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A new species of Freycinetia (Pandanaceae) from the Society Islands — New subgenus and new sections

KIM-LANG HUYNH

RÉSUMÉ

HUYNH, K.-L. (1995). Une espèce nouvelle de Freycinetia (Pandanaceae) des îles de la Société — Nouveau sous-genre et nouvelles sections. *Candollea* 50: 231-245. En anglais, résumés français et anglais.

Une espèce nouvelle de *Freycinetia* des îles de la Société (*F. moratii* Huynh) est décrite. Sont aussi décrits un nouveau sous-genre et deux nouvelles sections [subgen. *Gaudichaudiella* (B. C. Stone) Huynh, sect. *Malacandra* Huynh et sect. *Tahitiella* Huynh] tandis que la section *Gaudichaudiella* est amendée. L'existence de ce sous-genre vraisemblablement "naturel", le premier décrit chez *Freycinetia*, indique qu'il y en a d'autres, qui devront être définis à leur tour. L'utilité taxonomique de l'anatomie au niveau du sous-genre, de la section, et de l'espèce dans ce genre est soulignée. Les bractées de *F. impavida* et de *F. samoensis*, respectivement types de la section *Gaudichaudiella* et de la section *Malacandra*, sont décrites. L'anatomie bractéale de *F. impavida* est aussi décrite, de même que sa fleur mâle, en particulier son pistillode. Ces caractères peuvent plus tard permettre de distinguer les espèces considérées à l'heure actuelle comme synonymes de *F. impavida* (p. ex. *F. marquisensis*) quand ils y seront aussi connus. Un exemple montrant comment utiliser le pistillode à cet effet est donné.

ABSTRACT

HUYNH, K.-L. (1995). A new species of Freycinetia (Pandanaceae) from the Society Islands — New subgenus and new sections. *Candollea* 50: 231-245. In English, French and English abstracts.

A new species of *Freycinetia* from the Society Islands (*F. moratii* Huynh) is described. A new subgenus and two new sections are also described [subgen. *Gaudichaudiella* (B. C. Stone) Huynh, sect. *Malacandra* Huynh and sect. *Tahitiella* Huynh], while sect. *Gaudichaudiella* is emended. The existence of this most probably "natural" subgenus, which is the first subgenus defined in *Freycinetia*, indicates that other subgenera also exist and should be defined in their turn. The taxonomic utility of anatomy at the subgeneric, sectional and specific levels in this genus is emphasized. The bracts of *F. impavida* and *F. samoensis*, types of sect. *Gaudichaudiella* and sect. *Malacandra* respectively, are described. The bract anatomy of *F. impavida*, as well as its staminate flower, in particular its pistillode, are also described. This may make it possible to further distinguish those species considered at present to be synonymous to *F. impavida* (e.g. *F. marquisensis*), when their bract anatomy and staminate flower will also be known. An example showing how the pistillode can be used for this purpose is given.

KEY-WORDS: Anatomy — *Freycinetia* — PANDANACEAE — Society Islands — Taxonomy.

Introduction

Present state of knowledge on the taxonomy of Freycinetia in the Society Islands

Freycinetia impavida (sect. *Gaudichaudiella*) and *F. arborea* (sect. *Freycinetia*) are the only species of this genus known to this date in the Society Islands (STONE, 1981: 48). The former species was considered to be endemic to these islands, but was later also identified in the Marquesas (*F. marquisensis*, *F. delmasiana*), Fiji (*F. parksii*), New Hebrides, and the Solomon Islands by STONE

(1981: 55-56). The latter species was traditionally regarded to be native to the Hawaii Islands, but was also found in the Society Islands, New Caledonia (*F. longispica*), New Hebrides, Cook Islands (*F. wilderi*), the Marquesas (*F. hivaensis*, *F. kiekie*), and the Tubuai Islands (*F. rapensis*) by STONE (1979: 151; 1981: 52), and also in the Samoa Islands by COX (1981: 196) and STONE (1990: 1479). These cases of synonymy seemed to be based on the infructescences or pistillate inflorescences only, which are very similar within each of these two aggregate species. In fact, apart from leaves, infructescences and pistillate inflorescences were most frequently collected for *Freycinetia*, and therefore still constitute an essential basis for the interspecific distinction. However, bracts and staminate inflorescences also proved essential for this distinction but were little collected.

Recently, the structure of both pistillate and staminate flowers, and the anatomy of both bract and leaf were studied (HUYNH, 1991, 1992, 1993a, 1993b, 1994; HUYNH & COX, 1992; HUYNH & SAMPSON, 1992). As a result, a large number of new specific characters were found some of which also prove diagnostic of sections and subgenera. For *F. arborea* sensu Stone 1981, several facts indicate that it is an aggregate species. For example: *F. wilderi* differs from the Hawaiian *F. arborea* in the texture and anatomy of its leaves which are thinner and more flexible, and in the anatomy of its pistillode, pistil, and intermediate bracts; *F. longispica* in the texture and anatomy of its intermediate bracts which are thicker and more rigid. Likewise, *F. rapensis* in the shape and anatomy of its seed: this seed is straight, and the cells around the vascular bundle in the raphe are lignified; that of the Hawaiian *F. arborea* is generally crescent-shaped, sometimes U-shaped, and these cells are not lignified. These facts simply confirm the species endemism commonly observed in the family Pandanaceae.

In particular, the pistillode proved the most useful in distinguishing "close" species — other organs (pistil, leaf, bract, etc.) showing less variation —, especially as in *Freycinetia* each staminate flower bears a pistillode (MOORE & EDGAR, 1970: 98; HUYNH, 1991: 303; HUYNH, 1992: 430; HUYNH, 1993a: 267; HUYNH & COX, 1992: 238; HUYNH & SAMPSON, 1992: 186). In fact, in four component species of the aggregate *F. arborea* where staminate flowers have been studied — viz. the Hawaiian *F. arborea*, *F. wilderi*, the Society Islands *F. arborea* mentioned below, and *F. coxii* (this is the former Samoan *F. arborea*: HUYNH, 1994) —, the pistillodes are so different that they can make it possible to recognize them (see HUYNH, 1994). In *Pandanus* sect. *Martellidendron* also, which is the only section in this genus which has a pistillode in its staminate flowers (MARTELLI & PICHI-SERMOLLI, 1954; HUYNH, 1981), each species can be recognized by its pistillode (HUYNH, 1981: 46-48: "gynécée rudimentaire") except for *P. cruciatus* whose staminate plants have not been collected.

Concerning the *F. arborea* of the Society Islands, it was first recognized by STONE (1981: 52) in three pistillate specimens: *Raynal 18088* and *18121* (P!) from Tahiti, and *Grant 4987* (BISH!) from Bora Bora. These are studied in the present paper, as are two other pistillate specimens: *Florence 3940* (P!) from Tahiti, and *Grant 5165* (BISH!) from Tahaa. It is found that all five belong to one and the same species (viz. the *F. arborea* of the Society Islands), and that there is no significant difference between them and pistillate specimens of the Hawaiian *F. arborea* with regard to the aspect of leaf and syncarp and to the anatomy of pistil and leaf. In particular, the Society Islands *F. arborea* and the Hawaiian *F. arborea* are similar in having leaf abaxial stomates with papillate polar cells and berries without fusiform/elliptic fibre-bundles (for these two features, see below). Nevertheless, the former *F. arborea* has quite a different seed: this is slightly curved, never crescent-shaped or U-shaped, and has lignified cells around the vascular bundle in the raphe (the seed of the Hawaiian *F. arborea* is described above). Also, in its shape and anatomy, the pistillode of the Society Islands *F. arborea* as seen in the staminate specimen *St. John 17313* (BISH!) from Raiatea (Society Islands) cannot be confused with that of the Hawaiian *F. arborea* as observed in the staminate specimens *Lorence 7248* and *7249* (NEU!) from Kauai (Hawaii Islands). These differences indicate that the Society Islands *F. arborea* is a distinct species. However, in awaiting its formal description, it is simply called "*Freycinetia arborea*" in the following paragraphs.

In the Society Islands, *F. impavida* and *F. arborea* can be distinguished by the aspect of leaf and berry. In *F. impavida*: the leaves narrow abruptly from about the top sixth to the apex and are abundantly tessellate; the berries are strongly adherent along their infrapileal parts and therefore cannot be separated without some damage to their epicarp; the pileus is rostrate in lateral view,

± rotundate in apical view; in addition, they do not narrow beneath the pileus and are covered with a dense carpet of whitish "scales" (Fig. 1). These are the subepicarpic fusiform/elliptic fibre-bundles of the berries (Fig. 3). They are visible through the very thin epicarp because most of them are large; as to their whitish colour, it is due to the fibres. In *F. arborea*: the leaves narrow gradually from about the middle and are not tessellate or only slightly so; the berries are separate almost down to their bases and therefore can be removed without any tearing to their epicarp; the pileus is rectangular tabuliform in lateral view, generally elliptic in apical view; in addition, they narrow beneath the pileus, and never have whitish "scales". Another difference: the pistillate pedicels are scabrid in *F. impavida* but glabrous in *F. arborea*. It should be emphasized here that the term "pileus" as applied to *F. impavida* and some species which have similar berries (*F. samoensis*, *F. storckii*, etc.) is used in a wide sense to designate the upper, free part of their berries, by analogy with the pileus of *F. arborea* and other species. The pileus is very distinct in the latter group of species, but only slightly so in the former group.

F. impavida and *F. arborea* can also be distinguished by stomate morphology and berry anatomy. In *F. impavida*: the polar cells of the leaf abaxial stomates are smooth, and the berry is rich in fusiform/elliptic fibre-bundles (Fig. 2 and 3). In *F. arborea*: these cells are papillate (Fig. 16), and these fibre bundles are entirely lacking.

F. moratii described below is the third species recorded from the Society Islands. In general aspect it is intermediate between the other two species. In some fruit features it represents an unknown section (sect. *Tahitiella*) which is related to sect. *Gaudichaudiella*. For this reason, subgen. *Gaudichaudiella* is defined below to accommodate these sections and sect. *Malacandra*, a new section closely related to sect. *Gaudichaudiella*.

Material and methods

The herbarium material used to study the anatomy of pistil and staminate flower was rehydrated overnight in 65°C water, embedded in paraffin, microtome-sectioned, stained in Safranin and Astrablue, and mounted in a synthetic resin. For pistillodes, the data from these sections were completed with those from the pistillodes excised from the rehydrated material with a scalpel and allowed to lie by one of the larger lateral-faces in a drop of water on a slide, then observed without using a coverslip. These pistillodes are called "free" pistillodes in the present paper, and the shape they show may be considered to be the normal shape of the pistillode. They were also used to observe the apical parts of the carpelloses (Fig. 11 and 15). Subsequently, they were bleached by eau de Javelle, passed in Safranin (for staining xylem), mounted in Euparal, and used to observe anatomical features. The same method was applied to staminodes.

Leaf micromorphology was investigated with hand-made sections at the midlevel and with cuticles removed by using the method described in HUYNH (1971), the former for observing the leaf anatomy, the latter the leaf-surface details (stomates and epidermal cells: Fig. 16 and 17).

Results

Key to the Freycinetias of the Society Islands

1. Leaves narrowing abruptly in apical part; berries rich in fusiform/elliptic fibre-bundles; stomate polar cells of leaf abaxial face smooth or each with a short verruca; staminodes without raphide cells 2
- 1a. Leaves narrowing gradually from about middle; berries entirely devoid of fusiform/elliptic fibre-bundles; stomate polar cells of leaf abaxial face each with a long papilla; staminodes rich in raphide cells 3

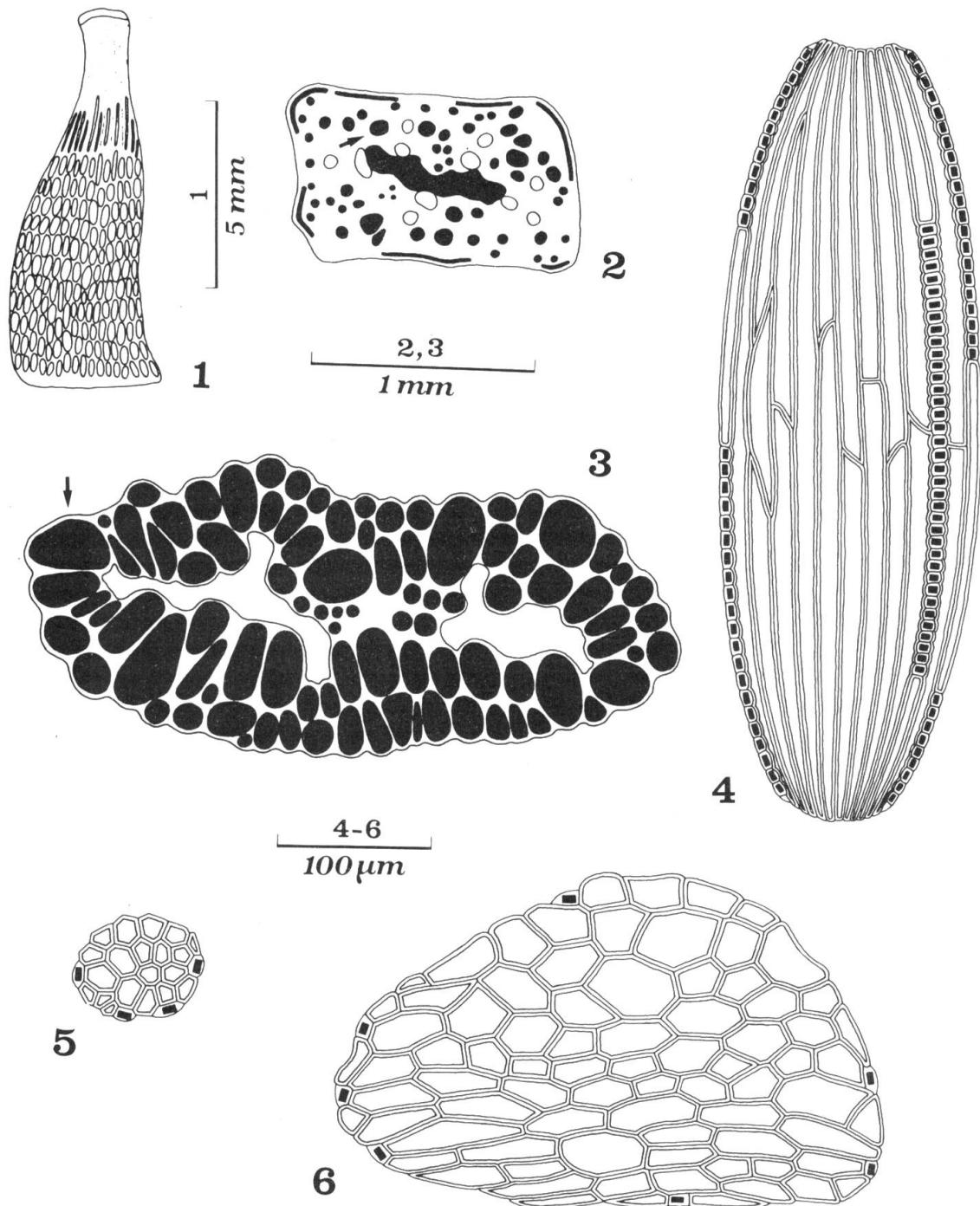


Fig. 1-6. — *Freycinetia impavida* (Raynal & Taureau 16551). — 1: Berry in lateral view, showing subepicarpic fusiform/elliptic fibre-bundles (ellipses). 2: Transverse section of 5-stigmatic berry about 9.2 mm long at about 1.1 mm from apex, showing central sclerenchyma (black mass in centre), five fertilization canals (blank ellipses in close proximity to central sclerenchyma), vascular bundles (the other blank ellipses), lignified hypodermis (black lines), and fusiform/elliptic fibre-bundles (small/large black spots). 3: Transverse section of the same berry at about 5.1 mm from apex, showing fusiform/elliptic fibre-bundles (black spots) and two triforked locules in the longer axis of the section. 4: Fusiform fibre-bundle at lower part of berry in longitudinal section (cells with black rectangle: crystal cells). 5, 6: The arrowed fibre-bundles in Fig. 2 and 3 respectively, magnified (cells with black rectangle: crystal cells). — Note. For Fig. 3: the vascular bundles, very narrow at this level, were probably destroyed by sectioning; the locules will fuse into one locule at lower levels.

2. Berries strongly adherent along their infrapileal parts in syncarp, and not narrowing beneath the pileus; pileus rostrate in lateral view, generally rotundate in apical view; fusiform/elliptic fibre-bundles generally broad beneath pileus hence the subepicarpic fibre-bundles in the infrapileal part are visible to the naked eye and appear whitish; leaf auricles deciduous; pistillate pedicels scabrid; stomate polar cells of leaf abaxial face smooth

F. impavida (sect. **Gaudichaudiella**)
- 2a. Berries separate almost down to their bases in syncarp, and narrowing beneath the pileus; pileus rectangular tabuliform in lateral view, generally elliptic in apical view; fusiform/elliptic fibre-bundles but all narrow, therefore the subepicarpic fibre-bundles are invisible to the naked eye; leaf auricles persistent; pistillate pedicels glabrous; stomate polar cells of leaf abaxial face each with a short verruca.

F. moratii (sect. **Tahitiella**)
3. Berries separate almost down to their bases in syncarp, and narrowing beneath the pileus; pileus rectangular tabuliform in lateral view, generally elliptic in apical view; leaf auricles persistent; pistillate pedicels glabrous

F. arborea (sect. **Freycinetia**)

Note:

The stomates of the family Pandanaceae are tetracytic, the guard cells being surrounded by two polar cells and two lateral cells (Fig. 17). In those species where the leaf epidermis is papillate (or verrucate, with short or slightly visible verrucas), these processes are generally observed at the abaxial face only, where the processes of the polar cells are in general at least as differentiated as those of the non stomatic cells. In some species of *Pandanus* and *Freycinetia*, the adaxial polar cells also bear papillas/verrucas but these are always less differentiated than those of the abaxial polar cells. For these reasons, the abaxial polar cells are used to characterize species (for example, species with stomates of class I, II, III, etc.: see HUYNH, 1974: 199-200).

Freycinetia subgen. **Gaudichaudiella** (B. C. Stone) Huynh, subgen. nov.

Basionym: *Gaudichaudiella* (as section) B. C. Stone, Blumea 16: 369. 1968.

Type species: *F. impavida*.

It seems useful to indicate here the diagnostic characters of this subgenus for further suitable identification: inflorescences terminal; berries pluristigmatic, rich in fusiform/elliptic fibre-bundles from apex to base when mature, only in pileus when immature.

This is the first subgenus defined in *Freycinetia* which comprises about 180 species according to STONE (1983: 5) and DAHLGREN & al. (1985: 485) but certainly more at present. It includes those species which are more or less closely related to *F. impavida* by having fusiform/elliptic fibre-bundles in their berries. These fibre bundles are very characteristic (Fig. 4), and have not been observed in the other species studied, which seems to indicate that subgen. *Gaudichaudiella* is "natural". The fact that a "natural" subgenus exists in *Freycinetia* indicates that others also do, and should be defined in their turn, not less than 25 sections being now known in this genus. For example, sect. *Racemosiflorae* on one hand, and sect. *Lateriflorae* and sect. *Solmsiella* on the other hand, stand apart from the other sections — the first section by its racemose inflorescences, the other two by their lateral inflorescences (see STONE, 1968: 363) — and therefore can form the nuclei of two other subgenera while other sections may further be found. As an example, in subgen. *Gaudichaudiella*, sect. *Malacandra* has been separated from sect. *Gaudichaudiella* when it was found that it has different bracts and staminate flowers (see below).

These fibre bundles do not seem to have been investigated in *Freycinetia*; neither does the anatomy of the berry of *F. impavida*. It would therefore be of interest to make as detailed a study of these fibre bundles and this anatomy as possible. Consider for example *Raynal & Taureau 16551* (P!), a Tahitian specimen of *F. impavida*. The berries in this specimen are about 10.5 mm long and show a dense carpet of whitish "scales" on the infrapileal part (Fig. 1). They already have seeds

although these are immature. In longitudinal sections, they comprise two main parts. The upper part is about 2 mm long and corresponds approximately to the pileus; the lower part is the cavity. Both are very rich in fusiform/elliptic fibre-bundles. These are composed of longitudinal rows of fibres and of crystal cells (Fig. 4). Although variable in length and width, they are always fusiform or elliptic in longitudinal section (Fig. 4) and more or less elliptic, never folded or elbow-shaped, in transverse section (Fig. 5 and 6). The largest of them are up to half a millimeter or more broad and are found along the infrapileal part almost to the base. In transverse sections in the middle part of the pileus, a very large number of fibre bundles of variable sizes and in several rows is observed between the central sclerenchyma and the partially lignified hypodermis (Fig. 2). In transverse sections in the middle zone of the berry, a very large number of other fibre bundles in 2-3 rows is observed in the cavity walls (Fig. 3). Most of these bundles are big, each comprising 200 or more fibres, which are generally broader than those in the pileus (compare Fig. 6 to Fig. 5). In transverse sections in lower zones, the fibre bundles are also large but distributed in only one row and generally with a little broader fibres. It is the largest subepicarpic fibre-bundles in the cavity walls that are visible on the berries and resemble whitish "scales". The berries in *Raynal & Taureau 16551* described above are similar to those in the type of *F. impavida* (P!), also studied in the present paper. The only difference is that in this latter specimen, the infrapileal parts of the berries are dissociated into a multitude of free whitish fusiform/elliptic fibre-bundles, which look like small seeds.

The fusiform/elliptic fibre-bundles in the berry of *F. impavida* are formed at first in the pileus, then in the lower part and along the ovary walls. This is indicated by the berries of *Raynal & Taureau 16551* described above and by those of *Grant 3676* (BISH!), another Tahitian specimen of this species. In contrast to the former berries where these fibre bundles are found from apex to base, the latter berries, which are younger (they are about 8.5 mm long), have them only in the pileus. As far as known, only the berries of subgen. *Gaudichaudiella* have fibres in the ovary walls when mature. This peculiar feature provides further grounds to this subgenus. The fact that the fusiform/elliptic fibre-bundles in the berries of *F. impavida* and allied species are peculiar may be revealed by *F. reineckei* (sect. *Filiformicarpea*) which is taken here as an example. The berry of this species has fibre strands (HUYNH & COX, 1992: Fig. 51) but these are neither distinct nor fusiform/elliptic in longitudinal section, as are the fusiform/elliptic fibre-bundles in *F. impavida*. In fact, they extend in single stretches along the fibrous zones of the berry in this section, and show a jagged or elbowed/folded shape in transverse section. In addition, they are observed in the pileus only, the berries being mature or not.

Subgen. *Gaudichaudiella* appears to comprise a large number of species and several sections, but only one section was previously described (sect. *Gaudichaudiella*) and two in the present paper (sect. *Tahitiella* and *Malacandra*). Some other sections have been distinguished and will further be described. Concerning the relationships of subgen. *Gaudichaudiella*, sect. *Freycinetia* (or, rather, subgen. *Freycinetia* which is to be defined) appears to be a very close group (see also STONE, 1968: 369). A link is sect. *Tahitiella*, which belongs to subgen. *Gaudichaudiella* but shows several similar features to those of sect. *Freycinetia* (see the comparison of *F. moratii* with *F. arborea* below). In particular, by its unrostrate berries (Fig. 20) sect. *Tahitiella* is probably the most remote section from sect. *Gaudichaudiella*. Another link is sect. *Gaudichaudiella* itself which has some similarity in bract aspect and pistillode anatomy to those of sect. *Freycinetia* (see the description of the bracts and pistillode of *F. impavida* below). Another very close group is sect. *Devriesella* (or, rather, subgen. *Devriesella* which is to be defined), whose berries are rostrate — as are those of *F. impavida* and several allied species —, but devoid of fusiform/elliptic fibre-bundles.

Freycinetia sect. **Gaudichaudiella** B. C. Stone, emend. Huynh

Definitio originalis: "Plantae subrobustae vel robustae. Folia elongata acuminata. Inflorescentia terminalis ternata, cephalis cylindraceis. Bacca apice rostrata. Stigmata plerumque 4-10" (STONE, 1968: 369).

Definitio emendata: Baccae lageniformes, infra pileum haud constrictae valde applicatae; pileo rostrato in aspectu laterali rotundato in apicali; hypoderme pilei lignescenti; fasciculis fibra- rum fusiformis/ellipticis numerosissimis, statura variabilissimis, infra pileum ad basim plerumque latissimis ergo visilibus super epicarpio; parietibus ovarii crassissimis propter fasciculos fibrarum plerumque latissimos. Anthera endothelialiter incrassata. Pistillodium in superficie spadicum locatum ergo visible inter filamenta, apice pilis longis destitutum, parietibus haud applicatis ergo cavitate distincta. Bractae inferae ensiformes sursum versus foliaceae; intermediae naviculares, sursum versus haud foliaceae. Auriculae foliorum deciduae. Charactere secundarii: syncarpia cylindracea, pedicellis apicem versus inflatis et omnino scaberis, basim versus in costis scaberis.

Type: *F. impavida*.

The bract and staminate characters in this diagnosis are deduced from the staminate plant of *F. impavida* described below. In its original conception, sect. *Gaudichaudiella* comprised *F. impavida* (type), *F. hivaoensis*, *F. marquisensis*, *F. samoensis*, *F. solomonensis*, *F. parksii*, *F. storckii*, and *F. urvilleana* (Stone, 1968: 369). Later *F. bicolor*, *F. insolita*, and *F. milnei* were also included (Stone, 1970), while *F. hivaoensis* was moved to sect. *Freycinetia* (Stone, 1981). *F. membranacea* may be another species of sect. *Gaudichaudiella*. Other species can further be known. Recently, it was possible to study the bracts and staminate flowers of *F. impavida* and *F. samoensis*; and it was found that they are quite different from one species to the other (see below). This indicates that the latter species represents a distinct section (sect. *Malacandra*), and suggests that these two organs should further be also investigated in the other species.

Staminate inflorescence and staminate flower of *Freycinetia impavida*

The staminate inflorescence and staminate flower of *F. impavida* are studied for the first time in the present paper, using *Florence 3222* (P!), from Tahiti. This is the only specimen of this species which was found to bear bracts. The interest of the bracts and staminate flower of *F. impavida* in the taxonomy of *Freycinetia* is evident, given the wide variation of these organs in this genus and considering the following points. Firstly, *F. impavida* being the type of sect. *Gaudichaudiella*, comparison of its bracts and staminate flower with those of the other species may make it possible to know if this section is “natural” or not. Secondly, this staminate flower, in particular its pistillode, may further be used to distinguish those species described or not which are differentiated in the Marquesas, New Hebrides, and the Fiji and Solomon Islands and which are at present considered to be synonymous to *F. impavida*. As mentioned above, each of the four component species of the aggregate *F. arborea* whose staminate flowers were studied can be recognized by its pistillode: this may also be the case in the aggregate *F. impavida*. Bract anatomy is also studied in *F. impavida* since it showed similar utility in the aggregate *F. arborea* (for example, in distinguishing *F. longispica* and *F. wilderi* from the Hawaiian *F. arborea*: see above). For these reasons, the first priority is ascertaining the identity of *Florence 3222* because staminate specimens of *Freycinetia* can easily be mis-identified (see HUYNH, 1994: 293-294). The fact that this specimen is a plant of *F. impavida* is indicated by its abundantly tessellate leaves and the scabrid pedicels of the pistillate plants in the same population (the scabridity is field-noted in this specimen). It is further corroborated by the smooth polar cells of the leaf abaxial stomates of the specimen. In the Society Islands, abundantly tessellate leaves and scabrid pistillate pedicels are observed only in this species.

Two kinds of bracts are field-noted in *Florence 3222*: outer bracts, pale yellow, and inner bracts, fleshy (“inflorescences entourées de bractées jaune pâle finalement rabattues, les internes charnues”). They seem to correspond to two ensiform bracts (Fig. 7 and 8) and two boat-shaped bracts (Fig. 9) respectively, found in the specimen. The former bracts comprise two parts: the lower brown, the upper greenish and of foliaceous texture. They correspond to the lowermost, leaf-like bracts normally observed in *Freycinetia*. The latter bracts are entirely brown and of rigid texture. In their shape and texture, they resemble the intermediate bracts of sect. *Freycinetia* as observed in the Hawaiian *F. arborea*, *F. coxii* (Huynh, 1994: Fig. 6-8), *F. rapensis*, *F. wilderi*, etc., and may therefore

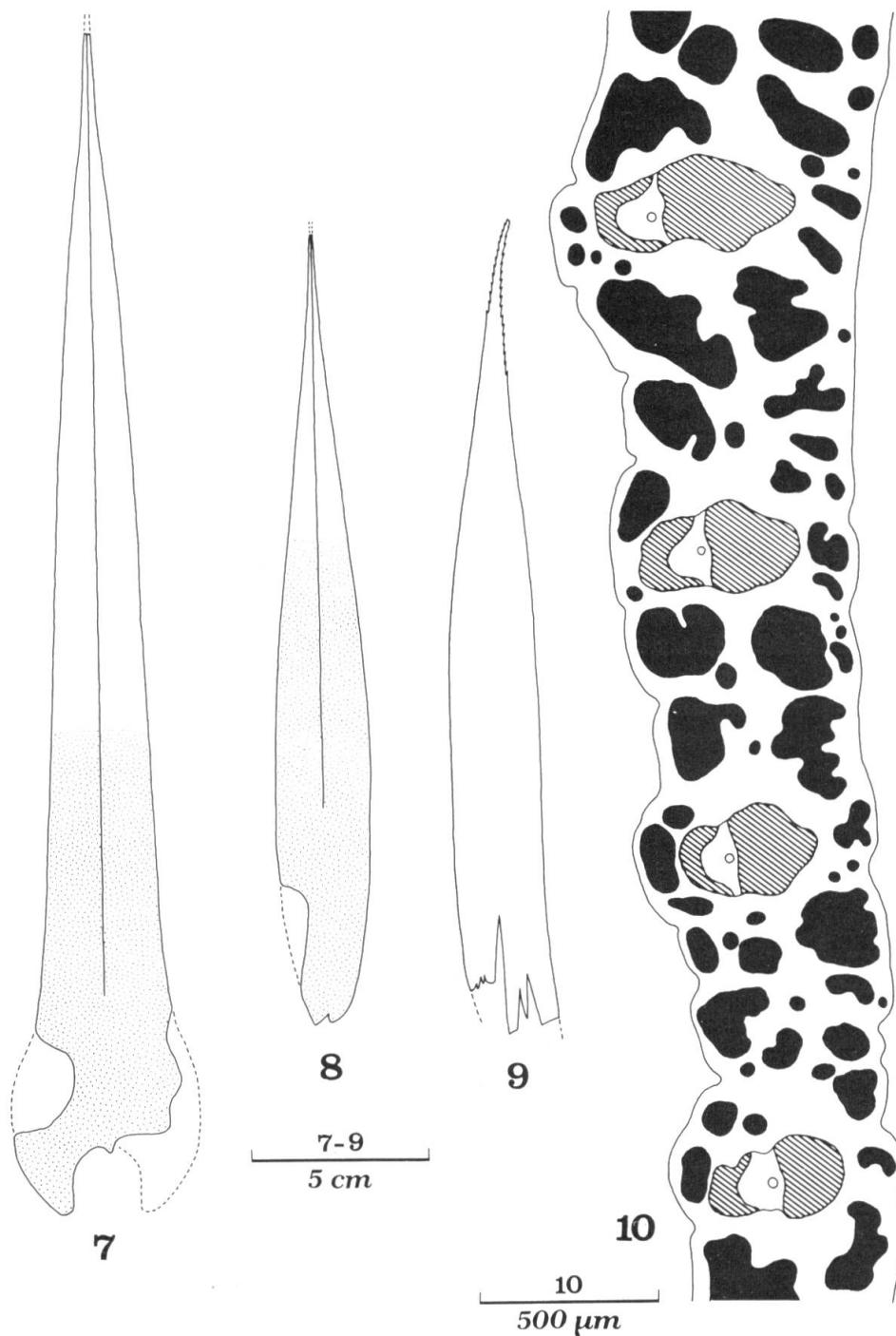


Fig. 7-10. — *Freycinetia impavida* (Florence 3222). — 7, 8: "Outer bracts" viewed by adaxial face (dotted: brown zone; blank: greenish foliaceous-textured zone). 9: "Inner bract" folded along midnerve, this latter on left. 10: Transverse section of the bract represented in Fig. 9 at 12 cm from apex, showing four fibrovascular bundles (hatched) and extra-vascular fibre-strands (black). — Note. For Fig. 7: the margins are minutely denticulate along 4 cm beneath apex, the midnerve along 22 cm beneath apex. For Fig. 8: the margins are minutely denticulate along 3 cm beneath apex, the midnerve along 13 cm beneath apex. For Fig. 10: adaxial face on left; the uppermost fibrovascular bundle corresponds to the middle of a pleat; in each fibrovascular bundle, the two hatched parts indicate the approximate extent of the zones of thick fibres, and the small circle represents the largest tracheary element, viz. the tracheary element furthest away from the adaxial face.

indicate an existence of close relationships between subgen. *Gaudichaudiella* and subgen. *Freycinetia*. It is probable that *F. impavida* also has other bracts, smaller and thinner, as do the species of sect. *Freycinetia* for example, but it was not possible to observe them in this specimen. The bract anatomy of *F. impavida* is studied in the middle part of an inner bract. At this level, no middle parenchyma is found between the adaxial chlorenchyma and the abaxial chlorenchyma, and big strands of extra-vascular fibres (= fibres outside of fibrovascular bundles) are observed at the adaxial side and the abaxial side (Fig. 10). This richness in fibres explains the rigidity of these bracts. Generally speaking, fibres are more abundant at the adaxial side than at the abaxial side, and there is no clear separation between the adaxial and the abaxial fibre-strands. In each half of the bract blade, the middle fibrovascular bundle which corresponds to the middle of a pleat is flanked by adaxial fibre-strands larger than those at either side (Fig. 10). Crystal cells are very abundant in the abaxial epidermis, less so in the adaxial epidermis. The abaxial hypodermis is not lignified.

The staminate characters of *F. impavida* observed are as follows. The anthers have endothecial thickenings, and are 1.3-1.5 mm long. They are rich in raphide cells along the connective, 5 or 6 large raphide cells being visible in the transverse sections. The filaments are papillate and 3.3-3.5 mm long, and some contain some raphide cells. The pollen is smooth. The pistillodes appear on the surface of the spike as soon as the filaments are removed. The "free" pistillodes (see Material and methods) show truncato-pyramidal shape, and their carpelloses have no distinct apices except for the prominent carpelloses at either side (Fig. 11). It is therefore not possible to determine the carpellose numbers. In the pistillodes studied with microtome sections, the walls are separate from top to base and very rich in both crystal cells (located in the outer hypodermis: Fig. 14) and raphide cells (Fig. 12 and 13). The great abundance of both types of cells, in particular of crystal cells, is further confirmed by the pistillodes bleached by eau de Javelle, which also show tracheids in the pistillode walls where they extend to a little above the middle. The height of the pistillode walls from the apex to the cavity bottom is about 450 μm (Fig. 12). A long apical placentode is frequently found (Fig. 13); sometimes two are visible, each at an end of the transverse sections. In particular, a high percentage of hypodermal cells and some epidermal cells both with walls thicker than those of the other cells in these two tissues are observed in the apical part of the pistillodes (Fig. 14). By their thick walls, both types of cells are also distinct in the pistillodes bleached by eau de Javelle. The chemical nature of their secondary thickenings is obscure. In the "free" pistillodes placed in Phloroglucinol-HCl, they do not stain while tracheids stain slightly violet. In those placed in Iodin-H₂SO₄, they stain yellow as do the unlignified cells. This seems to indicate that the secondary thickenings are cellulosic, which remains to be corroborated with fresh or ethanol-fixed material. The pistillode features of *F. impavida* described above are also observed in various species of sect. *Freycinetia*. This seems to indicate an existence of close relationships between subgen. *Gaudichaudiella* and subgen. *Freycinetia*.

Comparison of the above-mentioned pistillode of *F. impavida* with that of the Hawaiian *F. arborea* reported next shows how the former pistillode may further be used to distinguish those species which are at present considered to be synonymous to *F. impavida*. The use of the latter pistillode for comparison is determined by the fact that it is very different from the former. A large number of features can therefore be involved in order to render this example of comparison as extensive as possible. In the Hawaiian *F. arborea*, the "free" pistillodes are generally about twice as small as those of *F. impavida*, and have a subrectangular shape (Fig. 15). All their carpelloses are distinct, each having a prominent apex; therefore, the carpellose numbers can be determined by counting the carpellose apices. The pistillodes studied with microtome sections show other different features. Firstly, there is no vascularization in their walls, tracheids being observed beneath the pistillode cavity only. Secondly, no cells with secondary thickenings are visible in the pistillode walls. Thirdly, both crystal cells and raphide cells are lacking or rare. All three features are further corroborated by the pistillodes bleached by eau de Javelle. Fourthly, apical placentodes are short or undifferentiated. Fifthly, the height of the pistillode walls from the apex to the cavity bottom is about 300 μm . As a conclusion, the pistillode characters that can be used for distinguishing any two "close" species (for example two component species of an aggregate species) are those deduced from comparing their "free" pistillodes (pistillode shapes and sizes; carpellose apices), the pistillodes

bleached by eau de Javelle and those studied with microtome sections (height of the pistillode walls; existence or not of vascularization in these walls, of cells with secondary thickenings, and of raphide cells and crystal cells; density of these cells).

***Freycinetia moratii* Huynh, spec. nov.**

Folia circa 90 cm longa 3.5 cm lata in medio, in circa 1/4 supera abrupte attenuata; marginibus fere inermibus, basi apiceque minute denseque denticulatis; costa media inermi in dimidio infero minute denticulata in supero; auriculis circa 10 cm longis, subrigidis, persistentibus; cellulis polaribus stomatum in pagina abaxiali (= dorsali) breviter verrucatis. Inflorescentia foeminea terminalis; spadicibus probabiliter 3, usque ad 25 cm longis, syncarpiis cylindraceis interdum curvatis ad 19 cm longis 2.8 cm latis maturitate rubris, pedicellis glabris 4-6 cm longis 0.7 cm latis; bracteis in 14 cm axis distributis; pistillis circa 1 cm longis 5 mm latis 1.5 mm crassis, plerumque 8-10-stigmaticis, usque ad basim separatis, infra pileum circa 2.5 mm longum 3 mm latum 1.5 mm crassum rectangulo-tabuliformem in aspectu laterali elongato-ellipticum in apicali abrupte constrictis, basim versus secus axem spadicis dilatatis, intra fasciculis fibrarum numerosissimis sed omnibus anguste ellipticis tenuibusque (ut maximum circa 120 μ m latis 20 fibris compositis) ergo invisibilibus super epicarpio praeditis; staminodiis numerosis, sine cellulis raphidiphoris.

Type: *Morat* 7037 (BISH! holo-), Tahiti Island, Orohena Ridge, alt. 1100 m, 1 Sept. 1982; sheltered ridge-forest in small basin; fruits red at maturity. Iso- (P!).

F. moratii is named after Ph. Morat (P!). Since *F. moratii* is the type of sect. *Tahitiella* (see below), it would be of interest to also study the anatomy of its berry. Longitudinal sections of this berry show three parts — the pileus, the narrowing infrapileal part, and the cavity —, corresponding to the aspect of the berry (Fig. 20). Narrow fusiform/elliptic fibre-bundles are abundant at various levels. The hypodermis is lignified only in the pileus. In transverse sections in the middle part of the pileus (Fig. 21), a very large number of narrow fibre-bundles in several rows are found between the hypodermis and the central sclerenchyma; some single fibres are also observed. The central sclerenchyma does not extend to within the narrowing infrapileal part. In transverse sections in the middle part of the berry (Fig. 22), a very large number of fibre bundles in one row is observed, some of which are larger than those in the upper two parts. In transverse sections in the lower zones, fibre bundles are also abundant and in one row but the largest bundles are a little smaller than those in the middle part.

As seen above (Key to the Freycinetias of the Society Islands), *F. moratii* is intermediate between *F. impavida* and *F. arborea* but may appear more similar to the latter species. In particular, in aspect the syncarps and berries of *Morat* 7037 resemble so closely those of *Florence* 3940 (P!), a Tahitian specimen of *F. arborea*, that it is not possible to observe any difference between them. This shows that different species can have quite the same infructescences or pistillate inflorescences. This conclusion can be applied to the component species of the aggregates *F. arborea* and *F. impavida*. However, *F. moratii* shows closer taxonomic affinity with *F. impavida* by having fusiform/elliptic fibre-bundles in its berry. In *F. moratii* these fibre bundles are very narrow, therefore the subepicarpic bundles are not visible on the berry. In fact, the thickest of these are perceptible only from about $\times 12$ magnification onwards (when the berry is observed under a $\times 6-50$ stereo-microscope). *F. moratii* is thus a typical case which demonstrates the utility/necessity of micromorphology (anatomical features and surface details of various organs) in the taxonomy of *Freycinetia*. This is not without giving cause for some apprehension. In fact, if the berry of this species were not studied anatomically, it would certainly have been placed in sect. *Freycinetia* with *F. arborea*. Also, as seen in the Key to the Freycinetias of the Society Islands, the pistillate specimens of *F. moratii* that have leaves amputated of the apical parts cannot be distinguished from those of *F. arborea* if their berry anatomy and leaf surface (Fig. 16 and 17) are not studied. Such specimens of *Freycinetia* are very frequent in herbaria.

Although the fusiform/elliptic fibre-bundles in its berry reveal that *F. moratii* belongs to subgen. *Gaudichaudiella* (see above), it stands apart in this subgenus by having a pileus which is

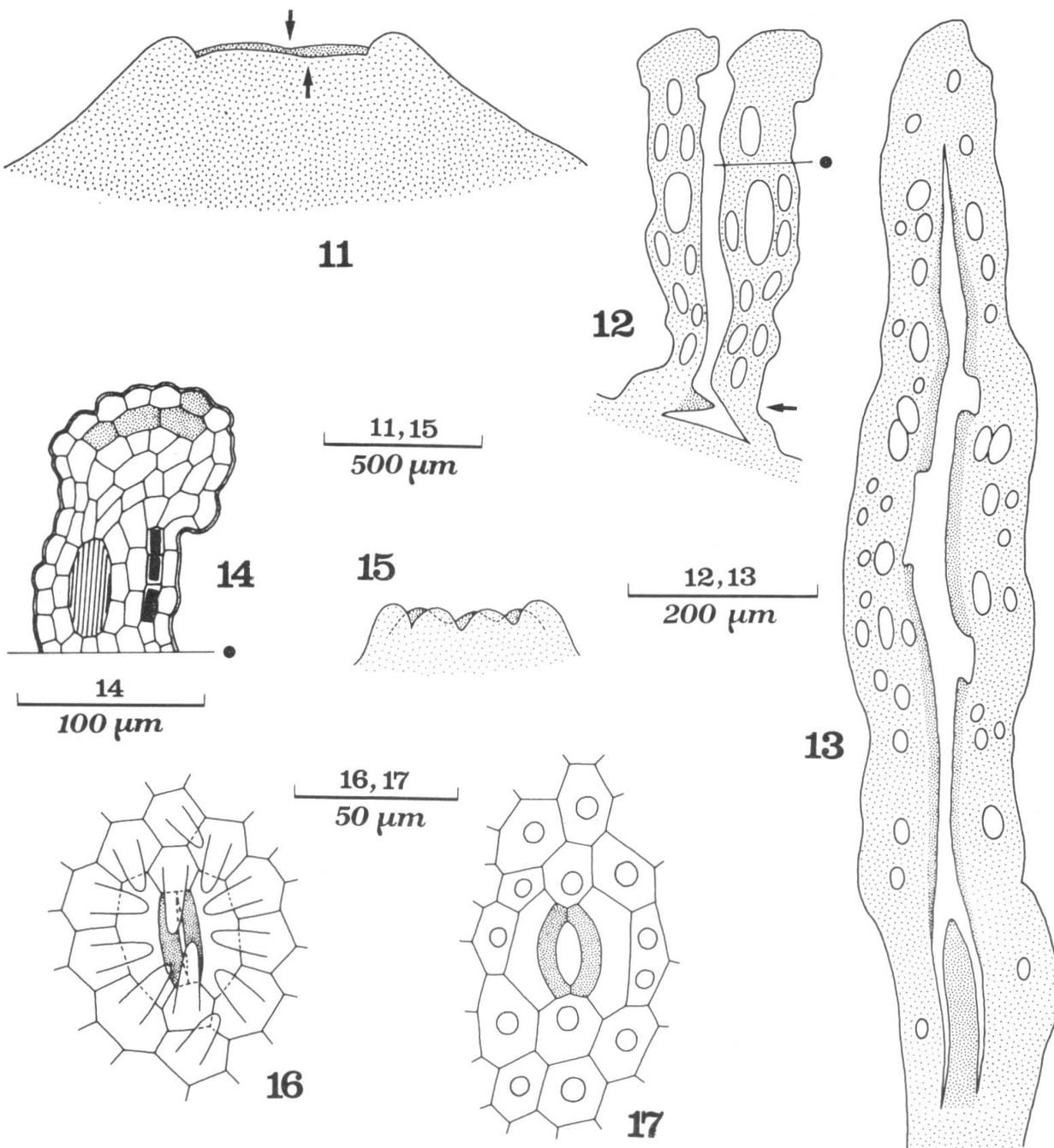


Fig. 11-17. — *Freycinetia impavida* (Florence 3222) (11-14), *F. arborea* of Hawaii Islands (Lorence 7249) (15), *F. arborea* of Society Islands (Raynal 18088) (16), and *F. moratii* (Morat 7037) (17). — 11: "Free" pistillode, showing a larger lateral-face in front view (lower arrow: limit almost indiscernible between two carpelloides of this face; upper arrow: limit between two carpelloides of the other larger lateral-face, this being almost entirely hidden; densely dotted: exposed part of the latter face). 12: Pistillode in longitudinal section passing by its shorter axis (arrow: lower limit of distribution zone of crystal cells and apex of pistillode cavity). 13: Pistillode in transverse section passing by its cavity (apical placentode below and finger-like). 14: The upper-right part of pistillode in Fig. 12, magnified (dotted: cells with secondary thickenings; cells with black rectangle: crystal cells). 15: "Free" pistillode, showing seven carpelode apices and a larger lateral-face in front view (densely dotted: exposed parts of the other larger lateral-face, this being almost entirely hidden). 16: Stomate-bearing area of leaf abaxial face, showing guard cells (dotted) and finger-like papillae. 17: Stomate-bearing area of leaf abaxial face, showing guard cells (dotted) and verrucas (circles), these being viewed by optical transverse section. — Note. For Fig. 12 and 13: each ellipse represents a raphide cell; the placentodes are densely dotted; crystal cells are very abundant in the outer hypodermises but not represented.

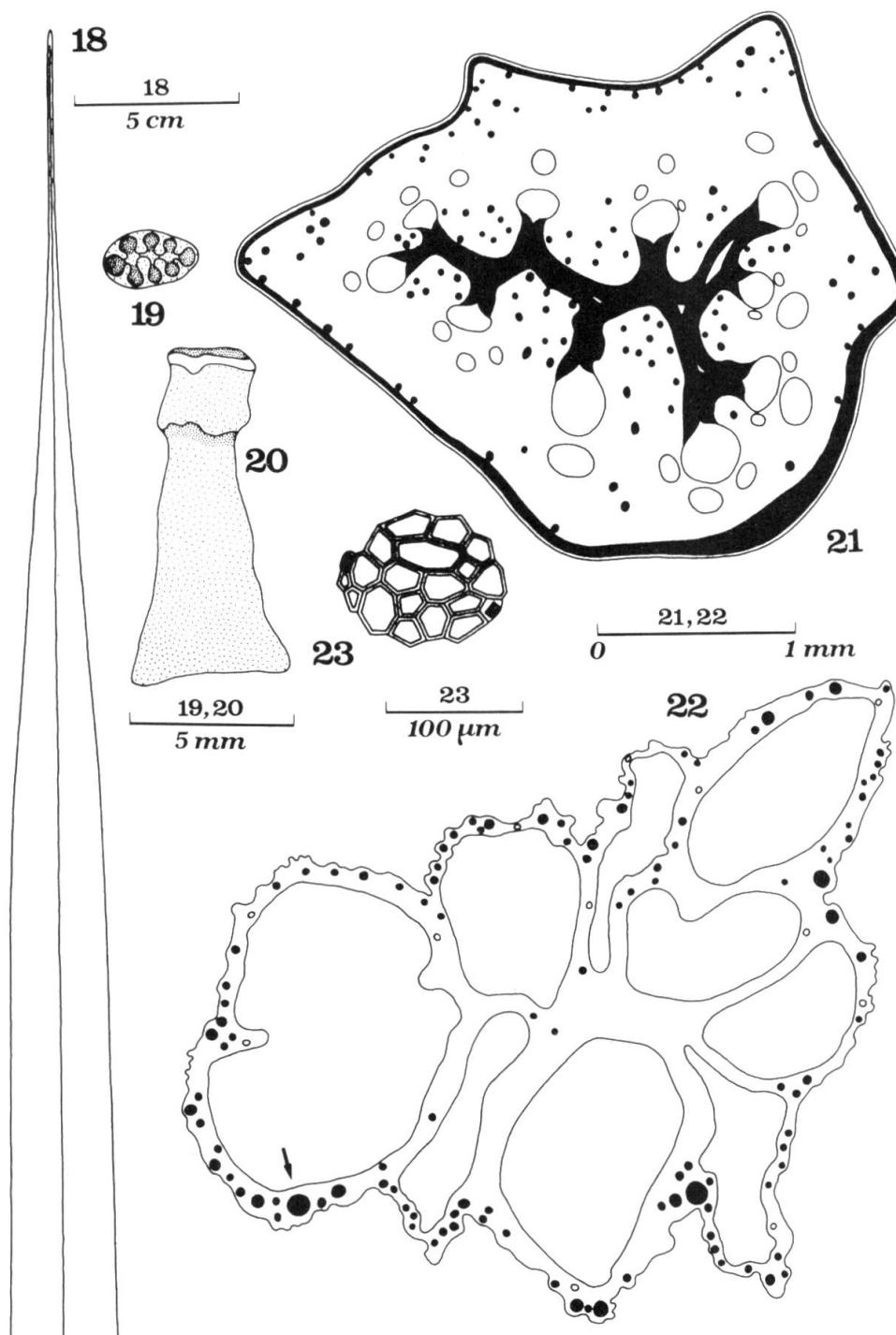


Fig. 18-23. — *Freycinetia moratii* (Morat 7037). — 18: Upper part of leaf, viewed by adaxial face. 19, 20: Berries in apical view and lateral view respectively, the former showing eight stigmata (densely dotted), the latter, the rectangular tabuliform pileus, the narrowing infrapileal part and the petticoat- like lower part. 21: Transverse section of 10-stigmatic berry about 7.9 mm long at about 0.8 mm from apex, showing central sclerenchyma (branched black mass in centre), ten fertilization canals (blank drop-like ellipses at apices of branchlets of central sclerenchyma), vascular bundles (the other blank ellipses), lignified hypodermis (black girdle), and fusiform/elliptic fibre-bundles (black spots). 22: Transverse section of the same berry at about 5.2 mm from apex, showing ten locules two of which fused, vascular bundles (small blank ellipses), and fusiform/elliptic fibre-bundles (black spots). 23: The arrowed fibre-bundle in Fig. 22, magnified (cells with black rectangle: crystal cells). — Note. For Fig. 22: the locules will fuse into one locule at lower levels.

rectangular tabuliform in lateral view and generally elliptic in apical view (Fig. 19 and 20). Therefore, sect. *Tahitiella* is described below to accommodate it. Also, its thin ovary-walls (Fig. 22) and persistent leaf-auricles are rare features in this subgenus.

In addition, the berries of *F. moratii* are separate almost down to their bases in syncarp; therefore, they can be removed without any tearing to their epicarp. In contrast, those of *F. impavida* (type of sect. *Gaudichaudiella*) and *F. samoensis* (type of sect. *Malacandra*) are so strongly adherent along their infrapileal parts that they cannot be removed without some damage to their epicarp. This difference may be explained. In *F. impavida*, *F. samoensis* and their allied species, the fusiform/elliptic fibre-bundles formed in the infrapileal part during the process of berry maturation are generally very broad; it follows that the ovary walls become very thick (Fig. 3) with the consequence that the berries adhere strongly to each other. In *F. moratii*, these fibre bundles are narrow; therefore the ovary walls remain thin during this stage (Fig. 22) and the berries do not adhere or not strongly to each other. This explanation seems to be corroborated by *F. nesiotica* (Solomon Islands), which also belongs to subgen. *Gaudichaudiella* but to another section which is to be described. The berries of this species show some resemblance to those of *F. moratii* in that the fusiform/elliptic fibre-bundles in the ovary walls are narrow and that these walls are thin. This anatomical similarity probably explains why the berries of *F. nesiotica* are also separate down to their bases in syncarp.

Freycinetia sect. *Tahitiella* Huynh, sect. nov.

Baccae usque ad basim separatae, infra pileum rectangulo-tabuliformem in aspectu laterali elongato-ellipticum in apicali abrupte constrictae; hypoderme pilei lignescenti; fasciculis fibrarum numerosissimis, anguste ellipticis, omnibus tenuibus ergo invisibilibus super epicarpio; parietibus ovarii tenuissimis propter fasciculos fibrarum omnes tenues. Auriculae foliorum persistentes. Charactere secundarii: syncarpia cylindracea, pedicellis glaberis, apice haud inflatis.

Type: *F. moratii*.

This section is probably unispecific. The anther, pistillode and bracts of *F. moratii* should further be investigated in order to complete this diagnosis.

Freycinetia sect. *Malacandra* Huynh, sect. nov.

Baccae lageniformes, infra pileum haud constrictae valde applicatae; pileo rostrato in aspectu laterali rotundato in apicali; hypoderme pilei lignescenti; fasciculis fibrarum fusiformis/ellipticis numerosissimis, statura variabilissimis, infra pileum ad basim plerumque latissimis ergo visibilibus super epicarpio; parietibus ovarii crassissimis propter fasciculos fibrarum plerumque latissimos. Anthera haud endothecialiter incrassata. Pistillodium infra superficiem spadicum locatum ergo invisible inter filamenta, apice pilis longis praeditum, parietibus arte applicatis ergo cavitate indistincta. Bracteae inferae intermediaeque sublineares foliaceaeque in parte supera. Auriculae foliorum deciduae. Charactere secundarii: syncarpia cylindracea/globosa, pedicellis scaberis, apice inflatis.

Type: *F. samoensis*.

Sect. *Malacandra* (Gr. malakos, andros) is named with reference to its anthers which appear soft because devoid of endothelial thickenings. *F. hombronii*, another Samoan species, also belongs to this section. It is very close to *F. samoensis* in which it can be included as being a form or variety. Therefore it probably has the same bracts and staminate flower.

F. samoensis differs from *F. impavida* (sect. *Gaudichaudiella*) in its anthers devoid of endothelial thickenings and in its pistillode which is located beneath the spike surface (hence it is invisible when the filaments are removed) and has long apical hairs and closely applied walls, as seen for example in Cox 167 (UC!). *F. samoensis* is the only known species of *Freycinetia* which has these

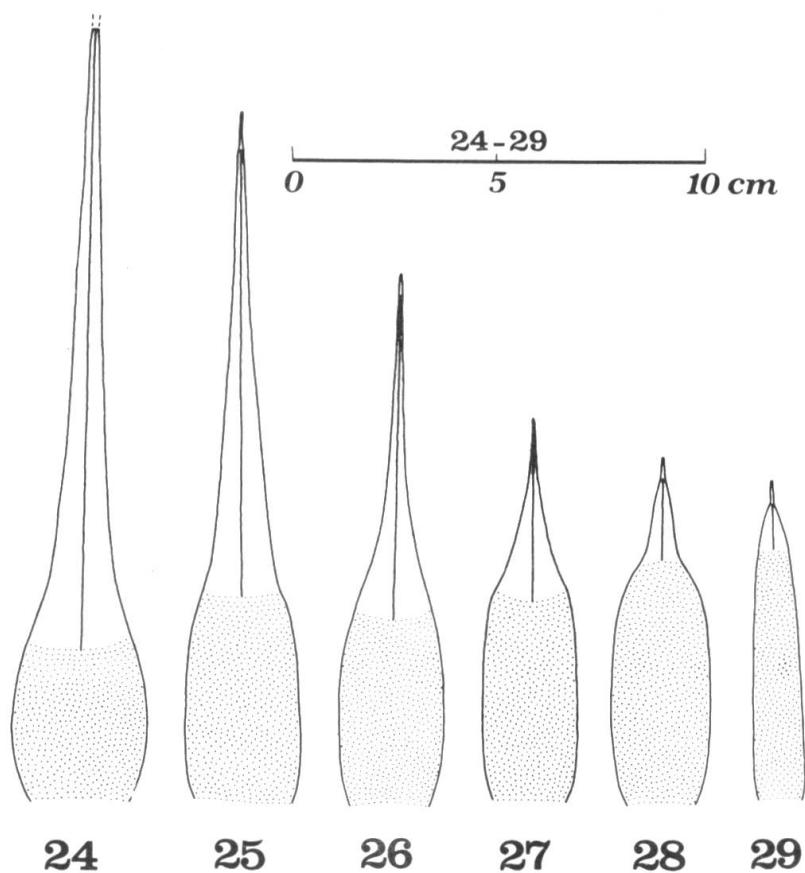


Fig. 24-29. — *Freycinetia samoensis* (Cox 132): Bracts viewed by adaxial face (dotted: membranaceous zone; blank: greenish foliaceous-textured zone). — Note. In all bracts, both the margins and midnerve are minutely denticulate along the foliaceous part, the uppermost prickles being a little larger than the other prickles.

staminate features. It also differs in its bracts, which are studied for the first time in the present paper, using Cox 132, 167 and 205 (GH!). Consider for example Cox 132, whose bracts are field-noted as being "white fleshy". Except for the floral bracts which are membranaceous and adhere closely to the pistillate spikes, thus making their study impossible, the other bracts at lower levels show two different parts (Fig. 24-29): the lower part is membranaceous, the upper part greenish and of foliaceous texture and may be termed sublineary. Neither ensiform nor boat-shaped bracts are observed, in contrast to *F. impavida* (Fig. 7-9). This wide difference in bract and staminate flower of *F. samoensis* from *F. impavida* upholds the separation of sect. *Malacandra*. However, both sections have quite the same berries; therefore sect. *Malacandra* is probably closest to sect. *Gaudichaudia*. Nevertheless, its anthers and pistillode appear unique in *Freycinetia*; therefore it should further be examined if a subgeneric rank may better be assigned to it. From another viewpoint, this difference in bract and staminate flower is quite unexpected, for in a recent past *F. samoensis* and *F. impavida* were considered to be closely related and placed in the same section. This reveals the difficulty of the taxonomy at the sectional level in *Freycinetia*, bracts and staminate plants having not been collected for most species.

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