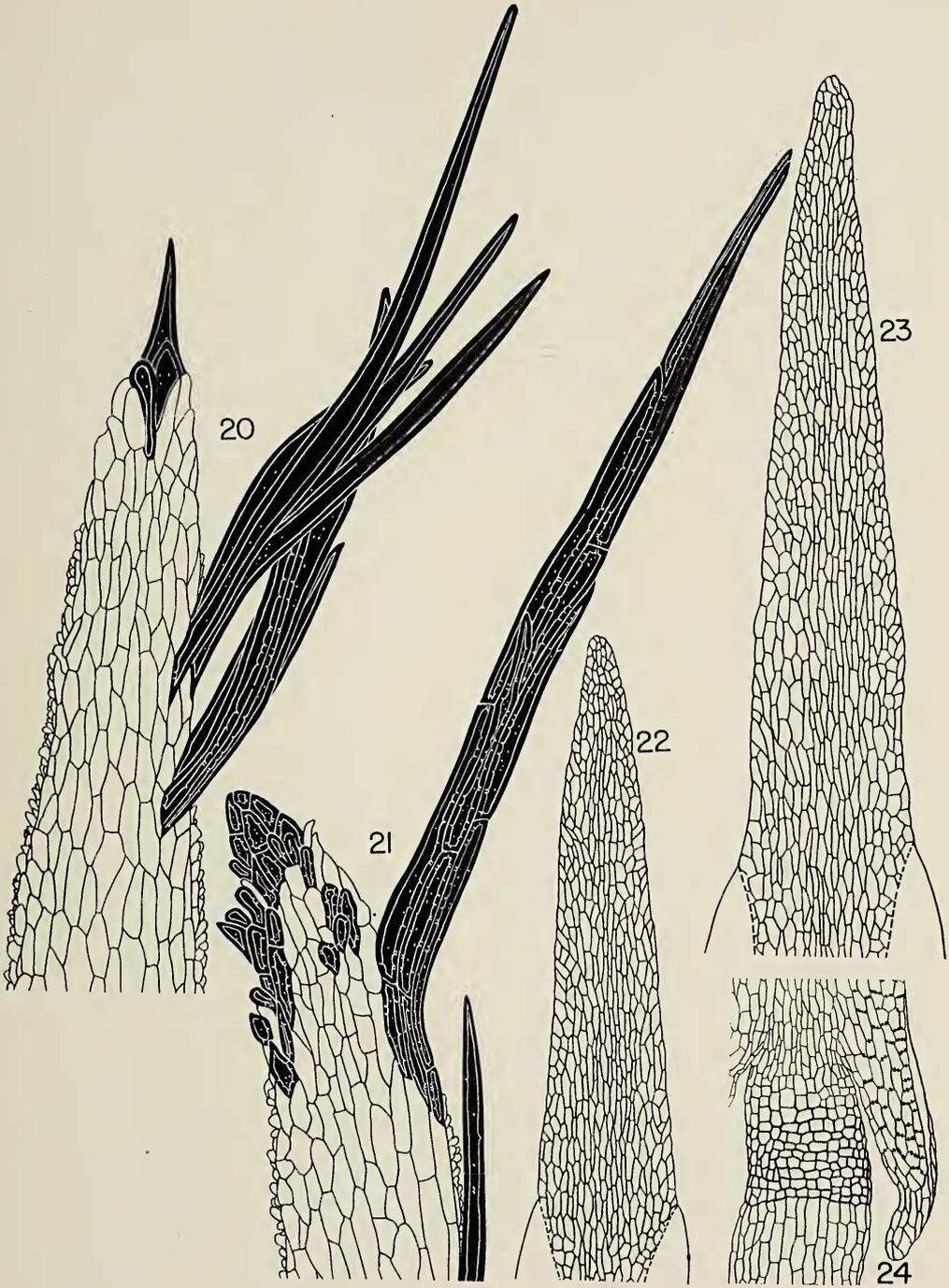
Histological features of leaves of the new taxa also distinguish them. *Fitchia cordata* possesses fibers in bundle sheaths of many veins,

but they are lacking in sheaths of finer veinlets. No secretory cavities are present in the mesophyll, although secretory canals occur adaxially or abaxially to the veins, or both (Fig. 7). Mesophyll is about 10 layers thick. These characteristics are not matched by any other *Fitchia* collection. Presence of a few fibers would ally *F. cordata* to *F. nutans* or *F. tabitensis*, but these two species possess secretory cavities. Absence of secretory cavities does characterize *F. speciosa* and the typical *F. cuneata*, but these taxa lack sclerenchyma in bundle sheaths.

Leaves of *F. cuneata* ssp. *tabaaensis* (Fig. 9) lack sclerenchyma along all but the largest veins. In addition to the secretory canals above and below veins (Fig. 9, left), secretory cavities are present in the mesophyll (Fig. 9, right). The mesophyll is about 10 cells thick. This description agrees closely with that of typical *F. cuneata* except for the presence of secretory cavities. Although such a difference might conceivably arise from a difference in maturity of a plant, it seems more likely a valid difference, for specimens of both subspecies were of flowering age.

INVOLUCRE: The heads of *F. cordata* are small, and the involucre of a living specimen would probably measure about 2 cm in diameter—the smallest involucre size in the genus except for *F. tabitensis* and *F. cuneata*. Involucral bracts of *F. cordata* (Fig. 13) have a thickness comparable to some bracts of *F. nutans*, but differ in their lack of the abundant sclerenchyma which characterizes bracts of *F. nutans*. The mature state of the bracts of *F. cordata* illustrated is certain, because they came from a head in fruit which was in the process of shattering. Occasional lignified thick-walled cells may be seen along the inner face of the bract and around the larger veins. In presence of sclerenchyma and other histological characteristics, the involucral bracts of *F. cordata* are midway between those of *F. nutans* and *F. cuneata*. The receptacular bracts of *F. cordata* (Fig. 14) show similar characteristics. As might be expected, lignified thick-walled cells are more frequent than in the involucral bracts.

Fitchia cuneata ssp. *tabaaensis* also has very narrow involucres, like those of the typical *F. cuneata* or *F. tabitensis*. Histologically, involu-



FIGS. 20–24. Figs. 20, 23, *Fitchia cordata*. Figs. 21, 22, 24, *F. cuneata* ssp. *tabaaensis*. Figs. 20, 21: Tips of corolla lobes, showing exterior surface. Sclerenchymatous cells are shown in black. Figs. 22, 23: Stamen tips, showing inner surface. Anther sacs shown in outline, below. Fig. 24: Base of anther and adjacent filament. Note caudate anther sac, right. All, $\times 65$.

cral bracts of *F. cuneata* ssp. *tabaaensis* (Fig. 17) resemble closely the description given for typical *F. cuneata* in the monograph. This resemblance is especially evident in the lack of sclerenchyma. Only an occasional lignified cell (usually near a vein) can be found. Collenchymatic thickening may occur near outer or inner faces of the bract. In the section shown, more than a single series of bundles may be seen; some of these bundles have distorted orientation of xylem and phloem, a condition mentioned in the monograph for *F. speciosa*. This condition is probably occasional among larger bracts of several species. The thickness of the involucre bract, as well as its lack of sclerenchyma, identifies the two subspecies of *F. cuneata* closely with each other. The receptacular bract (Fig. 18) of a head at anthesis certainly lacks sclereids, although a greater degree of lignification might be apparent in bracts of a head in fruit.

ACHENES: Awn shape and anatomy proved useful characteristics in distinguishing species of *Fitchia*. In comparing illustrations of these (Carlquist, 1957: plate 8) with these of the new taxa (Figs. 8, 10) this also proves to be true. In *F. cordata* (Fig. 8), the awns tend to be rounded in transectional shape, like those of *F. nutans*. However, they show a tendency to be wider than those of *F. nutans*. They have a single vascular bundle and, unlike at least some awns of *F. nutans*, they lack a secretory canal. Awns of *F. cuneata* ssp. *tabaaensis* (Fig. 10) are like those figured for the typical *F. cuneata* in all respects. Presence of three longitudinal zones of trichomes tends to make them triangular as seen in transectional view. Where such trichomes are absent, awns may have a more rounded shape.

COROLLA: In the monograph, considerable attention was focused on the importance of venation patterns of *Fitchia* corollas, both for their phylogenetic importance within Compositae and for their usefulness in distinguishing species. Corolla venation patterns are not illustrated here for the new taxa because they contribute relatively few novel features and can be referred to patterns illustrated in the monograph. Although few flowers of *F. cordata* could be studied in this respect (on account of the

ravages of the living plant by insects), the venation pattern of this species is substantially like that figured for *F. cuneata* or *F. tabitensis*. There is some variation in the levels at which adjacent lateral veins in each lobe join beneath sinuses, but differences in these levels are not nearly so extreme as the condition figured for *F. nutans* (Carlquist, 1957: 10). In their relatively short length (ca. 18 mm) the corollas of *F. cordata* approximate those of *F. tabitensis* also.

Corollas of *F. cuneata* ssp. *tabaaensis* have similar size and venation features. Typically, the patterns are the same as mentioned for *F. cordata*. However, occasionally a pair of adjacent laterals do not join beneath a sinus, but continue into the tube and achene without joining. This condition does occur occasionally in the other species, such as *F. speciosa*. A feature of interest in the corolla of *F. cuneata* ssp. *tabaaensis* is the presence of one or two supernumerary veins in each lobe. In addition to the median and lateral veins, these fine supernumerary veins may be present for a short distance near the base of the lobe. Such veins were not seen in the typical *F. cuneata*, for which, however, mature corollas were not available. Supernumerary veins are occasional in corollas of *F. speciosa*, and characteristically abundant in those of *F. mangarevensis*.

The occurrence of larger numbers of veins in corollas of *F. mangarevensis* is particularly interesting, since that species is close to *F. rapensis*. Corollas, now available, of *F. rapensis* confirm this relationship in the similarly elaborate venation pattern (Fig. 26). This similarity is shown in the presence of five veins per lobe, rather than three. Such a condition is basic in the construction of the *F. rapensis* corolla, although additional veins or vein fragments may be present. The outermost veins of each lobe fuse at the tips of many corolla lobes. The corolla venation of *F. mangarevensis* (Carlquist, 1957:14) is somewhat more complicated than this, because although the five-vein condition may be observed in some lobes in that species, additional veins are more frequent. The presence of complex corolla venation in both *F. rapensis* and *F. mangarevensis* is interesting in that it raises the question of how complex

venation may have been present ancestrally in *Fitchia*. Is the more complex condition primitive or a specialization? The question cannot be answered in terms of the data available, and cytological information would be very desirable as a line of supporting evidence.

Distribution of thin-walled and thick-walled trichomes and occurrence of sclereids on corolla-lobe tips have proved useful features in the systematics of *Fitchia*. In the two new taxa these features are also of interest. *Fitchia cordata* (Fig. 21) possesses lobe tips not identical to those of any species previously figured. The frequency of sclereids at the lobe tip is notable. Long multiseriate trichomes, all the cells of which are sclereids, are present. No trichomes composed of nonlignified cells were observed. This condition is most closely matched in the genus only in the new subspecies of *F. cuneata* (Fig. 20). In *F. cuneata* ssp. *tabaaensis* sclereids are rare or absent at the lobe tips. The trichomes are long, multiseriate (rarely uniseriate), and composed wholly of sclereids. This condition is not unlike the condition in typical *F. cuneata*, except that the trichomes in the Tahaa plants are few and long.

The corolla-lobe tips of *F. rapensis* (Fig. 25) are, as might be expected, rather similar to those of *F. mangarevensis* (Carlquist, 1957: 27). They are different in that in *F. rapensis* the sclerified trichomes are slightly longer, in general, and extend farther down the lobe. Occasional thin-walled hairs may be seen on the terminal portion of lobes of *F. rapensis*, but the extremely dense coating of thick-walled lignified trichomes clearly marks this pattern as closest to that of *F. mangarevensis*.

STAMENS: Stamen tips likewise offer taxonomic criteria. The long stamen tips of *F. cordata* (Fig. 23) exceed those of *F. nutans* in size, and are thus the longest of the Society Islands species of *Fitchia*. The stamen tips of *F. cuneata* ssp. *tabaaensis* (Fig. 22) are longer than those of the typical *F. cuneata*, but do not differ markedly from those of *F. tabitensis* or *F. nutans*.

The stamen tips of *F. rapensis* (Fig. 27) are 1.5 mm long, thus matching those of *F. mangarevensis*. This is particularly interesting because the two species are so much alike in this respect and because they have longer stamen

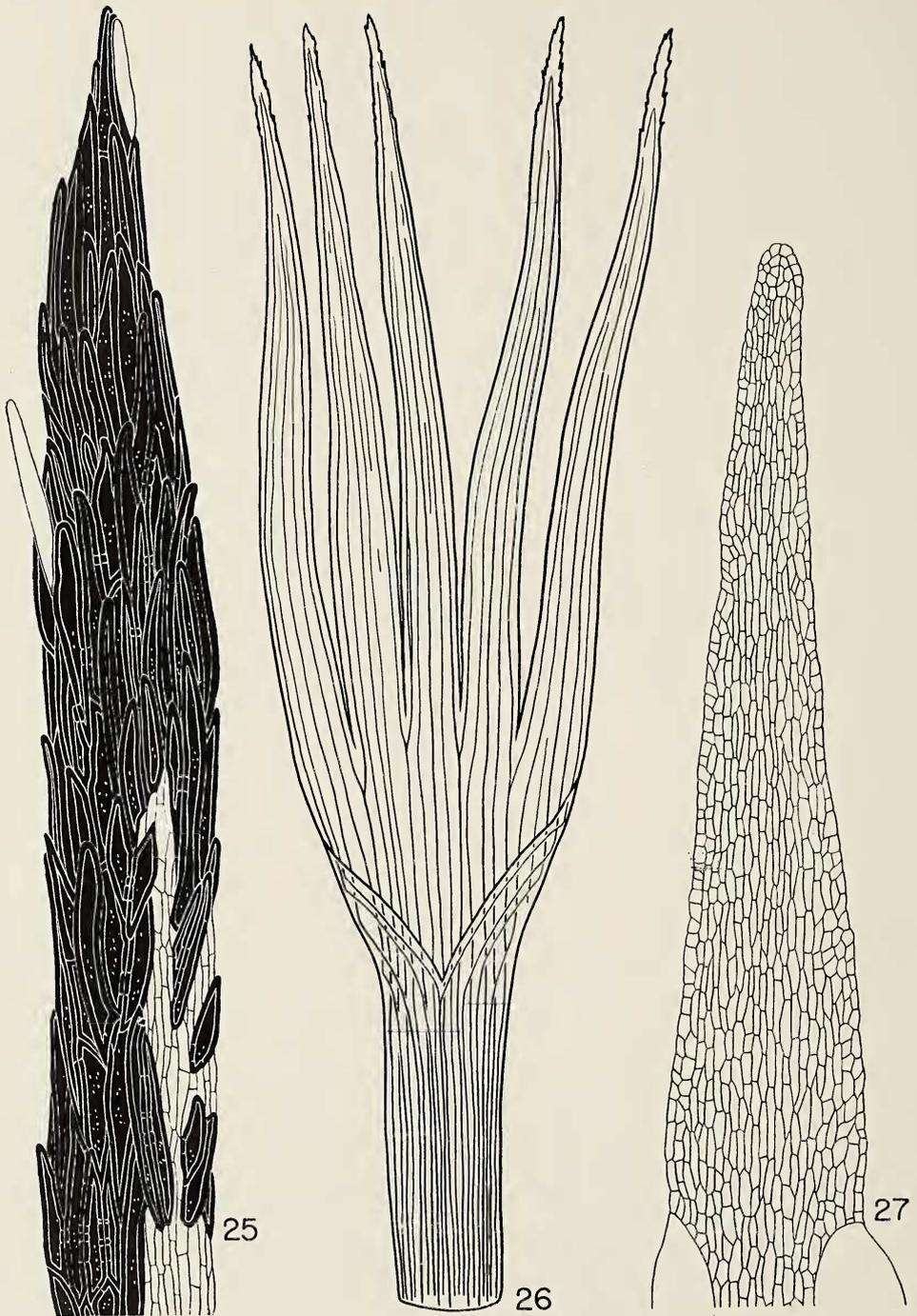
tips than the other species of the genus, with the exception of *F. speciosa*.

A feature of some interest not previously observed is the occurrence of somewhat caudate anther sacs in *F. cuneata* ssp. *tabaaensis* (Fig. 24) and the other taxa of *Fitchia*. In view of Cronquist's (1955) dictum that anthers of Compositae are primitively tailless, this would seem curious, because *Fitchia* possesses so many anatomical and morphological characteristics which appear primitive for the family. Cronquist's dictum, for which no appreciable evidence is adduced, seems highly questionable.

In transection the anthers of *F. cuneata* ssp. *tabaaensis* (Fig. 19) exhibit a feature of interest. One or two secretory canals may be observed in the connective of each anther. This condition occurs sparingly in *F. speciosa*, but was not observed in other species of *Fitchia*. The occurrence of anther secretory canals has been noted in other genera which may be related to *Fitchia*, such as *Petrobium* and *Oparanthus* (Carlquist, 1957).

STYLE: Like the anthers, the style of *F. cuneata* ssp. *tabaaensis* (Fig. 19) seems to exhibit more numerous secretory canals than those of other species of *Fitchia*. One canal (or occasionally a pair) is present exterior to each of the four style bundles. Liquid-preserved material is required for accurate demonstration of this phenomenon. In the only other species for which such material was available, *F. speciosa*, canals were much less abundant in styles (Carlquist, 1957). However, as indicated in the monograph, many other Heliantheae do show abundance of stylar secretory canals.

POLLEN GRAINS: The drawings of pollen grains of *Fitchia* (Figs. 28–30) show some differences in representation compared with those of the monograph. Although the outer sculptured layer (ectosexine) is composed of fine rods and spaces, as illustrated earlier, a lacunose inner sculptured layer (endosexine) has now been observed. The endosexine consists of rods interspersed in large spaces. In addition, an inner and outer layer of nexine (below in each figure) may be distinguished. Size and spine shape are of especial interest, however, in comparison of the species. The markedly blunt spines of *F. cuneata* ssp. *tabaaensis* (Fig. 29)

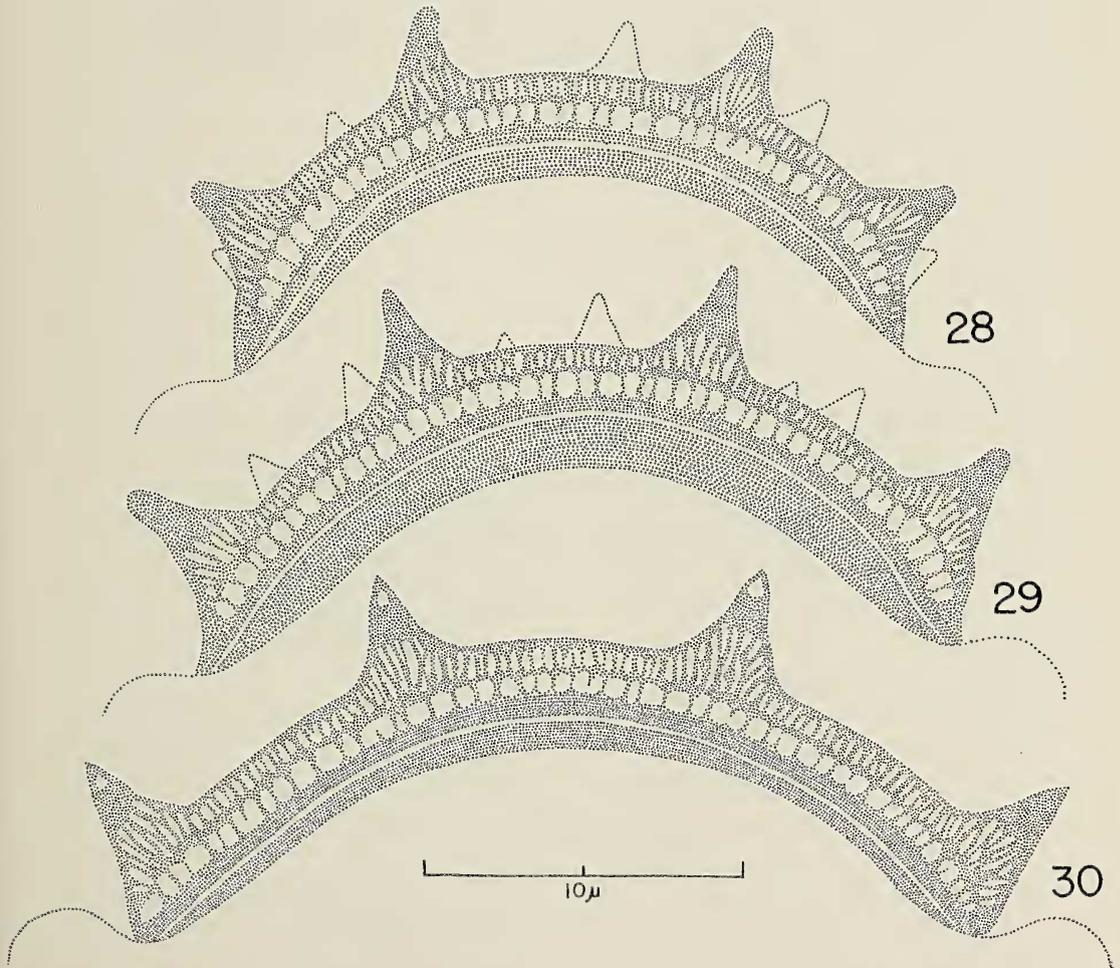


FIGS. 25-27. *Fitchia rapensis*. Fig. 25: Tip of corolla lobe, showing exterior surface; sclerenchymatous cells in black. Fig. 26: Corolla, showing venation. Fig. 27: Stamen tip, showing inner surface. Figs. 25, 27, $\times 65$. Fig. 26, $\times 8$.

match those of the typical *F. cuneata* (Carlquist, 1957:32). In *F. cordata* (Fig. 28) the spines are even more markedly blunt. Pollen grains of *F. cordata* (range, 39–51 μ ; average, 42 μ) are the smallest in the genus. The pollen grains of *F. cuneata* ssp. *tabaaensis* (range, 45–51 μ ; average, 48 μ) closely match those of ssp. *cuneata* in size. The slightly smaller size of grains in the latter may be caused by the fact that flowers of *F. cuneata* ssp. *cuneata* from which grains were taken were not quite mature. Pollen grains of *F. rapensis* (Fig. 30) average 60 μ in diameter, and have a range from 51 to 66 μ . They are thus slightly larger than those of *F.*

mangarevensis, although the difference is not significant. The spines of pollen grains of *F. rapensis* have an inverted-funnelform shape, like those of *F. mangarevensis*, but appear to be more sharply pointed. In addition, lacunae in spine tips were observed for the first time in the genus in *F. rapensis*. This feature, however, is not unexpected in *Fitchia*, since other Heliantheae have lacunae in spine tips (Carlquist, 1957:33).

SPECIES CHARACTERISTICS: In the monograph three species groups were recognized: (1) *F. speciosa*; (2) *F. nutans*, *F. tabitensis*, and *F. cuneata*; and (3) *F. mangarevensis* and



FIGS. 28–30. Optical sections of equator of pollen grains, showing a third of each grain. Germ pores indicated at left and right in each. Fig. 28, *F. cordata*. Fig. 29, *F. cuneata* ssp. *tabaaensis*. Fig. 30, *F. rapensis*.



FIGS. 31-32. Type specimens of *Fitchia*. Fig. 31, *F. cordata*. Fig. 32, *F. cuneata* ssp. *tahaensis*.

F. rapensis. The new taxa clearly belong to the second group. The present study also emphasizes the distinctness of the third group and the close relationship between the two species it contains.

Fitchia cuneata ssp. *tahaaensis* agrees with typical *F. cuneata* in most respects. Those by which it differs include: presence of sclerified tyloses in wood (not yet observed in wood of typical *F. cuneata*); leaves with wider and longer laminae; secretory cavities present in leaf mesophyll; involucre bracts thicker; sclerified trichomes on corolla-lobe tips longer and fewer; anther tips longer. These differences are relatively minor. Close identity of the two subspecies is revealed by such critical features as general leaf shape, pith structure, bract anatomy, corolla vascularization, awn shape and anatomy, and pollen size and ornamentation. The two taxa are therefore best regarded as subspecifically different. This situation is precisely what one would expect on account of the closeness of Tahaa to Raiatea, sister-islands (within a common fringing reef).

The nearest island to the sister-islands of Raiatea is Bora Bora. One might expect, therefore, a similarity between *F. cuneata* and *F. cordata*. These two do appear similar in their small heads, relative lack of sclerenchyma in involucre bracts, venation and size of corollas, lack of secretory cavities in leaves (excepting ssp. *tahaaensis*) and blunt shape of spines on pollen grains. They are dissimilar in that *F. cordata* possesses secretory canals and thin-walled nonlignified cells in the pith, has cordate leaves, and some sclerenchyma along veins of leaves. These characteristics are reminiscent of *F. nutans*. From *F. nutans*, however, *F. cordata* differs by such respects as those in which it resembles *F. cuneata*. Features of *F. cordata* which do not match those of any species in the *F. nutans*-*F. cuneata*-*F. tabitensis* group include the presence of nonlignified cells in pith, the small leaf size and cordate shape combined with relatively long petiole length, the presence of both long multiseriate sclerified trichomes and sclerified epidermal cells on corolla-lobe tips, long stamen tips, small pollen size, and blunt spines on pollen grains. These characteristics, combined with the distinction furnished by its geographical isolation on Bora Bora, mark *F. cordata* as worthy of recognition as a new species.

PHYLOGENETIC CONSIDERATIONS: The new taxa described here, although they contribute no anomalous features to the genus, do enlarge our picture of it and permit more detailed observations in this regard. The monograph of the genus provided some notions on the relationships of *Fitchia*. These ideas do not seem to require alteration. The new taxa do enhance the diversity of the Society Islands *Fitchias*. Indeed, Papy (1955) notes that the Society Islands form a center of diversity for *Fitchia*, and that the variability of *Fitchia* on Tahiti is suggestive of this. The latter phenomenon remains a problem worthy of study when more material from Tahiti becomes available.

Postulation of phylogenetic trends within each species group seems inadvisable, both because of the limited quantity of material known and the fact that the species seem to be variations on a basic theme rather than stages along a phylogenetic pathway. However, some interpretations of relationship among the species groups may be offered here.

The larger size—in all parts of the plant—of *F. speciosa*, as compared with the remaining species, seems specialized. The larger pollen size suggests the possibility of a greater chromosome number, and the morphology of the awn base seems clearly a specialized feature. The fact that *F. speciosa* has such an isolated geographical position, the westernmost species of *Fitchia*, in contrast with the likelihood of an American ancestry of this helianthoid (e.g., Brown, 1935; Papy, 1955), reinforces this supposition. The extremely large seeds of *F. speciosa* seem less adapted to long-distance dispersal than the smaller seeds of the Society Islands species. The most likely interpretation, seemingly, is that seed size, and the peculiar adnation of achene summit to awn base in *F. speciosa* are characteristics acquired subsequent to arrival of its ancestors in Rarotonga. *Fitchia speciosa* may be regarded as a highly distinct derivative of the Society Islands stock. Although corollas of *F. speciosa* are the largest in the genus, their venation is like that of the Society Islands species, not that of *F. rapensis* and *F. mangarevensis*, which have complex corolla venation.

If pollen-grain size is an indication of chromosome number, then one would expect the Society Islands species to have the lowest num-

ber, and progressively higher chromosome numbers would be indicated for the *F. rapensis*-*F. mangarevensis* group and *F. speciosa*. If this were true, and it were a criterion of phylogeny within the genus, the complex floral venation of *F. rapensis* and *F. mangarevensis* would be a specialization. Information on comparative cytology within the genus, in any case, is highly desirable.

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