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New species and sections of *Freycinetia* (Pandanaeae) from the Solomon Islands

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Abstract

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A new species and two new sections of *Freycinetia* (*F. stonei*, sect. *Solomoniella*, and sect. *Stoneella*) are described from the Solomon Islands. New characters of *F. nesiotica*, *F. membranacea* and *F. stonei* are found and can be used to distinguish these species which were often confused with one another in the past. In particular, the seed anatomy proves useful in distinguishing species and sections in this genus. It is further emphasized that *Freycinetia* has a very variable morphological differentiation which should be extensively investigated and used in its taxonomy.

Key words: berry and seed anatomy, *Freycinetia*, Pandanaeae, Solomon Islands, taxonomy.

Introduction

When Merrill & Perry (1939) described several species of *Freycinetia* from the Solomon Islands, they had no problem in distinguishing them except for *F. nesiotica* and *F. membranacea*. These two species are similar in that they have syncarps which are ellipsoid or shortly oblong, pistillate pedicels scabrid, and leaves mostly about 60 cm long and 1–1.5 cm broad, by which characters they differ from the other species (Stone 1963: 2). The characters found by Merrill & Perry (1939) which may to some extent be used to distinguish these species are as follows. For *F. nesiotica*: the leaves are distinctly coriaceous, and possibly the auricles split lengthwise into fibres. For *F. membranacea*: the leaves are of membranaceous texture, and the auricles break transversely into pieces.

In his second revision of *Freycinetia* in the Solomon Islands, Stone (1970) listed 23 species, all of which he was able to distinguish except, again, for *F. nesiotica* and *F. membranacea* (Stone 1970: 372–375), which he found “difficult to discriminate” and requiring “further comparative study”. He also considered the two above-mentioned leaf characters found by Merrill & Perry (1939) as “rather trivial”, and proposed to use “the different sort of scabridity on the pedicel” (of pistillate spikes) as a possible “better distinction”. That is: “in *F. nesiotica* the angles of the pedicel are beset by a rather robust,

wave-like series of antrorse, deltoid flat teeth, spreading out rather than much appressed; in *F. membranacea* the scabridity is much more minute, much more appressed, squamulose, and much more sparse; on first glance, in fact, the pedicels appear smooth". Nevertheless, again, this distinction is not unquestionable because difficult to use, and because the scabridity of pistillate pedicels may vary in one and the same species. As a result, there was much uncertainty about the identity of these species in herbaria.

Therefore, recently Stone (in litt. 16 Jan. 1993) suggested to the present author a special investigation of these two species in order to tentatively find other evidence that could be used to distinguish them. This was the primary purpose of the present study. However, in revising specimens from the Solomon Islands that belong or are comparable to these species, an unknown species and two unknown sections were also found which are described below.

Material and methods

For the anatomy of berry and seed, berries were rehydrated overnight in 65 °C water, embedded in paraffin, microtome-sectioned, stained in Safranin and Astrablue, and mounted in a synthetic resin.

The following specimens all of which are pistillate were investigated:

F. marquisensis F. Brown: Wagner, Lorence & Florence 6187 (BISH, PTBG), Marquesas Islands, Fatu Hiva, 23 July 1988.

F. membranacea Merr. & Perry: Waterhouse 168 (GH, NY), type, Solomon Islands, Bougainville, Siwai, December 1932. – Craven & Schodde 380 (GH), Solomon Islands, Bougainville, Barilo, 2 September 1964. – Schodde & Craven 4103 (GH), Solomon Islands, Bougainville, Aku, 21 September 1964. – Croft LAE. 65534 (GH), Solomon Islands, New Ireland, District New Ireland, subdistrict Lamet, 11 October 1974. – Kajewski 2184 (BISH, GH), Solomon Islands, Bougainville, Marmoromino, 28 September 1930 (fruits immature). – RSS 2388, Royal Society Expedition 1965 (GH), Solomon Islands, Kolombangara (fruits immature).

F. nesiotica Merr. & Perry: Brass 2929 (GH), type, Solomon Islands, San Cristoval, Hinuahaoro, 22 September 1932.

F. stonoi Huynh: Stone 2475 (BISH), type, Solomon Islands, Santa Ysabel, 12 October 1957.

Results

1. Differences in leaf shape and berry morphology between *Freycinetia nesiotica* and *F. membranacea*

These two species can be readily distinguished either by leaves or berries. The leaves of *F. nesiotica* narrow very gradually from about the middle to the apex (Fig. 1). Those of *F. membranacea* narrow abruptly from about the top seventh or eighth (Fig. 6). This tapering, observed in the type of this species, was corroborated by five other specimens all of which were also from the Solomon Islands (see above).

The berries of *F. nesiotica* differ from those of *F. membranacea* by the following features. Firstly, they narrow clearly in the middle part, and their pileus is pyramidal (Fig. 2). Such berries are unusual in subg. *Gaudichaudiella*, to which both species belong (see below). Those of *F. membranacea* do not narrow in the middle part, and their pileus is cylindrical above, pyramidal below (Fig. 7). Such berries are also observed in sect. *Gaudichaudiella* and sect. *Malacandra*, another section of subg. *Gaudichaudiella*. Secondly, the berries of *F. nesiotica* are clearly separate from each other (when they are in syn-

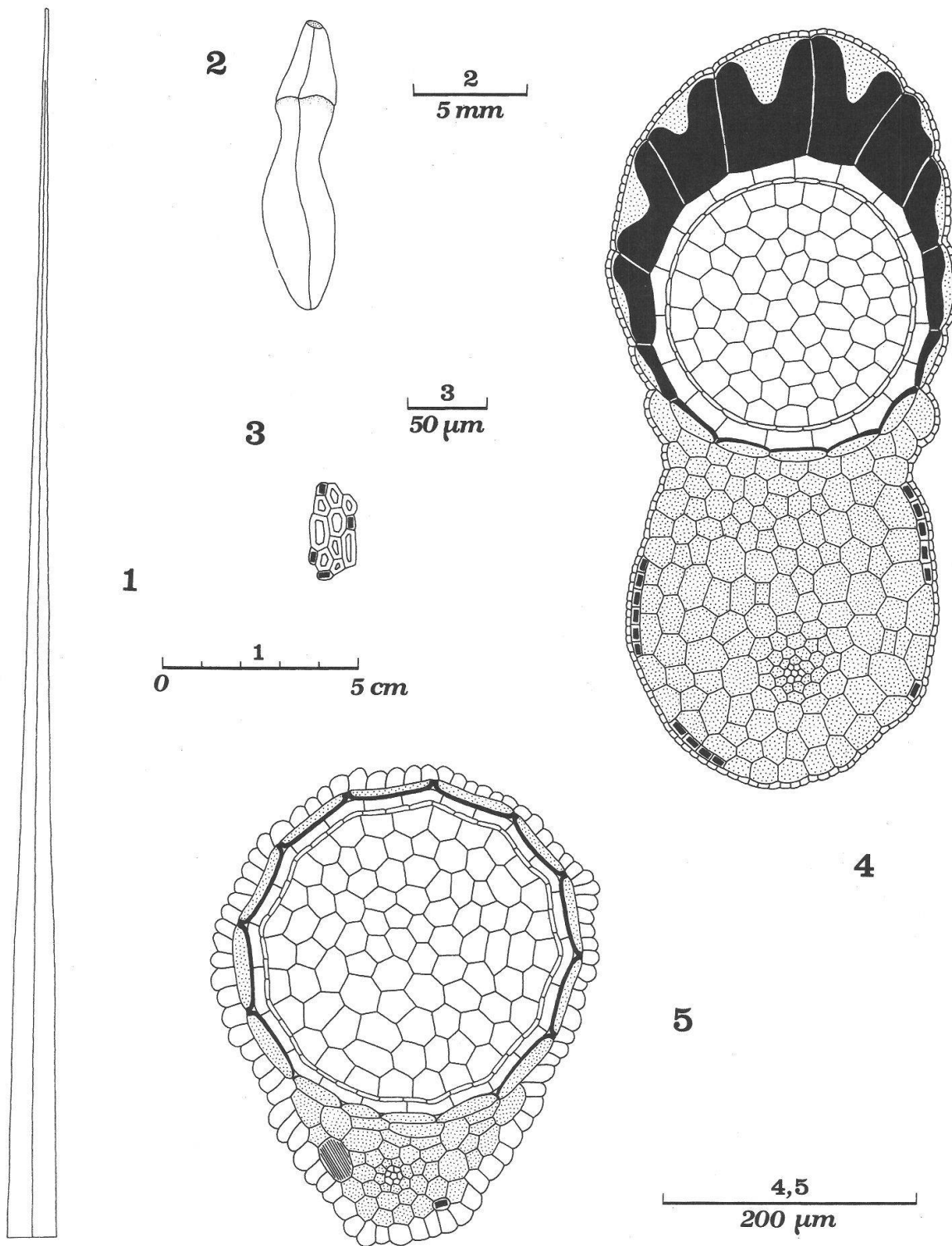


Fig. 1–5. *Freycinetia nesiotica* (1–4) (Brass 1929) and *F. marquisensis* (5) (Wagner, Lorence & Florence 1987). – 1: Upper part of a leaf about 66 cm long, viewed by adaxial face. – 2: Berry in lateral view, showing pyramidal pileus in the upper part. – 3: Middle transverse section of one of the largest fusiform/elliptic fibre-bundles in the basal part of the ovary walls (cells with black rectangle = crystal cells). – 4: Middle transverse section of seed, showing raphe in the lower half and integuments around endosperm in the upper half (for further caption, see Fig. 5). – 5: Middle transverse section of seed, showing raphe in the lower third and integuments around endosperm in the upper thirds (dotted cells = lignified cells; undotted cells = unligified cells; cell with black rectangle = crystal cell; hatched cell = raphide cell; outward-curved bold black-lines = lignified thickenings; the vascular bundle in the raphe is represented by the smallest undotted cells midway between the crystal cell and the raphide cell) (the integuments are represented each by two cell layers; however, the inner “layer” of the inner integument, which is visible as being the circle of thinnest cells, is very thin, therefore its observation was not satisfactory).

carp in dry state); as a result, they can be removed without any damage to their epicarp. Those of *F. membranacea* are strongly adherent to each other along their lower part with the consequence that they cannot be removed without some tearing to their epicarp. Both types of berry are also observed in other species of *Freycinetia*: the former type for example in the species of sect. *Freycinetia* and sect. *Devrieseella*, the latter type in those of sect. *Gaudichaudiella* and sect. *Malacandra*. In such a species, no variation from one type to the other has been found to occur. A third difference resides in the fibre bundles visible on the berries. These bundles are the thickest of the subepicarpic fibre bundles, but several other similar bundles of various sizes also exist beneath and at various levels from apex to base in the berry. Both sorts of fibre bundles are very characteristic, being fusiform/elliptic in longitudinal section and composed of longitudinal rows of fibres and of crystal cells. They have been observed in subg. *Gaudichaudiella* only (see Huynh 1995). Therefore, their presence in *F. nesiotica* and *F. membranacea* indicates that these species belong to this subgenus. The subepicarpic fusiform/elliptic fibre-bundles as seen in *F. membranacea* are fairly common in subg. *Gaudichaudiella* since they are also observed in several other species: for example *F. impavida* (sect. *Gaudichaudiella*), *F. samoensis* (sect. *Malacandra*), and their allied species. Those of *F. nesiotica* are narrower and generally twice as long.

2. Anatomical differences in berry and seed between *Freycinetia nesiotica* and *F. membranacea*

The berries of these two species also differ in their anatomy. The most visible difference lies in the fusiform/elliptic fibre-bundles in the basal part of the ovary walls as observed in transverse sections. In *F. nesiotica*, these fibre bundles are all small, the largest generally do not exceed about 60 μm in width and comprise about ten fibres (Fig. 3). This type of basal part of ovary walls is rare in subg. *Gaudichaudiella*. In *F. membranacea*, they are all much larger, up to 250 μm or more in width and with about sixty fibres, which are about twice larger (Fig. 8). This type of basal part of ovary walls and these fibres are also observed in several other species of subg. *Gaudichaudiella*: for example *F. impavida* (sect. *Gaudichaudiella*), *F. samoensis* (sect. *Malacandra*), and their allied species.

F. nesiotica and *F. membranacea* can also be easily distinguished by the anatomy of their seeds. In the former species, the lignified thickenings in the inner epidermis of the outer integument that are furthest away from the raphe are very strong, especially on the radial walls where they are up to 160 μm or more thick (Fig. 4), like the lignified thickenings in the inner epidermis of the outer integument of the seed coat of *Brassica* and *Sinapis* (Esau 1977: 461–462). Such thickenings have not been observed in any other species of *Freycinetia*. In the latter species, the lignified thickenings do not exceed about 10 μm on the radial walls and 2.5 μm on the inner tangential walls where they are just perceptible (Fig. 9). Other differences: In *F. nesiotica*, at the seed midlevel the vascular bundle is very excentric in the raphe and this latter is thinner than the remainder of the seed (Fig. 4); in *F. membranacea*, the vascular bundle is slightly excentric and the raphe is \pm as thick as the remainder of the seed (Fig. 9).

The seed anatomy of these two species reveals the taxonomic utility of this anatomy in *Freycinetia*. It also indicates their taxonomic isolation in subg. *Gaudichaudiella*. In fact, they have “thick” raphes, which comprise several layers of lignified cells (Fig. 4 and 9). In contrast, sect. *Gaudichaudiella* as seen in *F. impavida* and *F. marquisensis*, and sect. *Malacandra* as observed in *F. samoensis* and *F. hombronii*, have “thin” raphes, in which

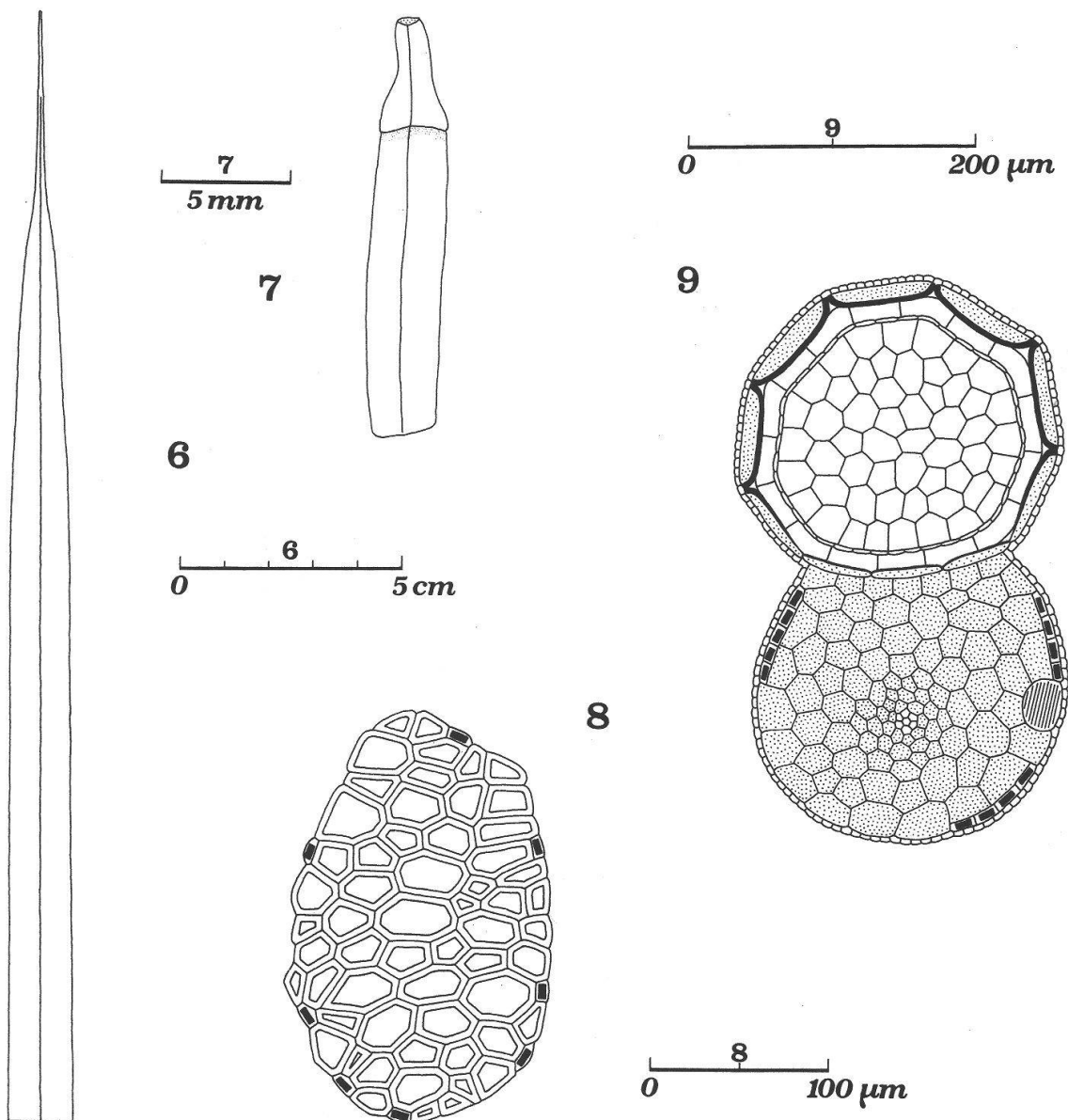


Fig. 6–9. *Freycinetia membranacea* [Craven & Schodde 380 (6) and Waterhouse 168 (7–9)]. – 6: Upper part of a leaf about 77 cm long, viewed by adaxial face. – 7: Berry in lateral view, showing pileus in the upper part, the pileus being cylindrical above pyramidal below. – 8: Middle transverse section of one of the largest fusiform/elliptic fibre-bundles in the basal part of the ovary walls (cells with black rectangle = crystal cells). – 9: Middle transverse section of seed, showing raphe in the lower half and integuments around endosperm in the upper half (for further caption, see Fig. 5).

only 2–4 layers of lignified cells are visible (Fig. 5). *F. nesiotica* also stands apart by having an inner epidermis of outer integument with exceptionally strong lignified thickenings at the side furthest away from the raphe but only faint thickenings at the opposite side, in contrast to *F. stonei* for example (compare Fig. 4 with Fig. 13). The peculiar seed of *F. nesiotica* and its unusual berry mentioned above indicate that it represents an unknown section, which is described below. As for *F. membranacea*, it is provisionally placed in sect. *Gaudichaudiella* despite its “thick” raphe, pending other noticeable fea-

tures to be found, especially from its staminate flower since these flowers vary from one section to another in subg. *Gaudichaudiella* (staminate plants of this species have not been collected). For example, in sect. *Gaudichaudiella* as seen in *F. impavida*, the anthers have endothelial thickenings, and the pistillode is located on the surface of the staminate spike and devoid of apical hairs; in sect. *Malacandra* as seen in *F. samoensis*, the anthers have no endothelial thickenings, and the pistillode is beneath the surface of the staminate spike and bears long apical hairs.

3. *Freycinetia* sect. *Solomoniella* Huynh, sect. nov.

Baccae 4-6-stigmaticae, pileo pyramidalis in aspectu laterali rotundato in apicali praeditae, valde longaeque attenuatae in medio, in syncarpio usque ad basim separatae, sursum versus longitudinaliter sulcatae; hypoderme sparsim lignescenti in strato subepidermico pilei; fasciculis fibrarum numerosis ex apice ad basim, anguste ellipticis, omnibus tenuibus; parietibus ovarii tenuissimis propter fasciculos fibrarum omnes tenues. Semen: raphe crassa, fasciculo vasorum in medio valde excentrico; crassificationes lignosae epidermidis internae integumentii externi a raphe remotae fortes in parietibus interno-tangentialibus fortissimae in radialibus (usque ad 160 μm), proximae tenues in ambobus parietibus. Auriculae foliorum deciduae.

Type: *F. nesiotica*.

4. *Freycinetia stonei* Huynh, sp. nov.

Scandens, ramis usque ad 5–6 mm crassis, omnino corneis nitidisque, internodis 1–1.3 cm longis. Folia 50–60 cm longa, circa 1.1 cm lata in medio 1.2 cm in basi; lamina subcoriacea, gradatim attenuata in tertia supra, acumine 3.5–4 cm longo 1 mm lato in basi 0.7 mm in medio, plicis leviter visibilibus in basi; marginibus omnino armatis, in basi acute denticulatis sursum versus ad apicem minute denticulatis; costa media inermi in tertia infera, sursum versus ad apicem minute denticulata, dentibus generaliter remotioribus et leviter longioribus quam marginalibus sub isdem libramentis; vagina circa 3 cm longa, dense forata in superficie adaxiali (= ventrali); auriculis circa 3 cm longis 8 mm latis in basi, subrigidis, persistentibus, corneis, brunneis, leviter nervatis, sursum versus generaliter minute denticulatis. Inflorescentia foeminea terminalis, 3 (interdum 4) spadicebus usque ad 6 cm longis praedita; syncarpiis late oblongis, ad 3 cm longis 2 cm latis; pedicellis ad 3 cm longis 3 mm crassis, omnino denticulatis in costis, omnino dense scabris inter costas; pedunculo infra pedicellos circa 5 cm longo 7 mm lato in apice 4 mm basi, 2 internodis circa 2.5 cm longis composito. Baccae plerumque 4–6-stigmaticae, 8–9 mm longae 4.5 mm latae 3.5 mm crassae, breviter lageniformes, in syncarpio valde applicatae; parte supraambitali 3.7–4 mm longa, rostrata in aspectu laterali rotundata in apicali, cornea plana; parte infraambitali partim cornea plana interdum usque ad basim, partim non cornea; hypoderme zonarum cornearum lignescenti omnino et in 2–4 stratis; intra fasciculis fibrarum fusiformis/ellipticis numerosis ex apice ad basim, statura variabilibus interdum latissimis usque ad 500 μm latis 350 μm crassis 200 fibris compositis ergo visibilibus super epicarpio zonarum non-cornearum (sed nunquam zonarum cornearum); semine circa 1.3 mm longo 0.5 mm lato, cellulis extimis tenuissimis, raphe crassa, perspicue crassiore quam reliquiis seminis, stratis cellularum lignosarum numerosis et cellulis crystalliferis numerosissimis sed cellulis raphidiphoris sparsis praedita, fasciculo vasorum in medio valde excentrico, crassificationibus lignosis epidermidis internae integumentii externi fortibus circum endospermium, usque ad 15 μm in parietibus

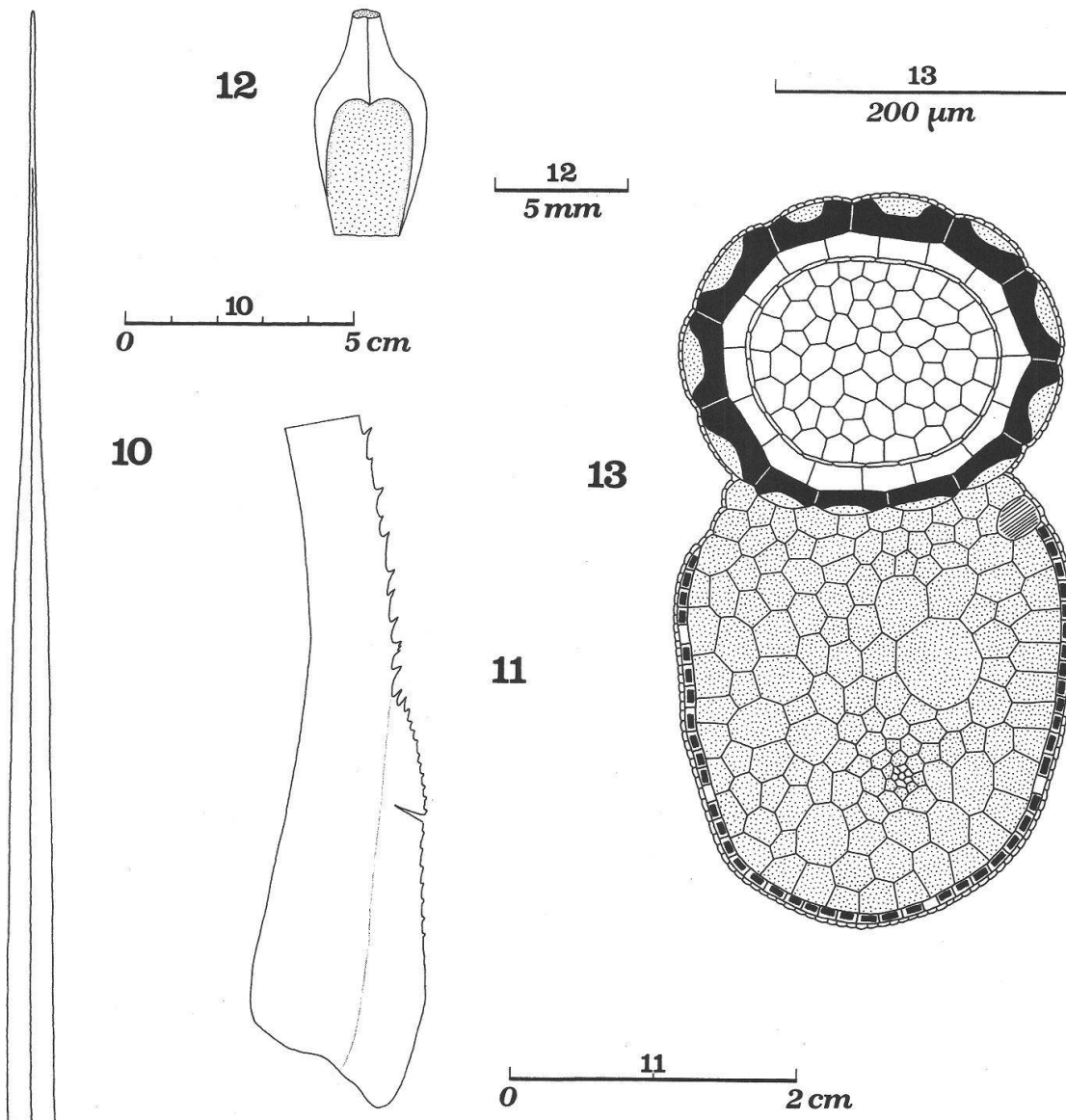


Fig. 10–13. *Freycinetia stonei* (Stone 2475). – 10: Upper part of a leaf about 48 cm long, viewed by adaxial face. – 11: Basal part of the same leaf folded along midnerve, showing auricle on right and midnerve on left. – 12: Berry in lateral view, showing corneous part (undotted) and non-corneous part (dotted). – 13: Middle transverse section of seed, showing raphe in the lower half and integuments around endosperm in the upper half (for further caption, see Fig. 5).

interno-tangentialibus a raphe remotissimis, 25 μm in radialibus; staminodiis circum basim baccae praesentibus.

Type: Stone 2475 (BISH, holo-), Solomon Islands, Santa Ysabel, Mainland of Santa Ysabel, near South tip; swamp forest near Nagolau village; 12 October 1957; vine climbing on mangrove trees; leaves 60 \times 1.1 cm, syncarps 3, oblong; berries acuminate.

F. stonei and sect. *Stoneella* described below are named after Benjamin C. Stone. A former professor of Botany, Stone was an indefatigable student of the morphology and taxonomy of the Pandanaceae during three decades and half and has immensely contributed to the taxonomy of *Pandanus* and *Freycinetia* in particular by greatly improving

their infrageneric classification. Besides a very large number of new species he described in both genera, most of the now known sections in *Freycinetia* and a large number of sections in *Pandanus* were defined by him.

Some features of *F. stonei* described above should be emphasized. All the leaf auricles observed are of rather rigid texture although some show transverse cracks (Fig. 11), and none of the leaves has lost its auricles. This texture indicates that the auricles are persistent. In the leaf sheath, the holes are dense and broad enough to be clearly visible, and are located between the auricles; each hole is a sunken area with one stomate located in centre; their abundance seems to be a specific character since observed in all leaves. Although none of the berries examined are entirely corneous, some show corneous zones extending from apex down to base (Fig. 12), as indicated by the presence of staminodes at the base of corneous zones in some berries (in *Freycinetia*, staminodes are always located at the base of the pistils/berries). These zones are smooth (=not longitudinally grooved) probably because their hypodermis is lignified throughout and in 2–4 layers.

The type of *F. stonei* was at first identified as being *F. membranacea* (Stone 1963: 4), then, as *F. nesiotica* (Stone 1970: 374). However, it corresponds to neither species given the following features: leaf narrowing gradually in the upper part; leaf auricles persistent; berry wholly corneous (hence not grooved) in the upper part, sometimes down to the base; hypodermis of the berry lignified in 2–4 layers throughout the corneous zones; lignified thickenings in the inner epidermis of the outer integument of the seed strong all around the endosperm, and the raphe much thicker than the remainder of the seed (Fig. 13). Only the first character and the shortly oblong syncarps of this specimen may be considered to be similar to those of *F. nesiotica*; for berry hypodermis, it is irregularly lignified in the subepidermal layer of the pileus in both *F. membranacea* and *F. nesiotica*. In addition, the berry of *F. stonei* does not exceed 9 mm in length, while those of *F. nesiotica* and *F. membranacea* are up to 13 mm and 16 mm respectively. In berry anatomy, as far as the fusiform/elliptic fibre-bundles are concerned, *F. stonei* differs clearly from *F. nesiotica* but not from *F. membranacea* since the bundles in the basal part of its ovary walls are more or less the same size as those of *F. membranacea* (Fig. 8) and therefore about four times as broad as those of *F. nesiotica* (Fig. 3).

Concerning the taxonomic position of *F. stonei*, the existence of fusiform/elliptic fibre-bundles in its berry indicates that it belongs to subg. *Gaudichaudiella*, as do *F. nesiotica* and *F. membranacea* (see above). In this subgenus however, none of the known sections can fit it because of its berry (Fig. 12), which is corneous and smooth (=not longitudinally grooved) throughout in the upper part and also in the lower part, sometimes down to the base, in contrast to the other species of this subgenus. The hypodermis of its berry is also peculiar by being lignified throughout and in 2–4 layers in the corneous zones, consequently sometimes down to the base. Likewise, its seed (Fig. 13) appears most noticeable by having a “thick” raphe in which the vascular bundle is strongly excentric – like *F. nesiotica* (Fig. 4) – but strong lignified thickenings all around the endosperm; in particular, the raphe is much thicker than the remainder of the seed, a rare feature in *Freycinetia*. Also, its persistent leaf-auricles are a rare feature in subg. *Gaudichaudiella*. These facts contribute to indicate that *F. stonei* represents an unknown section, which is described below.

Although *F. stonei*, *F. membranacea* and *F. nesiotica* belong to three different sections, they form in the Solomon Islands an artificial group which can be recognized by the following characters: inflorescence terminal; syncarps 3 sometimes 4, shortly ellipsoid or shortly oblong, 3–6 cm long by 2–3.5 cm wide; berries mostly 4–6 stigmatic, with apex generally rotundate and fusiform/elliptic fibre-bundles present from apex to base; pistil-

Tab. 1. Different features between *Freycinetia membranacea*, *F. nesiotica* and *F. stonei*

	<i>Freycinetia membranacea</i>	<i>Freycinetia nesiotica</i>	<i>Freycinetia stonei</i>
	Sect. <i>Gaudichaudiella</i>	Sect. <i>Solomoniella</i>	Sect. <i>Stoneella</i>
Leaves	Abruptly attenuate in the upper part (Fig. 6); auricles deciduous	Gradually attenuate in the upper part (Fig. 1); auricles deciduous	Gradually attenuate in the upper part (Fig. 10); auricles persistent
Berries	Up to 1.6 cm long, strongly adherent in syncarp when dry, not narrowing in middle, non-corneous and longitudinally grooved in the upper part; pileus distinct, cylindrical above pyramidal below (Fig. 7)	Up to 1.3 cm long, clearly separate in syncarp when dry, narrowing in middle, non-corneous and longitudinally grooved in the upper part; pileus distinct, pyramidal (Fig. 2)	Up to 0.9 cm long, strongly adherent in syncarp when dry, not narrowing in middle, corneous and smooth in the upper part; pileus generally indistinct (Fig. 12)
Seeds	Lignified thickenings on the inner tangential walls of the inner epidermis of the outer integument at the side furthest away from the raphe just perceptible in microscope; vascular bundle slightly excentric in the raphe; raphe \pm as thick as the remainder of the seed (Fig. 9)	Lignified thickenings on the inner tangential walls of the inner epidermis of the outer integument at the side furthest away from the raphe up to about 45 μ m thick; vascular bundle very excentric in the raphe; raphe thinner than the remainder of the seed (Fig. 4)	Lignified thickenings on the inner tangential walls of the inner epidermis of the outer integument at the side furthest away from the raphe up to about 15 μ m thick; vascular bundle very excentric in the raphe; raphe thicker than the remainder of the seed (Fig. 13)
Pistillate pedicels	Smooth between the angles	Scabrid between the angles in the upper part	Scabrid between the angles from apex to base

late pedicels scabrid/hispidulous; leaves mostly 60–70 cm long by 1–1.5 cm wide. They can in their turn be distinguished as indicated in Table 1.

5. *Freycinetia* sect. *Stoneella* Huynh, sect. nov.

Baccae 4–6-stigmaticae, breviter lageniformes, rostratae in aspectu laterali rotundatae in apicali, in syncarpio valde applicatae, corneae planaeque interdum usque ad basim, pileo generaliter indistincto; hypoderme zonarum cornearum omnino et in 2–4 stratis lignescenti; fasciculis fibrarum fusiformis/ellipticis numerosis ex apice ad basim, visibilibus super zonas non-corneas nunquam zonas corneas; parietibus ovarii crassissimis propter fasciculos fibrarum plerumque latissimos. Semen: raphe crassa, perspicue crassior quam reliquiae seminis, fasciculo vasorum in medio valde excentrico; crassificationes lignosae epidermidis internae integumentii externi fortes circum endospermium. Auriculae foliorum persistentes.

Type: *F. stonei*.

6. Conclusion

As seen above, the confusion in the past between *F. membranacea*, *F. nesiotica* and *F. stonei* was due to the fact that only a small number of characters were used for

distinguishing them. The present study shows that all three are distinct species and can be readily distinguished if other characters are also used, for example anatomical features of berry and seed. The distinction would have been more substantial if it were also possible to investigate their pistillodes (staminate plants of all three species have not been collected). This organ appears to be the most useful in distinguishing “difficult” species in *Freycinetia* (see for example Huynh 1994) since it is more variable than other organs, for example pistil, stamen, leaf and bract.

The case of these three “difficult” species should be applied to similar cases, which are numerous in this genus, while also tentatively using several other specific characters recently found from anatomy (see for example Huynh 1993: 508–509). It now becomes evident that *Freycinetia* has a very variable morphological differentiation but this has not been extensively investigated and used in its taxonomy, also because this genus has generally not been suitably collected. In fact, this was difficult task, since its specific characters which are very numerous became apparent only as morphological and taxonomic investigation progressed; therefore when collecting it was not easy to determine which organs can further be used in taxonomy and which others not. For example, the taxonomic utility of the seed anatomy as applied above seemed to be formerly unknown in *Freycinetia*. In this respect, the wide difference between *F. nesiotica*, *F. membranacea* and *F. stonei* (Fig. 4, 9 and 13) strongly suggests that seed anatomy in particular should be used in further taxonomic revisions of *Freycinetia* in the Solomon Islands and in any other area.

7. General view of subg. *Gaudichaudiella*

It seems useful to give here a general view of subg. *Gaudichaudiella*. This is characterized essentially by: inflorescences terminal; berries pluristigmatic, rich in fusiform/elliptic fibre-bundles from apex to base. It has been recognized in various islands in Polynesia and Melanesia: the Society Islands, Marquesas, Samoa Islands, Fiji, New Hebrides, Solomon Islands, and New Guinea. It comprises at present five sections as indicated below.

1. Berries separate in syncarp when dry; pedicels of pistillate spikes scabrid or glabrous 2
 - Berries strongly adherent in syncarp when dry; pedicels of pistillate spikes scabrid 3
2. Berries narrowing in the middle part; pileus pyramidal in lateral view, rotundate in apical view; raphe “thick”; pedicels of pistillate spikes scabrid; leaf auricles deciduous sect. *Solomoniella* (type: *F. nesiotica*)
 - Berries not narrowing in the middle part; pileus rectangular tabuliform in lateral view, elliptic in apical view; raphe?; pedicels of pistillate spikes glabrous; leaf auricles persistent sect. *Tahitiella* (type: *F. moratii*)
3. Berries smooth (= not longitudinally grooved) and corneous in the upper part, sometimes down to the base; raphe “thick”; leaf auricles persistent sect. *Stoneella* (type: *F. stonei*)
 - Berries longitudinally grooved and not corneous in the upper part; raphe “thin”; leaf auricles deciduous 4
4. Lower bracts ensiform, foliaceous in the upper part; intermediate bracts boat-shaped, not foliaceous in the upper part; anthers with endothelial thickenings; pistillode located on the surface of the staminate spike and devoid of apical hairs sect. *Gaudichaudiella* (type: *F. impavida*)

- Lower and intermediate bracts sublinear, foliaceous in the upper part; anthers without endothelial thickenings; pistillode located beneath the surface of staminate spike and provided with long apical hairs sect. *Malacandra* (type: *F. samoensis*)

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