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Monograph

Survey of the fruits and endocarps of Icacinaceae (Lamiids, Icacinales)

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Abstract. Icacinaceae Miers are a well-described family. However, the family lacks a comprehensive guide to endocarp morphology, which would be an important tool for interpreting the family's extensive fossil record of endocarp remains. In this survey, we describe fruits and endocarps of 88 species of Icacinaceae s. str., four of Icacinaceae s. lat. (now Metteniusaceae) and one of Oncothecaceae. We investigated the value of the endocarp in species recognition. In addition, we generated an Xper[3] database with an associated e-key to increase the availability of raw data and the understanding of the characters used. This study documents great diversity in epicarp hairs, mesocarp thickness, endocarp ornamentation, tubercle shape (if present), endocarp structure and thickness, and the locule lining. Some morphological features appear diagnostic for individual genera. In particular, the genus *Iodes* Blume, which is very common in the fossil record, is the only clade with the three following characters: papillae on the inner locule lining, ridged ornamentation on the endocarp surface, and a vascular bundle embedded within the endocarp wall. Finally, we discuss issues related to the preservation of fruit material in herbarium collections.

Keywords. E-Key, paleobotany, *Iodes*, morphoanatomy, monograph.

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Introduction

Icacinaceae Miers are a pantropical family in the lamiid clade with ca 23 genera and 160 species (Stull *et al.* 2015). Our knowledge of the family's morphology, systematics, ecology and distribution

is largely based on regional floristic treatments (e.g., Kerr 1911; Perrier de la Bâthie 1952; Boutique 1960; Sleumer 1971; Villiers 1973; Jansen-Jacobs 1979; De Roon 1994, 2003; Peng & Howard 2008; Utteridge & Schori 2011; Duno de Stefano 2013). The flowers, inflorescences, vegetative parts, and wood anatomy vary across the family and have been used for taxonomic classification. Fruit morphology, however, has been poorly documented in the previous literature, with usually only succinct descriptions of general fruit features (e.g., Engler 1893; Howard 1940, 1942a, 1942b; Sleumer 1971). Exceptions include detailed carpological studies of selected species of *Pyrenacantha* Hook. (*P. grandifolia* Eng., *P. scandens* Planch. ex Harv. and *P. kaurabassana* Baill.; Potgieter & van Wyk 1994) and *Cassinopsis* Sond. (*C. ilicifolia* (Hochst.) Sleumer and *C. tinifolia* Harv.; Potgieter & van Wyk 1993). Paleobotanical studies (e.g., Reid & Chandler 1933; Manchester 1994; Stull *et al.* 2012; Allen *et al.* 2015; Del Rio *et al.* 2019a) have provided the most information about fruit morphology across the family, as means of interpreting the rich fossil record of Icacinaceae, which consists primarily of endocarp remains (Del Rio & De Franceschi 2020). But lacking is a comprehensive examination of fruit structure across Icacinaceae, especially in light of recent phylogenetic studies of the family (e.g., Kårehed 2001; Byng *et al.* 2014; Stull *et al.* 2015). Although only drupaceous fruits are found in this family, the diversity of shape, anatomy and ornamentation is nevertheless substantial. Moreover, a comprehensive study of Icacinaceae fruit morphology would provide an invaluable resource for interpreting the family's rich fossil record of endocarp remains (Reid & Chandler 1933; Manchester 1994; Collinson *et al.* 2012).

In taxonomic research, the utility of many studies is often limited owing to the unavailablity of the 'raw data' upon which the work is based and the lack of standardization in descriptions and terminology used to communicate results. Ambiguity in terminology / descriptions can lead to 'noise' in taxonomic studies, and different methods of morphological examination can lead to different results, e.g., in measurements of characters such as endocarp thickness or tubercle length. Thus, taxonomic studies should include clear definitions (and / or explanatory diagrams) for critical characters / character states examined. In this spirit, a manual of leaf architecture was made (Leaf Architecture Working Group 1999; Ellis *et al.* 2009) to establish universal standards for analysis of leaf morphological characters. Similarly, for angiosperm wood, a database was created (InsideWood) to standardize the examination of wood characters and to host raw data (Wheeler 2011). In addition, this database uses the International association of wood anatomists (IAWA) list of characters, which are well illustrated and explained (Wheeler *et al.* 1989). Recently, new databases have been made using the Xper^2 software (Ung *et al.* 2010); important botanical examples include Palm-ID (Thomas 2011; Thomas & De Franceschi 2013), Pl@ntWood (Sarmiento *et al.* 2011) and a key to Amazonian ferns (Zuquim *et al.* 2017). These databases allow us to define items (species) and descriptive models (characters). Diverse functionalities are available, including interactive identification of a specimen starting from any descriptor. These tools can be used to complement descriptions and dichotomous keys, especially in cases like the study presented here.

In this survey, we describe fruits and endocarps of Icacinaceae species (ca 56% of the total diversity). We aim to (1) provide a detailed reference for endocarp morphology across the family, (2) provide the first database using Xper^3 (the online version of Xper^2) dedicated to the Icacinaceae fruits and endocarps from modern species, and (3) discuss patterns of endocarp diversity and the value of endocarp characters in fossil identification and species assignment.

Materials and methods

Samples and preparation

Endocarps were obtained from fruits removed from herbarium sheets. Preliminary tests showed that removing the mesocarp might damage the cellular structure of the outer part of the endocarp. Thus, when only one specimen was available for a given species, we used the following protocol: fruits were first hydrated in boiling water for ten minutes. Then, using a scalpel, fruit cross-sections were made

and dried with silica gel. Samples were then coated with gold-palladium for 5 minutes for examination with a scanning electron microscope (SEM, Jeol JCM6000, 15 kV), facilitating the observation of anatomical features, especially the endocarp wall layers and the locule surface (which sometimes bears papillae). Then, we rehydrated the specimens in boiling water for 10 minutes and removed the exocarp and mesocarp using a scalpel and a binocular microscope (Wild M3Z). Finally, the endocarp surface was studied using a binocular microscope (Wild M3Z) and imaged with a Leica DFC 420 camera. The technique of stacking was used for the macrophotography of the endocarps, and the final image was reconstructed using Photoshop CC 2014 software. When at least two specimens were available for a species, we conducted the anatomical and morphological studies separately using two fruits. The adhesion and hardness of the mesocarp vary considerably among species and genera. In extreme cases of hardness (e.g., *Rhyticaryum macrocarpum* Becc.), the mesocarp was slashed and reimmersed in boiling water for a few additional minutes. Measurements were taken from the digital photographs using ImageJ software (Rasband 2016). Measurements of cells were based on 10 cells per row. In addition, fruit size was obtained directly from the herbarium sheets. We measured at least five fruits per species. In many cases, a given fruit measurement is close to the endocarp measurement, because the mesocarp is usually highly collapsed / shriveled in herbarium samples.

The sampling comprises 88 species of the approximately 160 accepted extant species of Icacinaceae s. str. (Stull *et al.* 2015). We added four species of Metteniusaceae H.Karst. ex Schnizl. (formerly included in Icacinaceae s. lat.) and one species of Oncothecaceae Kobuski ex Airy Shaw to provide out-group comparisons in our analysis. Fruit samples were obtained from numerous herbaria, mainly the Muséum national d'histoire naturelle in Paris (P), but also the Royal Botanic Garden Kew (K), the Naturalis Biodiversity Center (L, U, WAG), the Meise Botanic Garden (BR), Kunming Institute of Botany (KUN), the Missouri Botanical Garden (MO) and the University of California (UC). Acronyms of herbaria follow Holmgren *et al.* (1990) and Index Herbariorum online. The voucher information (country, date, collector and herbarium repository) can be found at the beginning of each species description. The specimen(s) used for the endocarp and fruit descriptions are under the heading 'Specimens used for endocarp and fruit description', whereas the specimens used only for the fruit description are under the heading 'Other material'. Although generally only one or two endocarp specimens were examined for each species, we nevertheless consider these specimens to represent critical sources of information concerning the diversity in anatomy and morphology across the family. Information about living material (e.g., color of the mature fruit) was derived from the herbarium labels.

The sampling covers all the major geographic areas of the family: Africa (39 / 54 species), Asia (32 / 60), Madagascar (12 / 18) and South America (5 / 20). Our sampling lacks three monospecific Asian genera (*Merrilliodendron* Kaneh., *Natsiatopsis* Kurz and *Sleumeria* Utteridge, Nagam. & Teo) and the South American genus *Casimirella* Hassl., which contains seven species. The absence of this genus largely explains our poorer sampling in this region compared to the Old World.

Elements of description

We adopted description elements used in other studies (e.g., Reid & Chandler 1933; Stull *et al.* 2012), especially regarding the orientation of the fruit as used for other families (Jacques 2009). The endocarps are oriented along two axes, apical-basal and dorsal-ventral (Fig. 1). The primary vascular bundle runs inside or on / above the dorsal part of the endocarp. Overall, most species of Icacinaceae (but not all, e.g., *Mappia* Jacq., *Nothapodytes* Blume and *Merrilliodendron*) exhibit two basic endocarp types: ridged (Fig. 1.1) and / or pitted (Fig. 1.2). In the ridged type, vertical ridges form a diffuse pattern, often with additional horizontal ridges that span the vertical ridges, creating a reticulate pattern of areoles. In these areoles, simple or arbuscular freely ending ridgelets are occasionally found. In the pitted type, circular to elongate pits are randomly or longitudinally arranged. Small ridges are often found at the apical part,

but diffuse ridges are also present in some species. The diameter and number of pits vary among species, as they are often associated with tubercles, protruding more or less into the locule.

For the pit and tubercle shapes, we partially followed the nomenclature developed by Stull *et al.* (2012), but we adapted the descriptions for this new survey (Fig. 2.1– 2.7). We defined two main categories—pits with tubercles protruding into the endocarp locule (Fig. 2.1– 2.5) and pits lacking tubercles (Fig. 2.6–2.7). For the first category, we defined five forms, all based on observations made from transversely sectioned fruits. The bullate shape (Fig. 2.1) is defined as a tubercle wider than long, composed of short sclerotic cells. The elongate-flattened shape (Fig. 2.2) corresponds to a tubercle longer than wide and vertically flattened like a blade, composed of short sclerotic cells. The peg-shaped tubercles (Fig. 2.3) have parallel sides, a truncated apex and are composed of elongated sclerotic cells. The cylindrical tubercles (Fig. 2.4) are the largest, often longer than 2 mm, composed of numerous elongated cells forming a cylindrical structure, with a capitate (or at least inflated) apex. The spiny tubercles (Fig. 2.5), which are the most common type, are much longer than wide and have tapering sides with elongated sclerotic cells. The pit category without tubercles is divided in two clear types: a broad, concave pit (Fig. 2.6) with a polygonal cavity delimited by the wall, and a narrow pit (Fig. 2.7) with a cylindrical cavity and an acute pit base.

The shape of Icacinaceae hairs has been discussed for the pistil, corolla, filaments and endocarp locule (Heintzelman & Howard 1948), but not for the epicarp. We partially follow the former nomenclature, but we add some other shapes, which are described for the first time for fruits of Icacinaceae. The papillate shape (Fig. 2.8) corresponds to small structures on the epicarp comparable to the papillae on the locule lining of some endocarps (e.g., as in *Iodes* Blume species). The small ovoid hairs with an acuminate apex (Fig. 2.9) are the thickest hair type. The uncinate hairs (Fig. 2.10) and the simple hairs with granular ornamentation (Fig. 2.11) are the most common types on the epicarp of Icacinaceae. Finally, the long and thin hairs (Fig. 2.12) are visible with the naked eye and form a pilose indumentum. Occasionally, the long and thin hairs are associated with small and thin hairs at their base (4 to 5 times smaller), forming a cluster of hairs (not shown in Fig. 2).

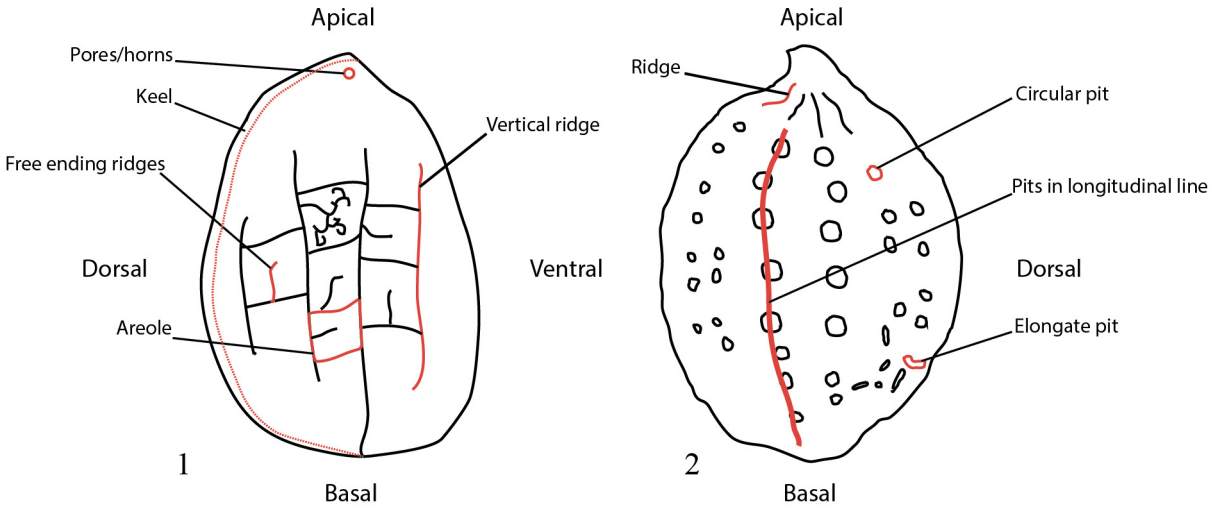

Fig. 1. General ornamentation of Icacinaceae Miers endocarps. **1**. Ridged endocarp. **2**. Pitted endocarp. Image taken from Del Rio (2018).

The endocarp wall structure is relatively constant across all Icacinaceae fruits (Fig. 2.13). The cells are digitate in shape, the cell walls are sclerotic (not shown in Fig. 2). The basal cells rows of the endocarp wall are composed of periclinally oriented, thin-walled cells (Fig. 2.13 (5)), with the innermost row lining the locule surface (Fig. 2.13 (4)). This inner row can either exhibit rounded to elongate papillae (Fig. 2.13 (1, 2)) or inflated cells (Fig. 2.13 (3)). Papillae and inflated cells are occasionally difficult to distinguish. To better characterize the rows above, we occasionally evaluated the adjacent rows of anticlinally oriented and/or isodiametric cells (Fig. 2.13 (6)), which were relatively easy to distinguish. We often observed a row between the mesocarp and the endocarp, with small anticlinally oriented or isodiametric cells; this row is difficult to attribute to the inner part of the mesocarp vs the outer part of the endocarp. However, this layer is likely part of the endocarp because its cells seem to be sclerotic, in contrast with the cells of the mesocarp, which are collapsed (Fig. 2.13 (8)).

Database and E-key online

The Xper[3] online database (Ung *et al.* 2010) was used to record descriptions and observations. The interface includes tabs (Fig. 3.1) with the following categories: items (specimens), descriptive model (characters and states), description (the link between the two previous tabs) and identification, which generates an interface for assisted identification (Figs 4–5). The database also was implemented in the

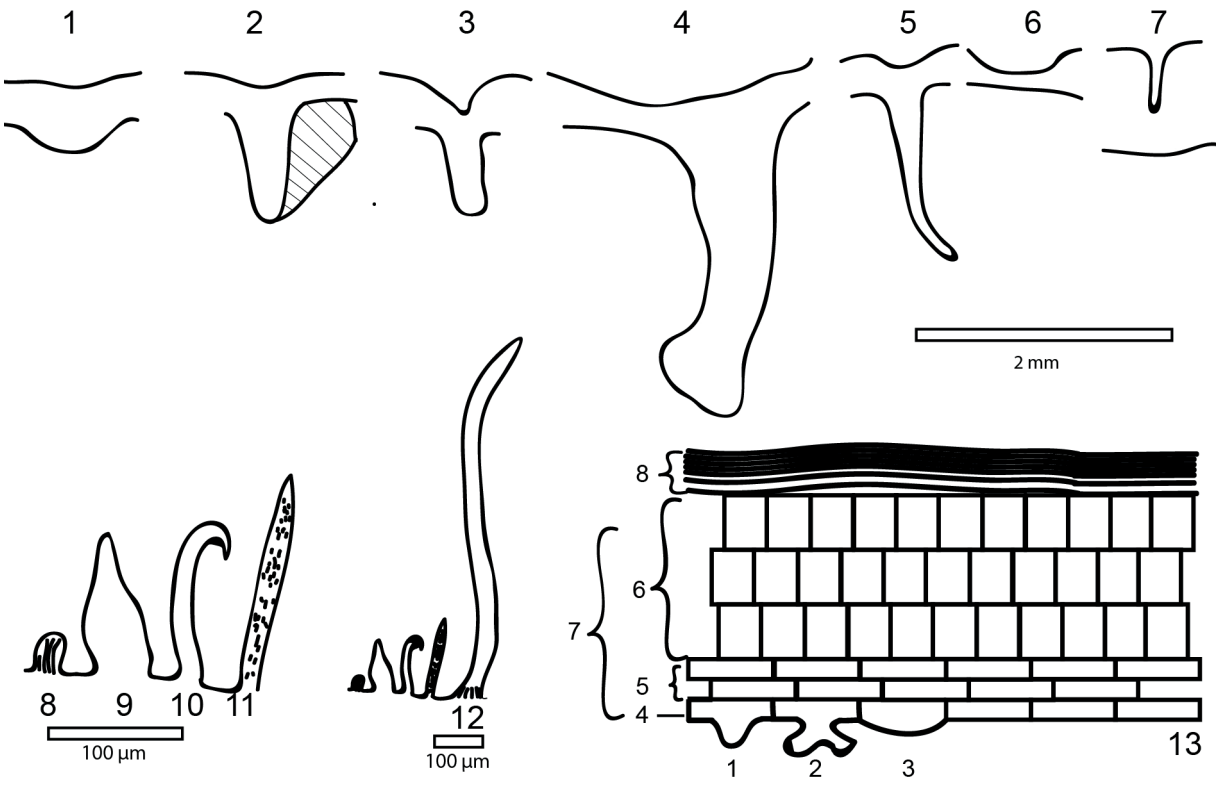

Fig. 2. Shapes of tubercles and hairs and the endocarp wall anatomy of Icacinaceae Miers. **1**–**7**. Tubercle shapes in transverse section. **1**. Bullate. **2**. Elongate-flattened. **3**. Peg-shaped. **4**. Cylindrical. **5**. Spiny. **6**. broad, concave pit. **7**. Narrow pit. – **8**–**12**. Hairs shapes. **8**. Papillae like. **9**. Small ovoid hairs with an acuminate apex. **10**. Uncinate hairs. **11**. Simple hairs with granular ornamentation. **12**. Long and thin hairs. **13**. Endocarp wall anatomy: 1 = rounded papillae; 2 = elongate papillae; 3 = inflated cell; 4 = periclinally oriented cells lining the locule; 5 = layer of periclinally oriented cells; 6 = layer of anticlinally oriented cells; 7 = endocarp wall; 8 = mesocarp wall when dry. Image modified from Del Rio (2018).

local software Xper[2], permitting access to the statistical part of the database (power of discrimination of characters, number of pictures, etc.).

Results

Online database

The Xper[3] key for the Icacinaceae (online version) is available at the following link: http://icacinaceae-fruits.identificationkey.org/mkey.html

This Xper[3] key, based on the following information, is a convenient means of synthesizing the data obtained from our study, and it offers a useful tool for identifying fruits of Icacinaceae, which is particularly relevant for studies of the fossil record.

The database contains 93 items (Fig. 3.2), with each including associated specimens (Fig. 3.3) and morphological and anatomical pictures (Fig. 3.4). The database contains 646 pictures associated with these items and descriptors.

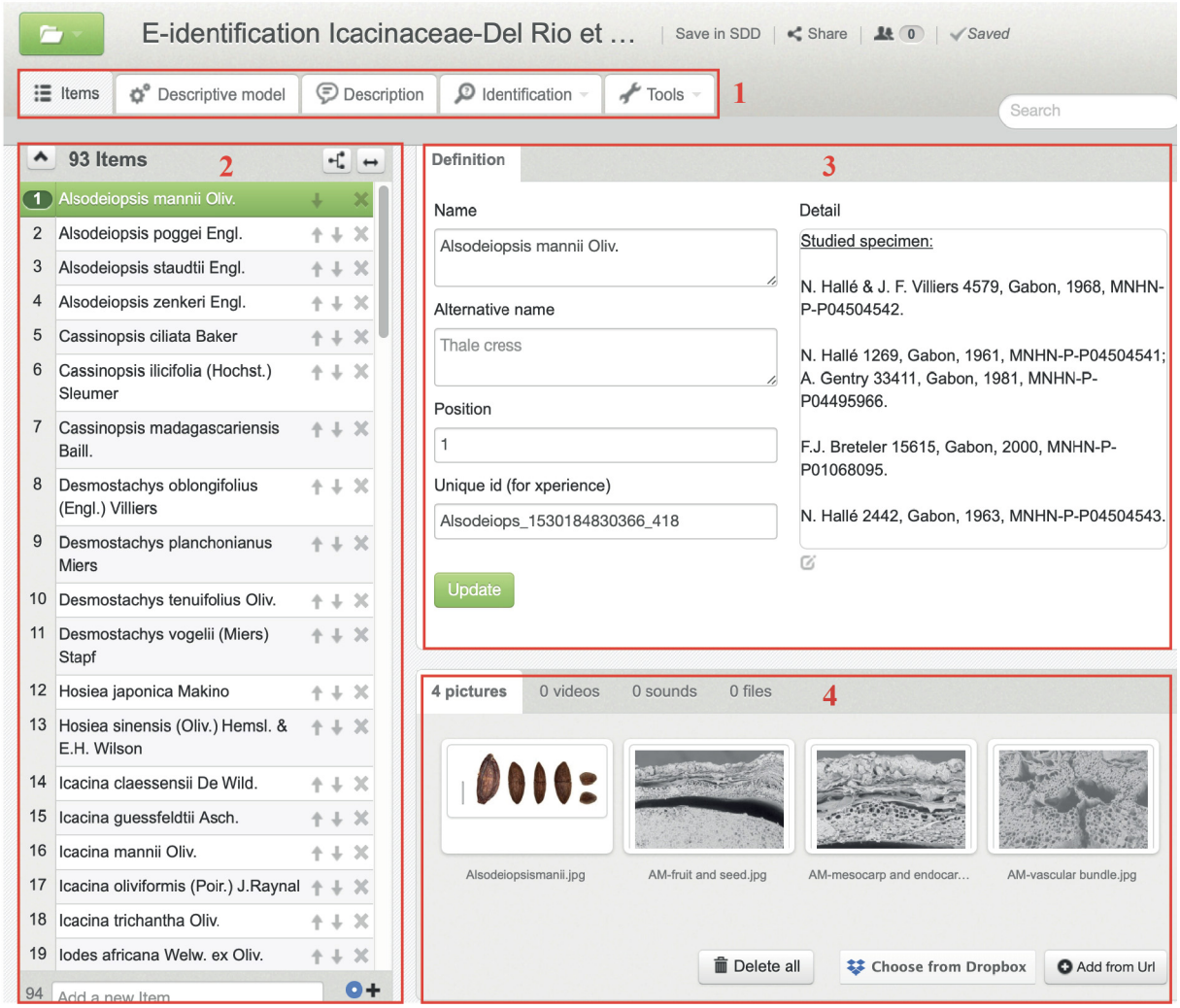

Fig. 3. Item view in the Xper[3] database. **1**. Tabs. **2**. List of items. **3**. Sheet of *Alsodeiopsis mannii* Oliv. with studied specimens. **4**. Pictures attached to the sheet. Image taken from Del Rio (2018).

Fifty-six descriptors (i.e., characters) were defined, 52 of them with associated images, and 121 states were used (average number of states per descriptor = 2.16); among them, 103 are illustrated. Six descriptors were divided into 23 sub-descriptors. Depending on the choice made by the user, some sub-descriptors can be unavailable for the user. For example, the length of the tubercle depends on the presence of tubercles. The dataset includes 18 numerical and 38 categorical descriptors. The descriptors are in a dependent hierarchy (Appendix 1). The discriminative power of all descriptors is available in Appendix 2. In addition, we can apply different descriptor weights (one to three) as a means of emphasizing the most pertinent characters. We gave more importance to the following characters: fruit gynophore, epicarp hairs; endocarp keel, shape in lateral view, apex structure, base morphology, outer surface ornamentation; primary vascular bundle position; locule number, presence of tubercles, and presence of locule hairs.

The database contains 5208 potential combinations. The database is 95.5% complete with 194 unknown data points. These unknown data mainly reflect fungal degradation of pertinent features on herbarium specimens. However, the species with the most missing data, *Miquelia assamica* (Griff.) Mast. ex B.D.Jacks., is 82.1% complete, demonstrating the overall robustness of the dataset.

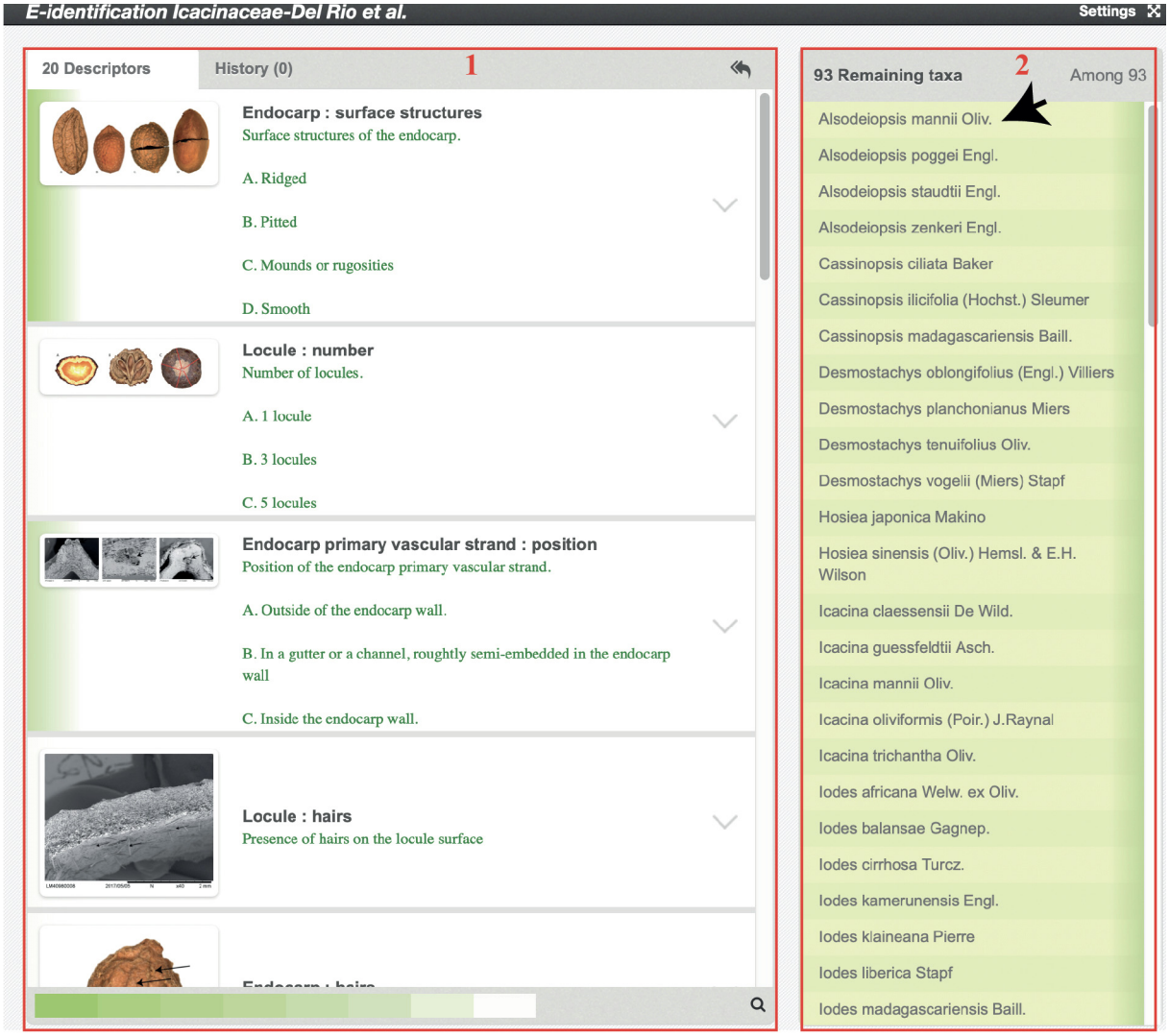

Fig. 4. Interactive identification view in Xper[3] database. **1**. Descriptors. **2**. Remaining items.

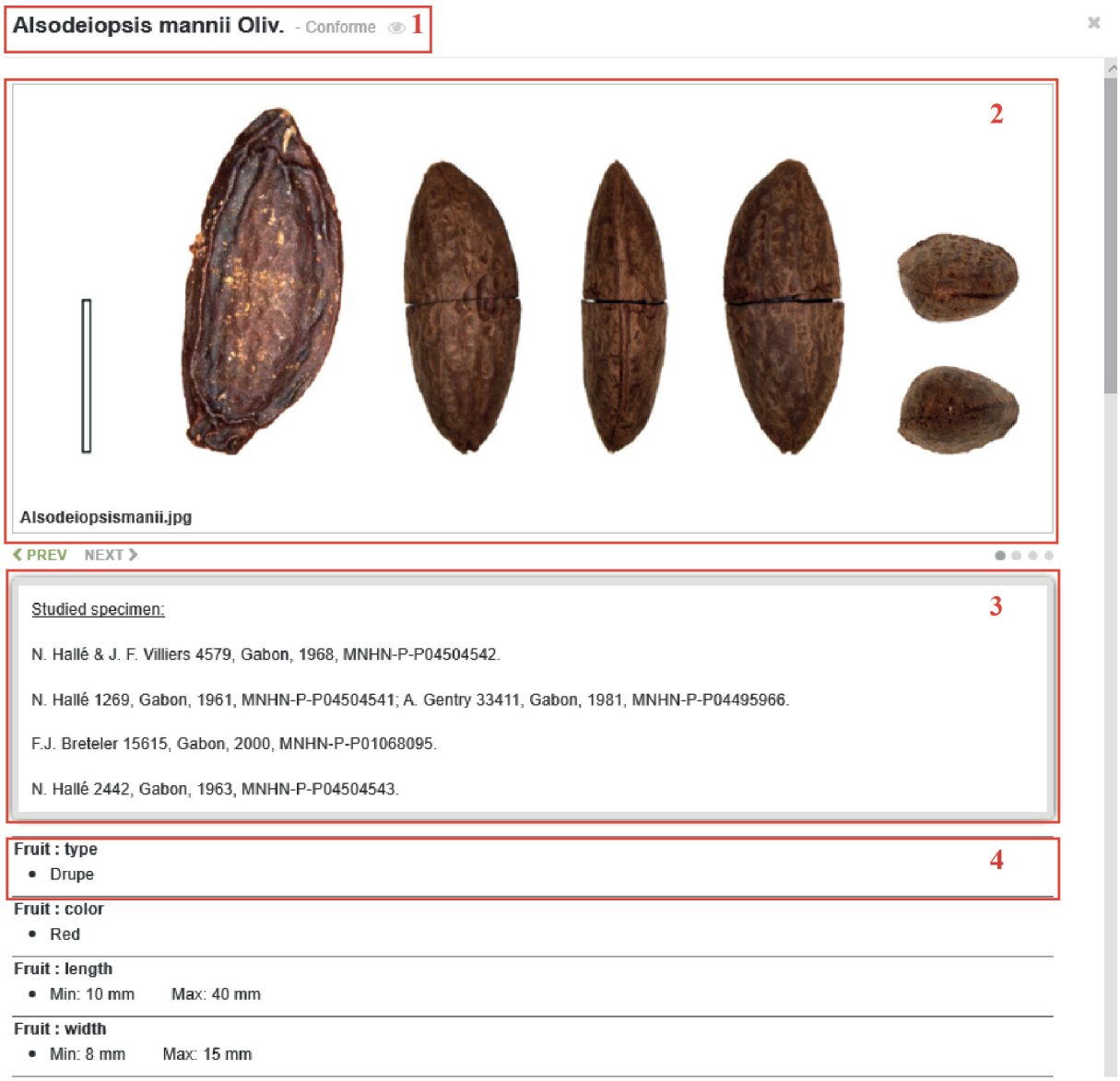

Fig. 5. View of remaining taxa in Interactive identification tab. **1**. Scientific name of the species. **2**. Pictures associated with the species. **3**. Studied specimens. **4**. Characters and character states of the species.

Fruit description of Icacinaceae *s. str.*

Class Magnoliopsida Brongn.
Subclass Lamiidae
Order Icacinales Tiegh.

Family **Icacinaceae** Miers
Figs 6–34

Description

Fruit. Drupaceous, elliptical to globose, asymmetrical at the apex, occasionally including an accrescent perianth; laterally compressed, mainly red-black when mature; glabrous or pubescent with a wide diversity of hair shapes. Calyx usually persistent, occasionally separated from the fruit by a gynophore.

Endocarp. Cream to brown, bilaterally symmetrical, unilocular, single-seeded, elliptical to globose in lateral view, lenticular to globose in transverse section. Keel often surrounding the endocarp in the plane of symmetry, occasionally faintly apparent or with a channel. Apex acute to flattened, asymmetrical or slightly asymmetrical; base symmetrical or cleft on one side, rounded to acute. Outer surface of the endocarp smooth, rugose, ridged, or pitted (or often ridged and pitted). Endocarp primary vascular bundle positioned outside the endocarp wall (in the mesocarp), often in a channel on the keel, or embedded within the endocarp wall. Endocarp wall composed of interlocking digitate and sclerotic cells with different orientations, rarely homogeneous. Locule surface (= inner endocarp surface) macromorphology smooth, lacunate or with tubercles protruding into the locule. Locule surface micromorphology smooth, papillate or with inflated cells, occasionally hairy.

Key to genera of Icacinaceae s.str.

1. Endocarp wall homogeneous comprised of isodiametric cells ..... ***Cassinopsis*** Sond.
– Endocarp wall not homogeneous or cells not exclusively isodiametric 2

2. Hairs present on the locule surface 3
– Hairs absent from the locule surface 4

3. Endocarp width ca 40 mm, endocarp wall more than 700 μm thick ..... ***Lavigeria*** Pierre
– Endocarp width ca 13 mm, endocarp wall less than 400 μm thick ..... ***Leretia*** Vell.

4. Locule surface papillate 5
– Locule surface not papillate 6

5. Outer endocarp surface pitted 7
– Outer endocarp surface not pitted 8

6. Hairs-like unit present on the endocarp surface ..... ***Pleurisanthes*** Baill.
– Hairs-like unit absent from the endocarp surface 9

7. Tubercles bullate ..... ***Miquelia*** Meisn.
– Tubercles spiny, cylindrical, peg-shaped or elongate-flattened ..... ***Pyrenacantha*** Hook.

8. Endocarp primary vascular bundle embedded within endocarp wall ..... ***Iodes*** Blume
– Endocarp primary vascular bundle outside endocarp wall or in a channel 10

9. Outer endocarp surface pitted 11
– Outer endocarp surface not pitted 12

10. Outer endocarp surface completely smooth ..... ***Iodes*** Blume
– Outer endocarp surface ridged or rugose, irregular 13

11. Pits within shallow mounds slightly protruding inside the locule ..... ***Phytocrene*** Wall.
– Pits within tubercles protruding inside the locule 14

12. Endocarp thickness >12 mm ..... ***Icacina*** A.Juss.
– Endocarp thickness <10 mm 15

13. Endocarp length ca 12 mm ..... ***Hosiea*** Hemsl. & E.H.Wilson
– Endocarp length >15 mm 16

14. Tubercles bullate ..... ***Stachyanthus*** Engl.
– Tubercles spiny, cylindrical, peg-shaped or elongate-flattened ..... ***Pyrenacantha*** Hook.

15. Endocarp ridged and reticulate 17
– Endocarp rugose, irregular 18

16. Endocarp almost smooth, irregularly rugose but without clear protuberant structures .....
..... ***Sarcostigma*** Wight & Arn.
– Endocarp rugose with clear protuberant structures or ridged 19

17. Endocarp oblong ..... ***Alsodeiopsis*** Oliv. in Benth.
– Endocarp elliptical 20

18. Endocarp apex with prominent bulge or pores 21
– Endocarp apex without ornamentation ..... ***Mappia*** Jacq.

19. Endocarp rugose, irregular ..... ***Mappianthus*** Hand.-Mazz.
– Endocarp ridged with a reticulate or diffuse ornamentation ..... ***Rhyticaryum*** Becc.

20. Endocarp length ca 9 mm, 4–5 areoles formed by ridges on each face .....
..... ***Natsiatum*** Buch.-Ham. ex Arn.
– Endocarp length >11 mm, 20–30 areoles formed by ridges on each face .....
..... ***Vadensea*** Jongkind & O.Lachenaud

21. Endocarp with subapical pores ..... ***Vadensea*** Jongkind & O.Lachenaud
– Endocarp with apical bulge 22

22. Ornamentation bullate, occuring in Madagascar ..... ***Desmostachys*** Planch. ex Miers
– Ornamentation more granular, occuring in Asia ..... ***Nothapodytes*** Blume

Genus ***Alsodeiopsis*** Oliv. in Benth.
Figs 6, 7.1–7.9

Description

Fruit. Oblong to slightly elliptical, asymmetrical at the apex, laterally compressed, red when mature. Epicarp strigose with yellow simple hairs with granular ornamentation, more or less shriveled when dry, revealing the underlying reticulum of endocarp ridges; calyx persistent.

Endocarp. Cream to brown, oblong in lateral view, lenticular in transverse section. Keel surrounding the endocarp in the plane of symmetry. Apex asymmetrical in lateral view; base rounded and symmetrical.

Outer surface of the endocarp ridged, with a reticulate pattern of thin rounded to angular ridges. Ridges delimit irregular, small to expansive areoles with simple or arbuscular freely ending ridgelets. Vasculature of the endocarp follows the reticulum. Endocarp primary vascular bundle outside the endocarp wall or in a channel on the keel. Endocarp wall forming two or three layers, each with at least one row of periclinally oriented cells; locule surface smooth, often clearly lacunate.

Key to the genus *Alsodeiopsis*

1. Endocarp brown with thick ridges ..... ***A. mannii*** Oliv.
– Endocarp cream with thin ridges 2

2. Endocarp primary vascular bundle outside the endocarp wall, base rounded .... ***A. staudtii*** Engl.
– Endocarp primary vascular bundle in a channel on the keel, base flattened 3

3. Endocarp wall ca 180–232 µm thick ..... ***A. poggei*** Engl.
– Endocarp wall ca 256–302 µm thick ..... ***A. zenkeri*** Engl.

Alsodeiopsis mannii Oliv.
Fig. 6.1–6.9

Material examined

Specimens used for endocarp and fruit description

GABON • "Monts de Cristal, route de Kinguélé"; 19 Jan. 1968; *N. Hallé & J.F. Villiers 4579*; P[MNHN-P-P04504542] • Bélinga; 20 Feb. 1961; *N. Hallé 1269*; P[MNHN-P-P04504541].

Other material

GABON • Ogoué-Ivindo, M'Passa Field Station, near Makokou on Riviere l'Ivindo; alt. 480 m; 18 Jul. 1981; *A. Gentry 33411*; P[MNHN-P-P04495966] • Ogooué-Lolo, Bambidie; ca 0°45′ S, 13°6′ E; 15 Aug. 2000; *F.J. Breteler 15615*; P[MNHN-P-P01068095] • "Abanga chantier C.E.F.A."; 11 Jun. 1963; *N. Hallé 2442*; P[MNHN-P-P04504543].

Description

Fruit. Oblong, shriveled when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp ca 200–250 µm thick when dry. Length 10–40 mm, width 8–15 mm, thickness 5–8 mm.

Endocarp. Brown, length ca 19.2 mm, width ca 7.7 mm, thickness ca 6 mm. Outer surface of the endocarp ridged, with 4–6 main ridges longitudinally, two of them reaching the point of the base on each face. Ridges rounded and thick, delimiting a reticulate pattern, faintly apparent, enclosing ca 40 small areoles with simple freely ending ridgelets. Endocarp wall 120–136 µm thick excluding ridges (163–185 µm thick including ridges). Endocarp primary vascular bundle outside the endocarp wall. Endocarp wall with three cell layers: outermost layer with 2–3 rows of isodiametric to periclinally oriented cells, cells 12.7–21.7 µm in width, followed by a layer of 6–7 rows of periclinally oriented cells, cells 8–19 µm in width. Innermost row contains small, periclinally oriented cells, cells ca 6.7 µm in width. Locule surface smooth.

Alsodeiopsis poggei Engl.
Fig. 6.10–6.18

Material examined

Specimen used for endocarp and fruit description

REPUBLIC OF THE CONGO • "Plateau des Cataractes"; 24 Oct. 1969; *P. Sita 1872*; P[MNHN-P-P04495916].

Other material

CAMEROON • "Colline Nssas dans le village Pan-Pan à 15 km au Sud, Sud-Ouest de Matomb, Matomb-Botmakak"; 11 Mar. 1986; *M. Ekitiké 48*; P[MNHN-P-P04495907] • "Akonolinga, Frès de Mendong (25 km N. d'Akonolinga)"; 7 Mar. 1962; *R. Letouzey 4485*; P[MNHN-P-P04495897].

GABON • "Ile de l'éléphant"; 9 Dec. 1971; *A. Hladik 1859*; P[MNHN-P-P04495893].

REPUBLIC OF THE CONGO • Bouenza; 3°53′ S, 13°42′ E; 23 Aug. 1965; *C. Farron 4577*; P[MNHN-P-P04495914].

Description

Fruit. Oblong, smooth when dry. Mesocarp ca 75 µm thick when dry. Length 10–19 mm, width 5–10 mm, thickness 4.0–5.1 mm.

Endocarp. Cream, length ca 13.1 mm, width ca 6.9 mm, thickness ca 4.5 mm. Outer surface of the endocarp ridged, with ca three main longitudinal ridges (with other small longitudinal ridges); the median ridge reaching the point of the base. Ridges rounded-angular and thin, delimiting a reticulate pattern, enclosing ca 20–60 small areoles with arbuscular freely ending ridgelets. Endocarp wall 135–156 µm thick excluding ridges (180–232 µm thick including ridges). Endocarp primary vascular bundle in a channel on the keel. Endocarp wall with three cell layers: outermost layer with 1–2 rows of isodiametric to periclinally oriented cells, cells 12.3–24.1 µm in width, followed by a layer with 8–12 rows of periclinally oriented cells, cells 9–23 µm in width. Innermost row with small periclinally oriented cells, cells ca 9 µm in width and inflated into the locule surface.

Fig. 6. Fruits of Icacinaceae Miers. **1**–**9**. *Alsodeiopsis mannii* Oliv. (*N. Hallé & J.F. Villiers 4579*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing a reticulate pattern of ridges. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of seed and pericarp in transverse section. **8**. Detail of the same section showing the mesocarp on the top and the endocarp wall at the bottom. **9**. SEM image of the vascular bundle in a channel (arrow). **– 10**–**18**. *Alsodeiopsis poggei* Engl. (*P. Sita 1872*). **10**. Dried fruit, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing a reticulate pattern of ridges. **12**. Dorsal view showing a keel surrounding the endocarp. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of simple the hairs on the epicarp surface. **17**. SEM image of the endocarp wall in transverse section. **18**. SEM image of the vascular bundle in a channel (arrow). **– 19**–**27**. *Alsodeiopsis staudtii* Engl. (*J.J.F.E. de Wilde 8304*). **19**. Dried fruit, lateral view. **20**–**25**. Endocarp. **20**. Lateral view showing a reticulate pattern of ridges. **21**. Dorsal view showing a keel surrounding the endocarp. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. Lateral view showing the vascularisation on the ridges. **26**. SEM image of the pericarp in transverse section with a vascular bundle (arrow). **27**. SEM image of the simple hairs on the epicarp surface. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–24 = 10 mm; 7, 25 = 1 mm; 9, 18, 26 = 500 µm; 8, 16–17, 27 = 200 µm.

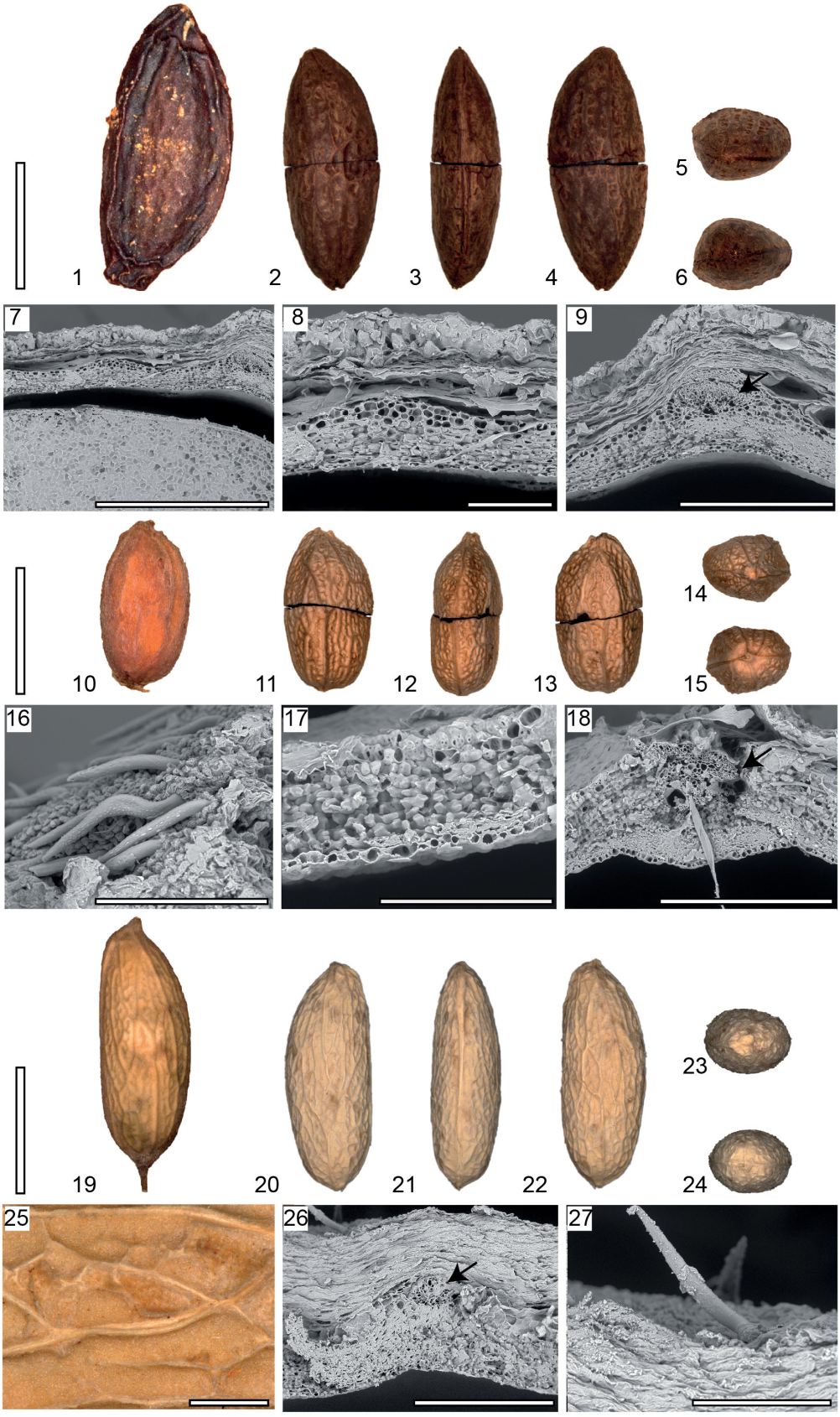

Fig. 6. (see full caption on page 12)

Alsodeiopsis staudtii Engl.
Fig. 6.19–6.27

Material examined

Specimens used for endocarp and fruit description

CAMEROON • 16 km on the road from Kribi to Ebolowa, than turning right on forest exploitation Rouillon, exploitation track followed in about S direction for 24 km, on bank of the Niété River.; 2°42′ N, 10°3′ E; 21 Jun 1975; *J.J.F.E. de Wilde 8304*; BR[BR0000021246852] • Lolodorf, Mt. Minn; 22 Nov. 1967; *H. Jacques-Felix 9190*; P[MNHN-P-P04495847].

Other material

CAMEROON • Galery forest of Kienke R., just E of Kribi; 2°56′ N, 9°55′ E; 5 Apr. 1969; *J.J. Bos 4276*; P[MNHN-P-P05036812] • Korup National Park; 24 Mar. 1998; *D. Kenfack 1073*; P[MNHN-P-P05036862] • 16 km on the road from Kribi to Ebolowa, than turning right on forest exploitation Rouillon, exploitation track followed in about S direction for 24 km, on bank of the Niété River.; 2°42′ N, 10°3′ E; 21 Jun. 1975; *J.J.F.E. de Wilde 8304*; P[MNHN-P-P04534452].

TANZANIA • Tanga, Korogwe District, Ambangulu Forest Reserve, W of Ambangulu cam site above Makweli village; 5°4′16″ S, 38°24′16″ E; 5 Nov. 1998; *M.A. Mwangoka & C. Kayombo 101*; P[MNHN-P-P05036843].

Description

Fruit. Oblong, reticulate when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp ca 300–400 µm thick when dry. Length 10–22 mm, width 5–15 mm, thickness 5.6–7.0 mm.

Endocarp. Cream, length ca 18.9 mm, width ca 7.1 mm, thickness ca 3.5 mm. Outer surface of the endocarp ridged, with ca 2–3 main longitudinal ridges, highly branched, with the median ridge reaching the point of the base. Ridges slightly angular and thin, delimiting a reticulate pattern with a random global aspect, enclosing ca 40–45 irregular areoles with arbuscular freely ending ridgelets. Endocarp wall 151–295 µm thick excluding ridges (256–302 µm thick including ridges). Endocarp primary vascular bundle outside endocarp wall. Endocarp wall with ca 14 rows of periclinally oriented cells, cells 13–20 µm in width. Locule surface smooth.

Alsodeiopsis zenkeri Engl.
Fig. 7.1–7.9

Material examined

Specimen used for endocarp and fruit description

CAMEROON • Ca 40 km S of Badjob, ca 50 km SW of Eséka; 18 Dec. 1963; *W.J.J.O. de Wilde 1549*; P[MNHN-P-P04495824].

Other material

CAMEROON • Ca 40 km S of Badjob, ca 50 km SW of Eséka; 18 Dec. 1963; *W.J.J.O. de Wilde 1549*; P[MNHN-P-P04495824] • Left bank of Sanaga River near ferry Nachtigal, ca 20 km N of Obala; alt. ca 400 m; galery forest; 11 Jun. 1964; *W.J.J.O. de Wilde 2662b*; P[MNHN-P-P04495825].

Description

Fruit. Oblong, reticulate when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp ca 70–80 µm thick when dry. Length 12.0–17.3 mm, width 5–8 mm, thickness 2.0–5.9 mm.

Endocarp. Cream, length ca 16 mm, width ca 7.2 mm, thickness ca 4.4 mm. Outer surface of the endocarp ridged, with ca three main longitudinal ridges, which span from the apex to the base of the endocarp. Ridges slightly angular and thin, delimiting a reticulate pattern, enclosing ca 50–60 polygonal areoles with more or less arbusclular freely ending ridgelets. Endocarp wall 102–157 µm thick excluding ridges (ca 186 µm thick including ridges). Endocarp primary vascular bundle in a channel on the keel. Endocarp wall with two layers: outermost layer with 10–11 rows of periclinally oriented cells, cells 9–15 µm in width; innermost layer with a single row of small periclinally oriented cells, cells ca 8–9 µm in width, inflated into the locule.

Genus ***Cassinopsis*** Sond.
Figs 7.10–7.26, 8.1–8.9

Description

Fruit. Globose to elliptical, occasionally laterally compressed, brown-black when mature. Epicarp glabrous. Calyx persistent.

Endocarp. Cream to brown, elliptical to globose in lateral view, lenticular to globose in transverse section. Keel surrounding the endocarp in the plane of symmetry. Apex asymmetrical in lateral view; base symmetrical. Outer surface of the endocarp ridged with thin to thick rounded and diffuse ridges (i.e., not reticulate), sometimes absent. Vasculature of the endocarp follows the reticulum of ridges or resides in a channel. Endocarp primary vascular bundle outside or within the endocarp wall. Endocarp wall thick, homogeneous, without preferential orientations of cells. Locule surface smooth, occasionally lacunate or with clusters of hairs.

Key to the genus *Cassinopsis*

1. Endocarp primary vascular bundle within the endocarp wall .....***C. madagascariensis*** Baill.
– Endocarp primary vascular bundle outside the endocarp wall 2

2. Endocarp globose, surface smooth .....***C. ilicifolia*** (Hochst.) Sleumer
– Endocarp elliptical, surface clearly ridged .....***C. ciliata*** Baker

Cassinopsis ciliata Baker
Fig. 7.10–7.18

Material examined

Specimen used for endocarp and fruit description
MADAGASCAR • 1932; *H. Perrier de la Bâthie 4671*; P[MNHN-P-P00441031].

Description

Fruit. Elliptical, apex acute, smooth when dry. Mesocarp 200–400 µm thick when dry. Length 13–23 mm, width 5–7 mm, thickness 8.0–9.4 mm.

Endocarp. Brown, compressed in the dorsoventral axis, elliptical in lateral view, lenticular in transverse section, length ca 12.9 mm, width ca 6.5 mm, thickness ca 8.8 mm. Apex acute. Outer surface of the endocarp ridged, with ca three main longitudinal ridges; the median ridge is thicker than other ridges, spanning from the base to the apex. Ridges thin and rounded, forming a diffuse pattern of small interconnected ridges running from the main ridge. Endocarp wall 544–761 µm thick excluding ridges (744–940 µm thick including ridges). Vasculature on the endocarp surface resting on ridges, with the endocarp primary vascular bundle positioned outside the endocarp wall. Endocarp wall with ca 20 rows of isodiametric cells, homogeneous; outermost layer with 13–17 rows of cells, cells 45–60 µm in

diameter; innermost layer with 5–7 rows of cells, cells 20–35 µm in diameter. Locule surface smooth and lacunate.

Cassinopsis ilicifolia (Hochst.) Sleumer
Fig. 7.19–7.25

Material examined

Specimen used for endocarp and fruit description
SOUTH AFRICA • Natal, Ngome; 15 Dec. 1969; *C.D. Louwsburg 2730*; WAG[WAG.1462859].

Other material
SOUTH AFRICA • 1948; *R.J. Rodin 3952*; P[MNHN-P-P05193345].

Description

Fruit. Globose, asymmetrical at the apex, laterally compressed, with traces left by the vasculature when dry. Mesocarp 210–272 µm thick when dry. Length ca 9.5 mm, width ca 8.6 mm, thickness ca 5.2 mm.

Endocarp. Cream, globose in lateral view, lenticular in transverse section, length 7.6–8.7 mm, width ca 7.8 mm, thickness ca 4.4 mm. Outer surface of the endocarp smooth, with only minute channels. Endocarp wall 600–640 µm thick. Vasculature of the endocarp resting in the channels, with the endocarp primary vascular bundle outside the endocarp wall. Endocarp wall with ca 24 rows of isodiametric cells, homogeneous, cells 25–55 µm in diameter. Locule surface smooth, not lacunate.

Cassinopsis madagascariensis Baill.
Fig. 8.1–8.9

Material examined

Specimen used for endocarp and fruit description
MADAGASCAR • 1999; *P.P. Lowry et al. 5162*; P[MNHN-P-P00724815].

Description

Fruit. Elliptical, asymmetrical at the apex, ridged when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp ca 100 µm thick when dry. Length 5–8 mm, width 3.5–5.0 mm, thickness 3.0–4.8 mm.

Fig. 7. Fruits of Icacinaceae Miers. **1**–**9**. *Alsodeiopsis zenkeri* Engl. (*W.J.J.O. de Wilde 1549*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing a reticulate pattern of ridges. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the pericarp in transverse section. **8**. SEM image of simple hairs on the epicarp surface. **9**. SEM image of the vascular bundle in a channel (arrow). – **10**–**18**. *Cassinopsis ciliata* Baker (*H. Perrier De La Bâthie 4671*). **10**. Dried fruit, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing a reticulate pattern of ridges. **12**. Dorsal view showing a keel surrounding the endocarp. **13**. Opposite lateral view. **14**. Apical view. **15.** Basal view. **16**. Transverse section of the fruit. **17**. SEM image of the endocarp wall in transverse section. **18**. Detail of the same section showing endocarp cells at the center of the wall. – **19**–**25**. *Cassinopsis ilicifolia* (Hochst.) Sleumer (*C.D. Louwsburg 2730*). **19**. Dried fruit, lateral view. **20**–**23**. Endocarp (apex missing). **20**. Lateral view. **21**. Dorsal view showing a keel surrounding the endocarp. **22**. Opposite lateral view. **23**. Basal view. **24**. SEM image of the pericarp in transverse section. **25**. Detail of the same section showing the cells. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15 = 10 mm; 16, 19–23 = 2.5 mm; 17 = 1 mm; 9, 24 = 500 µm; 7–8, 25 = 100 µm; 18 = 50 µm.

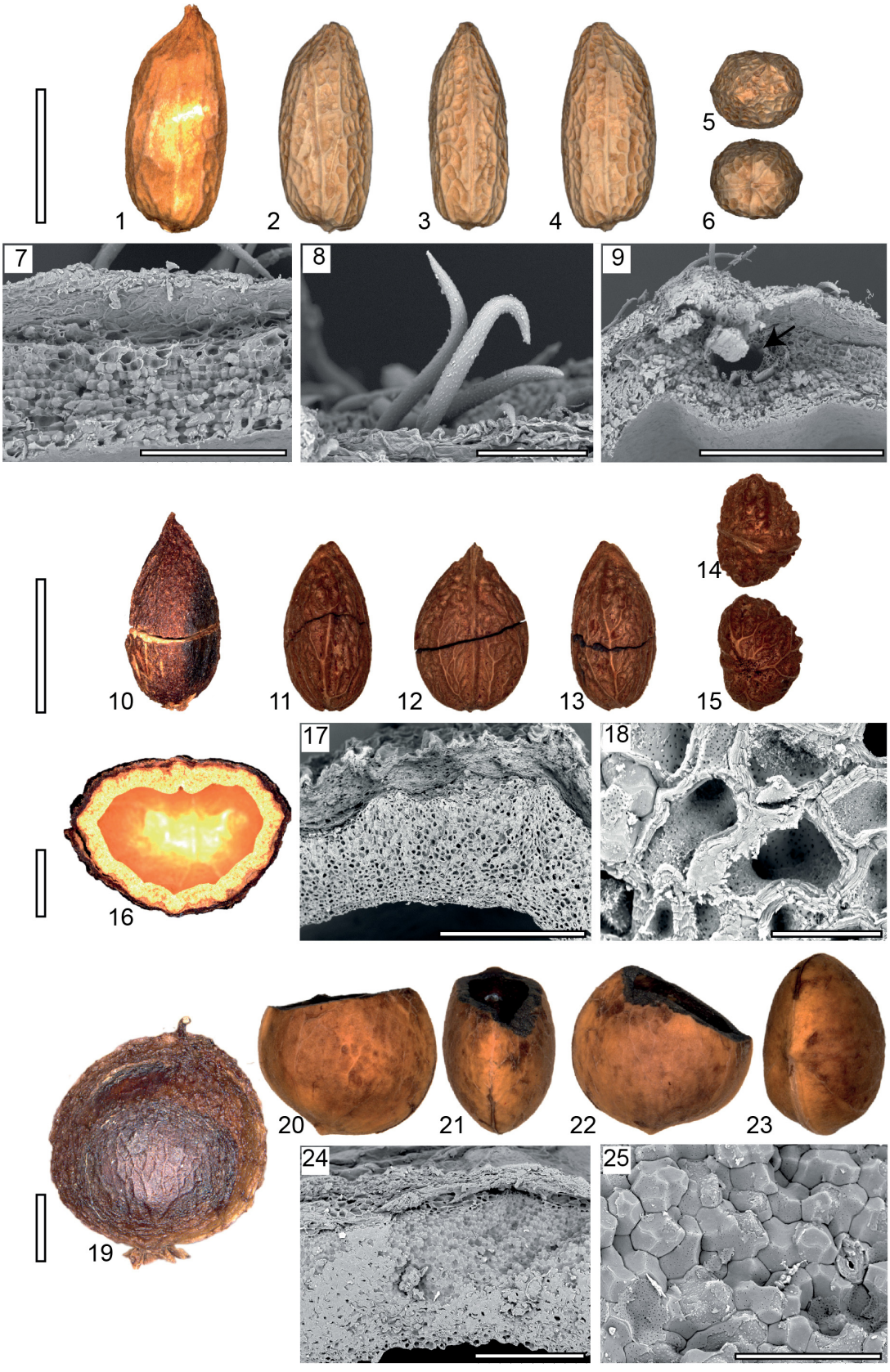

Fig. 7. (see full caption on page 14)

Endocarp. Cream, elliptical to globose in lateral view, globose in transverse section, length ca 6 mm, width ca 5 mm, thickness ca 4 mm. Apex slightly flattened. Outer surface of the endocarp ridged, with ca 5–6 main longitudinal ridges; the median and two lateral ridges reaching the point of the base. Ridges thin and rounded, forming a diffuse pattern, interconnected with the main ridges. Endocarp wall 520–750 µm thick excluding ridges (660–980 µm thick including ridges). Vasculature of the endocarp resting on ridges, with the primary vascular bundle embedded within the endocarp wall in the thicker part of the keel. Endocarp wall with ca 20 rows of isodiametric to anticlinally oriented cells, cells 30–55 µm in width. Inflated cells line the locule surface, cells 15–18 µm in width. Locule surface not lacunate, ornamented with clusters of 3–6 simple and wide hairs.

Genus ***Desmostachys*** Planch. ex Miers

Description

See description of *Desmostachys planchonianus* Miers, the sole member of the genus.

Desmostachys planchonianus Miers
Fig. 8.17–8.25

Material examined

Specimen used for endocarp and fruit description

MADAGASCAR • 1993; *B. Lewis & S. Razafimandimbison 735*; P[MNHN-P-P04561640].

Other material

MADAGASCAR • 2003; *R. Rabevohitra et al. 4810*; P[MNHN-P-P04561628] • 2003; *R. Rabevohitra et al. 4658*; P[MNHN-P-P04561629] • 2002; *J. Rabenantoandro et al. 1155*; P[MNHN-P-P04561630].

Description

Fruit. Elliptical, asymmetrical at the apex, laterally compressed, red when mature. Epicarp strigose with yellow simple hairs with granular ornamentation, rugose when dry, revealing the underlying rugosities of the endocarp. Mesocarp 250–300 µm thick when dry. Length 10–16 mm, width 7–12 mm, thickness 5.0–5.8 mm. Calyx persistent.

Fig. 8. Fruits of Icacinaceae Miers. **1**–**9**. *Cassinopsis madagascariensis* Baill. (*P.P. Lowry et al. 5162*). **1**. Broken fruit, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing a reticulate pattern of ridges. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the pericarp in transverse section. **8**. Detail of the same section showing the cells. 9. SEM image of the inner endocarp surface showing cluster of hairs inside. – **10**–**16**. *Vadensea oblongifolia* (Engl.) Jongkind & O.Lachenaud (*R. Letouzey 8309*). **10**. Dried fruit, lateral view. **11**–**15**. Broken endocarp. **11**. Lateral view showing a reticulate pattern of ridges. **12**. Dorsal view showing a keel surrounding the endocarp. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of the pericarp in transverse section. – **17**–**25**. *Desmostachys planchonianus* Miers (*B. Lewis & S. Razafimandimbison 735*). **17**. Dried fruit, lateral view. **18**–**22**.Endocarp. **18**. Lateral view showing the roughness. **19**. Dorsal view showing a keel surrounding the endocarp. **20**. Opposite lateral view. **21**. Apical view. **22**. Basal view. **23**. SEM image of the endocarp in transverse section. **24**. Detail of the basal part of 23. showing periclinally oriented cells. **25**. Detail of the upper part of 23. showing anticlinally oriented cells. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 17–22 = 5 mm; 7 = 1 mm; 16 = 500 µm; 23 = 300 µm; 9 = 200 µm; 25 = 100 µm; 8, 24 = 50 µm.

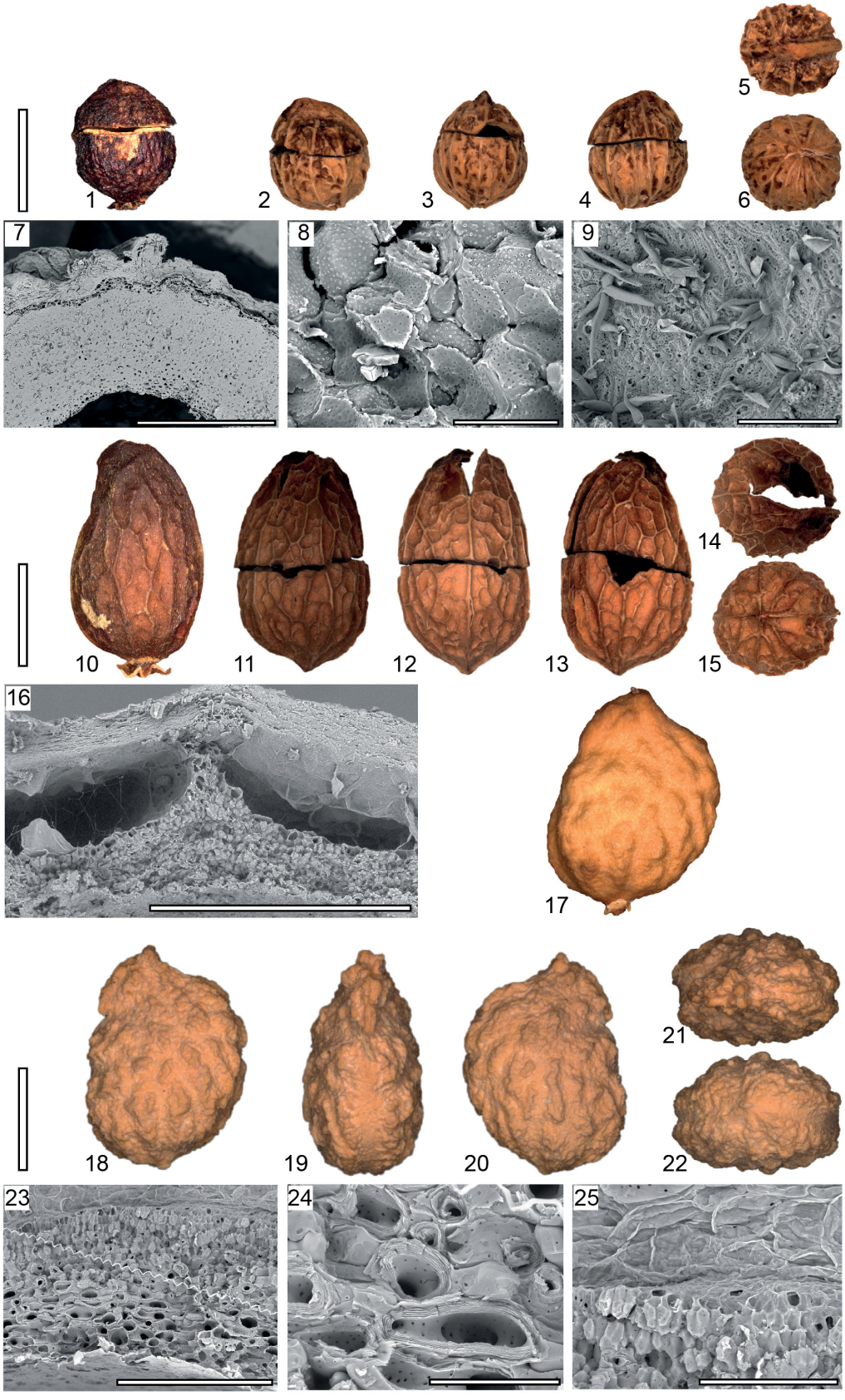

Fig. 8. (see full caption on page 18)

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 11.1 mm, width ca 7.8 mm, thickness ca 3.5 mm. Apex with an asymmetrical bulge; base rounded, slightly asymmetrical. Outer surface of the endocarp rugose, irregular, with 20–25 mounds arranged longitudinally and interspaced by 4–5 channels. Channel surrounding the endocarp in the plane of symmetry. Vasculature of endocarp lies in the channels between mounds. Endocarp primary vascular bundle positioned outside the endocarp wall. Endocarp wall 245–290 µm thick excluding mounds (338–474 µm thick including mounds). Endocarp wall with two layers: outermost layer with 7–10 rows of anticlinally oriented cells, cells 16–21 µm in length; innermost layer with 7–10 rows of periclinally oriented cells, cells 20–27 µm in width. Locule surface smooth.

Genus ***Vadensea*** Jongkind & O.Lachenaud
Figs 8.10–8.16, 9.1–9.18

Description

Fruit. Elliptical, laterally compressed, red when mature. Epicarp strigose to puberulent with yellow simple hairs with granular ornamentation, smooth to reticulate when dry, revealing the underlying reticulum of endocarp ridges. Calyx persistent.

Endocarp. Cream to brown, elliptical in lateral view, lenticular to globose in transverse section. Keel often surrounding the endocarp in the plane of symmetry, occasionally not visible. Apex more or less asymmetrical in lateral view; base symmetrical. Outer surface of the endocarp ridged, with diffuse or reticulate pattern of sharp to angular ridges. When reticulate, ridges delimit polygonal areoles with or without freely ending ridgelets. Endocarp with a symmetrical pair of pores compressed on the keel, positioned eccentrically and subapically on the endocarp faces, each with a central pit, or replaced by an apical bulge. Vasculature on the endocarp surface follows the reticulum of ridges. Endocarp primary vascular bundle outside the endocarp wall or in a channel on the keel. Endocarp wall with at least one row of periclinally oriented cells. Locule surface smooth, more or less lacunate.

Taxonomic remark

This work was largely completed before the taxonomic modification of the genus *Desmostachys* s. l. (Jongkind & Lachenaud 2019). For practical reasons, we decided to keep the structure of this survey, but we included the taxonomic modifications. The probable polyphyly of *Desmostachys* s. l. had already been outlined in the discussion, and we decided to keep these comments as a means of corroborating the study of Jongkind & Lachenaud (2019).

Key to the genus *Vadensea*

1. Endocarp ridged and rugose, with a diffuse pattern of ridges .....
..... ***V. vogelii*** (Miers) Jongkind & O.Lachenaud
– Endocarp exclusively ridged, with a reticulate pattern of ridges 2

2. Fruit length ca 11 mm, ridges sharp, areoles with freely ending ridgelets .....
.....***V. oblongifolia*** (Engl.) Jongkind & O.Lachenaud
– Fruit length ca 20–25 mm, ridges angular, areoles without freely ending ridgelets .....
.....***V. tenuifolia*** (Oliv.) Jongkind & O.Lachenaud

Vadensea oblongifolia (Engl.) Jongkind & O.Lachenaud
Fig. 8.10–8.16

Material examined

Specimen used for endocarp and fruit description
CAMEROON • 1966; *R. Letouzey 8309*; P[MNHN-P-P04495051].

Description

Fruit. Epicarp strigose, reticulate when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp 50–70 µm thick when dry. Length 9–15 mm, width 6.3–10.0 mm, thickness 5.0–6.6 mm.

Endocarp. Cream, lenticular to globose in transverse section, length ca 11.3 mm, width ca 6.8 mm, thickness ca 4.5 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical; base rounded, slightly asymmetrical. Outer surface of the endocarp ridged, with ca 4–5 main longitudinal ridges; the median and occasionally a lateral ridge reaching the point of the base. Ridges sharp and thin, delimiting a reticulate pattern enclosing 20–25 polygonal areoles with freely ending ridgelets. Endocarp wall 112–154 µm thick excluding ridges (260–330 µm thick including ridges). Endocarp primary vascular bundle outside the endocarp wall. Endocarp wall with 9–11 rows of periclinally oriented cells, cells 8–15 µm in width. Locule surface smooth, lacunate.

Vadensea tenuifolia (Oliv.) Jongkind & O.Lachenaud
Fig. 9.1–9.9

Material examined

Specimen used for endocarp and fruit description
CAMEROON • 1969; *J.J. Bos 4277*; P[MNHN-P-P04495129].

Description

Fruit. Epicarp strigose, smooth when dry. Mesocarp 750–820 µm thick when dry. Length 21–25 mm, width 9–15 mm, thickness 5.0–10.2 mm.

Endocarp. Cream, lenticular in transverse section, length ca 18.4 mm, width ca 9.2 mm, thickness ca 8.5 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical, bulged; base subacute, symmetrical. Outer surface of the endocarp ridged, with 4–6 main longitudinal ridges; the median and a lateral ridge reaching the point of the base on each face. Ridges angular and broad, almost rectangular, with a median channel clearly visible, delimiting a reticulate pattern enclosing 20–24 polygonal longitudinally elongate areoles. The ridges merge with the bulge at the apex. Endocarp primary vascular bundle in a channel on the keel. Endocarp wall 180–200 µm thick excluding ridges (320–385 µm thick including ridges). Endocarp wall with ca 17 rows of periclinally oriented cells, cells 7–16 µm in width. Locule surface smooth and lacunate.

Vadensea vogelii (Miers) Jongkind & O.Lachenaud
Fig. 9.10–9.18

Material examined

Specimen used for endocarp and fruit description
IVORY COAST • “Côte d’Ivoire”; 1931; *Service forestier 364*; P[MNHN-P-P04495087].

Other material

IVORY COAST • "Côte d'Ivoire"; 1931; *Service forestier 446*; P[MNHN-P-P04495088] • 1963; *W.J.J.O. de Wilde 514*; P[MNHN-P-P04495094] • Tabou, along road via Irputou to Cavally River; 8 Apr. 2000; *C.C.H. Jongkind 4975*; WAG[WAG.1463136].

Description

Fruit. Epicarp puberulent, reticulate-rugose when dry, revealing the underlying rugosities and ridges of the endocarp. Mesocarp thin. Length 14–21.4 mm, width 10.0–11.1 mm, thickness 7.0–11.2 mm.

Endocarp. Brown, globose in transverse section, length ca 19.4 mm, width ca 10.7 mm, thickness ca 10 mm. Sharp keel, sinuous and serrated, surrounding the endocarp in the plane of symmetry. Apex acute and asymmetrical; base rounded, slightly asymmetrical. Outer surface of the endocarp rugose and ridged. Ridges sharp and diffuse with only a median ridge serrated. Surface covered by ca 70 rugged protuberances, evenly distributed, and by 'ridges' that form small, vertically and longitudinally elongate mounds. Endocarp with a symmetrical pair of pores situated at the merging of the apex and the median ridge. Endocarp primary vascular bundle positioned outside the endocarp wall. Endocarp wall 370–477 µm thick excluding ridges (1200–1380 µm including ridges). Endocarp wall with three cell layers: outermost layer with 1–2 rows of isodiametric cells, cells ca 27–40 µm in diameter; followed by a layer of 15–21 rows of anticlinally oriented cells, cells ca 19–24 µm in length; innermost layer with 5–6 rows of periclinally oriented cells, cells ca 9–14 µm in width. Locule surface smooth and lacunate.

Genus ***Hosiea*** Hemsl. & E.H.Wilson
Figs 9.19–9.25, 10.1–10.9

Description

Fruit. Elliptical, slightly asymmetrical at the apex, laterally highly compressed, red-brown when mature. Epicarp glabrous. Calyx persistent.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section. Small keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical in lateral view; base rounded and symmetrical. Outer surface of the endocarp ridged, with thin rounded to sharp ridges delimiting a reticulate pattern enclosing areoles; most areoles with freely ending ridgelets. Vasculature of the endocarp free or

Fig. 9. Fruits Icacinaceae Miers. **1**–**9**. *Vadensea tenuifolia* (Oliv.) Jongkind & O.Lachenaud (*J.J. Bos 4277*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing a reticulate pattern of ridges. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of pericarp in transverse section. **8**. SEM image of endocarp in transverse section. **9**. SEM image of the vascular bundle in a channel. – **10**–**18**. *Vadensea vogelii* (Miers) Jongkind & O.Lachenaud (*Service forestier 364*). **10**. Dried fruit, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing the ridges and roughness. **12**. Dorsal view showing a keel surrounding the endocarp. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of a ridge in transverse section. **17**. SEM image of the endocarp wall in transverse section. **18**. SEM image of simple hairs on the epicarp surface. – **19**–**25**. *Hosiea japonica* Makino (*Okudai 60474*). **19**–**21**. Endocarp. **19**. Lateral view showing a reticulate pattern of ridges. **20**. Dorsal view showing a keel surrounding the endocarp. **21**. Opposite lateral view. **22**. SEM image of the endocarp wall in transverse section. **23**. Detail of the same section showing the cells. **24**. SEM image of the inner layer of the endocarp wall, showing papillae. **25**. Detail of the same section. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–21 = 10 mm; 7, 16, 22 = 1 mm; 9, 17 = 500 µm; 8 = 100 µm; 23 = 300 µm; 8, 18 = 200 µm; 24–25 = 20 µm.

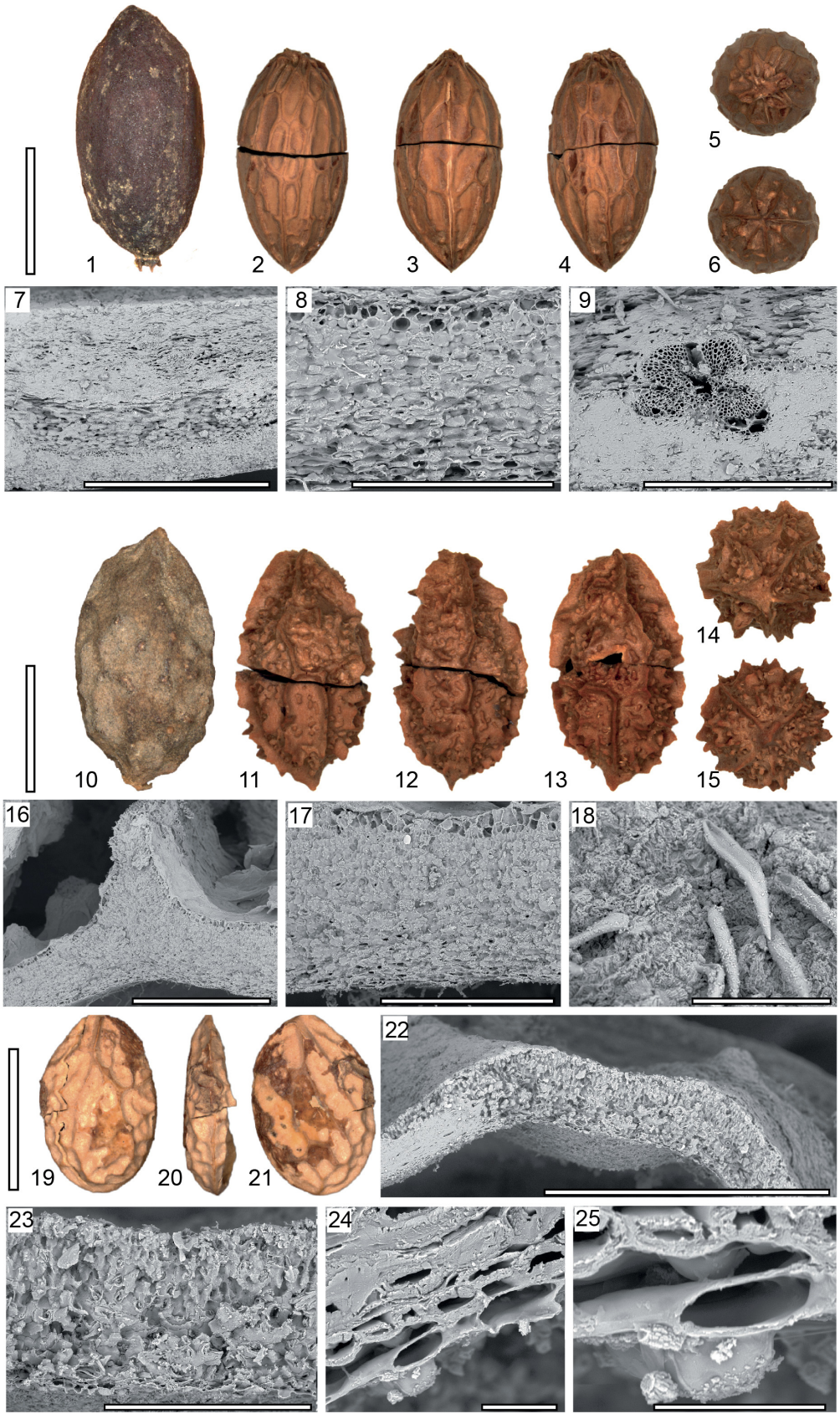

Fig. 9. (see full caption on page 22)

resting on the ridges; endocarp primary vascular bundle positioned outside the endocarp wall. Endocarp wall thin, divided into distinctive layers, at least one layer with anticlinally oriented cells (outer part) and another with periclinally oriented cells (inner part). Locule surface with regularly spaced and large papillae, irregular in shape. Locule surface lacunate.

Key to the genus *Hosiea*

1. Endocarp ridges acute ..... ***H. japonica*** Makino
– Endocarp ridges rounded ..... ***H. sinensis*** (Oliv.) Hemsl. & E.H.Wilson

Hosiea japonica Makino
Fig. 9.19–9.25

Material examined

Specimen used for endocarp and fruit description
JAPAN • *Okudai 60474*; UC.

Description

Fruit. Mesocarp ca 200 µm thick when dry.

Endocarp. Length ca 12.5 mm, width ca 8.1 mm, thickness ca 1.5 mm. Outer surface of the endocarp ridged with 2–3 main longitudinal ridges; the median ridge reaching the point of the base. Ridges thin and sharp, delimiting a reticulate pattern enclosing 15–18 irregular areoles generally with freely ending ridgelet inside. Vasculature of the endocarp resting on the ridges. Endocarp wall 180–235 µm thick excluding ridges (262–302 µm including ridges). Endocarp wall with three layers: outermost layer with 11–12 rows of anticlinally oriented cells, cells 14–26 µm in length; middle layer with 3–4 rows of periclinally oriented cells, cells 11–22 µm in width; innermost layer with periclinally oriented cells, cells 6 µm in width, lining the locule with regularly spaced and elongate to rounded papillae; papillae 12.2–21.0 µm (av. 14.6 µm) in diameter. Locule surface lacunate.

Fig. 10. Fruits of Icacinaceae Miers. **1**–**9**. *Hosiea sinensis* (Oliv.) Hemsl. & E.H. Wilson (*M. l'abbé Farges s.n.*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing a reticulate pattern of ridges. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of pericarp in transverse section. **8**. SEM image of the endocarp cells in transverse section. **9**. SEM image of papillae lining the locule. – **10**–**17**. *Icacina claessensii* De Wild (*C. Evard 5094*). **10**. Dried fruit, lateral view. **11**–**15**. Broken endocarp. **11**. Lateral view showing the ridges. **12**. Dorsal view showing a keel surrounding the endocarp. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of the endocarp with ridges and separated mesocarp in transverse section. **17**. SEM image of the endocarp wall in transverse section. – **18**–**26**. *Icacina guessfeldtii* Asch. (*J. Gillet 2674*). **18**. Dried fruit, lateral view. **19**–**24**. Broken endocarp. **19**. Lateral view showing a reticulate pattern of ridges. **20**. Dorsal view. **21**. Opposite lateral view. **22**. Apical view. **23**. Basal view. **24**. Detail of the apical view showing the pair of pores. **25**. SEM image of the pericarp in transverse section showing the vascular bundle in the endocarp wall (arrow). **26**. SEM image of the endocarp periclinally oriented cells. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 18–23 = 10 mm; 24 = 2 mm; 16, 25 = 1 mm; 7, 17, 26 = 200 µm; 8–9 = 50 µm.

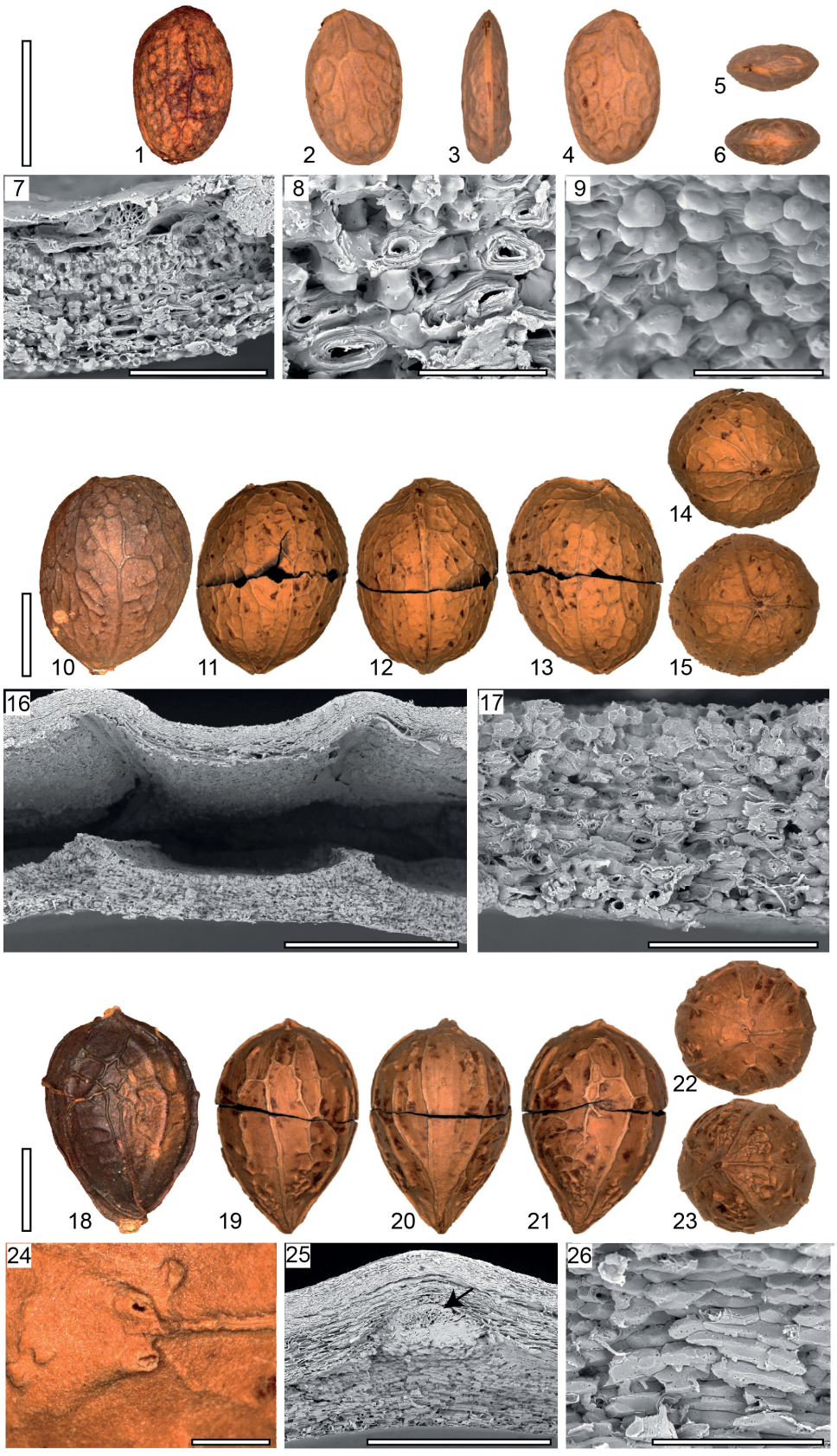

Fig. 10. (see full caption on page 24)

Hosiea sinensis (Oliv.) Hemsl. & E.H.Wilson
Fig. 10.1–10.9

Material examined

Specimen used for endocarp and fruit description
CHINA • "District de Tchen-Kéou-Tin"; s.d.; *M. l'abbé Farges s.n.*; P[MNHN-P-P04513501].

Description

Fruit. Epicarp glabrous, reticulate when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp ca 70 µm thick when dry. Length 13–18 mm, width 8.1 mm, thickness 3.9 mm.

Endocarp. Length ca 12.6 mm, width ca 7.8 mm, thickness ca 1.1 mm. Outer surface of the endocarp ridged, with 3–4 main longitudinal ridges; the median ridge reaching the point of the base. Ridges thin and rounded, forming a reticulate pattern enclosing 14–20 areoles, generally with a freely ending ridgelet inside. Vasculature of the endocarp free. Endocarp wall 161–202 µm thick excluding ridges (ca 250 µm thick including ridges). Endocarp wall with three cell layers: outermost layer with 5–10 rows of anticlinally oriented cells, cells 10–13 µm in length; followed by a layer of 5–7 rows of periclinally oriented cells, cells 15–19 µm in width; innermost layer with a single row of periclinally oriented cells, cells ca 6 µm in width, lining the locule with regularly spaced and elongate papillae; papillae 11–21 µm in diameter, ca 1000 papillae per 0.25 mm^2. Locule surface lacunate.

Genus ***Icacina*** A.Juss.
Figs 10.10–10.26, 11

Description

Fruit. Elliptical, occasionally slightly globose, asymmetrical at the apex, red-brown to black when mature. Epicarp glabrous or yellowish puberulent with small ovoid hairs to papillate hairs, which line the surface, and simple hairs with granular ornamentation or only simple hairs without granular ornamentation; ridged when dry, revealing the underlying reticulum of endocarp ridges. Calyx persistent.

Endocarp. Cream, elliptical to obovate in lateral view, globose to lenticular in transverse section. Keel surrounding the endocarp in the plane of symmetry or faintly visible. Apex truncate or acute, always asymmetrical in lateral view; base symmetrical. Outer surface of the endocarp irregularly rugose or ridged, with a diffuse or reticulate pattern of rounded to sharp ridges. Vasculature follows the ridges or rests between rugosities. Endocarp primary vascular bundle positioned outside or within the endocarp wall. Endocarp wall with at least one row of periclinally oriented cells. Locule surface smooth and faintly lacunate.

Key to the genus *Icacina*

1. Keel surrounding the endocarp clearly visible, ornamentation rugose with numerous mounds 2
– Keel faintly apparent, ornamentation ridged 3

2. Apex truncate, endocarp length ca 18 mm ..... ***I. oliviformis*** (Poir.) J.Raynal
– Apex acute, endocarp length ca 25 mm ..... ***I. mannii*** Oliv.

3. Ridges sharp, reticulate 4
– Ridges rounded, not reticulate ..... ***I. guessfeldtii*** Asch.

4. Ridges up to 430 µm thick, keel faintly apparent, vascular bundle outside the endocarp wall ..... ***I. claessensii*** De Wild.
– Ridges up to 730 µm thick, keel thick, vascular bundle within the endocarp wall ..... ***I. trichanta*** Oliv.

Icacina claessensii De Wild.
Fig. 10.10–10.17

Material examined

Specimen used for endocarp and fruit description
DEMOCRATIC REPUBLIC OF THE CONGO • "Baringa/S/Maringa (Terr. Befale) Forêt"; 26 Oct. 1958; *C. Evard 5094*; BR[BR0000015572356].

Other material
GABON • 1897; *R.P. Klaine 959*; P[MNHN-P-P04495392].

Description

Fruit. Elliptical, red when mature. Epicarp glabrous, ridged, with diffuse long arbuscles, revealing the underlying reticulum of endocarp ridges. Mesocarp 200–250 µm thick. Length 24–26 mm, width 18.3 mm, thickness 14.0–17.5 mm.

Endocarp. Elliptical in lateral view, globose in transverse section, length ca 23 mm, width ca 17.6 mm, thickness ca 17 mm. Keel faintly apparent, with a median channel, surrounding the endocarp in the plane of symmetry. Apex truncate; base rounded and slightly asymmetrical, positioned in opposition to the apex asymmetry. Outer surface of the endocarp ridged with 3–4 main longitudinal ridges; the median and a lateral ridge reaching the point of the base. Ridges sharp and thin, with a median channel (corresponding to the trace left by the vasculature of the fruit), forming a partial and sparse reticulum with ca 16–17 areoles, some areoles transversally extended, others small and randomly positioned, with freely ending ridgelets, occasionally arbusclular. Endocarp possessing a symmetrical pair of pores positioned eccentrically and subapically at the apical end of the median ridge. Vasculature of the endocarp resting in the channels of the ridges; endocarp primary vascular bundle positioned outside the endocarp wall. Endocarp wall 240–362 µm thick excluding ridges (400–430 µm including ridges). Endocarp wall with two layers: outermost layer with 3–4 rows of isodiametric cells, cells 18–28 µm in diameter, innermost layer with 10–13 rows of periclinally oriented cells, cells 13–21 µm in width. Locule surface smooth and lacunate.

Icacina guessfeldtii Asch.
Fig. 10.18–10.26

Material examined

Specimen used for endocarp and fruit description
DEMOCRATIC REPUBLIC OF THE CONGO • 1902; *J. Gillet 2674*; BR[BR0000015572677].

Other material
REPUBLIC OF THE CONGO • "Route de Kinkala, Itineraire Mahitou - Boutsouka - Tonkama"; Jun. 1964; *A. Bouquet 28*; P[MNHN-P-P04495336].

Description

Fruit. Elliptical to obovate, red when mature. Epicarp glabrous, ridged when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp 400–600 µm thick when dry. Length 21–30 mm, width 15–20 mm, thickness 12.0–19.4 mm.

Endocarp. Obovate in lateral view, globose in transverse section, length ca 26.3 mm, width ca 17 mm, thickness ca 16.5 mm. Keel surrounding the endocarp wall in the plane of symmetry, with one part flattened and containing a vascular bundle embedded within the endocarp wall. Apex truncate; base

acute, slightly asymmetrical. Outer surface of the endocarp ridged and rugose, with a median ridge reaching the point of the base and running nearly to the apex. Lateral ridges irregular and disconnected, running along more or less the entirety of the endocarp length. Ridges rounded with a slight median channel, forming a diffuse pattern, occasionally forming an arbuscle-like branch. A few isolated mounds cover the surface randomly. Endocarp possessing a symmetrical pair of pores compressed on the keel, positioned eccentrically and subapically on the apical endocarp faces, each with a central pit. Endocarp wall 263–306 µm thick excluding ridges (470–560 µm including ridges). Vasculature of the endocarp resting in the channels of the ridges but also free. Endocarp wall with ca 15 rows of periclinally oriented cells, cells 20–27 µm in width. Locule surface smooth, slightly lacunate.

Icacina mannii Oliv.
Fig. 11.1–11.9

Material examined

Specimen used for endocarp and fruit description
REPUBLIC OF THE CONGO • Brazzaville; 1953; *J. Koechlin 2334*; P[MNHN-P-P04495011].

Other material
GABON • 1897; *R.P. Klaine 489*; P[MNHN-P-P04495007].

REPUBLIC OF THE CONGO • Brazzaville; 1950; *J. Koechlin 633*; P[MNHN-P-P04495012].

Description

Fruit. Elliptical with acute apex, laterally compressed, brown when mature. Epicarp puberulent with two types of hairs, simple hairs with granular ornamentation and small papillae-like hair expansions that line the fruit; faintly rugose when dry, revealing the underlying endocarp ridges. Mesocarp 200–400 µm thick when dry. Length 25–35 mm, width 16.5–26.0 mm, thickness 10–17 mm.

Endocarp. Elliptical in lateral view, lenticular in transverse section, length ca 25.6 mm, width ca 16.3 mm, thickness ca 12 mm. Keel running along the dorsal length of the endocarp, flanked by two channels, with the vascular bundle embedded within keel / endocarp wall; a single channel runs along the ventral length of the endocarp. Apex acute, asymmetrical, forming a rectangular protuberance; base

Fig. 11. Fruits of Icacinaceae Miers. **1**–**9**. *Icacina mannii* Oliv. (*J. Koechlin 2334*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing the mounds. **3**. Dorsal view. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the vascular bundle embedded within endocarp wall in transverse section (arrow). **8**. SEM image of the endocarp wall in transverse section. **9**. SEM image of the papillae-like hairs on epicarp. **– 10**–**18**. *Icacina oliviformis* (Poir.) J.Raynal (*M. Dybowski 698*). **10**. Broken fruit, lateral view. **11**–**15**. Broken endocarp. **11**. Lateral view showing the mounds. **12**. Dorsal view. **13**. Apical view. **14**. Basal view. **15**. Detail of apical view showing pores (arrows). **16**. SEM image of the vascular bundle embedded within endocarp wall in transverse section (arrow). **17**. SEM image of the endocarp wall in transverse section. **18**. SEM image of the ovoid hairs with an acuminate apex on the epicarp. – **19**–**27**. *Icacina trichantha* Oliv. (*J.C. Okafor fhi 34969*). **19**. Dried fruit, lateral view. **20**–**24**. Broken endocarp. **20**. Lateral view showing the ridges. **21**. Dorsal view showing a keel surrounding the endocarp. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. SEM image of the vascular bundle embedded within endocarp wall in transverse section (arrow). **26**. SEM image of a ridge in transverse section. **27**. SEM image of the endocarp wall in transverse section. Images taken from Del Rio (2018). Scale bars: 1–6, 10–14, 19–24 = 10 mm; 7, 15, 25 = 1 mm; 16, 26 = 500 µm; 8, 27 = 300 µm, 17 = 200 µm; 9, 18 = 100 µm.

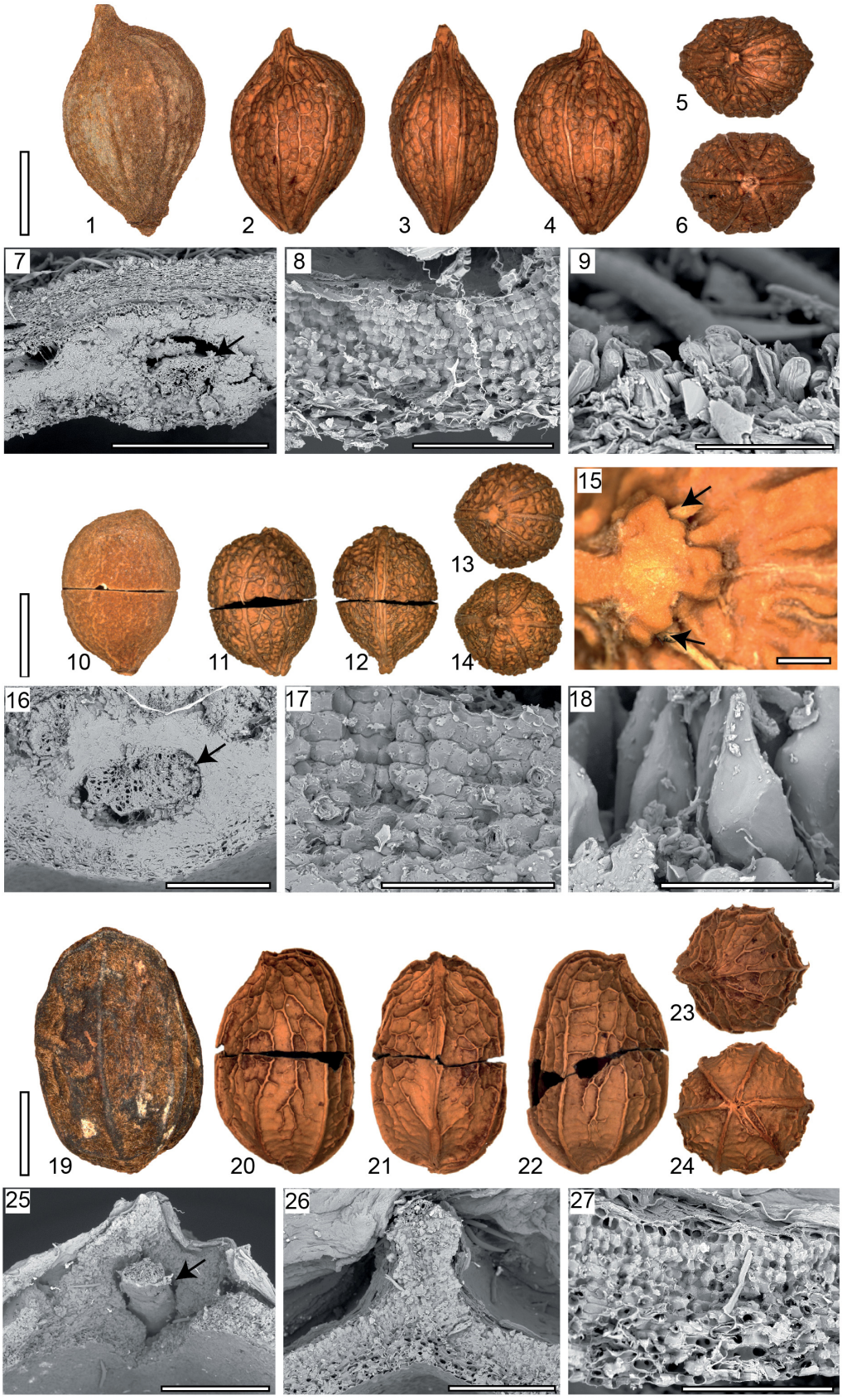

Fig. 11. (see full caption on page 28)

rounded-acute and slightly asymmetrical. Outer surface of the endocarp rugged with ca 90 mounds, more or less square-polygonal, with freely ending channels inside, more or less branched. Mounds organized in 9–12 longitudinal lines separated by 5–6 main longitudinal channels. The main channel on each face reaching the pore positioned subapically on the apical protuberance. Vasculature of the endocarp resting in the channels between mounds and along the channel branches inside the mounds. Endocarp wall 289–372 µm thick excluding mounds (460–544 µm including mounds). Endocarp wall with two cell layers: outermost layer with 8–9 rows of anticlinally oriented to isodiametric cells, cells 22–31 µm in length; innermost layer with 5–6 rows of periclinally oriented cells, cells 14–21 µm in width. Locule surface smooth, lacunate.

Icacina oliviformis (Poir.) J.Raynal
Fig. 11.10–11.18

Material examined

Specimen used for endocarp and fruit description
REPUBLIC OF THE CONGO • 1892; *M. Dybowski 698*; P[MNHN-P-P04495750].

Other material
CENTRAL AFRICAN REPUBLIC • 1978; *Peyre de Fabrègues 3610*; P[MNHN-P-P04495743].

SENEGAL • 1933–1934; *J. Trochain 3367*; P[MNHN-P-P04495790].

Description

Fruit. Elliptical, red-brown when mature. Epicarp puberulent with small ovoid hairs with an acuminate apex. Mesocarp 420–620 µm thick when dry. Length 17–23 mm, width 13–16 mm, thickness 9–14 mm.

Endocarp. Elliptical in lateral view, globose in transverse section, length ca 18 mm, width ca 13.1 mm, thickness ca 14 mm. Keel running along the dorsal length of the endocarp, flanked by two channels, with the vascular bundle embedded within keel / endocarp wall; a single channel runs along the ventral length of the endocarp. Apex truncate; base rounded-acute and slightly asymmetrical. Outer surface of the endocarp rugose with ca 70–80 mounds, more or less square-polygonal, with a freely ending channels inside, more or less branched. Mounds organized in 7–8 longitudinal lines separated by three main longitudinal channels. The main channel on each face reaching a pore positioned subapically, each pore with a central pit. Vasculature of the endocarp resting in the channels between mounds and along the channel branches inside the mounds. Endocarp wall 288–307 µm thick excluding mounds (588–661 µm including mounds). Endocarp wall with two cell layers: outermost layer with 7–8 rows of anticlinally oriented to isodiametric cells, cells 24–34 µm in width; innermost layer with 8–9 rows of periclinally oriented cells, cells 16–21 µm in width. Locule surface smooth, lacunate.

Icacina trichantha Oliv.
Fig. 11.19–11.27

Material examined

Specimen used for endocarp and fruit description
NIGERIA • 1955; *J.C. Okafor fhi 34969*; P[MNHN-P-P04495708].

Description

Fruit. Elliptical, brown-black when mature. Epicarp puberulent with yellow simple hairs, reticulate when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp ca 300 µm thick when dry. Length 30.8–34.0 mm, width 17–24 mm, thickness 12.0–18.7 mm.

Endocarp. Elliptical in lateral view, globose in transverse section, length ca 27.4 mm, width ca 17 mm, thickness ca 14 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing a vascular bundle embedded within the endocarp wall. Apex greatly asymmetrical in lateral view; base rounded, slightly asymmetrical. Outer surface of the endocarp ridged, with ca four main ridges, two lateral ridges reaching the point of the base. Ridges sharp and rectangular with a median channel, delimiting a reticulate pattern well developed in the upper half of the endocarp and more diffuse in the lower half. The reticulum encloses 10–20 irregular, more or less polygonal areoles with freely ending ridgelets inside. Endocarp possessing a symmetrical pair of pores compressed on the keel, positioned eccentrically and subapically on the endocarp faces, each with a central pit. Endocarp wall 270–315 µm thick excluding ridges (362–735 µm including ridges). Vasculature of the endocarp resting in the channels of the ridges. Endocarp wall with three cell layers: outermost layer with 4–6 rows of anticlinally oriented to isodiametric cells, cells 19–30 µm in length; middle layer with 4–8 rows of periclinally oriented cells, cells 20–27 µm in width; innermost layer with one row of periclinally oriented cells, which line the locule surface with inflated cells, cells 8–13 µm in width. Locule surface smooth, lacunate.

Genus ***Iodes*** Blume
Figs 12–15, 16.1–16.18

Description

Fruit. Elliptical, occasionally globose, asymmetrical at the apex, laterally compressed, red to brown when mature. Epicarp strigose or puberulent, scarcely pilose, with simple hairs with granular ornamentation and/or uncinate hairs or long and thin hairs, ridged or rugged-rugose to smooth when dry, revealing the underlying endocarp ornamentation. Calyx persistent or not.

Endocarp. Cream to brown, elliptical, occasionally globose in lateral view, lenticular, occasionally globose in transverse section. Keel often surrounding the endocarp in the plane of symmetry, with the thicker margin containing a vascular bundle embedded within the endocarp wall; occasionally replaced by channel containing the primary vascular bundle. Apex asymmetrical in lateral view; base symmetrical or cleft. Outer surface of the endocarp smooth, rugged-rugose, and/or ridged, with ridges rounded to sharp comprising a diffuse to reticulate pattern with or without freely ending ridgelets. Secondary ridges (i.e., small ridges delimiting a reticulum inside or between the primary reticulation/ridges) occasionally present. Endocarp possessing a symmetrical pair of horn-like protrusions compressed on the keel, sometimes much reduced and forming pores, positioned eccentrically and subapically on the endocarp faces, absent in African species. Vasculature resting on ridges when present, occasionally between ridges or rugosities. Endocarp wall with two or three cell layers. Locule surface with regularly spaced and rounded papillae. Locule surfaces more or less lacunate.

Key to the genus *Iodes*

1. Endocarp with pores or horn-like protrusions at the apex 2
– Endocarp lacking pores or horn-like protrusions 3

2. Endocarp with pores 4
– Endocarp with horn-like protrusions 5

3. Outer surface of the endocarp smooth ..... ***I. seguinii*** (H.Lév.) Rehder
– Outer surface of the endocarp ridged 6

4. Endocarp globose in lateral view, endocarp length < 12 mm ..... ***I. perrieri*** Sleumer
– Endocarp elliptical in lateral view, endocarp length > 30 mm ..... ***I. yatesii*** Merr.

5. Endocarp base cleft on one side 7
– Endocarp base symmetrical 8

6. Pattern of ridges not reticulate ..... ***I. liberica*** Stapf
– Pattern of ridges reticulate 9

7. Pattern of ridges delimiting a few areoles, endocarp length >12.6 mm ..... ***I. ovalis*** Blume
– Pattern of ridges diffuse, endocarp length <12.6 mm 10

8. Endocarp ca 32 mm in length ..... ***I. balansae*** Gagnep.
– Endocarp ca 15 mm in length ..... ***I. scandens*** (Becc.) Utteridge & Byng

9. Fruit pilose, endocarp wall 222–245 µm thick excluding ridges ..... ***I. seretii*** (De Wild.) Boutique
– Fruit glabrous, puberulent, endocarp wall <200 µm thick excluding ridges 11

10. Endocarp ornamentation rugose, secondary ridges absent ..... ***I. cirrhosa*** Turcz.
– Rugose ornamentation absent, secondary ridges present ..... ***I. philippinensis*** Merr.

11. Areoles few in number, ca 1 to 3 ..... ***I. kamerunensis*** Engl.
– Areoles numerous (>13) 12

12. Fruit glabrous, endocarp with numerous areoles, ridges faintly distinct, freely ending ridgelets absent, endocarp length <8 mm ..... ***I. madagascariensis*** Baill.
– Fruit puberulent, endocarp with (at most) 25 areoles, freely ending ridgelets present, ridges distinct, endocarp length >10 mm 13

13. Areoles 13–15 on each face, surface rugose ..... ***I. klaineana*** Pierre
– Areoles 21–25 on each face, surface not rugose ..... ***I. africana*** Welw. ex Oliv.

Iodes africana Welw. ex Oliv.
Fig. 12.1–12.9

Material examined

Specimen used for endocarp and fruit description

CENTRAL AFRICAN REPUBLIC • Oubangui, Boukoko; 20 Mar. 1948; *R.P. Tisserant s.n.*; P[MNHN-P-P03951984].

GABON • 1904; *R.P. Klaine 3505*; P[MNHN-P-P03951995].

Other material

CAMEROON • 1969; *J.J. Bos 5089*; P[MNHN-P-P03951958].

REPUBLIC OF THE CONGO • 1964; *A. Bouquet 833*; P[MNHN-P-P03951922].

Description

Fruit. Elliptical, laterally compressed, brown when mature. Epicarp puberulent with yellow simple hairs with granular ornamentation, reticulate when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp ca 300 µm thick when dry. Length 11.2–15.0 mm, width 8.4–11.1 mm, thickness ca 6 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length 10.8–11.7 mm, width 8.5–9.1 mm, thickness ca 4.5 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing a vascular bundle embedded within the endocarp wall. Apex asymmetrical in lateral view; base rounded, slightly flattened, symmetrical. Outer surface of the endocarp ridged with three main longitudinal ridges (up to eight counting small longitudinal ridges) more or less branched, all reaching the point of the base. Ridges rounded and thin, enclosing 21–25 longitudinal and polygonal areoles with small freely ending ridgelets, occasionally absent. Vasculature of the endocarp resting on the ridges and free in the mesocarp. Endocarp wall 154–171 µm thick excluding ridges (268–277 µm including ridges). Endocarp wall with three cell layers: outermost layer with ca 0–6 row(s) of isodiametric cell, cells 24–32 µm in diameter; followed by a layer with 5–10 rows of periclinally oriented cells, cells 9–13 µm in width; innermost layer with one row of periclinally oriented cells, cells ca 8.5 µm in width, covering the inner endocarp surface with regularly spaced and rounded papillae; papillae 14.3–17.4 µm (av. 16.1 µm) in diameter, ca 810–840 papillae per 0.25 mm^2. Locule surface lacunate.

Iodes balansae Gagnep.
Fig. 12.10–12.13

Material examined

Specimen used for endocarp and fruit description
CHINA • *Liu 171*; KUN[KUN-0647593].

Other material
VIETNAM • 1888; *B. Balansa 3981*; P[MNHN-P-P00698073].

Description

Fruit. Elliptical, laterally compressed, red when mature. Epicarp strigose-puberulent with yellow simple hairs with granular ornamentation, reticulate when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp ca 200 µm thick when dry. Length 25–38 mm, width 14–20 mm.

Endocarp. Brown, elliptical in lateral view, lenticular in transverse section, length ca 32.7 mm, width ca 15.2 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing a vascular bundle embedded within the endocarp wall. Apex greatly asymmetrical; base acute, symmetrical. Outer surface of the endocarp ridged, with two types of ridges; the primary ridges composed of one main median ridge, which reaches the point of the base, and two lateral ridges that run close to the apex. Primary ridges rectangular and thin with a median channel, forming a diffuse pattern with short lateral freely ending ridgelets. Secondary ridges thin and rounded, delimiting a dense reticulum enclosing numerous areoles. Endocarp possessing a symmetrical pair of horn-like protrusions compressed on the keel, positioned eccentrically and subapically on the endocarp faces, each with a central pit. Vasculature of the endocarp resting on the channels of the ridges and free in the mesocarp. Endocarp wall 434–450 µm thick excluding ridges (550–600 µm thick including secondary ridges and 1300 µm thick including primary ridges). Endocarp wall with three cell layers: outermost layer with ca 12 rows of isodiametric to anticlinally oriented cells, followed by a layer with ca 7 rows of periclinally oriented cells, innermost layer periclinally oriented, lining the locule surface with rounded papillae, papillae ca 20 µm in diameter. Locule surface lacunate.

Remarks

The cellular details of the specimen examined were not clearly visible; thus, we were unable to obtain cell size information. The inner endocarp surface was also decayed but we were able to distinguish a few papillae.

Iodes cirrhosa Turcz.
Fig. 12.14–12.23

Material examined

Specimen used for endocarp and fruit description
VIETNAM • "Indo-chine, Ba Drang"; 18 May 1921; *B. Hayata 672*; P[MNHN-P-P06672331].

Other material
VIETNAM • "Indo-chine", Annam; 23 May 1923; *E. Poilane 6622*; P[MNHN-P-P06672332].

Description

Fruit. Elliptical, cleft at the base, red when mature. Epicarp puberulent with yellow simple hairs with granular ornamentation, shriveled when dry, revealing the underlying endocarp ridges. Mesocarp 270–320 µm thick when dry. Length 12–20 mm, width 10–15 mm, thickness 7–10 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 12.6 mm, width ca 9.5 mm, thickness ca 4.5 mm. Keel thick, surrounding the endocarp in the plane of symmetry, with the thicker margin containing the primary vascular bundle embedded within the endocarp wall. Apex asymmetrical with an acute protuberance on either side in lateral view; base flat and cleft on one side. Outer surface of the endocarp ridged and faintly rugose, with two thin rectangular to sharp ridges on each face, the median ridge running from the base up to ⅔ of the endocarp length and the second ridge running up to the subapical part. Endocarp possessing a symmetrical pair of horn-like protrusions compressed on the keel, positioned eccentrically and subapically one on either endocarp face, each protrusion with a central pit. Endocarp wall 380–405 µm thick excluding ridges (813–1064 µm thick including ridges). Endocarp wall with three cell layers, sometimes homogeneous: outermost layer with 15–17 rows of isodiametric, occasionally anticlinally oriented cells, cells 22–49 µm in diameter, followed by a layer with 3–4 rows of small periclinally oriented cells, cells 7–10 µm in width; innermost layer with one row of periclinally oriented cells, cells ca 6.5 µm in width, covering the inner endocarp surface with regularly spaced, sessile rounded papillae, papillae 8.6–15.5 µm (av. 10.2 µm) in diameter, ca 460 papillae per 0.25 $mm^{2.}$ Locule surface lacunate.

Fig. 12. Fruits of Icacinaceae Miers. **1**–**9**. *Iodes africana* Welw. Ex Oliv. (*R.P. Tisserant s.n.*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view of the endocarp showing a reticulate pattern of ridges. **3**. Dorsal view of the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the pericarp in transverse section. **8**. SEM image of the endocarp wall in transverse section and papillae on the inner surface. **9**. SEM surface view of the papillae lining the locule. – **10**–**13**. *Iodes balansae* Gagnep. (*Liu 171*). **10**. Dried fruit, lateral view. **11**. Lateral view of a part of the endocarp showing the double reticulation (arrow = horn-like protrusions). **12**. SEM image of primary ridges in transverse section. **13**. SEM image of secondary ridges in transverse section. – **14**–**23**. *Iodes cirrhosa* Turcz (*B. Hayata 672*). **14**. Dried fruit, lateral view. **15**–**19**. Endocarp. **15**. Lateral view showing the ridges and roughness. **16**. Dorsal view showing a keel surrounding the endocarp. **17**. Opposite lateral view. **18**. Apical view. **19**. Basal view. **20**. SEM image of a vascular bundle embedded within endocarp wall in transverse section of the pericarp (arrow). **21**. SEM image of an endocarp ridge in a transverse section of the pericarp. **22**. SEM image of the lower part of the endocarp wall in transverse section and papillae on the inner surface. **23**. SEM surface view of the papillae lining the locule. Images taken from Del Rio (2018). Scale bars: 1–6, 10–11, 14–19 = 10 mm; 12 = 1 mm; 13, 20–21 = 500 µm; 7, 9 = 300 µm; 8, 23 = 50 µm; 22 = 20 µm.

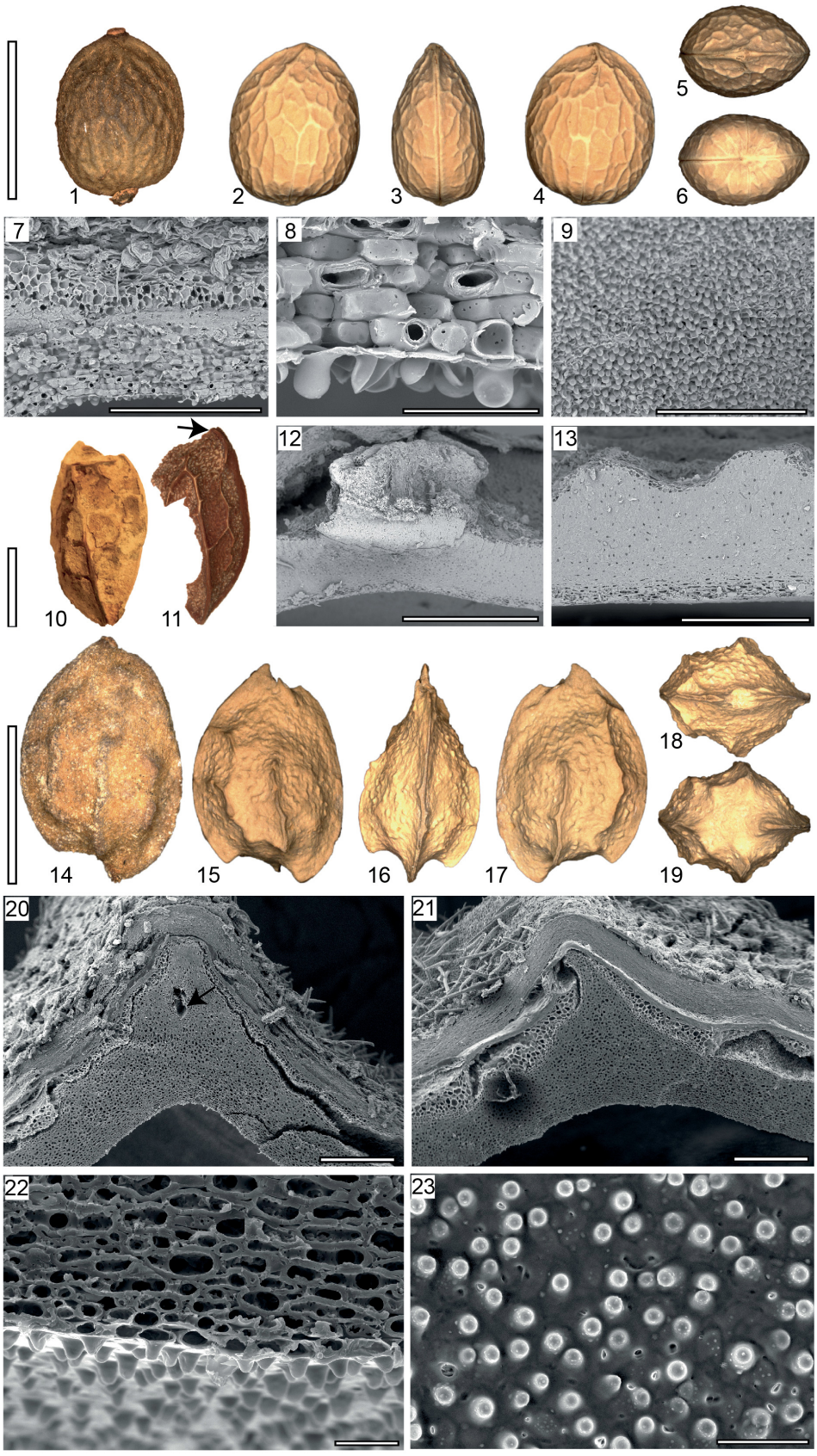

Fig. 12. (see full caption on page 32)

Remarks

The endocarp was considered "smooth inside" (Sleumer 1971). Here we demonstrate that the locule is densely covered by papillae. These papillae are difficult to observe without SEM.

Iodes kamerunensis Engl.
Fig. 13.1–13.9

Material examined

Specimen used for endocarp and fruit description
CAMEROON • 1899; *G.A. Zenker 2032*; P[MNHN-P-P03951972].

Description

Fruit. Elliptical; epicarp puberulent with yellow simple hairs with granular ornamentation, shriveled when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp 135–150 µm thick when dry. Length 10.0–12.4 mm, width 7.0–9.6 mm, thickness 6.0–8.9 mm.

Endocarp. Cream, elliptical in lateral view, globose in transverse section, length ca 10.9 mm, width ca 9.9 mm, thickness ca 7.5 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing the primary vascular bundle embedded within the endocarp wall, occasionally divided into two parts subapically. Apex asymmetrical in lateral view; base rounded-flat and symmetrical. Outer surface of the endocarp ridged, with three main longitudinal ridges; the median ridge beginning at the point of the base then dichotomizing at the ⅔ of the endocarp length; the apical ⅓ of the endocarp length is ridgeless. Ridges rounded and thin, each with a median channel, enclosing 1–3 polygonal areoles, extended transversally and longitudinally. Vasculature of the endocarp resting in the channels of the ridges. Endocarp wall 154–181 µm thick excluding ridges (460–470 µm thick including ridges). Endocarp wall homogenous, with 9–12 rows of isodiametric cells, 14–26 µm in diameter. Locule surface unknown, lacunate.

Remarks

A tissue (placenta?, degradation?) obscures the surface of the locule.

Fig. 13. Fruits of Icacinaceae Miers. **1**–**9**. *Iodes kamerunensis* Engl. (*G.A. Zenker 2032*). **1**. Dried fruit, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing a reticulate pattern of ridges. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of a vascular bundle embedded within the endocarp wall (arrow) in a transverse section of the pericarp. **8**. SEM image of a ridge in transverse section of the pericarp. **9**. SEM image of the endocarp wall in transverse section. – **10**–**18**. *Iodes klaineana* Pierre (*R.P. Klaine 3064*). **10**. Dried fruit, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing a reticulate pattern of ridges. **12**. Dorsal view showing the keel surrounding the endocarp. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of a vascular bundle embedded within the endocarp wall (arrow) in a transverse section of the pericarp. **17**. SEM image of a ridge in transverse section of the pericarp. **18**. SEM image of the cells of the endocarp. – **19**–**27**. *Iodes liberica* Stapf (*J.G. Adam 3833*). **19**. Broken dried fruit, lateral view. **20**–**24**. Broken endocarp. **20**. Lateral view showing a reticulate pattern of ridges. **21**. Dorsal view showing a keel surrounding the endocarp. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. SEM image of a vascular bundle embedded within the endocarp wall (arrow). **26**. SEM image of a ridge and endocarp wall in transverse section. **27**. Portion of the endocarp wall. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–24 = 10 mm; 7, 16, 25 = 1 mm; 8, 17 = 500 µm; 26 = 300 µm; 9 = 200 µm; 27 = 100 µm; 18 = 50 µm.

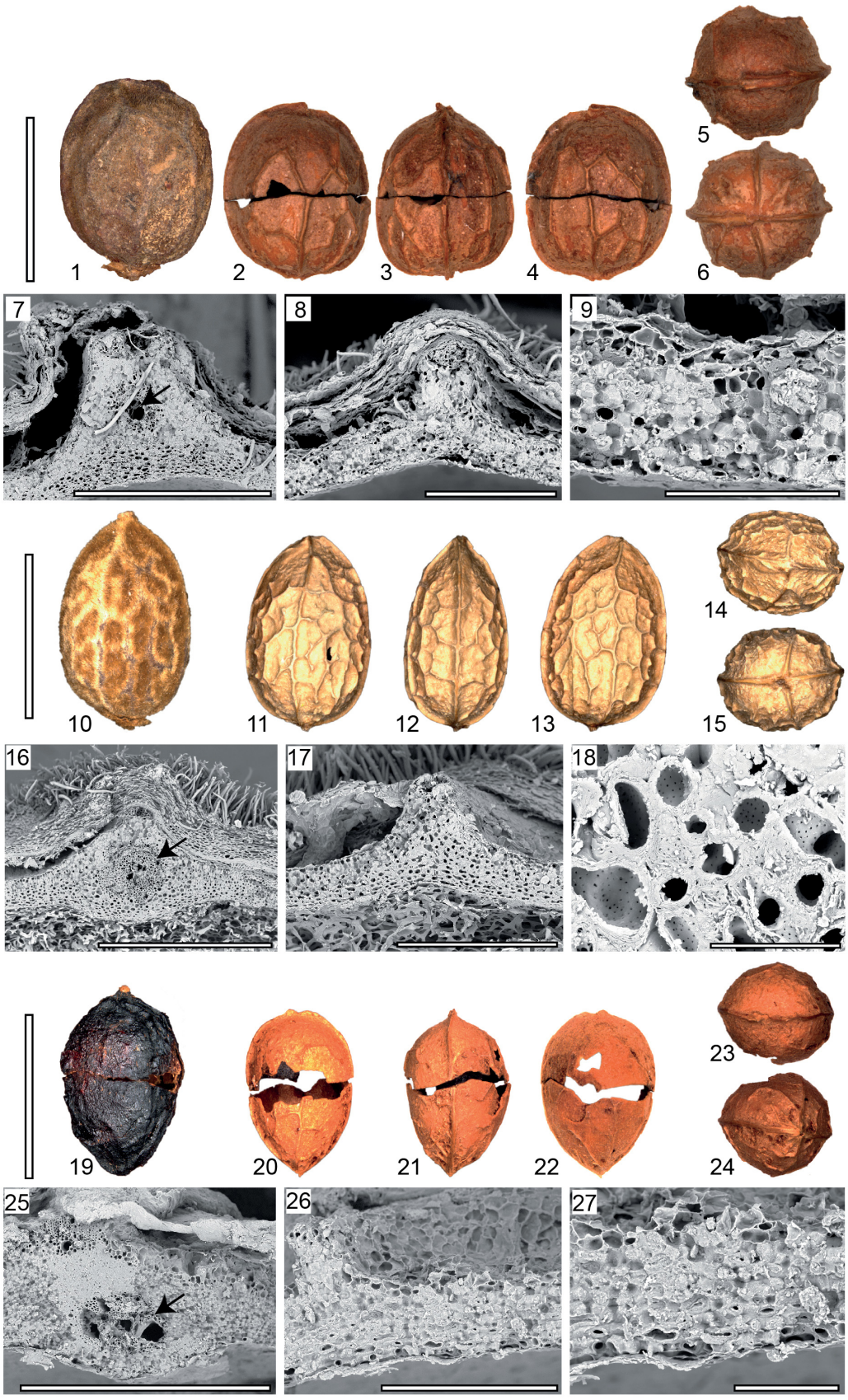

Fig. 13. (see full caption on page 36)

Iodes klaineana Pierre
Fig. 13.10–13.18

Material examined

Specimen used for endocarp and fruit description
GABON • 1902; *R.P. Klaine 3064*; P[MNHN-P-P04472306].

Other material
GABON • 1983; *J.J.F.E. de Wilde 606*; P[MNHN-P-P04472313].

Description

Fruit. Elliptical, red when mature. Epicarp densely puberulent with yellow short simple hairs with granular ornamentation and longer simple hairs without ornamentation, shriveled when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp 240–300 µm thick when dry. Length 11.0–13.6 mm, width 7.0–11.0 mm, thickness 4–7.1 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 12.1 mm, width ca 7.6 mm, thickness ca 6.3 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing the primary vascular bundle embedded within the endocarp wall. Apex slightly asymmetrical in lateral view, horn-like protrusions or pores absent; base rounded and symmetrical. Outer surface of the endocarp ridged, with 4–5 main longitudinal ridges; the median ridges running from the point of the base up to the point of the apex. Ridges rounded, thin, with a median channel, delimiting a reticulate pattern (sparse subapically and subbasally, but denser toward the middle), enclosing 13–15 polygonal areoles each with a freely ending ridge. Vasculature of the endocarp resting in the channels of the ridges. Endocarp wall 128–173 µm thick excluding ridges (300–360 µm thick including ridges). Endocarp wall with at least two cell layers: outermost layer with 5–9 rows of isodiametric to anticlinally oriented cells, cells 22.7–29.0 µm in width, innermost layer with 1–5 rows of periclinally oriented cells, cells 13–14 µm in width. Locule surface unknown, lacunate.

Iodes liberica Stapf
Fig. 13.19–13.27

Material examined

Specimen used for endocarp and fruit description
GUINEA • 1949; *J.G. Adam 3833*; P[MNHN-P-P04472332].

Other material
GUINEA • 1949; *J.G. Adam 5788*; P[MNHN-P-P04472335] • 1949; *J.G. Adam 5252*; P[MNHN-P-P04472330].

IVORY COAST • Bingerville; 27 Mar. 1906; *A. Jolly s.n.*; P[MNHN-P-P04472370] • 1959; *A.J.M. Leewenberg 2527*; P[MNHN-P-P04472371].

Description

Fruit. Elliptical to obovoid, red when mature. Epicarp sparsely strigose with yellow simple hairs with granular ornamentation. Mesocarp ca 200 µm when dry. Calyx not persistent. Length 8.0–11.9 mm, width 5.0–7.8 mm, thickness 5.5–7.4 mm.

Endocarp. Light brown, elliptical to obovoid in lateral view, globose in transverse section, length ca 10.4 mm, width ca 7.1 mm, thickness ca 7 mm. Keel surrounding the endocarp in the plane of symmetry,

with the thicker margin containing a vascular bundle embedded within the endocarp wall. Apex slightly asymmetrical in lateral view, without horn-like protrusions or pores; base rounded-acute, symmetrical. Outer surface of the endocarp sparsely ridged, with one median ridge running longitudinally, beginning at the point of the base and spanning ca ⅔ of the endocarp length. Ridges angular-sharp, thin, with a median channel, forming a sparse diffuse pattern from the median ridge, absent from the apical ⅓ of the endocarp length. Vasculature of the endocarp resting in the channels of the ridges. Endocarp wall 138–172 µm thick excluding ridges (257–266 µm thick including ridges). Endocarp wall with at least two cell layers: outermost layer with one row of anticlinally oriented to isodiametric cells, 16.1–22.7 µm in width; innermost layer with 8–9 rows of periclinally oriented cells, 8.8–22 µm in width. Locule surface unknown, not lacunate.

Iodes madagascariensis Baill.
Fig. 14.1–14.9

Material examined

Specimens used for endocarp and fruit description
MADAGASCAR • "Côte orientale de Madagascar"; s.d.; *Chapelier s.n.*; P[MNHN-P-P04472113] • *McPherson 18809*; MO[MO-2972314].

Other material
MADAGASCAR • s.d.; *Chapelier s.n.*; P[MNHN-P-P04472112].

Description

Fruit. Elliptical, brown when mature. Epicarp glabrous, granular, shriveled when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp 135–214 µm thick when dry. Calyx not persistent. Length 7–9 mm, width 4–5 mm, thickness 4.4–5.0 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length 7.6–8.0 mm, width ca 4.6 mm, thickness ca 4.3 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing the primary vascular bundle embedded within the endocarp wall. Apex slightly asymmetrical in lateral view, horn-like protrusions or pores absents; base rounded, symmetrical. Outer surface of the endocarp ridged delimiting a reticulate pattern of rounded ridges. Ridges thin and faintly apparent, with a median channel, enclosing more than 80 small polygonal areoles distributed over the entire surface of the endocarp. Vasculature of the endocarp resting in the channels of the ridges. Endocarp wall 165–201 µm thick excluding ridges (227–265 µm thick including ridges). Endocarp wall with at least two cell layers: outermost layer with ca 11 rows of periclinally oriented to isodiametric cells, cells 18.9–27.0 µm in width; innermost layer with one row of small periclinally oriented cells, cells 7.9–9.6 µm in width, covering the inner endocarp surface with regularly spaced and rounded papillae, papillae ca 13.3 µm in diameter. Locule not lacunate.

Iodes ovalis Blume
Fig. 14.10–14.18

Material examined

Specimen used for endocarp and fruit description
VIETNAM • *Hiep HLF 203*; MO[MO-2080935].

Other material

INDONESIA • "Celebes" [Sulawesi]; 1863; *Kunz?*; P[MNHN-P-P04504863].

Description

Fruit. Elliptical, cleft at the base, red when mature. Epicarp strigose with yellow simple hairs with granular ornamentation and small papillae-like hairs lining the fruit, shriveled when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp 142–242 µm thick when dry. Length 15–25 mm, width 10.0–11.4 mm, thickness 8–9 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 17.8 mm, width ca 11 mm, thickness ca 8.6 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing a vascular bundle embedded within the endocarp wall. Apex asymmetrical and acute in lateral view; base flattened and cleft. Outer surface of the endocarp ridged and faintly rugose, with 3–4 main longitudinal ridges delimiting a reticulate pattern, enclosing 3–4 large polygonal areoles. Ridges thin, rectangular, with a median channel, interconnected with some very short freely ending ridgelets. Rugosities distributed over the entire surface. Endocarp possessing a symmetrical pair of horn-like protrusions positioned eccentrically and subapically on the endocarp faces, each with a central pit. Endocarp wall 314–375 µm thick excluding ridges (ca 490 µm thick including ridges). Endocarp wall with three cell layers: outermost layer with 16–19 rows of isodiametric, occasionally anticlinally oriented cells, followed by a layer with 6–11 rows of periclinally oriented cells; innermost layer with one row of periclinally oriented cells, lining the locule surface with regularly spaced and rounded papillae; papillae 9.2–11.8 µm (av. 10.1 µm) in diameter, at least 220 papillae per 0.25 mm^2. Locule lacunate.

Iodes perrieri Sleumer
Fig. 14.19–14.27

Material examined

Specimen used for endocarp and fruit description

MADAGASCAR • 1926; *Perrier de la Bâthie 17843*; P[MNHN-P-P04472108].

Fig. 14. Fruits of Icacinaceae Miers. **1**–**9**. *Iodes madagascariensis* Baill. (*Chapelier s.n.*; MNHN-P-P04472113). **1**. Dried fruit, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing a reticulate pattern of ridges. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the pericarp in a transverse section showing the vascular bundle embedded within the endocarp wall (arrow). **8**. Other view of the pericarp in a transverse section showing the endocarp wall. **9**. Detail showing the papillae on the locule surface. – **10**–**18**. *Iodes ovalis* Blume (*Hiep HLF 203*). **10**. Broken dried fruit, lateral view. **11**–**15**. Broken endocarp. **11**. Lateral view showing the reticulation and roughness. **12**. Dorsal view showing a keel surrounding the endocarp. **13**. Opposite lateral view (arrow = horn-like protrusion). **14**. Apical view. **15**. Basal view. **16**. SEM image of the vascular bundle embedded within the endocarp wall (arrow). **17**. SEM image of a ridge in transverse section. **18**. SEM image of the papillae on the locule surface. – **19**–**27**. *Iodes perrieri* Sleumer (*Perrier de la Bâthie 17843*). **19**. Dried fruit, lateral view. **20**–**24**. Endocarp. **20**. Lateral view showing a reticulate pattern of faintly marked ridges. **21**. Dorsal view of endocarp. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. SEM image of a ridge and endocarp wall in transverse section. **26**. Detail showing the endocarp cells in the upper part. **27**. SEM image of the papillae on the locule surface. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–24 = 10 mm; 16 = 1 mm; 7–8, 17, 25 = 500 µm; 26 = 200 µm; 9, 18, 27 = 50 µm.

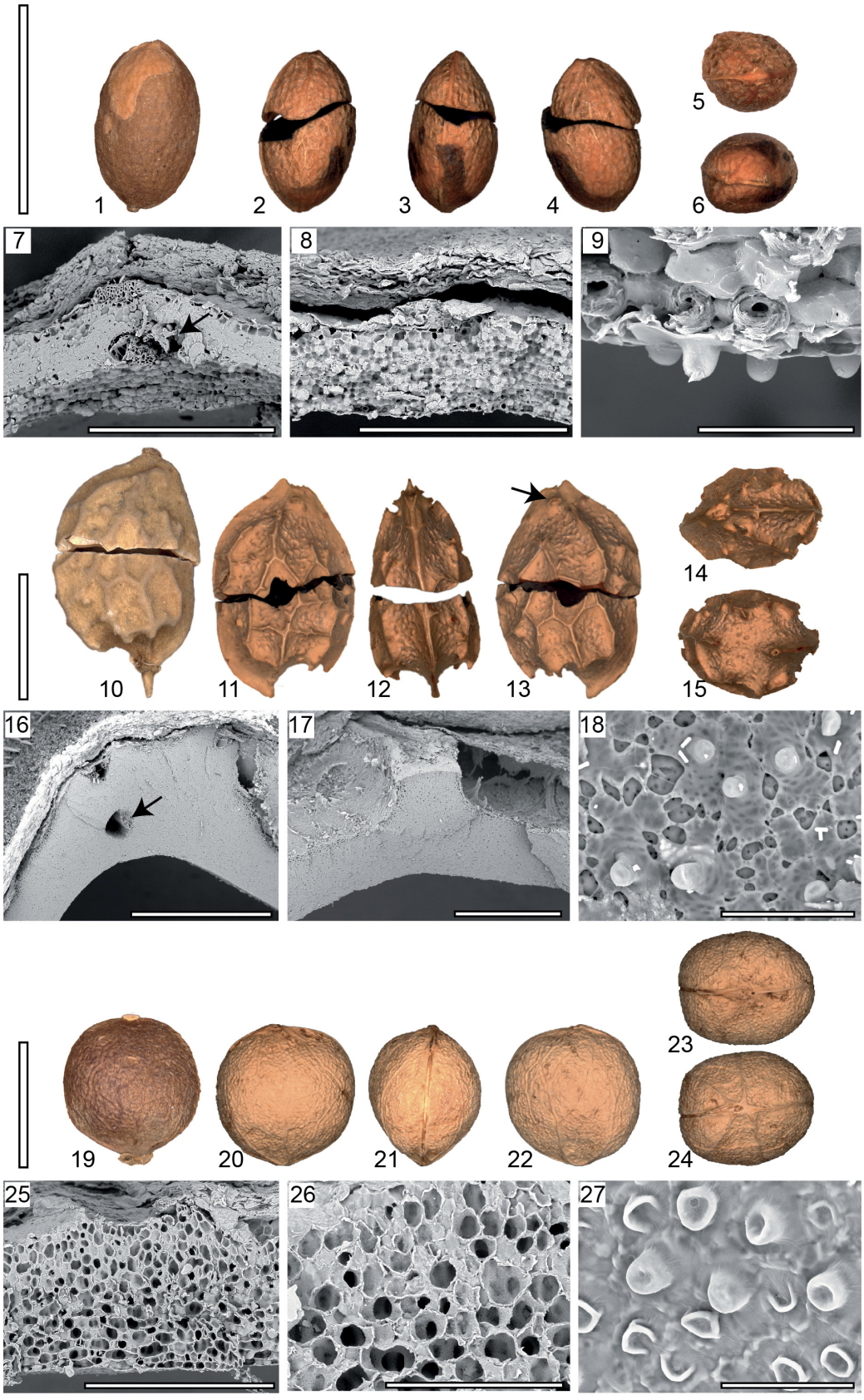

Fig. 14. (see full caption on page 40)

Other material

MADAGASCAR • 1932; *J. Leandri 468*; P[MNHN-P-P04472110] • 1996; *C.C.H. Jongkind 3385*; P[MNHN-P-P05279694] • 1997; *C.C.H. Jongkind 3696*; P[MNHN-P-P05274867].

Description

Fruit. Globose, brown when mature. Epicarp strigose, with yellow simple hairs with granular ornamentation, finely ridged when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp 88–111 µm thick when dry. Length 11–17 mm, width 11.3–15.0 mm, thickness 10–12 mm.

Endocarp. Cream, globose in lateral view and transverse section, length ca 11.5 mm, width ca 10.9 mm, thickness ca 9.2 mm. Keel thin and delicate, surrounding the endocarp in the plane of symmetry, with the thicker margin containing the primary vascular bundle embedded within the endocarp wall. Apex slightly asymmetrical; base rounded, symmetrical. Outer surface of the endocarp ridged with two types of ridges. The primary ridges comprise three main longitudinal ridges, two of them spanning from the apex to the base. Primary ridges thin, rounded and forming a sparse diffuse pattern. Secondary ridges thin and sharp, delimiting a dense reticulum enclosing numerous areoles. Endocarp possessing a symmetrical pair of pores positioned eccentrically and subapically on the endocarp faces. Vasculature of the endocarp resting on ridges. Endocarp wall 317–338 µm thick excluding ridges (340–426 µm thick including ridges). Endocarp wall with three cell layers: outermost layer with 3–11 rows of isodiametric to anticlinally oriented cells, cells 23.7–44.0 µm in width, followed by a layer with 3–9 rows of periclinally oriented cells, cells 20–27 µm in width, innermost layer with one row of periclinally oriented cells, cells 12–18 µm in width, covering the inner endocarp surface with regularly spaced and rounded papillae; papillae 12.3–18.0 µm (av. 14.9 µm) in diameter, ca 448 papillae per 0.25 mm^2. Locule lacunate.

Iodes philippinensis Merr.
Fig. 15.1–15.9

Material examined

Specimen used for endocarp and fruit description

PHILLIPINES • 1916; *A.D.E. Elmer 16418*; P[MNHN-P-P04504850].

Fig. 15. Fruits of Icacinaceae Miers. **1**–**9**. *Iodes philippinensis* Merr. (*A.D.E. Elmer 16418*). **1**. Dried fruit, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing the primary ridges and secondary reticulation. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the uncinate hairs on the epicarp surface. **8**. SEM image of the vascular bundle embedded within the endocarp wall (arrow) seen in a transverse section of the pericarp. **9**. SEM image of the endocarp wall in transverse section. – **10**–**17**. *Iodes scandens* (Becc.) Utteridge & Byng (MO). **10**. Lateral view of the endocarp showing a reticulate pattern of ridges. **11**–**14**. Endocarp. **11**. Dorsal view showing a keel surrounding the endocarp partially splitted in the same plane. **12**. Opposite lateral view. **13**. Apical view. **14**. Basal view. **15**. SEM image of a ridge in transverse section. **16**. SEM image of the endocarp wall in transverse section. **17**. SEM image of the endocarp cells and potential papillae on the locule surface (arrow). – **18**–**26**. *Iodes seguinii* (H.Lév.) Rehder (*Abbé Cavalerie 3932*). **18**. Dried fruit, lateral view. **19**–**23**. Endocarp. **19**. Lateral view showing the smooth surface with the vasculature on a faintly marked channel. **20**. Dorsal view showing the channel. **21**. Opposite lateral view. **22**. Apical view with the channel seen on the left side. **23**. Basal view. **24**. SEM image of the channel containing the vascular bundle. **25**. SEM image of endocarp wall in transverse section. **26**. Detail showing the endocarp basal cells. Images taken from Del Rio (2018). Scale bars: 1–6, 10–14, 18–23 = 10 mm; 7, 15 = 1 mm; 8, 16, 24 = 500 µm; 9, 25 = 200 µm; 26 = 50 µm; 17 = 30 µm.

Fig. 15. (see full caption on page 42)

Description

Fruit. Oblong, red when mature. Epicarp puberulent-strigose, with yellow simple hairs with granular ornamentation and uncinate hairs, shriveled when dry, revealing the underlying endocarp ridges. Mesocarp ca 50 µm thick when dry. Length 11–15 mm, width 7.5–12.0 mm, thickness 5–10 mm.

Endocarp. Brown, oblong in lateral view, hexagonal in transverse section, length ca 12.4 mm, width ca 7.6 mm, thickness ca 6.5 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing the primary vascular bundle embedded within the endocarp wall. Apex asymmetrical and almost flat with two uncinate protuberances in lateral view; base flattened and cleft on the opposite side. Outer surface of the endocarp ridged with two types of ridges. Primary ridges large and rectangular, composed of two main longitudinal ridges, running from the subbasal part up to the subapical part of the endocarp length and forming a diffuse pattern with only 2–3 lateral freely ending ridgelets. Secondary ridges thin and rounded, delimiting a dense reticulum enclosing numerous areoles. Endocarp possessing a symmetrical pair of horn-like protrusions positioned on the bigger uncinate protuberance at the apex. Vasculature of the endocarp resting on ridges. Endocarp wall 229–282 µm thick excluding ridges (285–296 µm including secondary ridges and 360–396 µm including primary ridges). Endocarp wall with four cell layers: outermost layer with ca 5 rows of isodiametric cells, cells 12.5–16.5 µm in diameter, followed by a layer with ca 6 rows of isodiametric to anticlinally oriented cells, cells 21.4–28.3 µm in width, then a layer with ca 5 rows of periclinally oriented cells, cells 8.1–11.9 µm in width; innermost layer with one row of periclinally oriented cells, cells 6.7–6.9 µm in width, covering the surface of the locule (detail of the surface unknown). Locule lacunate.

Iodes scandens **(**Becc.) Utteridge & Byng
Fig. 15.10–15.17

Material examined

Specimen used for endocarp and fruit description
NEW GUINEA • s. loc; s.d.; *s. col. s.n.*; MO.

Description

Fruit. Elliptical; epicarp puberulent. Calyx persistence and mesocarp thickness unknown. Length 20 mm, width 15 mm, thickness 15 mm.

Endocarp. Brown, elliptical in lateral view, lenticular in transverse section, length ca 14.7 mm, width ca 12.9 mm, thickness ca 11.2 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing the primary vascular bundle embedded within the endocarp wall. Apex rounded and asymmetrical; base rounded, slightly asymmetrical. Outer surface of the endocarp ridged with two main longitudinal ridges; the median ridge runs from the point of the base up the half of the endocarp length, then divides into several smaller ridges and a lateral ridge, which runs from the subbase up to the subapex. Ridges rectangular, thin, with a median channel, delimiting a reticulate pattern enclosing 13–18 irregular ridges with arbuscular freely ending ridgelets. Vasculature of the endocarp surface in the channels of the ridges. Endocarp possessing a symmetrical pair of horn-like protrusions compressed on the keel, positioned eccentrically and subapically on the endocarp faces, each with a central pit. Endocarp wall 502–564 µm thick excluding ridges (652–672 µm including ridges). Endocarp wall with three cell layers: outermost layer with 11–13 rows of anticlinally oriented cells, cells 14.0–43.1 µm in length, followed by a layer with 6–8 rows of periclinally oriented cells, cells 21.1–25.6 µm in width; innermost layer with one row of periclinally oriented cells, cells 9.3–9.8 µm in width, covering the locule surface, apparently with rounded papillae (detail of the surface poorly preserved). Locule lacunate.

Iodes seguinii (H.Lév.) Rehder
Fig. 15.18–15.26

Material examined

Specimen used for endocarp and fruit description
CHINA • Kouy-Tcheou Province; Jun. 1912; *Abbé Cavalerie 3932*; P[MNHN-P-P05279333].

Description

Fruit. Elliptical to oblong, red when mature. Epicarp puberulent, with yellow uncinate hairs, smooth when dry. Mesocarp thin when dry. Length 15–23 mm, width 10–16 mm, thickness 5.0–7.9 mm.

Endocarp. Brown, oblong in lateral view, lenticular in transverse section, length ca 16.5 mm, width ca 11 mm, thickness ca 8.1 mm. Channel surrounding the endocarp on only one side in the plane of symmetry. Apex asymmetrical, flattened in the lateral view; base flattened and symmetrical. Outer surface of the endocarp smooth with thin, faintly apparent channels, 3–4 main channels running longitudinally. Vasculature of the endocarp in the channels; primary vascular bundle positioned inside the channel surrounding the endocarp. Endocarp wall 173–226 µm thick. Endocarp wall with ca 12 rows of periclinally oriented cells, cells 9.9–15.4 µm in width. Locule surface smooth, not lacunate.

Iodes seretii (De Wild.) Boutique
Fig. 16.1–16.9

Material examined

Specimen used for endocarp and fruit description
CAMEROON • Forest near Boa Bakundu village, south west of Kumba; 19 Apr. 1986; *D. Thomas & M. Etuge 63*; BR[BR0000015596772].

Other material
NIGERIA • *Ekwuno PFO 370*; MO[MO-2730593].

Description

Fruit. Elliptical, red when mature. Epicarp pilose, with yellow long and thin hairs and yellow simple hairs with granular ornamentation. Mesocarp 132–162 µm thick when dry. Length 11.6–15.5 mm, width 8.5–10.0 mm, thickness 5.6 mm.

Endocarp. Brown, elliptical in lateral view, lenticular in transverse section, length ca 11.6 mm, width ca 8.7 mm, thickness ca 5.9 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing a vascular bundle embedded within the endocarp wall. Apex slightly asymmetrical in lateral view, with a central pit in apical view; base rounded, symmetrical. Outer surface of the endocarp ridged with 3–4 main longitudinal ridges (6–7 including small longitudinal ridges); the median and two lateral ridges reaching the point of the base and running along the endocarp length. Ridges thin, rounded to rectangular, with a median channel, delimiting a reticulate pattern enclosing 23–25 polygonal and longitudinally extended areoles. Surface of endocarp finely covered by ridgelets-rugosities. Vasculature of the endocarp resting in the channels of the ridges. Endocarp wall 227–245 µm thick excluding ridges (320–386 µm including ridges). Endocarp wall with three cell layers: outermost layer with 1–3 rows of isodiametric cells (mesocarp?), cells 12.2–17.2 µm in diameter, followed by a layer with 15 rows of periclinally oriented cells, cells 9.4–13.2 µm in width; innermost layer with one row of periclinally oriented cells, cells 5.4–8.7 µm in width, covering the inner endocarp surface with regularly spaced and rounded papillae; papillae 11.8–13.7 µm (av. 12.7 µm) in diameter. Locule lacunate.

Iodes yatesii Merr.
Fig. 16.10–16.18

Material examined

Specimen used for endocarp and fruit description
SUMATRA • 19 Nov. 1988; *Burley 1577*; L[L.2288996].

Other material
SUMATRA • s.d.; *H.S. Yates 1342*; P[MNHN-P-P04504846].

Description

Fruit. Elliptical, brown when mature, length 25–34 mm, width 15–17 mm, thickness 11–13 mm.

Endocarp. Cream, with a cork-like texture, elliptical in lateral view, lenticular in transverse section, length ca 33.8 mm, width ca 17 mm, thickness ca 10.7 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing the primary vascular bundle embedded within the endocarp wall. Apex asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp ridged with two types of ridges. Primary ridges comprising three main longitudinal ridges; the median ridge reaching the point of the base. Primary ridges large, rectangular, with a median channel and with wavelet ornamentation on both sides of the channel; delimiting a reticulate pattern enclosing 7–8 square-polygonal areoles transversally. Secondary ridges thin and sharp, delimiting a dense reticulum enclosing numerous areoles. Vasculature of the endocarp resting in the channels of the ridges. Endocarp possessing a symmetrical pair of pores positioned eccentrically and subapically on the endocarp faces. Endocarp wall 258–322 µm thick excluding ridges (433–597 µm thick including the secondary ridges and ca 959 µm thick including primary ridges). Endocarp wall with three cell layers: outermost layer with ca 2–4 rows of isodiametric to anticlinally oriented cells, cells 30.7–32.6 µm in width; middle layer with 11 rows of periclinally oriented cells, cells 11.9–21.0 µm in width; innermost layer with one row of periclinally oriented cells, cells 6.3–8.4 µm in width, covering the inner endocarp surface with papillae. Locule lacunate.

Fig. 16. Fruits of Icacinaceae Miers. **1**–**9**. *Iodes seretii* (De Wild.) Boutique (*D. Thomas & M. Etuge 63*). **1**. Broken dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view of the endocarp showing a reticulate pattern of ridges. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the pilose indumentum on the epicarp surface and of a transverse section of the pericarp. **8**. SEM image of the vascular bundle embedded within the endocarp wall (arrow) in a transverse section of the pericarp. **9**. SEM image of basal endocarp cells in a transverse section and papillae on the locule surface. – **10**–**18**. *Iodes yatesii* Merr. (*Burley 1577*). **10**–**15**. Endocarp. **10**. Lateral view showing the double reticulation. **11**. Dorsal view showing a keel surrounding the endocarp. **12**. Opposite lateral view. **13**. Apical view. **14**. Basal view. **15**. Magnification of areoles showing the secondary reticulation. **16**. SEM image of a vascular bundle embedded within the endocarp wall (arrow). **17**. SEM image of primary and secondary ridges in transverse view. **18**. Detail of the right part of the same section showing the cells organization in endocarp wall and secondary ridges. – **19**–**21**. *Lavigeria macrocarpa* (Oliv.) Pierre. **19**–**21**. Endocarp. **19**. Lateral view showing ridges / roughness (*R. Letouzey 8970*). **20**. Transverse section showing the vascular bundle (arrow) embedded within the endocarp wall (*N. Hallé 3734*). **21**. SEM image of the same section showing the endocarp wall and the locule with simple hairs (arrow) (*Bos 4098*). Images taken from Del Rio (2018). Scale bars: 1–6, 10–14, 19–20 = 10 mm; 7, 21 = 2 mm; 15, 17 = 1 mm; 8, 16, 18 = 500 µm; 9 = 50 µm.

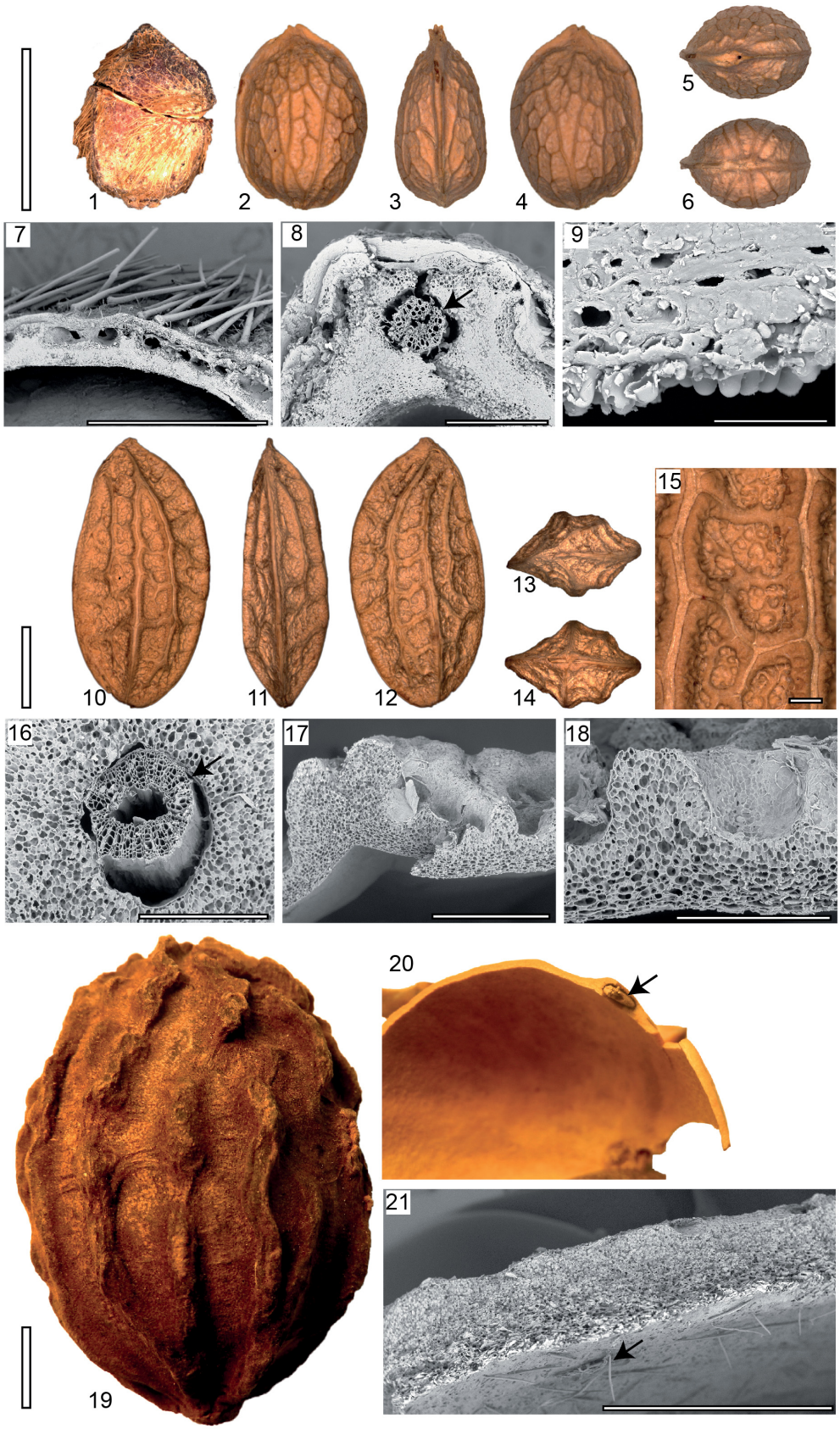

Fig. 16. (see full caption on page 46)

Genus ***Lavigeria*** Pierre

Description

See description of *Lavigeria macrocarpa* (Oliv.) Pierre, the only species of *Lavigeria* examined for this study.

Lavigeria macrocarpa (Oliv.) Pierre
Fig. 16.19–16.21

Material examined

Specimen used for endocarp and fruit description

CAMEROON • 17 km from Kribi, Edea road; 8 Mar. 1969; *Bos 4098*; WAG [WAG.1398990] • "Près de la rivière Niete au SSE Zingui (40 km SE de Kribi)"; 11 Mar. 1968; *R. Letouzey 8970*; P[MNHN-P-P04494818] • Bakingini, at edge of plantation area above Mile 11; 6 Mar. 2007; *J.J. Wieringa 5840*; WAG[WAG.1398985].

GABON • 1966; *N. Hallé 3734*; P[MNHN-P-P04494807].

Description

Fruit. Elliptical, red when mature. Epicarp pilose and puberulent, with long and thin red hairs and simple hairs with granular ornamentation, shriveled when dry, revealing the underlying endocarp rugosities. Mesocarp ca 14 mm thick. Calyx not persistent. Length 53–95 mm, width 40–58 mm.

Endocarp. Cream, elliptical in lateral view, globose in transverse section, length ca 58 mm, width ca 37 mm. Keel surrounding the endocarp in the plane of symmetry, with the thicker margin containing a vascular bundle embedded within the endocarp wall. Apex slightly asymmetrical in the lateral view; base rounded, symmetrical. Outer surface of the endocarp rugose, with large mounds in 3–4 major longitudinal rows. Mounds formed by folds of the wall. Endocarp wall 694–850 µm thick without and with ridges. Endocarp wall with two cell layers: outermost layer with 15 rows of isodiametric cells, cells 20.5–58.5 µm in diameter; innermost layer with 15 rows of periclinally oriented cells, cells 10.3–32.0 µm in width. Inner endocarp smooth with long and thin hairs. Locule surface folded, not lacunate.

Fig. 17. Fruits of Icacinaceae Miers. **1**–**9**. *Leretia cordata* Vell. (*J.C. Solomon 17073*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view of a broken endocarp showing channels and vascularization. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the vascular bundle embedded within the endocarp wall (arrow). **8**. SEM image of the endocarp wall in transverse section. **9**. Detail showing cells. – **10**–**18**. *Mappia longipes* Lundell (*M. Guillermo Ibarra 72*). **10**. Dried fruit, lateral view. **11**–**15**. Broken endocarp. **11**. Lateral view showing faint roughness. **12**. Dorsal view showing a keel surrounding the endocarp. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of the pericarp in transverse section. **17**. SEM image of the endocarp in transverse section. **18**. Detail showing anticlinally oriented cells. – **19**–**26**. *Mappia multiflora* Lundell (*Contreras 6781*). **19**–**23**. Endocarp. **19**. Lateral view showing the channels and the vasculature. **20**. Dorsal view (with a broken part at left apex). **21**. Second lateral view. **22**. Apical view. **23**. Basal view. **24**. SEM image of a transverse section showing a channel with the vascular bundle (arrow). **25**. SEM image of the endocarp wall in transverse section. **26**. Enlargement showing detail of anticlinally oriented cells and vasculature on the endocarp. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–23 = 10 mm; 7, 16, 24 = 1 mm; 17, 25 = 500 µm; 8 = 300 µm; 26 = 200 µm; 9 = 100 µm; 18 = 50 µm.

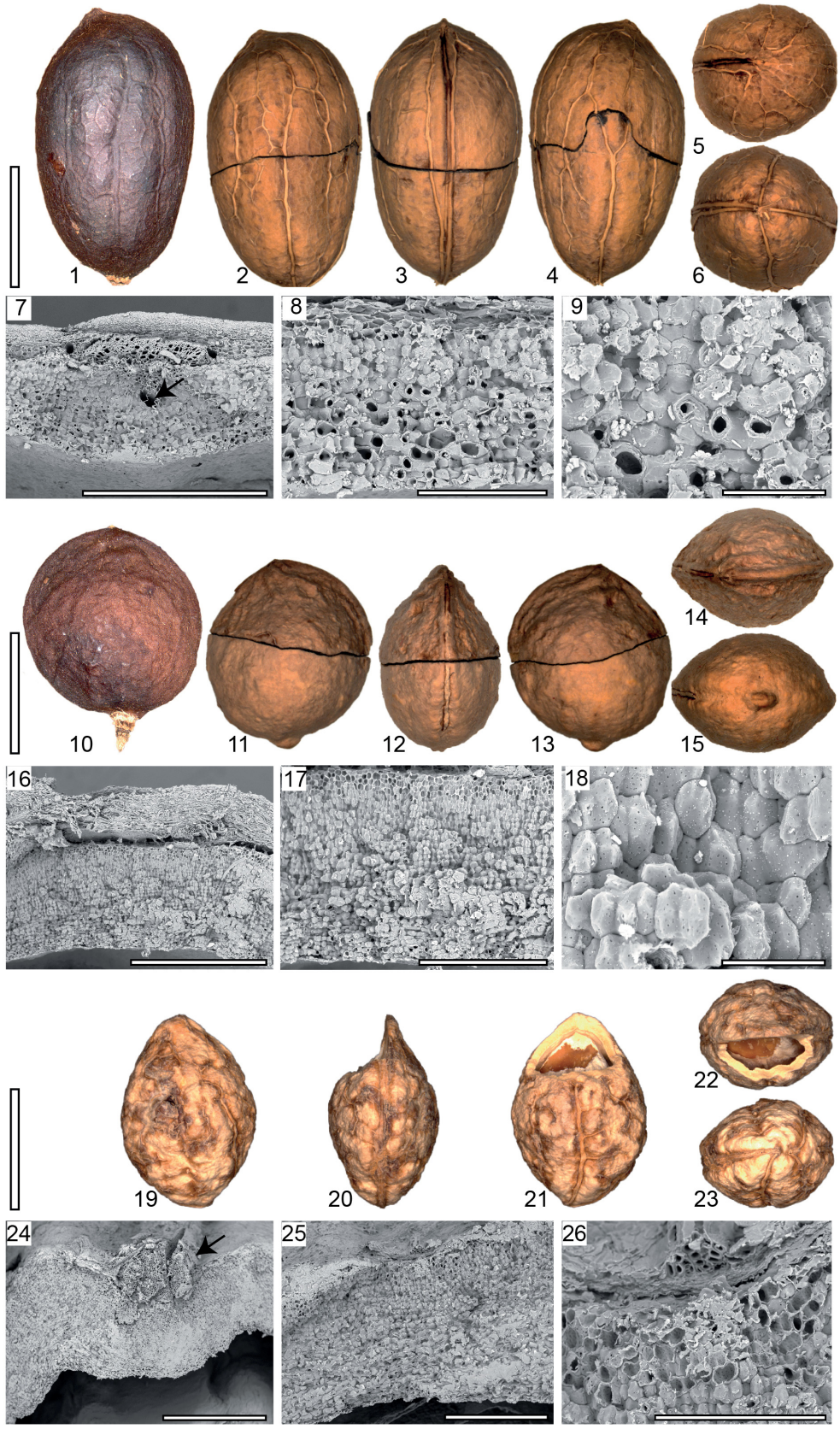

Fig. 17. (see full caption on page 48)

Genus ***Leretia*** Vell.

Description

See description of *Leretia cordata* Vell., the sole member of the genus.

Leretia cordata Vell.
Fig. 17.1–16.9

Material examined

Specimen used for endocarp and fruit description
BOLIVIA • Pando; 17 Jun. 1987; *J.C. Solomon 17073*; U[U.1343377].

Other material
FRENCH GUIANA • Crique Baboune; 29 Jul.1981; *Centre Orstom 4687*; P[MNHN-P-P05221896].

Description

Fruit. Elliptical, apex asymmetrical, red-black when mature. Epicarp glabrous, channels with vasculature marked when dry. Mesocarp 200–240 µm thick when dry. Calyx persistent. Length 20–50 mm, width 13–30 mm, thickness 12.7–16.0 mm.

Endocarp. Cream, elliptical to oblong in lateral view, globose in transverse section, length ca 22.5 mm, width ca 13 mm, thickness ca 12.3 mm. Channel surrounding the endocarp on one side in the plane of symmetry. Apex slightly asymmetrical in lateral view; base rounded, slightly asymmetrical. Outer surface of the endocarp smooth with ca 3 main shallow channels containing the vasculature of the endocarp. Endocarp primary vascular bundle embedded within the endocarp wall. Endocarp wall 353–386 µm thick. Endocarp wall with ca 12–14 rows of periclinally oriented cells, cells 16.3–33.0 µm in width. Inner endocarp surface smooth with long and thin hairs. Locule surface slightly lacunate.

Genus ***Mappia*** Jacq.
Figs 17.10–17.26, 18.1–18.8

Description

Fruit. Elliptical to globose, laterally compressed, red when mature. Epicarp glabrous.

Endocarp. Cream, elliptical to globose in lateral view, lenticular in transverse section. Keel surrounding the endocarp in the plane of symmetry. Apex asymmetrical in lateral view; base symmetrical. Outer surface of the endocarp rugose, almost smooth. Vasculature of the endocarp generally resting between rugosities. Endocarp primary vascular bundle outside the endocarp wall. Endocarp wall with two layers, including layer with rows of periclinally oriented cells and another with rows of anticlinally oriented cells. Locule surface smooth, sometimes slightly lacunate.

Key to the genus *Mappia*

1. Endocarp surface quite smooth 2
– Endocarp surface rugose with channels and mounds ..... ***M. multiflora*** Lundell

2. Endocarp elliptical, without clear ridges ..... ***M. racemosa*** Jacq.
– Endocarp globose, short ridge at the apex ..... ***M. longipes*** Lundell

Mappia longipes Lundell
Fig. 17.10–17.18

Material examined

Specimen used for endocarp and fruit description
MEXICO • 1982; *M. Guillermo Ibarra 72*; U[U.1343380].

Description

Fruit. Globose, symmetrical at the apex. Epicarp smooth or slightly rugose when dry, revealing the endocarp faint rugosities. Mesocarp ca 350 µm thick when dry. Calyx persistent. Length 18.8 mm, width 14.7 mm, thickness 10.4 mm.

Endocarp. Globose in lateral view, length ca 15.8 mm, width ca 13.6 mm, thickness ca 10.2 mm. Keel surrounding the endocarp in the plane of symmetry, with a central channel. Base with a small rounded protuberance at the point of the base. Outer surface of the endocarp smooth with sparse rugosities randomly distributed, and short ridge beginning the apex and running transversally and subapically over 0.5 mm at the most. Vasculature of the endocarp free. Endocarp wall 714–809 µm thick. Endocarp wall with two cell layers: outermost layer with ca 17 rows of anticlinally oriented cells, cells 21.7–32.8 µm in length; innermost layer with 14 rows of periclinally oriented cells, cells 16.9–26.7 µm in width. Inner endocarp surface smooth, not lacunate.

Mappia multiflora Lundell
Fig. 17.19–17.26

Material examined

Specimen used for endocarp and fruit description
GUATEMALA • Cadenas, in low forest bordering Rio Sarstun; 18 Mar. 1967; *Contreras 6781*; U[U.1343381].

Description

Fruit. Elliptical, apex slightly acuminate and asymmetrical, length 14–26 mm, width 10–20 mm, thickness 10–13 mm.

Endocarp. Elliptical-globose in lateral view, length ca 16.4 mm, width ca 11.3 mm, thickness ca 9.3 mm. Channel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical and acute. Outer surface of the endocarp rugose, with ca 2–3 main longitudinal channels that separate irregular mounds. Vasculature of the endocarp resting in the channels, between rugosities. Endocarp wall 692–795 µm thick with and without rugosities. Endocarp wall with two cell layers: outermost layer with 13 rows of anticlinally oriented cells, cells 16.8–30.2 µm in length, innermost layer with 20 rows of periclinally oriented cells, cells 13.5–28.2 µm in width. Inner endocarp surface smooth, lacunate.

Mappia racemosa Jacq.
Fig. 18.1–18.8

Material examined

Specimen used for endocarp and fruit description
CUBA • Province of Pinar del Rio, Guanajay; 1904; *H.A. Van Hermann 250*; P[MNHN-P-P04513543].

Other material
CUBA • Sep. 1859–Jan. 1860; *C. Wright 1389*; P[MNHN-P-P04513544].

Description

Fruit. Elliptical or globose, asymmetrical at the apex, length 10–23 mm, width 8–11 mm, thickness 6–13 mm.

Endocarp. Elliptical in lateral view, length ca 12 mm, width ca 8.8 mm, thickness ca 6.9 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical and acute; base with small rounded protuberance at the point of the base. Outer surface of the endocarp rugose, irregular; rugosities distributed randomly at the surface. Vasculature of the endocarp free. Endocarp wall 373–468 µm thick excluding rugosities (535–545 µm thick including rugosities). Endocarp wall with two cell layers: outermost layer with 10–12 rows of anticlinally oriented cells, cells 15.7–34.0 µm in length; innermost layer with 10 rows of periclinally oriented cells, cells 13.8–19.8 µm in width. Locule surface smooth, not lacunate.

Genus ***Mappianthus*** Hand.-Mazz.

Description

See description of ***Mappianthus iodoides*** Hand.-Mazz., the only species of *Mappianthus* examined for this study.

Mappianthus iodoides Hand.-Mazz.
Fig. 18.9–18.17

Material examined

Specimen used for endocarp and fruit description

CHINA • Kwangsi Province; 15 Sep. 1933; *A.N. Steward & H.C. Cheo 1093*; P[MNHN-P-P04513538].

Other material

CHINA • Kouy-Tcheou Province; s.d.; *Cavalerie 1518*; P[MNHN-P-P05274868].

Des ion

Fruit. Elliptical, asymmetrical at the apex, red-green when mature. Epicarp strigose with yellow simple hairs with granular ornamentation, faintly rugose when dry, revealing the underlying endocarp rugosities.

Fig. 18. Fruits of Icacinaceae Miers. **1**–**8**. *Mappia racemosa* Jacq. (*H.A. Van Hermann 250*). **1**–**5**. Endocarp. **1**. Lateral view showing rough surface. **2**. Dorsal view showing a keel surrounding the endocarp. **3**. Opposite lateral view. **4**. Apical view. **5**. Basal view. **6**. SEM image of the endocarp wall in transverse section. **7**. Detail showing anticlinally oriented outer layer cells. **8**. Detail showing periclinally oriented inner layer cells. – **9**–**17**. *Mappianthus iodoides* Hand.-Mazz. (*A.N. Steward & H.C. Cheo 1093*). **9**. Broken dried fruit, lateral view. **10**–**14**. Endocarp. **10**. Lateral view showing the mounds. **11**. Dorsal view. **12**. Opposite lateral view. **13**. Apical view. **14**. Basal view. **15**. SEM image of a pericarp transverse section showing the channel with the vascular bundle. **16**. SEM image of the pericarp transverse section. **17**. SEM image of the papillae in the locule. – **18**–**23**. *Miquelia assamica* (Griff.) Mast. ex B.D.Jacks. (*Wight s.n.*). **18**–**19**. Endocarp. **18**. Lateral view showing the pits and ridges. **19**. Opposite lateral view. **20**. SEM image of the endocarp wall in transverse section. **21**. Detail showing the rows of cells in the endocarp wall. **22**. Other detail showing the bullate tubercle. **23**. SEM image of the inner part of the endocarp and the papillae in transverse section. Images taken from Del Rio (2018). Scale bars: 1–5, 9–14, 18–19 = 10 mm; 20 = 1 mm; 6, 15–16, 22 = 500 µm; 17, 21 = 300 µm; 7–8 = 100 µm; 23 = 50 µm.

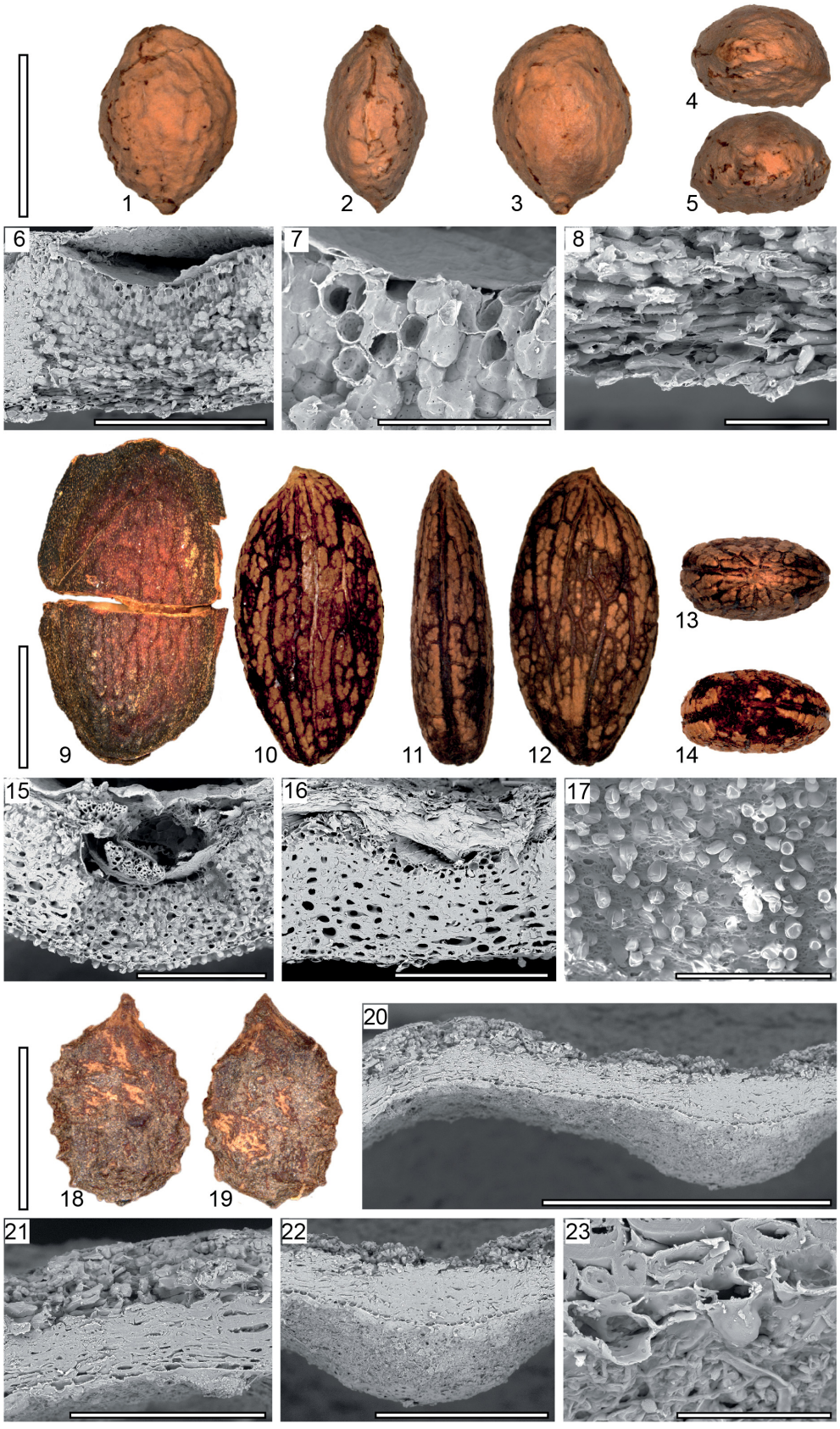

Fig. 18. (see full caption on page 52)

Mesocarp 100–200 µm thick when dry. Calyx persistent. Length 20–37 mm, width 10.0–17.7, thickness 4–8 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 25.5 mm, width ca 12.8 mm, thickness ca 6.9 mm. Channel surrounding the endocarp in the plane of symmetry. Apex asymmetrical, acute in lateral view; base rounded, symmetrical. Outer surface of the endocarp rugose with ca 73–91 mounds; mounds more or less square polygonal, each with more or less branched freely ending channel inside. Mounds organized in 5–6 longitudinal lines separated by four main longitudinal channels. The main channel on each face reaching a pore positioned subapically. Vasculature of the endocarp in the channels between mounds; primary vascular bundle half-embedded, positioned in the channel surrounding the endocarp. Endocarp wall 293–329 µm thick excluding mounds (484–496 µm thick including mounds). Endocarp wall with three cell layers: outermost layer with 1–4 rows of isodiametric, occasionally anticlinally oriented cells, cells 26–35 µm in length, followed by a layer with 7–10 rows of periclinally oriented cells, cells 24.6–29.0 µm in width; innermost layer with one row of periclinally oriented cells, cells 10.1–13.8 µm in width, lining the inner endocarp surface with regularly spaced and rounded papillae; papillae 21.9–30.6 µm (av. 25.6 µm) in diameter, ca 138 papillae per 0.25 mm^2. Locule lacunate.

Genus ***Miquelia*** Meisn.
Figs 18.18–18.23, 19.1–19.17

Description

Fruit. Ovoid to elliptical, with the apex occasionally acuminate, laterally compressed, red when mature. Epicarp strigose to puberulent with yellow simple hairs with granular ornamentation and uncinate hairs, more or less ridged when dry, revealing the underlying reticulum of endocarp ridges. Calyx persistent ,separated from the fruit by a gynophore.

Endocarp. Brown, elliptical to ovoid or partially globose in lateral view, lenticular in transverse section. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical in lateral view, with a subapical pore on each face, occasionally absent; base symmetrical. Outer surface of the endocarp pitted and ridged or rugose. Pits large, exclusively circular, organized in longitudinal lines. Pits associated with small, bullate tubercles protruding into the locule. Ridges thin to thick, forming a reticulate pattern, delimiting a few polygonal areoles. Vasculature of the endocarp resting on the ridges. Endocarp primary vascular bundle outside the endocarp wall. Endocarp wall with at least one layer with rows of periclinally oriented cells. Locule surface with regularly spaced and rounded papillae, occasionally lacunate, often hardly discernible.

Key to the genus *Miquelia*

1. Endocarp ovoid, ca 8 mm in length ..... ***M. celebica*** Blume
– Endocarp elliptic, >13.5 mm in length 2

2. Endocarp wall thick (>1 mm), 8–9 pits longitudinally ..... ***M. caudata*** King
– Endocarp wall thin (<0.2 mm), 3–4 pits longitudinally ..... ***M. assamica*** (Griff.) Mast. ex B.D.Jacks.

Miquelia assamica (Griff.) Mast. ex B.D.Jacks.
Fig. 18.18–18.23

Material examined

Specimen used for endocarp and fruit description

INDIA • 1871; *Wight s.n.*; K[sheet lacking barcode, same specimen series as K000700042]

Other material

INDONESIA • "Celebes" [Sulawesi]; P[MNHN-P-P04513530].

Description

Fruit. Elliptical, asymmetrical and acuminate at the apex. Epicarp glabrous, shrunken when dry, revealing the underlying reticulum of endocarp ridges. Length 9.0–13.5 mm, width 8.0–9.3 mm, thickness ca 5 mm.

Endocarp. Elliptical in lateral view, length ca 13.5 mm, width ca 8.9 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical, acute in lateral view, with apical hole in apical view. Outer surface of the endocarp pitted, ridged and rugose. Ridges large and rounded, faintly apparent, with three main longitudinal ridges delimiting a reticulate pattern enclosing a few polygonal areoles. Rugosities apparent on the ridges, mostly on the keeled margin and transversally oriented ridges. Pits large, 1–2 mm in diameter, exclusively circular, organized in longitudinal lines, 3–4 pits longitudinally and transversally (ca 12 pits per face). Pits associated with bullate tubercles, ca 240 µm in length inside the endocarp. Endocarp wall ca 182–210 µm thick (with and without ridges; the ridges are mainly formed by a fold of the wall rather than extra thickening). Endocarp wall with two cell layers: outermost layer with ca 12 rows of periclinally oriented cells, cells 13.4–28.0 µm in width; innermost layer with one row of periclinally oriented cells, cells 8.2–11.0 µm in width, covering the inner endocarp surface with regularly spaced and rounded papillae; papillae 13–18 µm (av. 16 µm) in diameter. Locule lacunate.

Miquelia caudata King

Fig. 19.1–19.8

Material examined

Specimen used for endocarp and fruit description

MALAYSIA • 26 Oct. 1988; *Othman S. 56069*; L[L.3807104] • Perak; 8 Dec. 1965; *Mohd, Shah & Sidek 1168*; L[L.2289517].

Description

Fruit. Elliptical, apex elongate. Epicarp strigose, with yellow simple hairs with granular ornamentation, shriveled when dry, faintly revealing the underlying endocarp ridges. Length 23–30 mm, width 13–18 mm, thickness 7–10 mm.

Endocarp. Elliptical in lateral view, length ca 17 mm, width ca 12.2 mm, thickness ca 8.2 mm. Apex slightly asymmetrical, acute in lateral view, with apical hole. Outer surface of the endocarp pitted and ridged. Ridges sharp and thin, with three main longitudinal ridges; the median ridge running from the point of the base up to ⅔ of the endocarp length, the two lateral ridges running from the point of the apex almost to the base, each connected with the keel by four transverse ridges enclosing three areoles. Pits large (0.4–1.2 mm in diameter), exclusively circular, organized in longitudinal lines, 8–9 pits longitudinally, ca 6 pits transversally with one pit between median ridge and lateral ridges, and two pits between lateral ridges and the keel (ca 44–48 pits per face). Pits associated with bullate tubercles, ca 302 µm in length inside the endocarp. Cellular details of endocarp wall unknown. Inner endocarp surface with regularly spaced and rounded papillae; papillae 13.2–18.0 µm (av. 15.9 µm) in diameter, ca 600–800 papillae per 0.25 mm^2. Locule lacunate.

Miquelia celebica Blume
Fig. 19.9–19.17

Material examined

Specimen used for endocarp and fruit description
INDONESIA • "Celebes" [Sulawesi], Tondano; 1923; *J.S.A. Kruiff 23*; L[L.2289530].

Other material
INDONESIA • "Celebes" [Sulawesi]; 1840; E.A. Forsten s.n.; L[L.0014929].

PHILIPPINES • *Ramos 80631*; K.

Description

Fruit. Ovoid. Epicarp strigose with yellow uncinate hairs, shriveled when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp 143–240 µm thick when dry. Length 8–17 mm, width 7–12 mm, thickness 6 mm.

Endocarp. Ovoid in lateral view, length ca 8 mm, width ca 7.8 mm, thickness ca 3 mm. Apex slightly asymmetrical, acute in lateral view, with subapical pore. Outer surface of the endocarp pitted and ridged. Ridges rounded and thin to thick, with three main longitudinal ridges; the median ridge running from the base up to ⅔ of the endocarp length, the two lateral ridges running from the apex almost to the base. The two lateral ridges are each connected with some transverse ridges; transverse ridges free or connected with the keel. Pits large (0.4–0.9 mm in diameter), exclusively circular and organized in longitudinal lines, 3–5 pits longitudinally, 4 pits transversally with one pit between median ridge and lateral ridges, and one pit between lateral ridges and the keel (ca 17–19 pits per face). Pits associated with bullate tubercles, ca 400 µm in length inside the endocarp. Endocarp wall ca 170–270 µm thick (with and without ridges; the ridges are mainly formed by a fold of the wall rather than by extra thickening). Endocarp wall with three cell layers: outermost layer with 2–4 rows of isodiametric cells, cells 13.0–22.7 µm in diameter, followed by a layer with ca 5 rows of periclinally oriented cells, cells 8.5–17.7 µm in width; innermost layer with one row of periclinally oriented cells, cells 8.6–15.4 µm in width, covering the inner endocarp surface with regularly spaced and rounded papillae; papillae 12.6–16.0 µm (av. 14 µm) in diameter. Locule lacunate.

Fig. 19. Fruits of Icacinaceae Miers. **1**–**8**. *Miquelia caudata* King (*Mohd, Shah & Sidek 1168*). **1**. Dried fruit with acuminate apex and an elongate gynophore (here broken), lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing ridges and pits. **3**. Dorsal view showing a keel surrounding the endocarp. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the bullate tubercle in the locule. **8**. SEM image of the papillae on the tubercle surface. – **9**–**17**. *Miquelia celebica* Blume (*J.S.A. Kruiff 23*). **9**. Dried fruit with an elongate gynophore, lateral view. **10**–**14**. Endocarp. **10**. Lateral view showing ridges and pits. **11**. Dorsal view showing a keel surrounding the endocarp. **12**. Opposite lateral view. **13**. Apical view. **14**. Basal view. **15**. SEM image of the pericarp in transverse section showing a ridge. **16**. SEM image of the pericarp in transverse section showing the bullate tubercle. **17**. SEM image of the inner part of the endocarp in transverse section showing papillae. – **18**–**26**. *Natsiatum herpeticum* Buch.-Ham. ex Arn. (*H.B. Cale s.n.*). **18**. Broken dried fruit, lateral view. **19**–**23**. Broken endocarp. **19**. Lateral view showing the ridges. **20**. Dorsal view showing a keel surrounding the endocarp. **21**. Opposite lateral view. **22**. Apical view. **23**. Basal view. **24**. SEM image of the pericarp in transverse section showing the channel with the vascular bundle (arrow). **25**. SEM image of the pericarp in transverse section showing the ridge. **26**. Detail showing cells of the endocarp. Images taken from Del Rio (2018). Scale bars: 1–6, 9–14, 18–23 = 10 mm; 15, 24 = 1 mm; 7, 16, 25 = 500 µm; 26 = 200 µm; 8, 17 = 50 µm.

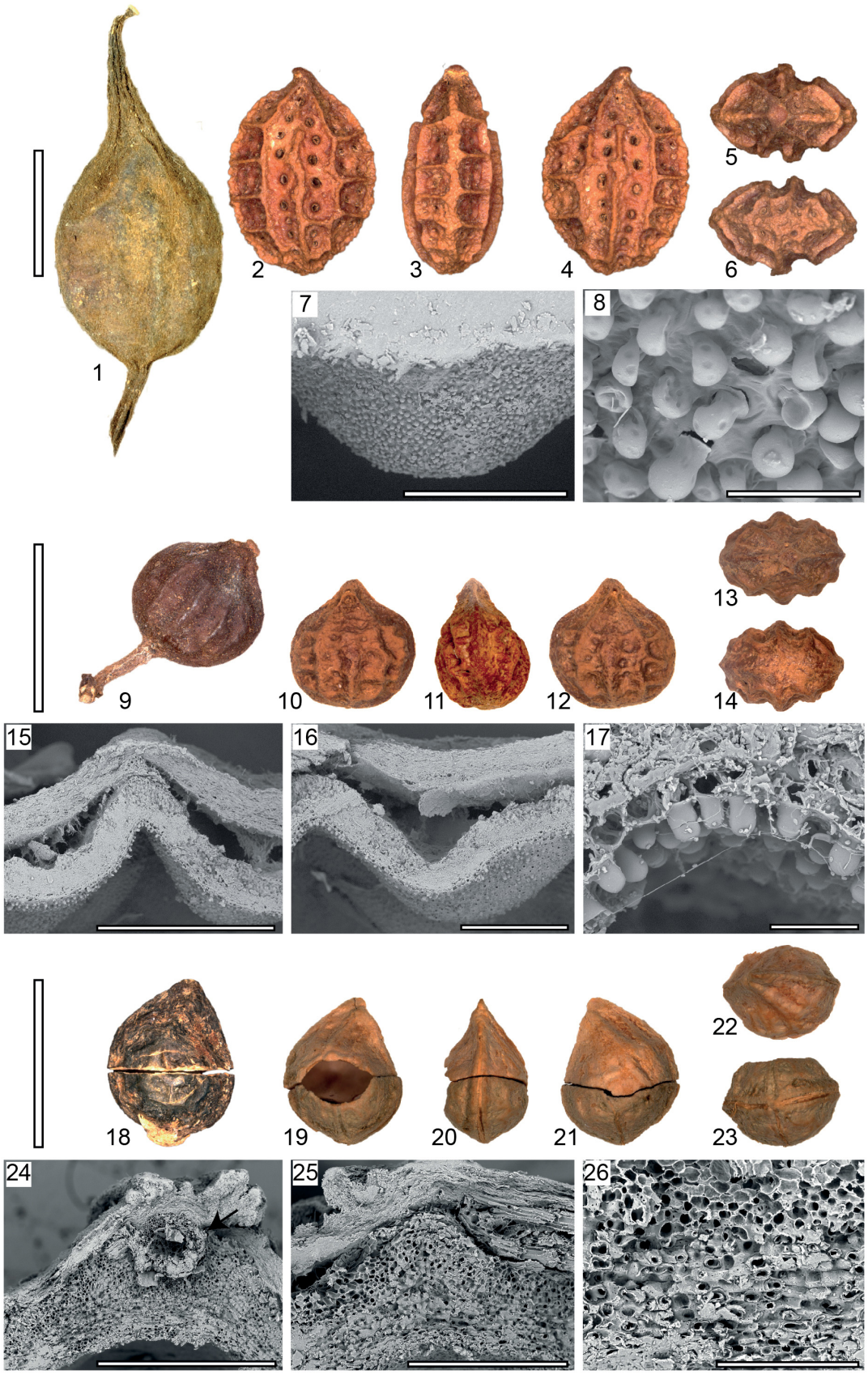

Fig. 19. (see full caption on page 56)

Genus ***Natsiatum*** Buch.-Ham. ex Arn.

Description

See description of *Natsiatum herpeticum* Buch.-Ham. ex Arn, the sole member of this genus.

Natsiatum herpeticum Buch.-Ham. ex Arn.
Fig. 19.18–19.26

Material examined

Specimen used for endocarp and fruit description
CHINA • 1903; *H.B. Cale s.n.*; P[MNHN-P-P04513511].

Description

Fruit. Elliptical to ovoid, apex slightly asymmetrical, black when mature. Epicarp strigose, with yellow simple hairs with granular ornamentation. Mesocarp 98–126 µm thick when dry. Calyx persistent. Length 10.2–15.0 mm, width 7.6–10.0 mm, thickness 5.6 mm.

Endocarp. Cream, elliptical to ovoid in lateral view, lenticular in transverse section, length ca 9 mm, width ca 7 mm, thickness ca 5.1 mm. Keel surrounding the endocarp in the plane of symmetry, with a central channel. Apex asymmetrical and acute in lateral view; base rounded, symmetrical. Outer surface of the endocarp ridged, ridges faintly apparent, with at least two main longitudinal ridges; the median ridge reaching the point of the base. Ridges thin and rounded, with a median channel, delimiting a sparse reticulum with only 3–4 polygonal areoles visible. Vasculature resting in the channels of the ridges; endocarp primary vascular bundle semi-embedded within the endocarp wall in the channel of the keel. Endocarp wall 280–370 µm thick excluding ridges (432–531 µm thick including ridges). Endocarp wall with two cell layers: outermost layer with 0–3 row(s) of isodiametric cells (mesocarp-endocarp cell transition), cells 15.1–19.7 µm in diameter; innermost layer with 12–16 rows of periclinally oriented cells, cells 12.7–21.5 µm in width. Locule surface unknown, lacunate.

Remarks

A figure from Stull *et al.* (2011) shows the endocarp of *Natsiatum herpeticum* Buch.-Ham. ex Arn. better preserved with more areoles and freely ending ridgelets than seen here. We speculate that the development of the endocarp in our sample was halted, or the endocarp was decayed by fungal attacks (see Discussion for preservation issues).

Genus ***Nothapodytes*** Blume
Fig. 20.1–20.18

Description

Fruit. Elliptical to almost oblong, asymmetrical at the apex, laterally compressed, red-black when mature. Epicarp strigose, with yellow simple hairs with granular ornamentation, shriveled when dry, revealing the underlying endocarp rugosities. Calyx persistent.

Endocarp. Cream to brown, elliptical to oblong in lateral view, lenticular to globose in transverse section. Channel surrounding the endocarp in the plane of symmetry. Apex asymmetrical in lateral view, with a subapical bulge; base symmetrical. Outer surface of the endocarp rugose, irregular. Vasculature of the endocarp resting between the rugosities. Primary vascular bundle positioned in the channel in the plane of symmetry or outside the endocarp wall. Endocarp wall composed of periclinally oriented cells. Locule surface smooth, not lacunate.

Key to the genus *Nothapodytes*

1. Endocarp oblong, globose in transverse section, endocarp wall >200 µm thick .....
.....***N. nimmoniana*** (J.Graham) Mabb.
– Endocarp elliptical, lenticular in transverse section, endocarp wall <200 µm thick .....
.....***N. pittosporoides*** (Oliv.) Sleumer

Nothapodytes nimmoniana (J.Graham) Mabb.
Fig. 20.1–20.9

Material examined

Specimen used for endocarp and fruit description
SRI LANKA • "Ceylon", Kandy District, E of Madugoda; 30 Apr. 1975; *A.H.H. Jayasuriya 1922*; L[L.2289443].

Other material
SRI LANKA • "Ceylan"; s.d.; *Thwaites 492*; P[MNHN-P-P04513579].

INDIA • Tamil Nadu, Nilgiri; s.d.; Hook. fil. & *Thomson 359*; P[MNHN-P-P04513576].

Description

Fruit. Oblong; mesocarp 108–189 µm thick when dry. Length 10–20 mm, width 6–10 mm, thickness 3.0–7.3 mm.

Endocarp. Brown, oblong in lateral view, globose in transverse section, length ca 14 mm, width ca 7.2 mm, thickness ca 6.6 mm. Rugosities extended longitudinally, organized in 3–4 longitudinal lines, separated by 3–4 main longitudinal channels. Endocarp wall 208–295 µm thick excluding the rugosities (336 µm thick including rugosities). Endocarp wall with ca 16 rows of periclinally oriented cells, cells 11.6–23.7 µm in width.

Nothapodytes pittosporoides (Oliv.) Sleumer
Fig. 20.10–20.18

Material examined

Specimen used for endocarp and fruit description
CHINA • s.d.; *s. col. 4118*; P[MNHN-P-P04513559].

Other material
CHINA • 1907; *J. Cavalerie 3164*; P[MNHN-P-P04449925].

Description

Fruit. Elliptical; mesocarp 72–129 µm thick when dry. Length 10–20 mm, width 6–9 mm, thickness 4.0–6.7 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 10.7 mm, width ca 7.3 mm, thickness ca 6.7 mm. Channel surrounding the endocarp in the plane of symmetry. Rugosities extended longitudinally, organized in 3–4 longitudinal lines, separated by 3–4 main longitudinal channels. Endocarp wall 164–197 µm thick excluding rugosities. Endocarp wall with ca 7–8 rows of periclinally oriented cells, cells 14.2–26.8 µm in width.

Genus ***Phytocrene*** Wall.
Figs 20.19–20.26, 21–22

Description

Fruit. Elliptical to oblong, symmetrical to highly asymmetrical and accrescent at the apex, laterally compressed, yellow-red when mature. Epicarp pilose, with clusters of yellow to red hairs or long and thin hairs. Calyx persistent or absent.

Endocarp. Brown to cream, elliptical to ovoid in lateral view, occasionally obovoid, lenticular to elliptical in transverse section. Keel surrounding the endocarp in the plane of symmetry in some species. Apex asymmetrical in lateral view; base symmetrical. Outer surface of the endocarp pitted, occasionally ridged or rugose, irregular. Pits associated with shallow mounds, narrow or polygonal in shape, not protruding beyond the endocarp wall. Endocarp possessing a symmetrical pair of pores, positioned eccentrically and subapically on the endocarp faces. Endocarp primary vascular bundle positioned outside the endocarp wall. Endocarp wall with two layers, one layer with rows of periclinally oriented cells and another with rows of anticlinally oriented cells. Locule surface smooth, generally not lacunate.

Key to the genus *Phytocrene*

1. Pits broad, concave 2
– Pits narrow 3

2. Endocarp ca 14 mm in length, endocarp wall thin (114–154 μm thick), pits with a median freely ending ridge or central dimple ..... ***P. anomala*** Merr.
– Endocarp ca 26 mm in length, endocarp wall thick (542–591 μm thick), pits without a freely ending ridge ..... ***P. oblonga*** Wall.

3. Endocarp clearly ridged ..... ***P. hirsuta*** Blume
– Endocarp not ridged 4

4. Pits 60–65 on each face ..... ***P. bracteata*** Wall.
– Pits >90 on each face 5

5. Endocarp 40–60 mm in length, oblong ..... ***P. macrophylla*** (Blume) Blume
– Endocarp <40 mm in length, not oblong 6

Fig. 20. Fruits of Icacinaceae Miers. **1**–**9**. *Nothapodytes nimmoniana* (J. Graham) Mabb. (*A.H.H. Jayasuriya 1922*). **1**. Dried fruit, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing the roughness. **3**. Dorsal view of the endocarp with a channel. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the pericarp in transverse section. **8**. Detail showing the inner part of the endocarp cells. **9**. Other detail showing the outer part of the endocarp cells. – **10**–**18**. *Nothapodytes pittosporoides* (Oliv.) (*s. col. 4118*). **10**. Dried fruit, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing the roughness. **12**. Dorsal view of the endocarp with a channel. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of a pericarp transverse section showing the vascular bundle in a channel. **17**. SEM image of a pericarp transverse section with a vasculature between mesocarp and endocarp. **18**. SEM image of the endocarp cells in transverse section. – **19**–**26**. *Phytocrene anomala* Merr. (*M. Ramos 1840*). **19**. Dried fruit with an accrescent apex, lateral view. **20**–**25**. Endocarp. **20**. Lateral view showing the pits in broad, concave pits. **21**. Dorsal view. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. SEM image of the endocarp showing a pit in transverse section. **26**. SEM image of the endocarp wall in transverse section. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–24 = 10 mm; 7, 16–17, 25 = 500 μm; 18 = 300 μm; 8–9 = 200 μm; 26 = 100 μm.

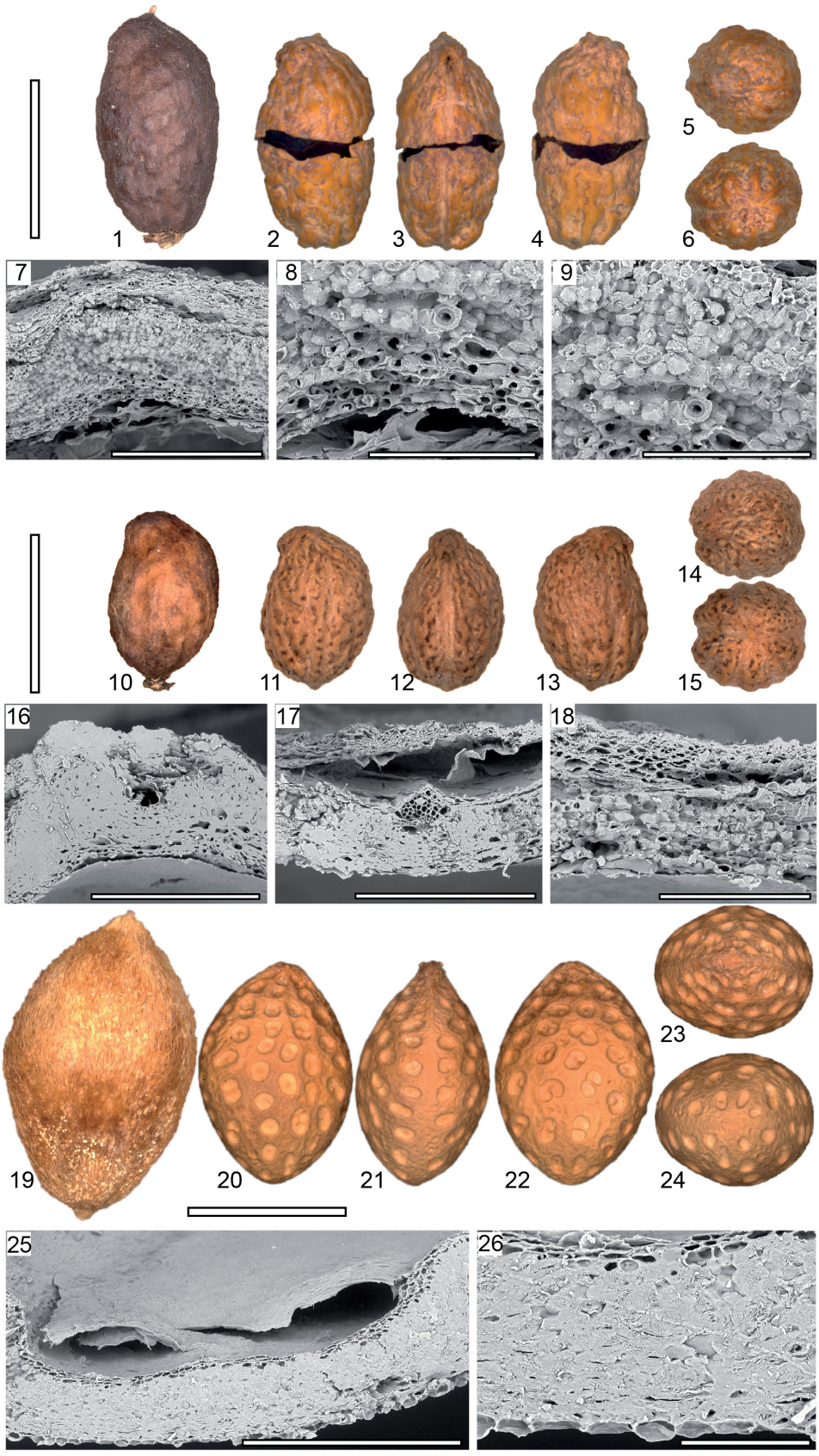

Fig. 20. (see full caption on page 60)

6. Endocarp obovoid, 125–130 pits per face .....***P. borneensis*** Becc.
– Endocarp ovoid, 168–178 pits per face .....***P. palmata*** Wall.

Phytocrene anomala Merr.
Fig. 20.19–20.26

Material examined

Specimen used for endocarp and fruit description
BORNEO • 1920; *M. Ramos 1840*; L[L.2289425].

MALAYSIA • 18 Jun. 1986; *Patrick et al. SAN 118639*; K[K000183648].

Description

Fruit. Elliptical, slightly asymmetrical and accrescent at the apex, yellow-orange when mature. Epicarp with clusters of yellow hairs. Calyx persistent. Length 20–25 mm, width 11–15 mm, thickness 8.0–10.1 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 14.4 mm, width ca 10 mm, thickness ca 6 mm. Marginal keel encircling the endocarp in the plane of symmetry, lacking except for a thin trace observable in the upper part. Apex slightly asymmetrical and acute in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted. Pits circular to elongate (concave area), ca 0.8–1.7 mm in diameter, representing most of the surface of the endocarp, more or less organized longitudinally with ca 8–10 pits longitudinally and 6–7 pits transversally (ca 35–45 pits per face). Each pit with a central dimple or one freely ending ridge inside. Pits without tubercles. Endocarp wall ca 330 µm thick excluding pits (114–154 µm thick including pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with 3–5 rows of anticlinally oriented cells, cells 12.3–24.5 µm in length; middle layer with 9–10 rows of periclinally oriented cells, cells 10.2–14.2 µm in width; innermost layer with a single row of periclinally oriented cells, cells 13.0–20.7 µm in width, lining the locule surface with inflated cells. Locule with slightly rounded protuberances due to the thickening of the wall under the pits.

Phytocrene borneensis Becc.
Fig. 21.1–21.8

Material examined

Specimen used for endocarp and fruit description
MALAYSIA • Borneo, Sarawak; 8 Jul. 1979; *B. Lee S.40246* ; L[L.2289394].

Description

Fruit. Obovoid, slightly asymmetrical and widely acuminate at the apex, yellow-brown when mature. Epicarp with clusters of yellow hairs. Mesocarp thin but thick at the accrescent part when dry. Calyx not persistent. Length ca 56 mm, width ca 14 mm.

Endocarp. Brown, obovoid in lateral view, lenticular in transverse section, length ca 39.1 mm, width ca 17.3 mm, thickness ca 9 mm. No clear keel surrounding the endocarp in the plane of symmetry, but thin trace of keel present in the upper part. Apex asymmetrical and emarginate in lateral view; base acute, symmetrical. Outer surface of the endocarp pitted. Pits circular in the upper half and more elongate in the lower half of the endocarp, relatively thin, 0.2–0.4 mm in width, randomly arranged with ca 12–13 pits longitudinally and 10–11 pits transversally (ca 125–130 pits per face). Pits narrow, without tubercles. Endocarp wall 681–766 µm thick excluding pits (307–351 µm thick including pits). Endocarp

wall (excluding pits), with three cell layers: outermost layer with ca 16 rows of anticlinally oriented cells, cells 32.8–45.7 µm in length, followed by a layer with ca 9 rows of periclinally oriented cells, cells 14.5–24.0 µm in width; innermost layer consist of periclinally oriented cells, cells 9.7–11.4 µm in width, lining the locule surface with inflated cells. Locule covered with rounded protuberances due to the thickening of the wall under the pits.

Phytocrene bracteata Wall.
Fig. 21.9–21.16

Material examined

Specimen used for endocarp and fruit description
MALAYSIA • s.d.; *W.S. Kurz s.n.*; P[MNHN-P-P00868411].

Other material
MALAYSIA • "British North Borneo, Elphinstone Province", Tawao; Oct. 1922–Mar. 1923; *A.D.E. Elmer 21444*; P[MNHN-P-P04513389].

Description

Fruit. Ovoid with a symmetrical and elongate apex, yellow-brown when mature. Epicarp with clusters of yellow hairs. Mesocarp thin, but thick at the accrescent part when dry. Calyx not persistent. Length 45–80 mm, width 15–23 mm, thickness 10.0–11.6 mm.

Endocarp. Brown, ovoid in lateral view, lenticular in transverse section, length 30.5–40.0 mm, width 16.4–20.0 mm, thickness 11–15 mm. No clear keel surrounding the endocarp in the plane of symmetry, but thin trace of keel present in the upper part. Apex slightly asymmetrical and emarginated in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and faintly ridged. Pits circular, occasionally elongate, relatively thin, 0.3–0.6 mm in diameter, randomly arranged with ca 11–12 pits longitudinally and 5–7 pits transversally (ca 60–65 pits per face). Pits narrow, without tubercles. Ridges faintly apparent, rounded, delimiting a pseudo-reticulum enclosing numerous areoles on the endocarp surface. Endocarp wall 615–684 µm thick (ridges height insignificant, ca 250 µm including pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with 10–11 rows of anticlinally oriented cells, 22.0–38.0 µm in length, followed by a layer with 17–18 rows of periclinally oriented cells, cells 11.7–21.9 µm in width; innermost layer with one row of periclinally oriented cells, cells 4.3–7.3 µm in width, lining the locule surface with inflated cells. Locule with rounded protuberances due to the thickening of the wall under the pits.

Phytocrene hirsuta Blume
Fig. 21.17–21.24

Material examined

Specimen used for endocarp and fruit description
INDONESIA • "Celebes" [Sulawesi]; 1874; *O. Beccari HB.2497/98*; L[L.2289338].

Description

Fruit. Elliptical, with a symmetrical and elongate apex, red when mature. Epicarp with clusters of yellow-red hairs. Mesocarp thin, but thick at the accrescent part when dry. Calyx not persistent. Length 30–45 mm, width 15–20 mm, thickness 15–16 mm.

Endocarp. Brown, elliptical in lateral view, lenticular in transverse section, length 20–35 mm, width ca 16 mm, thickness ca 11 mm. No clear keel surrounding the endocarp in the plane of symmetry, but trace

of keel present in the upper part. Apex asymmetrical, slightly emarginate in lateral view; base rounded and symmetrical. Outer surface of the endocarp pitted and ridged. Pits circular, thin, 0.4–0.8 mm in diameter, randomly arranged with ca 13–14 pits longitudinally and 8–11 pits transversally (ca 145–150 pits per face). Pits mainly narrow, occasionally capitate, without tubercles. Ridges large and flattened, diffuse, with three main ridges longitudinally (8–10 counting all longitudinal ridges); the median ridge reaching a subbasal area and spanning to the ⅔ of the endocarp length; the two adjacent ridges running from the apex and interconnected together at the location of the subapical pore, and becoming diffuse and faintly apparent in the middle of the endocarp length with some transverse and longitudinal freely ending ridgelets. Endocarp wall 1035–1055 µm thick excluding pits. Detail of wall unknown. Locule surface with inflated cells. Locule with rounded protuberances due to the thickening of the wall under the pits.

Phytocrene macrophylla (Blume) Blume
Fig. 22.1–22.9

Material examined

Specimen used for endocarp and fruit description
MALAYSIA • Borneo; Nov.–Dec. 1931; *J. & M.S. Clemens 26544 Bis*; L[L.2289632].

Other material
PHILIPPINE • 1916; *A.D.E. Elmer 15960*; P[MNHN-P-P04513397].

Description

Fruit. Elliptical, with a symmetrical and elongate apex, red when mature. Epicarp with clusters of yellow-red hairs. Mesocarp 330–400 µm thick, but thicker at the accrescent part when dry. Calyx not persistent. Length 55–130 mm, width 19–30 mm.

Endocarp. Cream, oblong in lateral view, lenticular in transverse section, length 40–60 mm, width 13.3–25.0 mm, thickness 8–20 mm. No clear keel surrounding the endocarp in the plane of symmetry, but with a trace of keel present in the upper part. Apex asymmetrical, emarginate in lateral view; base acute, slightly asymmetrical. Outer surface of the endocarp pitted and ridged. Pits primarily longitudinally elongate, occasionally two pits are merged, 0.4–1.0 mm in diameter, more or less longitudinally arranged, with ca 11–12 pits longitudinally and 7–9 pits transversally (ca 90–105 pits per face). Pits shortly rounded, without tubercles. Ridges rounded, limited to two lateral ridges, not branched, only present in the upper third (apical end) of the endocarp length. The two lateral ridges reaching the apex

Fig. 21. Fruits of Icacinaceae Miers. **1**–**8**. *Phytocrene borneensis* Becc. (*B. Lee S.40246*)**. 1**. Dried fruit with a widely accrescent apex, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing the pits. **3**. Dorsal view. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of endocarp wall in transverse section. **8**. SEM image of the narrow pit in transverse section. – **9**–**16**. *Phytocrene bracteata* Wall. (*W.S. Kurz s.n.*). **9**. Dried fruit with a widely accrescent apex, lateral view. **10**–**14**. Broken endocarp. **10**. Lateral view showing the reticulation and pits. **11**. Dorsal view. **12**. Opposite lateral view. **13**. Apical view. **14**. Basal view. **15**. SEM image of the endocarp wall in transverse section. **16**. SEM image of the narrow pit in transverse section. – **17**–**24**. *Phytocrene hirsuta* Blume (*O. Beccari HB.2497/98*). **17**. Dried fruit with a widely accrescent apex, lateral view. **18**–**22**. Endocarp. **18**. Lateral view showing the pits and ridges. **19**. Dorsal view. **20**. Opposite lateral view. **21**. Apical view. **22**. Basal view. **23**. SEM image of the endocarp wall in transverse section. **24**. SEM image of the narrow pit in transverse section, here enlarged towards the locule. Images taken from Del Rio (2018). Scale bars: 1–6, 9–14, 17–22 = 10 mm; 7–8, 15–16, 23–24 = 500 µm.

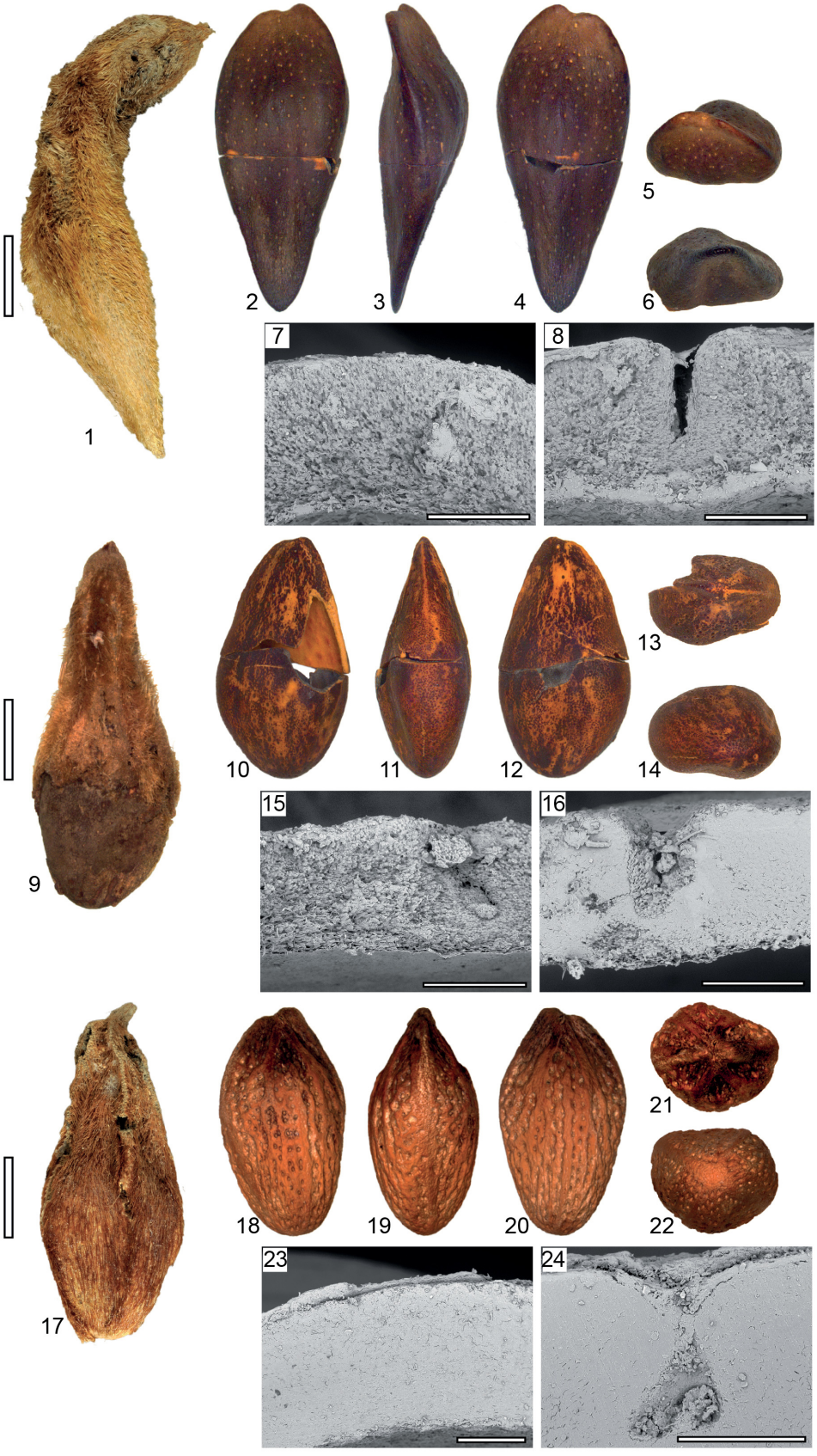

Fig. 21. (see full caption on page 62)

at the location of the subapical pore. Endocarp wall 550–660 µm thick excluding pits (285 µm thick including pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with ca 10–16 rows of anticlinally oriented cells, cells 15.5–23.3 µm in length, followed by a layer with ca 13–19 rows of periclinally oriented cells, cells 10.5–12.6 µm in width; innermost layer with one row of periclinally oriented cells, cells 8.2–9.02 µm in width, lining the locule surface with inflated cells. Locule with rounded protuberances due to the thickening of the wall under the pits.

Phytocrene oblonga Wall.
Fig. 22.10–22.18

Material examined

Specimen used for endocarp and fruit description
COUNTRY UNKNOWN • s. loc.; s.d.; *s. col. s.n.*; P.

Other material
VIETNAM • "Indochine", Annam; 4 Jun. 1920; *A. Chevalier 1499*; P[MNHN-P-P04513413].

Description

Fruit. Obovoid, symmetrical and elongated at the apex, red when mature. Epicarp with yellow long and thin hairs. Mesocarp thin but thicker in the accrescent part when dry. Calyx not persistent. Length 30–44 mm, width 15.0–25.0 mm, thickness 9–10 mm.

Endocarp. Brown, elliptical to oblong in lateral view, lenticular in transverse section, length ca 26.5 mm, width ca 12.3 mm, thickness ca 7 mm. No clear keel surrounding the endocarp in the plane of symmetry. Apex asymmetrical in lateral view; base rounded, slightly symmetrical. Outer surface of the endocarp pitted. Pits elongate longitudinally (concave area), ca 1.4–2.8 mm in length, representing most of the surface of the endocarp, organized longitudinally with ca 12 pits longitudinally and 7–12 pits transversally (ca 81–105 pits per face). Pits without tubercles. Endocarp wall ca 542–591 µm thick excluding pits (ca 200 µm thick including pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with ca 17 rows of anticlinally oriented cells, cells 10.3–19.3 µm in length, followed by a layer with ca 4 rows of periclinally oriented cells, cells 13.9–18.6 µm in width; innermost layer with one row of periclinally oriented cells, cells 17.0–29.8 µm in width, lining the locule surface with the inflated cells. Locule with rounded protuberances due to the thickening of the wall under the pits.

Fig. 22. Fruits of Icacinaceae Miers. **1**–**9**. *Phytocrene macrophylla* (Blume) Blume (*J. & M.S. Clemens 26544 Bis*). **1**. Dried fruit with an accrescent apex, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing the pits. **3**. Dorsal view. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of pericarp in transverse section. **8**. SEM image of the endocarp showing a narrow pit in transverse section. **9**. SEM image of the cluster of hairs on the epicarp surface. – **10**–**18**. *Phytocrene oblong*a Wall. (*s. col. s.n.*; P). **10**. Dried fruit with an accrescent apex, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing the broad, concave pits. **12**. Dorsal view. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of the endocarp showing a pit in transverse section. **17**. SEM image of the endocarp wall in transverse section. **18**. SEM image of inflated cells on the locule surface. – **19**–**26**. *Phytocrene palmata* Wall. (*Jacobs 8155*). **19**–**23**. Broken endocarp. **19**. Lateral view showing the pits. **20**. Dorsal view showing the keel. **21**. Opposite lateral view. **22**. Apical view. **23**. Basal view. **24**. SEM image of the endocarp in transverse section **25**. SEM image of the endocarp in transverse section showing a narrow pit. **26**. Detail showing cells on and around the pit. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–23 = 10 mm; 7–9, 16, 24–25 = 500 µm; 26 = 200 µm; 17–18 = 100 µm.

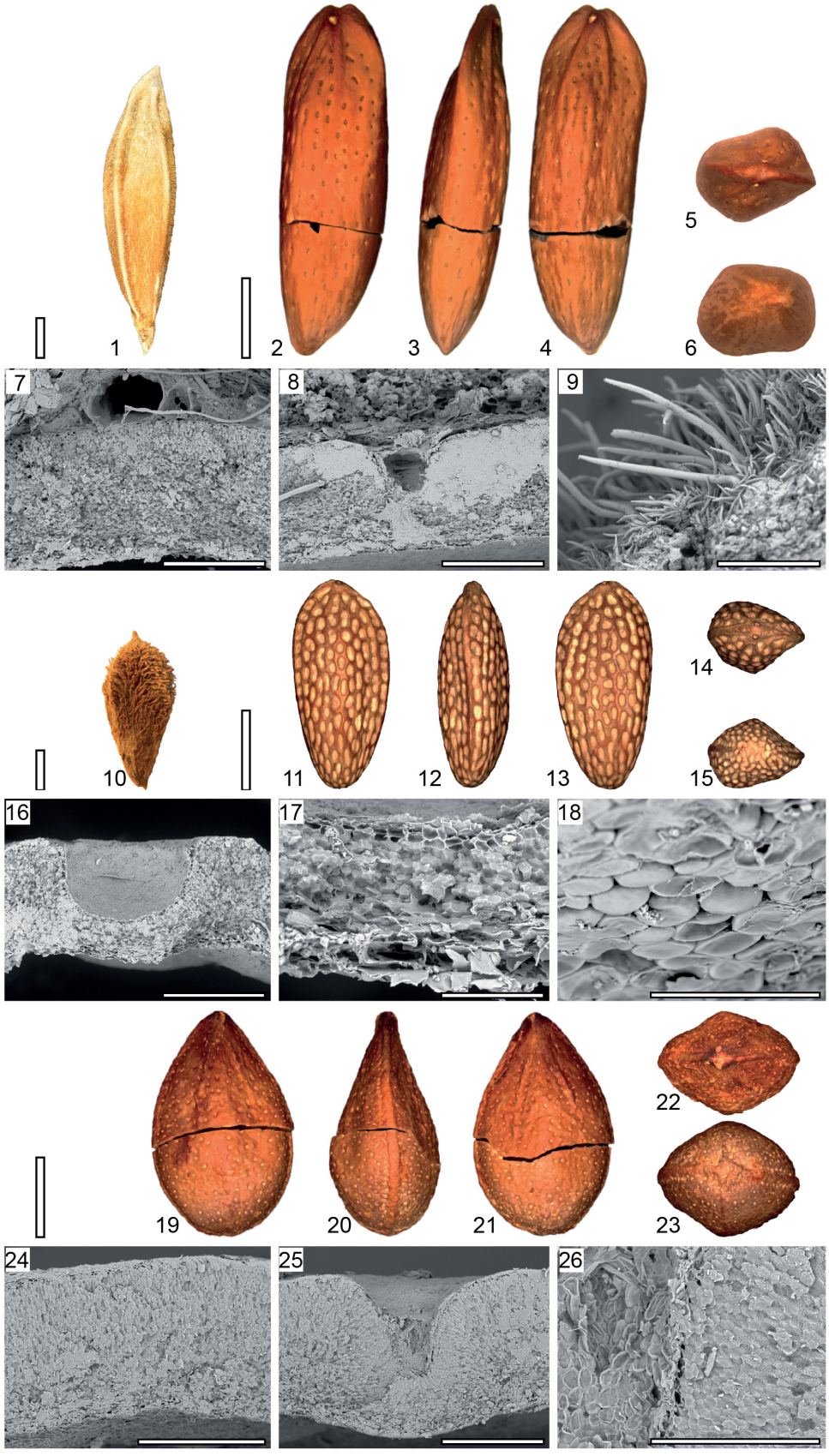

Fig. 22. (see full caption on page 66)

Phytocrene palmata Wall.
Fig. 22.19–22.26

Material examined

Specimen used for endocarp and fruit description
SUMATRA • 3 Apr. 1968; *Jacobs 8155*; L[L.2289602].

Description

Fruit. Ovoid, slightly asymmetrical and elongate at the apex, yellow when mature. Epicarp with clusters of hairs. Mesocarp thin, but thicker in the accrescent part when dry. Calyx not persistent. Length 35–55 mm, width 16–25 mm, thickness ca 13 mm.

Endocarp. Brown, ovoid in lateral view, lenticular in transverse section, length ca 29.3 mm, width ca 18 mm, thickness ca 13 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and faintly ridged. Pits circular, occasionally elongate, thin, 0.3–0.8 mm in diameter, randomly arranged with ca 11–13 pits longitudinally and 8–11 pits transversally (ca 168–178 pits per face). Pits narrow and shortly rounded, without tubercles. Ridges rounded, limited to two laterals ridges, not branched, only present in the apical third to half of the endocarp length. The two lateral ridges reaching the apex at the location of the pore, with one on each face. Endocarp wall 594–627 µm thick excluding pits (300–400 µm thick including pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with ca 14 rows of anticlinally oriented cells, cells 22.3–34.6 µm in length, followed by a layer with ca 5 rows of periclinally oriented cells, cells 15.8–22.9 µm in width; innermost layer with one row of periclinally oriented cells, cells ca 11 µm in width, lining the locule surface with inflated cells. Locule with rounded protuberances due to the thickening of the wall under the pits.

Genus ***Pleurisanthes*** Baill.

Description

See description of *Pleurisanthes flava* Sandwith, the only species of *Pleurisanthes* examined for this study.

Pleurisanthes flava Sandwith
Fig. 23.1–23.9

Material examined

Specimen used for endocarp and fruit description
GUYANA • Potaro-Siparuni; 1987; *J.J. Pipoly 10168*; P[MNHN-P-P05279044].

Description

Fruit. Elliptical, acuminate and slightly elongate at the apex, red when mature. Epicarp puberulent, with small ovoid hairs with an acuminate apex, rugose-ridged when dry, revealing the underlying endocarp ornamentation. Mesocarp 131–163 µm thick when dry. Calyx not persistent. Length 11.0–12.7 mm, width 9.0–10.2 mm, thickness 8.0–8.5 mm.

Endocarp. Cream, tomentose with long simple hairs forming a distinct ‘layer’ in transversal view ca 200 µm thick, elliptical in lateral view, lenticular to globose and folded in transverse section, length ca 11.6 mm, width ca 10.2 mm, thickness ca 8.6 mm. Channel surrounding the endocarp in the plane of symmetry. Apex asymmetrical in lateral view, with a central pit in apical view; base rounded,

symmetrical. Outer surface of the endocarp rugose with some elongate and large mounds organized in 4–5 longitudinal lines separated by four channels. Vasculature resting in the channels. Endocarp primary vascular bundle in the channel surrounding the endocarp. Endocarp wall 260–353 µm thick with and without mounds (the rugosities of the endocarp surface are formed by folds in the wall rather than thickenings). Endocarp wall with two cell layers: outermost layer with 6–7 rows of anticlinally oriented cells, cells 24.7–57.2 µm in length; innermost layer with 2–3 rows of periclinally oriented cells, cells 9.5–17.3 µm in width. Locule smooth, highly lacunate.

Genus ***Pyrenacantha*** Hook.
Figs 23.10–23.27, 24–30, 31.1–31.9

Description

Fruit. Elliptical to globose, apex accrescent elongate, sometimes widely inflated, laterally compressed or not, yellow to black when mature. Epicarp puberulent to pilose, with simple hairs, small ovoid hairs with an acuminate apex, long and thin hairs, or uncinate hairs, yellow, occasionally red or white; occasionally shriveled when dry, revealing the underlying reticulum of endocarp ridges. Calyx absent or persistent, often separated from the fruit by more or less extended gynophore.

Endocarp. Brown to cream, elliptical-ovoid to globose, rarely deltoid in lateral view, lenticular to globose in transverse section. Keel, more or less visible, surrounding the endocarp in the plane of symmetry. Apex asymmetrical in lateral view; base symmetrical. Outer surface of the endocarp pitted and ridged, with the ridges delimiting a reticulate pattern, which in general surrounds the pits. Sometimes the ridges are not visible except at the apex. Pits more or less circular, in longitudinal lines or randomly distributed, each pit associated with a tubercle protruding into the locule; tubercles spiny, peg-shaped, cylindrical, or elongate-flattened. Vasculature of the endocarp free; primary vascular bundle positioned outside the endocarp wall. Endocarp wall mainly with three stratified cell layers. Locule surface often with regularly spaced and rounded to large papillae, occasionally only present at the apex of the tubercles, smooth in some cases, not clearly lacunate.

Key to the genus *Pyrenacantha*

1. Endocarp elliptical-ovoid, obovoid or globose in lateral view 2
– Endocarp deltoid in lateral view ..... ***P. macrocarpa*** (A.Chev. ex Hutch. & Dalziel) Byng & Utteridge

2. Tubercles ≤ 1 mm long, elongate-flattened or peg-shaped 3
– Tubercles > 1 mm long, spiny or cylindrical 4

3. Tubercles peg-shaped 5
– Tubercles elongate-flattened 6

4. Tubercles spiny 7
– Tubercles cylindrical 8

5. Locule surface smooth, tubercles capitate at the apex, often bifid ..... ***P. klaineana*** Pierre ex Exell & Mendonça
– Locule surface with papillae, tubercles not capitate or bifid at the apex 9

6. Endocarp ovoid to globose in lateral view, fewer than 50 pits per face 10
– Endocarp elliptical to obovoid, more than 50 pits per face 11

7. Pits small, up to 400 µm in diameter 12
– Pits wider, up to 1450 µm in diameter 13

8. Endocarp ca 9 mm in length, with no reticulation .....***P. sylvestris*** S.Moore
– Endocarp more than 10 mm in length, with reticulation 14

9. Endocarp with more than 200 pits per face .....***P. vogeliana*** Baill.
– Endocarp with fewer than 190 pits per face 15

10. Endocarp wall 275–325 µm thick, at least 40 pits per face .....
.....***P. anhydathoda*** (Villiers) Byng & Utteridge
– Endocarp wall 420–500 µm thick, up to 36 pits per face .....
..... ***P. gossweileri*** (Exell) Byng & Utteridge

11. Endocarp obovoid, ca 18.5 mm in length, with a reticulum of ridges enclosing 37–55 areoles .....
.....***P. soyauxii*** (Engl.) Byng & Utteridge
– Endocarp elliptical, ca 14.8 mm in length, with a reticulum of ridges enclosing 5–7 areoles .....
.....***P. thomsoniana*** (Bail.) Byng & Utteridge

12. Endocarp width ca 15 mm ..... ***P. longirostrata*** Villiers
– Endocarp width ca 7.2 mm 16

13. Endocarp wall less than 400 µm thick 17
– Endocarp wall more than 400 µm thick 18

14. Endocarp length ca 19 mm, more than 100 pits per face ..... ***P. laetevirens*** Sleumer
– Endocarp length less than ca 12 mm, fewer than 45 pits per face 19

15. Endocarp length ca 15.4 mm, endocarp wall 290–300 µm thick, ca 100 pits per face .....
.....***P. rakotozafyi*** Labat, El-Achkar & R.Rabev.
– Endocarp length less than ca 14.4 mm, endocarp wall more than 400 µm thick, more than 120 pits per face 20

16. Endocarp ca 11 mm long 21
– Endocarp ca 14 mm long .....***P. lebrunii*** Boutique

17. Ca 80–93 pits per face .....***P. tropophila*** Labat, El-Achkar & R.Rabev.
– Ca 107–114 pits per face .....***P. capitata*** H.Perrier

18. Endocarp lenticular in transverse section, surface ridged and pitted or only pitted 22
– Endocarp globose in transverse section, surface only pitted 23

19. Tubercle length more than 2 mm, endocarp length ca 12 mm, endocarp wall more than 300 µm thick ..... ***P. cordicula*** Villiers
– Tubercle length less than 2 mm, endocarp length ca 10.8 mm, endocarp wall less than 300 µm thick .....***P. staudtii*** (Engl.) Engl.

20. Ridges sharp, pits less than 300 µm in diameter, 170–184 pits on each face .....
.....***P. kaurabassana*** Baill.
– Ridges rounded, pits more than 300 µm in diameter, 120–140 pits on each face .....
..... ***P. malvifolia*** Engl.

21. Endocarp with a prominent median ridge that crosses the endocarp in length .....
..... ***P. acuminata*** Engl.
– Endocarp without a prominent median ridge .....***P. puberula*** Boutique

22. Endocarp pitted and ridged, pits elongate ..... ***P. humblotii*** (Baill. ex Grandid.) Sleumer
– Endocarp pitted only, with circular pits ..... ***P. glabrescens*** (Engl.) Engl.

23. Endocarp with 145–150 pits on each face ..... ***P. ambrensis*** Labat, El-Achkar & R.Rabev.
– Endocarp with 159–173 pits on each face ..... ***P. andapensis*** Labat, El-Achkar & R.Rabev.

Pyrenacantha acuminata Engl.
Fig. 23.10–23.18

Material examined

Specimen used for endocarp and fruit description
CENTRAL AFRICAN REPUBLIC • Boukoko; 18 Apr. 1951; *R.P. Tisserant 2085*; P[MNHN-P-P04495460].

Other material
CAMEROON • 1968; *R. Letouzey 9166*; P[MNHN-P-P04495454].

COUNTRY UNKNOWN • s. loc.; 18 May 1900; *s. col. 1863*; P[MNHN-P-P04495455].

Description

Fruit. Elliptical, acuminate and accrescent at the apex. Epicarp puberulent, with yellow simple hairs with granular ornamentation, ridged when dry, revealing the underlying endocarp ridges. Mesocarp 192–612 µm thick when dry. Calyx persistent. Length 12–17 mm, width 8–12 mm, thickness 4–8 mm.

Endocarp. Brown, elliptical in lateral view, lenticular in transverse section, length ca 11 mm, width ca 8.4 mm, thickness ca 5.5 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical and acute in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits circular and thin, ca 0.2–0.3 mm in diameter, randomly arranged with 8–11 pits longitudinally and 8–9 pits transversally (ca 93–106 pits per face). Pits associated with spiny tubercles protruding into the locule; tubercles ca 983–1718 µm in length and 352–456 µm in diameter at the base, with 17–18 cells spanning the width. Tubercle cells sclerotic, digitate and elongate. Ridges rounded and thin, more or less diffuse, faintly apparent, with a prominent median ridge running longitudinally from the base up to the apex. Endocarp wall 243–302 µm thick (excluding pits). Endocarp wall (excluding pits) with three cell layers: outermost layer composed of 1–2 rows of isodiametric to periclinally oriented cells, cells 11.8–20.1 µm in width, middle layer with 9–11 rows of periclinally oriented cells, cells 7.0–35.6 µm in width; innermost layer with one row of periclinally oriented cells, cells 9.16–17.0 µm in width, lining the locule surface with inflated to papillate cells. Locule not lacunate.

Pyrenacantha ambrensis Labat, El-Achkar & R.Rabev.
Fig. 23.19–23.27

Material examined

Specimen used for endocarp and fruit description
MADAGASCAR • 1993; *O. Andrianantoanina & A. Solotiana 62*; P[MNHN-P-P00440603].

Description

Fruit. Elliptical to globose, accrescent at the apex, brown-orange when mature. Epicarp puberulent with yellow small ovoid hairs with an acuminate apex and simple hairs with granular ornamentation, shriveled when dry. Mesocarp 480–500 µm thick when dry. Calyx persistent, separated from the fruit by an extended gynophore. Length 25–30 mm, width 19–22 mm, thickness 15.0–16.6 mm.

Endocarp. Brown, elliptical to globose in lateral view, globose in transverse section, length ca 22.5 mm, width ca 17 mm, thickness ca 15 mm. Trace of keel present in the upper part. Apex with acute protuberance, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted. Pits circular, occasionally elongated longitudinally, 0.4–1.4 mm in length, randomly arranged with 11–12 pits longitudinally and 12–15 pits transversally (ca 145–150 pits per face). Pits associated with spiny tubercles protruding into the locule; tubercles ca 3–4 mm in length and 647–931 µm in diameter at the base, faintly capitate at the apex, with 26–27 cells in width. Tubercle cells sclerotic, digitate and elongate. Endocarp wall 569–601 µm thick (excluding pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with 8–14 rows of anticlinally oriented cells, cells 17.8–50.5 µm in length, followed by a layer with 3–9 rows of periclinally oriented cells, cells 17.7–23.7 µm in width; innermost layer with one row of periclinally oriented cells, cells 0.5–1.4 µm in width, lining the locule surface with regularly spaced and sessile rounded papillae; papillae 7.6–13.1 µm (av. 10.6 µm) in diameter, with ca 1000 papillae per 0.25 mm^2. Locule surface not lacunate.

Remarks

The innermost row of periclinally oriented cells, which have a small width, could be collapsed due to a dryness inside the locule.

Pyrenacantha andapensis Labat, El-Achkar & R.Rabev.
Fig. 24.1–24.9

Material examined

Specimen used for endocarp and fruit description
MADAGASCAR • 1994; *D. Ravelonarivo et al. 72*; P[MNHN-P-P00440605].

Description

Fruit. Elliptical to globose, accrescent at the apex, brown-orange when mature. Epicarp puberulent, with yellow small ovoid hairs with an acuminate apex and simple hairs with granular ornamentation, shriveled when dry. Mesocarp 620–1541 µm thick when dry. Calyx persistent, separated from the fruit by an extended gynophore. Length 20–26 mm, width 20–26 mm, thickness 17.4–26.0 mm.

Fig. 23. Fruits of Icacinaceae Miers. **1**–**9**. *Pleurisanthes flava* Sandwith (*J.J. Pipoly 10168*). **1**. Dried fruit, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing mounds and hairs-like fibres. **3**. Dorsal view. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the pericarp with a vasculature in an endocarp channel (arrow). **8**. SEM image of the endocarp wall in transverse section. **9**. SEM image of the small ovoid hairs with an acuminate apex on the epicarp surface. – **10**–**18**. *Pyrenacantha acuminata* Engl. (*R.P. Tisserant 2085*). **10**. Dried fruit, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing the pits and the main ridge. **12**. Dorsal view. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of the endocarp in transverse section showing spiny tubercles. **17**. SEM image of tubercle cells in longitudinal section of the tubercule. **18**. SEM image of the endocarp wall in transverse section. – **19**–**27**. *Pyrenacantha ambrensis* Labat, El-Achkar & R.Rabev. (*O. Andrianantoanina & A. Solotiana 62*). **19**. Dried fruit with an elongate gynophore here broken, lateral view. **20**–**24**. Broken endocarp. **20**. Lateral view showing circular pits. **21**. Dorsal view showing a keel. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. SEM image of the pericarp in transverse section. **26**. SEM image of the endocarp wall in transverse section. **27**. SEM image of cells of the tubercle in its longitudinal section. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–24 = 10 mm; 16, 25 = 2 mm; 7 = 1 mm; 18, 26 = 500 µm; 8, 27 = 300 µm; 9, 17 = 100 µm.

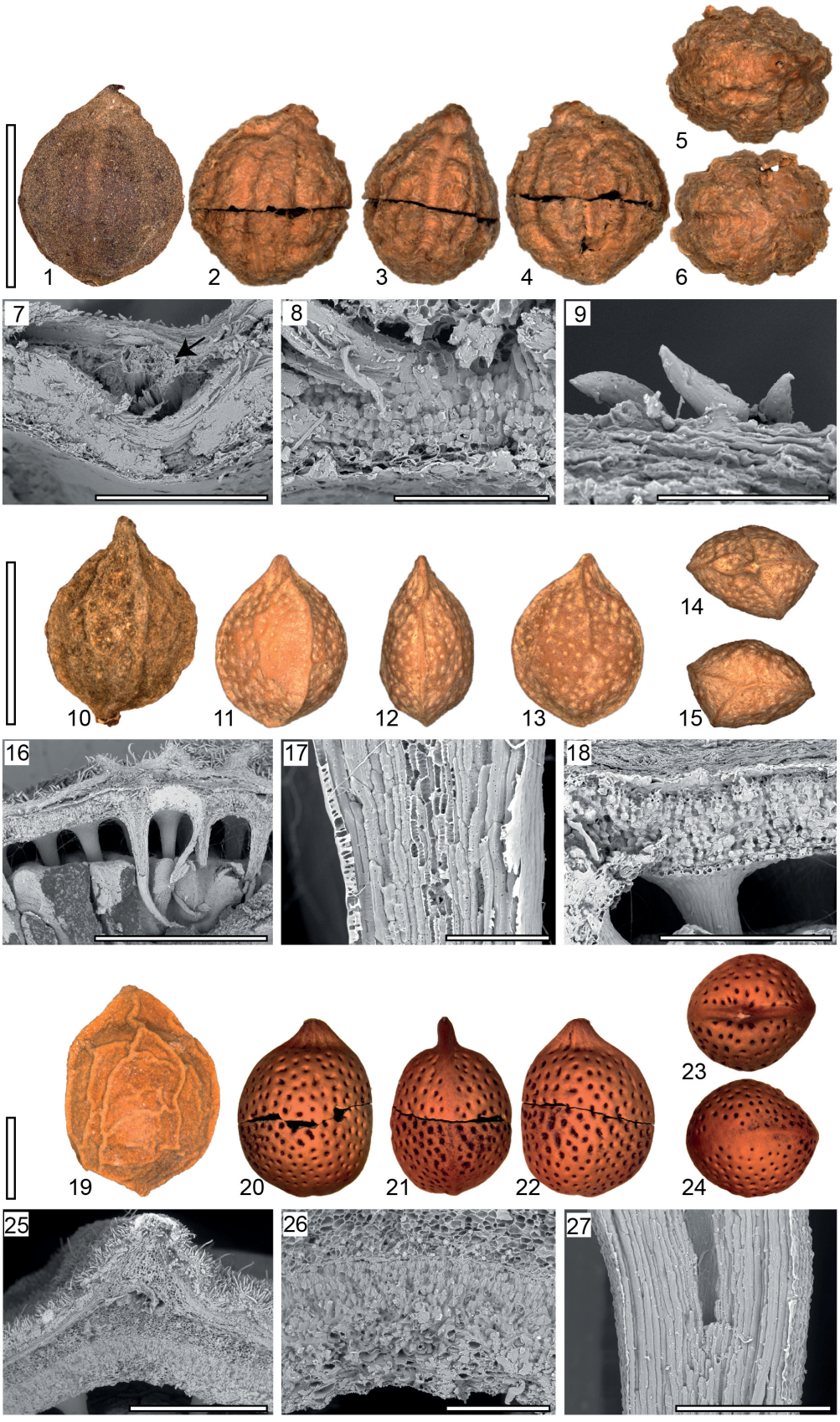

Fig. 23. (see full caption on page 68)

Endocarp. Brown, globose in lateral view, globose in transverse section, length ca 19.9 mm, width ca 18.2 mm, thickness ca 14 mm. Trace of keel present in the upper part. Apex with acute protuberance, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted. Pits circular, occasionally elongated longitudinally, 0.2–1.1 mm in length, randomly arranged with 10–11 pits longitudinally and 13–15 pits transversally (ca 159–173 pits per face). Pits associated with spiny tubercles protruding into the locule; tubercles ca 3–4 mm in length and 600–655 µm in diameter at the base, capitate at the apex, with 20–21 cells in width. Tubercle cells sclerotic, digitate and elongate. Endocarp wall 512–569 µm thick (excluding pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with ca 7–8 rows of anticlinally oriented cells, cells 19.0–29.9 µm in length, followed by a layer with 9–10 rows of isodiametric or occasionally periclinally oriented cells, cells 21.0–33.5 µm in diameter; innermost layer with one row of isodiametric cells, cells 14–18 µm in diameter, lining the locule surface with regularly spaced and rounded papillae; papillae 9.7–17 µm (av. 13.9 µm) in diameter. Locule surface not lacunate.

Pyrenacantha anhydathoda (Villiers) Byng & Utteridge
Fig. 24.10–24.17

Material examined

Specimen used for endocarp and fruit description

GABON • "Gabonia"; s.d.; *R.P. Teilles 100*; P[MNHN-P-P04494750].

Other material

GABON • 19 Feb. 1902; *R.P. Klaine 1571*; P[MNHN-P-P00418164].

Description

Fruit. Ovoid to globose, accrescent at the apex, red when mature. Epicarp puberulent, with red to yellow simple hairs with granular ornamentation, ridged when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp ca 100 µm thick when dry. Calyx persistent. Length 34–35 mm, width 12–20 mm, thickness 7–8 mm.

Fig. 24. Fruits of Icacinaceae Miers. **1**–**9**. *Pyrenacantha andapensis* Labat, El-Achkar & R.Rabev. (*D. Ravelonarivo et al. 72*). **1**. Dried fruit with an elongate gynophore here boken, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing the pits. **3**. Dorsal view. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the endocarp wall with spiny tubercles in transverse section. **8**. SEM image of cells in the inner part of the endocarp wall in transverse section and the innermost layer that line the locule with papillae. **9**. SEM image of the small ovoid hairs with an acuminate apex on the epicarp surface. – **10**–**17**. *Pyrenacantha anhydathod*a (Villiers) Byng & Utteridge (*R.P. Teilles 100*). **10**–**14**. Endocarp. **10**. Lateral view showing the pits and the main ridges. **11**. Dorsal view. **12**. Opposite lateral view. **13**. Apical view. **14**. Basal view. **15**. SEM image of the endocarp showing elongate-flattened tubercles. **16**. SEM image of the endocarp wall in transverse section. **17**. SEM image of spherical papillae lining the locule surface. – **18**–**26**. *Pyrenacantha capitata* H.Perrier (*F. Ratovoson et al. 678*). **18**. Dried fruit with a short gynophore, lateral view. **19**–**23**. Endocarp. **19**. Lateral view showing the pits. **20**. Dorsal view. **21**. Opposite lateral view. **22**. Apical view. **23**. Basal view. **24**. SEM image of the fruit in transverse section showing spiny tubercles and long and thin hairs on the epicarp. **25**. SEM image of the pericarp in transverse section. **26**. SEM image of the cells of the tubercle in its longitudinal section. Images taken from Del Rio (2018). Scale bars: 1–6, 10–14, 18–23 = 10 mm; 7, 24 = 2 mm; 15, 25 = 1 mm; 9 = 500 µm; 16, 26 = 300 µm; 8 = 200 µm; 17 = 30 µm.

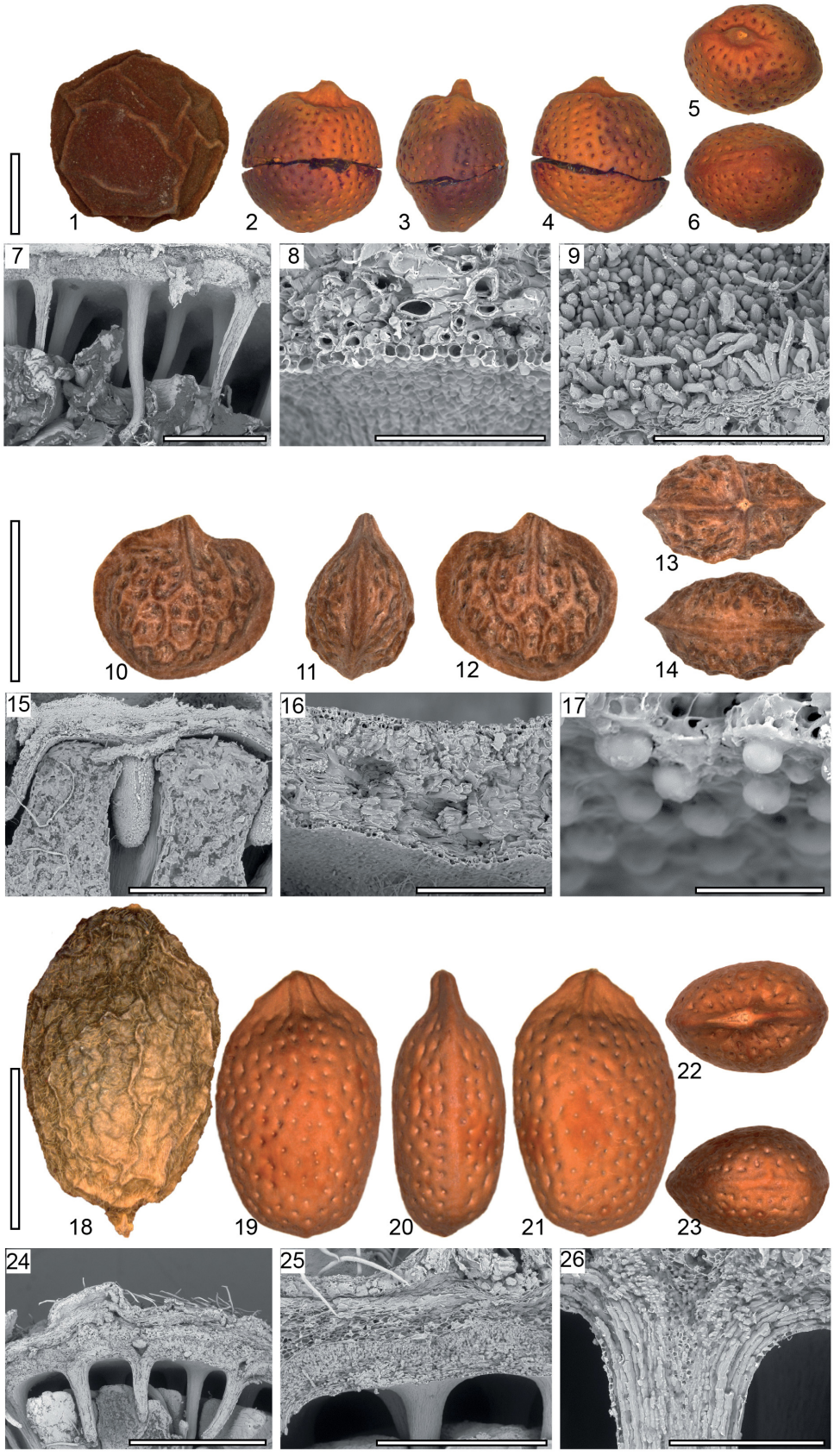

Fig. 24. (see full caption on page 74)

Endocarp. Brown, ovoid to globose in lateral view, lenticular in transverse section, length ca 10.6 mm, width ca 11.4, thickness ca 5.5 mm. Sharp keel surrounding the endocarp in the plane of symmetry. Apex acute, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits primarily elongated longitudinally, 0.3–0.9 mm in length, randomly arranged with ca 5 pits longitudinally and 8 pits transversally (ca 40–42 pits per face). Pits associated with an elongate-flattened tubercles protruding into the locule; tubercles ca 412–874 µm in length and 400–450 µm in diameter at the base. Ridges rounded and thin, with a median ridge running longitudinally from the point of the apex to the center of the endocarp length and then splitting into two parts, merging with two lateral ridges. Ridges delimiting a reticulate pattern with 12–14 areoles. Secondary ridges delimiting small areoles more or less enclosing each pit. Endocarp wall 276–326 µm thick excluding ridges (ca 460 µm thick including ridges). Endocarp wall (excluding pits) with three cell layers: outermost layer with 2–4 rows of anticlinally oriented cells, cells 15.4–27.4 µm in length, followed by a layer with 14–16 rows of periclinally oriented cells, cells 8.0–14.2 µm in width; innermost layer with one row of periclinally oriented cells, cells 7.7–15.6 µm in width, lining the locule surface with regularly spaced and rounded to elongate papillae; papillae 10.9–18.3 µm (av. 14.8 µm) in diameter. Locule surface not lacunate.

Pyrenacantha capitata H.Perrier
Fig. 24.18–24.26

Material examined

Specimen used for endocarp and fruit description
MADAGASCAR • 2002; *F. Ratovoson et al. 678*; P[MNHN-P-P00440639].

Other material
MADAGASCAR • 2005; *T. Andriamihajarivo et al. 638*; P[MNHN-P-P06807829].

Description

Fruit. Elliptical, slightly accrescent at the apex. Epicarp pilose with yellow long and thin hairs, shriveled when dry. Mesocarp 360–400 µm thick when dry. Calyx persistent. Length 17–21 mm, width 8–12 mm, thickness 4–6 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 17.1 mm, width ca 10.4 mm, thickness ca 4.5 mm. Trace of keel present in the upper part. Apex with acute protuberance but flattened laterally, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged with only 1–2 longitudinal ridges present in the flattened apical part. Pits circular, occasionally elongate, 0.2–0.6 mm in diameter, more or less randomly arranged with 10–13 pits longitudinally and 8–10 pits transversally (ca 107–114 pits per face). Pits associated with spiny tubercles protruding into the locule; tubercles ca 1500 µm in length and 420–620 µm in diameter at the base, with 20–23 cells in width. Tubercle cells sclerotic, digitate and elongate. Endocarp wall 246–289 µm thick (excluding pits). Endocarp wall (excluding pits), with three cell layers: outermost layer with 4–7 rows of anticlinally oriented to isodiametric cells, cells 15.4–28.9 µm in length, followed by a layer with 9–12 rows of periclinally oriented cells, cells 10.0–11.2 µm in width; innermost layer with one row of periclinally oriented cells, cells 5.0–9.9 µm in width, lining the locule surface with more or less flattened cells. Locule surface not lacunate.

Pyrenacantha cordicula Villiers
Fig. 25.1–25.9

Material examined

Specimen used for endocarp and fruit description
CAMEROON • 1986; *M. Etuge & D. Thomas 28*; P[MNHN-P-P00557873].

Description

Fruit. Elliptical, slightly accrescent at the apex. Epicarp puberulent with yellow simple hairs with granular ornamentation, shriveled when dry. Mesocarp 225–425 µm thick when dry. Calyx persistent, separated from the fruit by a small gynophore. Length 17 mm, width 11.6 mm, thickness 9.3 mm.

Endocarp. Brown, elliptical to obovoid in lateral view, lenticular in transverse section, length ca 12 mm, width ca 8 mm, thickness ca 5 mm. Trace of keel present in the upper part. Apex with acute protuberance, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits primarily elongate, occasionally circular, 0.6–1.3 mm in length, arranged in longitudinal lines with 6–7 pits longitudinally and transversally (ca 40–45 pits per face). Pits associated with cylindrical tubercles protruding into the locule; tubercles ca 2.5 mm in length and 1 mm in diameter at the base, capitate at the apex, with ca 45 cells in width. Tubercle cells sclerotic, digitate and elongate. Ridges rounded and large, delimiting a dense reticulum enclosing all pits in an areole. Endocarp wall 332–438 µm thick (excluding pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with 1–2 rows of isodiametric to periclinally oriented cells, cells 8.6–10.7 µm in width, followed by a layer with ca 17 rows of periclinally oriented cells, cells 9.5–25.3 µm in width; innermost layer with one row of periclinally oriented cells, cells 5.5–5.8 µm in width, lining the locule surface with more or less flattened cells. Locule surface not lacunate.

Pyrenacantha glabrescens (Engl.) Engl.
Fig. 25.10–25.18

Material examined

Specimen used for endocarp and fruit description
IVORY COAST • 1906; *A. Chevalier 17326*; P[MNHN-P-P04495475].

Other material
IVORY COAST • 1976; *J. de Koning 6802*; P[MNHN-P-P06807655].

Description

Fruit. Elliptical, slightly accrescent at the apex, red when mature. Epicarp strigose with yellow uncinate hairs, slightly ridged when dry. Mesocarp 250–300 µm thick when dry. Calyx persistent, separated from the fruit by a small gynophore. Length 24.3–35.0 mm, width 15–18 mm, thickness 10.0–11.4 mm.

Endocarp. Brown, with a cardboard-like texture (due to decay, see Remark and Discussion for preservation issues), elliptical in lateral view, lenticular in transverse section, length ca 21.7 mm, width ca 13.7 mm, thickness ca 10 mm. Trace of keel present in the upper part. Apex asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted. Pits circular, randomly arranged with 10–12 pits longitudinally and 8–9 transversally (ca 60–80 pits per face). Pits associated with spiny tubercles protruding into the locule. Endocarp wall 550–638 µm thick (excluding pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with 7–8 rows of anticlinally oriented cells, cells 31.3–56 µm in length, followed by a layer with 6–7 rows of periclinally oriented cells, cells 26.2–

31.0 µm in width; innermost layer with one row of periclinally oriented cell, cells 13.8–14.4 µm in width, lining the endocarp. Locule surface not lacunate.

Remark

The studied specimens were attacked by a saprophytic fungus. This could explain the peculiar texture of the endocarp. The tubercles are atrophied (see Discussion for preservation issues).

Pyrenacantha gossweileri (Exell) Byng & Utteridge
Fig. 25.19–25.27

Material examined

Specimen used for endocarp and fruit description

REPUBLIC OF THE CONGO • Mayombe, Mount Bamba; 6 Jan. 1969; *Y. Attims 42*; P[MNHN-P-P04494730].

Description

Fruit. Ovoid, accrescent at the apex, with an inflated cap that covers half of the length of the fruit. Epicarp strigose, with yellow simple hairs with granular ornamentation. Mesocarp 130–140 µm thick when dry. Calyx not persistent. Length 16.0–16.8 mm, width 11.3–16.0 mm, thickness 7.5–12.0 mm.

Endocarp. Brown, ovoid to globose in lateral view, lenticular in transverse section, length ca 10.7 mm, width ca 10.5 mm, thickness ca 7.1 mm. Sharp keel surrounding the endocarp in the plane of symmetry. Apex acute, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits primarily elongate, 0.5–1.7 mm in length longitudinally, randomly arranged with ca 6 pits longitudinally and 6 pits transversally (ca 33–36 pits per face). Pits associated with elongate-flattened tubercles protruding into the locule; tubercles ca 724 µm in length and 716 µm in diameter at the base, with ca 15 cells in width. Tubercle cells sclerotic, digitate and not elongate. Ridges rounded and thin, with three main ridges running longitudinally. Ridges delimiting a reticulate pattern with 14–15 areoles. Secondary ridges delimiting small areoles more or less enclosing each pit. Endocarp wall 423–498 µm thick excluding ridges (ca 700 µm thick including ridges). Endocarp wall (excluding pits) with three cell layers: outermost layer with 3–4 rows of isodiametric to anticlinally oriented cells, cells 10.4–43.2 µm in length, followed by a layer with 8–12 rows of periclinally oriented cells, cells

Fig. 25. Fruits of Icacinaceae Miers. **1**–**9**. *Pyrenacantha cordicula* Villiers (*M. Etuge & D. Thomas 28*). **1**. Dried fruit with a short gynophore, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing the pits and ridges. **3**. Dorsal view. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the endocarp showing cylindrical tubercles. **8**. SEM image of cells of the tubercle in its transverse section. **9**. SEM image of the endocarp wall in transverse section. – **10**–**18**. *Pyrenacantha glabrescens* (Engl.) Engl. (*A. Chevalier 17326*). **10**. Dried fruit with a short gynophore, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing the pits (decayed). **12**. Dorsal view. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of the atrophied spiny tubercles. **17**. SEM image of the pericarp in transverse section. **18**. SEM image of the uncinate hairs on the epicarp. – **19**–**27**. *Pyrenacantha gossweileri* (Exell) Byng & Utteridge (*Y. Attims 42*). **19**. Dried fruit with an inflated cap and ending with a short tube, lateral view. **20**–**24**. Endocarp. **20**. Lateral view showing the pits and ridges. **21**. Dorsal view showing the keel. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. SEM image of the fruit and seed in transverse section. **26**. SEM detail of transverse section of the endocarp showing an elongate-flattened tubercle. **27**. SEM image of the inner layers of the endocarp showing papillae lining the locule surface. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–24 = 10 mm; 7, 25 = 2 mm; 16–17 = 1 mm; 8, 26 = 500 µm; 9, 18 = 300 µm; 27 = 50 µm.

Fig. 25. (see full caption on page 78)

13.0–15.9 µm in width; innermost layer with one row of periclinally oriented cells, cells 6.3–10.3 µm in width, lining the locule surface with regularly spaced and rounded to elongate papillae; papillae 14.9–18.8 µm (av. 16.1 µm) in diameter. Locule surface not lacunate.

Pyrenacantha humblotii (Baill. ex Grandid.) Sleumer
Fig. 26.1–26.9

Material examined

Specimen used for endocarp and fruit description
MADAGASCAR • 1987; *M. Nicoll, P. Lowry & A. Rakotozafy 570*; P[MNHN-P-P00440635].

Other material
MADAGASCAR • s.d.; *REH 334*; P[MNHN-P-P06637527] • s.d.; *Humblot s.n.*; P[MNHN-P-P00440634].

Description

Fruit. Elliptical, slightly accrescent at the apex, red when mature. Epicarp pilose-puberulent with yellow simple hairs with granular ornamentation, shriveled when dry. Mesocarp 440–560 µm thick when dry. Calyx persistent, separated from the fruit by an elongated gynophore. Length 17–22 mm, width 11–20 mm, width 5–13 mm.

Endocarp. Reddish-brown, elliptical in lateral view, lenticular in transverse section, length ca 17 mm, width ca 11.7 mm, thickness ca 7.4 mm. Trace of keel present in the upper part. Apex with acute protuberance, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits primarily elongate, 0.4–1.3 mm in diameter, more or less randomly arranged with 9–13 pits longitudinally and 10–12 pits transversally (ca 115–130 pits per face). Pits associated with spiny tubercles protruding into the locule; tubercles ca 2–3 mm in length and 548–628 µm in diameter at the base, more or less capitate at the apex, with 16–20 cells in width. Tubercle cells sclerotic, digitate and elongate. Ridges rounded and large, delimiting a dense reticulum enclosing all pits in an areole. Endocarp wall 480–566 µm thick (excluding pits). Endocarp wall (excluding pits) with three cell layers:

Fig. 26. Fruits of Icacinaceae Miers. **1**–**9**. *Pyrenacantha humblotii* (Baill. ex Grandid.) Sleumer (*M. Nicoll, P. Lowry & A. Rakotozafy 570*). **1**. Dried fruit with a broken gynophore, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing the pits and ridges. **3**. Dorsal view. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the fruit in transverse section showing endocarp with spiny tubercles. **8**. SEM image of tubercle cells in its longitudinal section. **9**. SEM image of the papillae on the tubercle surface. – **10**–**18**. *Pyrenacantha kaurabassana* Baill. (*A. Gomes e Sousa 1584*). **10**. Dried fruit with a portion of the gynophore, lateral view. **11**–**15**. Broken endocarp. **11**. Lateral view showing the pits and sharp ridges. **12**. Dorsal view showing the keel. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of the peg-shaped tubercles in a transverse section of the pericarp (note the presence of fungal hyphae). **17**. SEM image of the endocarp wall in transverse section. **18**. SEM image of the papillae on the tubercle surface. – **19**–**27**. *Pyrenacantha klaineana* Pierre ex Exell & Mendonça (*A.J.M. Leewenber 4523*). **19**. Dried fruit with a gynophore here broken, lateral view. **20**–**24**. Endocarp. **20**. Lateral view showing the pits. **21**. Dorsal view showing the keel. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. SEM image of the capitate peg-shaped tubercles. **26**. SEM image showing cells of the tubercle in its longitudinal section. **27**. SEM image of the endocarp wall in transverse section. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–24 = 10 mm; 7 = 2 mm; 16, 25 = 1 mm; 17 = 500 µm; 8 = 300 µm; 18 = 200 µm; 26–27 = 100 µm; 9 = 50 µm.

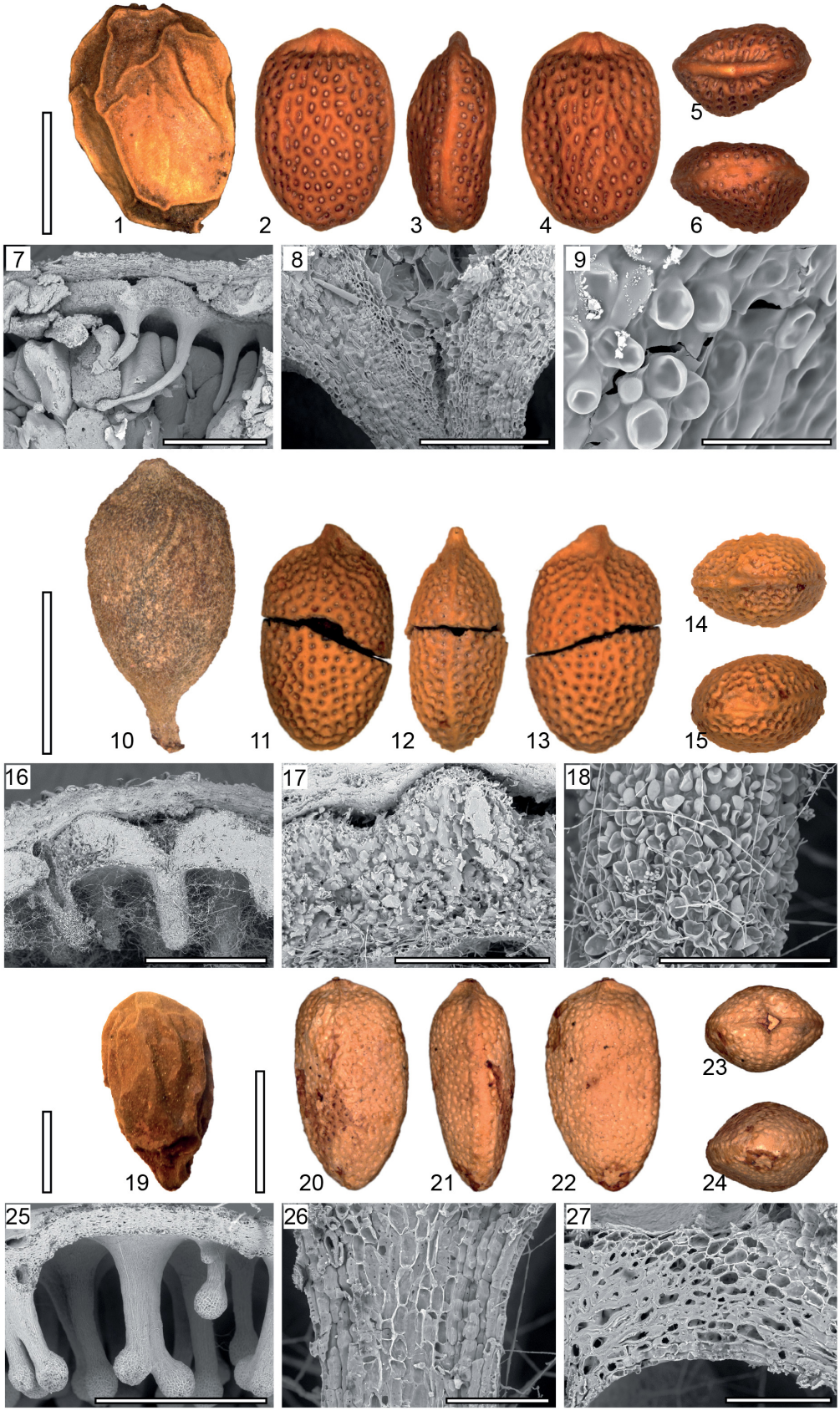

Fig. 26. (see full caption on page 80)

outermost layer with 3–4 rows of isodiametric to anticlinally oriented cells, cells 8.3–12.8 µm in length, followed by a layer with ca 13–14 rows of periclinally oriented cells, cells 16.9–56.3 µm in width; innermost layer with one row of periclinally oriented cells, cells 9.2–11.9 µm in width, lining the locule surface with regularly spaced and rounded papillae; papillae 10.5–20.0 µm (av. 15.3 µm) in diameter. Locule surface not lacunate.

Pyrenacantha kaurabassana Baill.
Fig. 26.10–26.18

Material examined

Specimen used for endocarp and fruit description
MOZAMBIQUE • 1933; *A. Gomes e Sousa 1584*; P[MNHN-P-P04495513].

Other material
AFRICA • "Côte orientale d'Afrique"; Nov. 1888; *R.P. Sacleux 787*; P[MNHN-P-P04495512] • "Cap"; s.d.; *Orège ? s.n.*; P[MNHN-P-P04495509].

Description

Fruit. Elliptical, accrescent at the apex. Epicarp strigose, with yellow simple hairs with granular ornamentation. Mesocarp 200–260 µm thick when dry. Calyx persistent, separated from the fruit by an elongated gynophore. Length 13–20 mm, width 8.0–9.2 mm, thickness 5–7 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 14.4 mm, width ca 8.2 mm, thickness ca 6 mm. Keel surrounding the endocarp in the plane of symmetry. Apex with acute protuberance, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits exclusively circular, 0.2–0.3 mm in diameter, more or less longitudinally arranged with 14–18 pits longitudinally and ca 10 pits transversally (ca 170–184 pits per face). Pits associated with peg-shaped tubercles protruding into the locule; tubercles ca 658–700 µm in length and 267–326 µm in diameter at the base. Ridges sharp and thin, delimiting a dense reticulum enclosing all pits in an areole. Endocarp wall 427–469 µm thick (excluding pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with 1–2 rows of isodiametric cells, cells 8.0–12.6 µm in diameter, followed by a layer with 11–12 rows of periclinally oriented cells, cells 15.0–44.3 µm in width; innermost layer with one row of periclinally oriented cells, cells 8.9–12.2 µm in width, lining the locule surface with regularly spaced and rounded papillae; papillae 12.3–27.8 µm (av. 21 µm) in diameter. Locule surface not lacunate.

Pyrenacantha klaineana Pierre ex Exell & Mendonça
Fig. 26.19–26.27

Material examined

Specimen used for endocarp and fruit description
IVORY COAST • 1962; *A.J.M. Leewenber 4523*; P[MNHN-P-P04495495].

Other material
GABON • s.d.; *R.P. Klaine 1299*; P[MNHN-P-P04495499] • 1899; *R.P. Klaine 1383*; P[MNHN-P-P04495503].

Description

Fruit. Elliptical, accrescent at the apex, black when mature. Epicarp puberulent, with yellow simple hairs with granular ornamentation, shriveled when dry. Calyx persistent, separated from the fruit by an elongated gynophore. Length 20–25 mm, width 11–16 mm, thickness 7–9 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 17.9 mm, width ca 9.5 mm, thickness ca 7 mm. No keel surrounding the endocarp in the plane of symmetry. Apex and base rounded, symmetrical or slightly asymmetrical in lateral view. Outer surface of the endocarp pitted. Pits circular, occasionally elongate, 0.1–0.3 mm in diameter, randomly arranged with 18–19 pits longitudinally and 12–17 pits transversally (ca 242 pits per face). Pits associated with peg-shaped tubercles protruding into the locule; tubercles ca 698–982 µm in length and 388–576 µm in diameter at the base, bifid and/or capitate at the apex, with 16–17 cells in width. Tubercle cells sclerotic, digitate and elongate. Endocarp wall 130–185 µm thick (excluding pits). Endocarp wall (excluding pits) with two cell layers: outermost layer with 8–10 rows of periclinally oriented cells, cells 9.2–17.2 µm in width; innermost layer with one row of periclinally oriented cells, cells 3.6–7.6 µm in width, lining the locule surface. Locule surface not lacunate.

Pyrenacantha laetevirens Sleumer
Fig. 27.1–27.9

Material examined

Specimen used for endocarp and fruit description
MADAGASCAR • s.d.; *H. Grevé 234*; P[MNHN-P-P00440649].

Other material
MADAGASCAR • 1923; *H. Perrier de la Bâthie 1985*; P[MNHN-P-P00440648].

Description

Fruit. Elliptical, accrescent at the apex. Epicarp puberulent, with yellow simple hairs with granular ornamentation, slightly shriveled when dry. Mesocarp 313–566 µm thick when dry. Calyx persistent, occasionally separated from the fruit by an elongated gynophore. Length 19–40 mm, width 13–26 mm, thickness 7–20 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 18.9 mm, width ca 12.3 mm, thickness ca 8 mm. Trace of keel present in the upper part. Apex with acute protuberance, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits primarily elongate, 0.3–1.3 mm in length, randomly arranged with ca 10 pits longitudinally and 9–10 pits transversally (ca 108–115 pits per face). Pits associated with cylindrical tubercles protruding into the locule; tubercles ca 1979–2340 µm in length and 675–1085 µm in diameter at the base, more or less capitate at the apex, with 26 cells in width. Tubercle cells sclerotic, digitate and elongate. Ridges faintly rounded to rectangular and large, delimiting a dense reticulum enclosing all pits in an areole. Endocarp wall 370–400 µm thick excluding pits. Endocarp wall (without pits) with three cell layers: outermost layer with ca 7 rows of isodiametric to occasionally anticlinally oriented cells, cells 16.1–33.4 µm in length, followed by a layer with ca 8 rows of periclinally oriented cells, cells 22.4–34.3 µm; innermost layer with one row of periclinally oriented cells, cells 5.0–8.3 µm in width, lining the locule surface. Locule surface not lacunate.

Pyrenacantha lebrunii Boutique
Fig. 27.10–27.18

Material examined

Other material

CAMEROON • 1962; *F.J. Breteler 2933*; P[MNHN-P-P04472184].

Description

Fruit. Elliptical, acuminate and accrescent at the apex. Epicarp puberulent, with yellow simple hairs with granular ornamentation, shriveled when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp 130–300 µm thick when dry. Calyx persistent, separated from the fruit by a short gynophore. Length 16.0–18.4 mm, width 9.6–11.0 mm, thickness 3–5 mm.

Endocarp. Brown, elliptical in lateral view, lenticular in transverse section, length ca 13.9 mm, width ca 8.8 mm, thickness ca 4.1 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical and acute in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits circular, occasionally elongate, 0.2–0.3 mm in diameter, randomly arranged with 9–11 pits longitudinally and ca 8 pits transversally (ca 105–107 pits per face). Pits associated with spiny tubercles protruding into the locule; tubercles ca 836–1500 µm in length and ca 500 µm in diameter at the base, with ca 22 cells in width. Tubercle cells sclerotic, digitate and elongate. Ridges rounded and thin, more or less diffuse, enclosing 4–5 areoles, faintly apparent, with a ridge running longitudinally from the base up to the apex. Endocarp wall 221–280 µm thick excluding ridges (370–455 µm including ridges). Endocarp wall (excluding pits) with three cell layers: outermost layer with ca 2 rows of isodiametric cells, cells 11.3–22.2 µm in diameter, followed by a layer with ca 11 rows of periclinally oriented cells, cells 16.3–33.2 µm in width; innermost layer with one row of periclinally oriented cells, cells 7.5–15.5 µm in width, lining the locule surface with more or less inflated, papillate cells. Locule surface not lacunate.

Fig. 27. Fruits of Icacinaceae Miers. **1**–**9**. *Pyrenacantha laetevirens* Sleumer (*H. Grevé 234*). **1**. Dried fruit with a short gynophore here partially broken, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing the pits and flattened reticulation. **3**. Dorsal view. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the cylindrical tubercle between seed cells. **8**. SEM image of the pericarp in transverse section showing the indumentum on the epicarp. **9**. SEM image of the endocarp in transverse section. – **10**–**18**. *Pyrenacantha lebrunii* Boutique (*F.J. Breteler 2933*). **10**. Dried fruit with a short gynophore and elongate apex, lateral view. **11**–**15**. Broken endocarp. **11**. Lateral view showing the pits and ridges. **12**. Dorsal view showing the keel. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of pericarp with the spiny tubercles and corresponding seed cavities separated from each other after retraction of the seed tissue due to drying. **17**. Detail of the endocarp in transverse section showing the wall and tubercle cells. **18**. Other detail showing simple hairs on the epicarp. – **19**–**25**. *Pyrenacantha longirostrata* Villiers (*R. Letouzey 14156*). **19**–**22**. Endocarp. **19**. Lateral view of the apical part of the endocarp showing the pits and ridges. **20**. Opposite lateral view. **21**. Internal view showing spiny tubercles. **22**. Apical view. **23**. SEM image of the endocarp in transverse section showing wall and tubercle cells. **24**. SEM image of uncinate hairs on the epicarp. **25**. SEM image of papillae on the locule surface. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–20, 22 = 10 mm; 7, 16 = 2 mm; 8, 21 = 1 mm; 23 = 500 µm; 9, 17–18 = 300 µm; 24 = 100 µm; 25 = 30 µm.

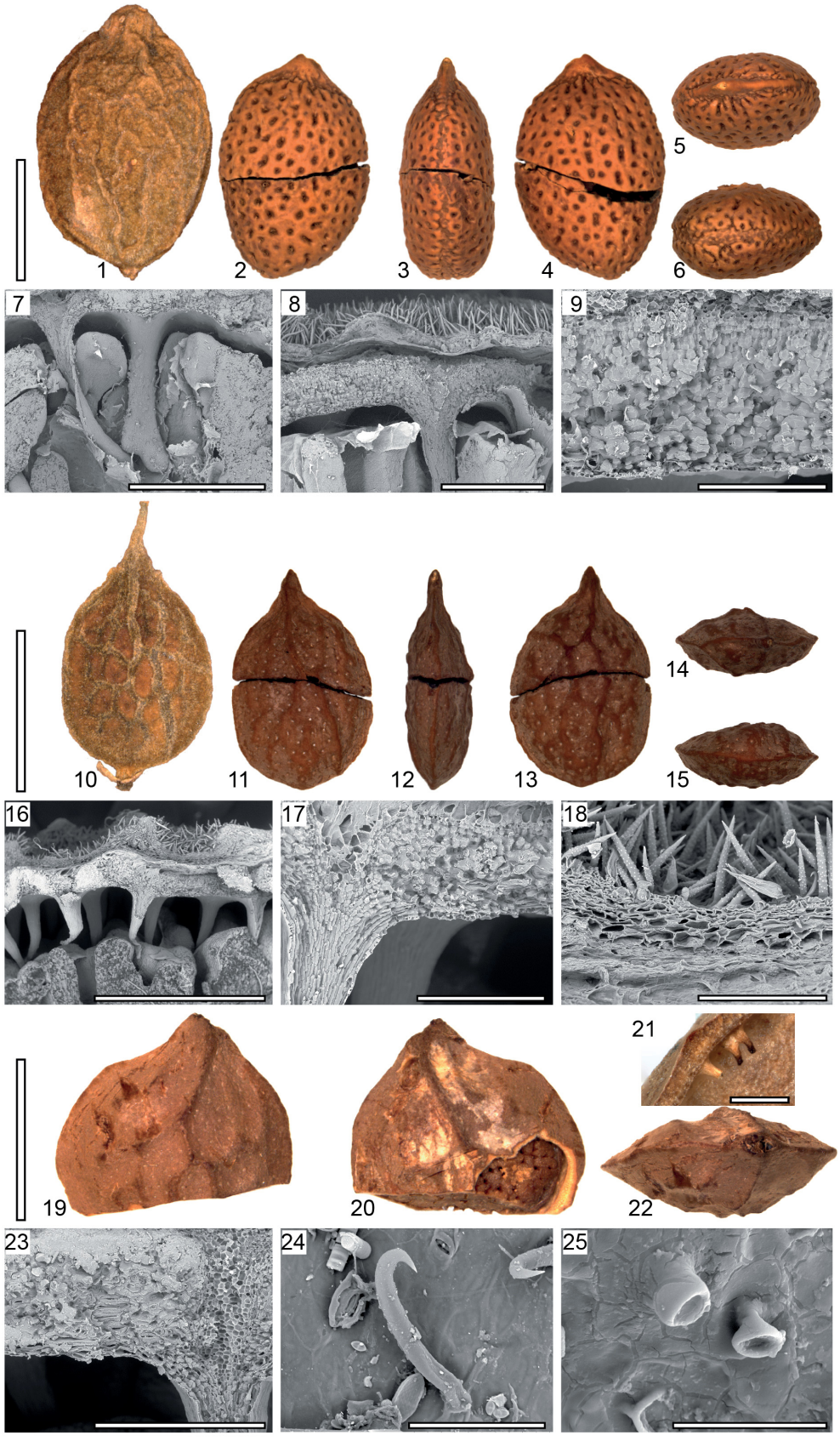

Fig. 27. (see full caption on page 84)

Pyrenacantha longirostrata Villiers
Fig. 27.19–27.25

Material examined

Specimen used for endocarp and fruit description
CAMEROON • "Cameroun"; s.d.; *R. Letouzey 14156*; K.

Description

Fruit. Elliptical, accrescent at the apex, red when mature. Epicarp strigose, with yellow uncinate hairs. Length 28–35 mm, width 16–20 mm, thickness 6–8 mm.

Endocarp. Brown, elliptical in lateral view, lenticular in transverse section, width ca 15 mm, thickness ca 6 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical and acute in lateral view. Outer surface of the endocarp pitted and ridged. Pits circular, occasionally elongate, 0.1–0.3 mm in diameter, randomly arranged with 11–12 pits transversally. Pits associated with spiny tubercles protruding into the locule; tubercles ca 1200 µm in length and ca 386–472 µm in diameter at the base, apex occasionally bifid, with ca 14 cells in width. Tubercle cells sclerotic, digitate and elongate. Ridges rounded and thin, diffuse, faintly apparent. Endocarp wall 350–400 µm thick excluding ridges (484–534 µm thick including ridges). Endocarp wall (excluding pits and ridges) with two cell layers: outermost layer with ca 11 rows of periclinally oriented cells, cells 11.2–32.8 µm in width; innermost layer with one row of periclinally oriented cells, cells 9.8–16.2 µm in width, lining the locule surface with regularly spaced and rounded papillae; papillae 8.7–15.7 µm (av. 13.7 µm) in diameter, ca 190 papillae per 0.25 mm^2. Locule surface not lacunate.

Remarks

Endocarp specimen with only the upper part preserved; fruits rare in herbarium collections.

Pyrenacantha macrocarpa (A.Chev. ex Hutch. & Dalziel) Byng & Utteridge
Fig. 28.1–28.8

Material examined

Specimens used for endocarp and fruit description
IVORY COAST • Abidjan; s.d.; *J. de Koning 4918*; BR[BR0000015570635] • 1954; *N. Lovi 3952*; P[MNHN-P-P04494747].

Other material
IVORY COAST • 1907; *A. Chevalier 17216*; P[MNHN-P-P00418166].

GHANA • 1999; *J. Stone, J. Amponsah & M. Chintoh 3421*; P[MNHN-P-P06807826].

Description

Fruit. Elliptical, accrescent at the apex and forming an inflated cap (representing about half of the length). Epicarp pilose, with long and thin hairs and yellow-white simple hairs with granular ornamentation. Mesocarp thin when dry. Calyx persistent, separated from the fruit by a more or less elongated gynophore. Length 42.4–70.0 mm, width 20–25 mm, thickness 9–10 mm.

Endocarp. Cream, deltoid in lateral view, lenticular in transverse section, length ca 20.6 mm, width ca 16.4 mm, thickness ca 9.5 mm. Keel surrounding the endocarp in the plane of symmetry. Apex truncate and slightly asymmetrical, with protuberance; base rounded, almost acute, symmetrical. Outer surface of the endocarp pitted and ridged. Pits circular, occasionally elongate, 0.5–1.6 mm in diameter, arranged

in longitudinal lines with 9–10 pits longitudinally and 8–9 pits transversally (ca 83–84 pits per face). Pits associated with elongate-flattened tubercles protruding into the locule; tubercles ca 710–1084 µm in length and 227–279 µm in diameter at the base. Ridges rounded-rectangular, thin, delimiting a dense reticulum enclosing all pits in an areole. Endocarp wall 534 µm thick excluding pits. Endocarp wall (excluding pits) with three cell layers poorly preserved except for the innermost layer including one row of periclinally oriented cells, cells 3.3–10.5 µm in width, lining the locule surface with inflated cells. Locule surface not lacunate.

Remarks

Endocarp wall poorly preserved in the specimens examined due to the preparation (see Discussion for preservation issues).

Pyrenacantha malvifolia Engl.
Fig. 28.9–28.17

Material examined

Specimen used for endocarp and fruit description
KENYA • 16 Sep. 1961; *R.M. Polhill & S. Paulo 475* ; BR[BR0000016755826].

Description

Fruit. Elliptical, shortly accrescent at the apex. Epicarp strigose, with yellow simple hairs with granular ornamentation, shriveled when dry. Mesocarp 450–560 µm thick when dry. Calyx persistent. Length 16 mm, width 10.2 mm, thickness 6.5 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 12.6 mm, width ca 8.7 mm, thickness ca 6 mm. Keel surrounding the endocarp in the plane of symmetry. Apex acute and asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits circular, occasionally elongate, ca 0.3 mm in diameter, randomly arranged with 9–14 pits longitudinally and 10–12 pits transversally (ca 120–140 pits per face). Pits associated with peg-shaped tubercles protruding into the locule; tubercles ca 625–693 µm in length, 227–279 µm in diameter at the base, with ca 15–16 cells in width. Tubercle cells sclerotic, digitate and shortly elongate. Ridges faintly apparent, rounded and diffuse, with a median ridge running from the base to the apex. Endocarp wall 440–516 µm (excluding pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with 2–3 rows of isodiametric to periclinally oriented cells, cells 11.5–17.0 µm in width, followed by a layer with ca 15 rows of periclinally oriented cells, cells 10.6–43.6 µm in width; innermost layer with one row of periclinally oriented cells, cells 5.7–12.3 µm in width, lining the locule surface with regularly spaced and rounded-large papillae. Locule surface not lacunate.

Pyrenacantha puberula Boutique
Fig. 28.18–28.26

Material examined

Specimen used for endocarp and fruit description
DEMOCRATIC REPUBLIC OF THE CONGO • Botuge; 25 Mar. 1955; *C. Evrard 601*; BR[BR0000013148430].

Description

Fruit. Elliptical, acuminate and accrescent at the apex. Epicarp strigose, with yellow uncinate hairs, slightly shriveled when dry. Mesocarp 230–312 µm thick when dry. Calyx persistent, separated from the fruit by a short gynophore. Length ca 19.7 mm, width ca 11.4 mm, thickness ca 4.6 mm.

Endocarp. Brown, elliptical in lateral view, lenticular in transverse section, length ca 11 mm, width ca 7.2 mm, thickness ca 4.5 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical and acute in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits circular, occasionally elongate, ca 0.2–0.4 mm in diameter, randomly arranged with 9–11 pits longitudinally and 8–10 pits transversally (ca 85–100 pits per face). Pits associated with spiny tubercles protruding into the locule; tubercles ca 977–1100 µm in length and 285–361 µm in diameter at the base, with ca 17 cells in width. Tubercle cells sclerotic, digitate and elongate. Ridges rounded and thin, more or less diffuse, faintly apparent, with a median ridge running longitudinally from the base to the apex. Endocarp wall 177–184 µm thick (excluding pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with 1–3 rows of isodiametric to periclinally oriented cells, cells 7.5–14.6 µm in width; followed by a layer with ca 10 rows of periclinally oriented cells, cells 10.2–32.5 µm in width; innermost layer with one row of periclinally oriented cells, cells 4.1–10.0 µm, lining the locule surface with inflated to papillate cells, cells 11.2–21.8 µm (av. 17.3 µm) in diameter. Locule not lacunate.

Pyrenacantha rakotozafyi Labat, El-Achkar & R.Rabev.
Fig. 29.1–29.9

Material examined

Specimen used for endocarp and fruit description
COMOROS • Mayotte; 2007; *F. Barthelat 1764*; P[MNHN-P-P00631418].

Fig. 28. Fruits of Icacinaceae Miers. **1**–**8**. *Pyrenacantha macrocarpa* (A.Chev. ex Hutch. & Dalziel) Byng & Utteridge (*J. De Koning 4918*). **1**. Dried fruit with a short gynophore and an inflated cap ending with an elongated tube, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing the pits. **3**. Dorsal view showing a keel. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the outer surface with pits and transverse section of the endocarp showing wall and elongate-flattened tubercles. **8**. SEM image of the inner layers of the endocarp wall. – **9**–**17**. *Pyrenacantha malvifolia* Engl. (*R.M. Polhill & S. Paulo 475*). **9**. Dried fruit with a short gynophore, lateral view. **10**–**14**. Broken endocarp. **10**. Lateral view showing the pits and ridges. **11**. Dorsal view showing the keel. **12**. Opposite lateral view. **13**. Apical view. **14**. Basal view. **15**. SEM image of the pericarp in transverse section showing peg-shaped tubercles on the inner part of the endocarp. **16**. Detail of longidudinal section of the tubercle showing the cells. **17**. Other detail showing the papillae and one stoma (arrow) on the apex of a tubercle. – **18**–**26**. *Pyrenacantha puberula* Boutique (*C. Evrard 601*). **18**. Dried fruit with a short gynophore and a short acuminate apex, lateral view. **19**–**23**. Endocarp. **19**. Lateral view showing the pits. **20**. Dorsal view showing the keel. **21**. Opposite lateral view showing the pitted seed in the right bottom part (endocarp missing in this part). **22**. Apical view. **23**. Basal view. **24**. SEM image of the fruit in transverse section showing spiny tubercles. **25**. SEM image of the endocarp in transverse section showing the wall and the base of tubercle. **26**. SEM image of the papillae on the apex of the tubercle. Images taken from Del Rio (2018). Scale bars: 1–6, 9–14, 18–23 = 10 mm; 7, 15, 24 = 2 mm; 25 = 300 µm; 16, 26 = 200 µm; 8, 17 = 50 µm.

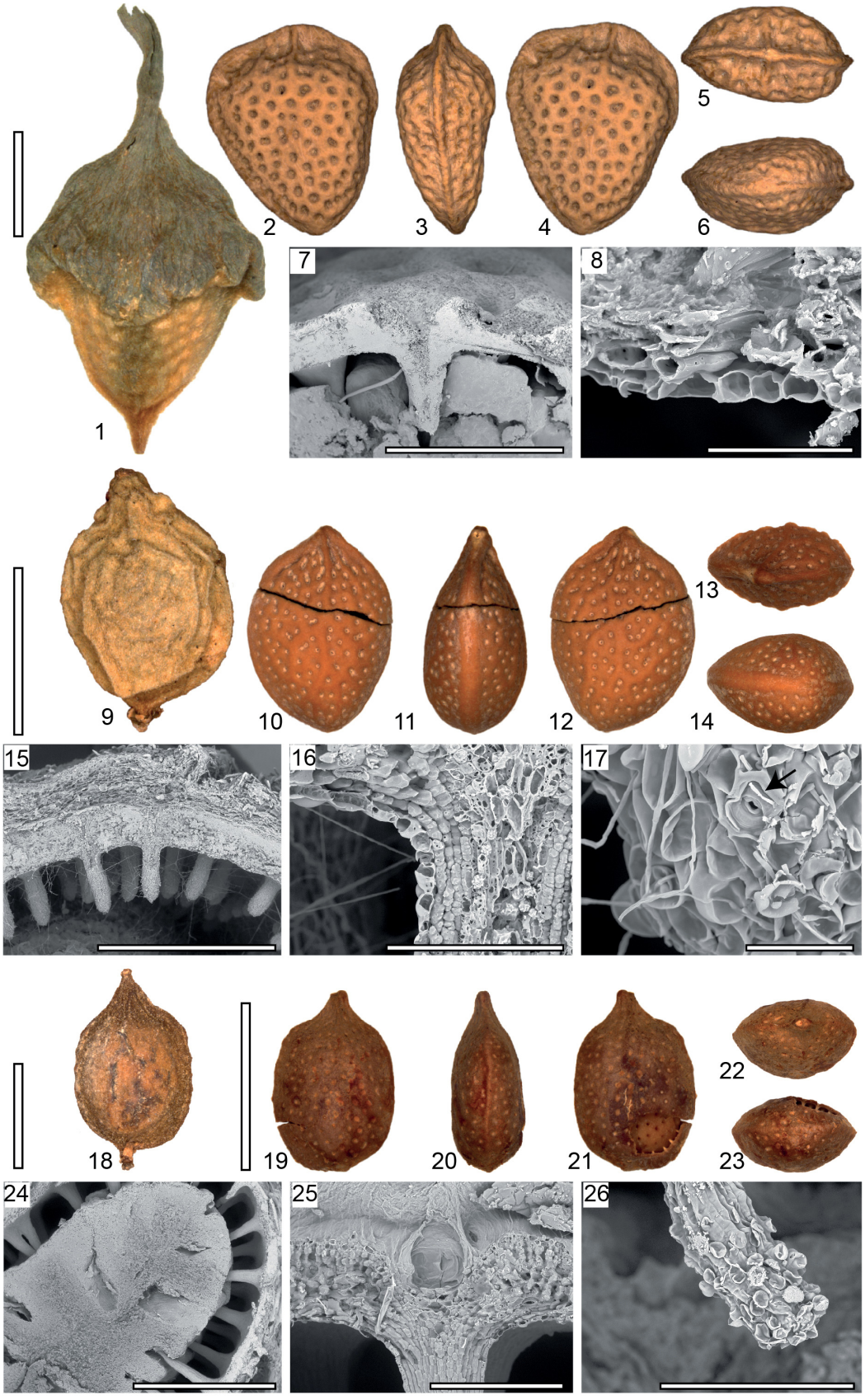

Fig. 28. (see full caption on page 86)

Description

Fruit. Elliptical, slightly accrescent at the apex. Epicarp strigose, with yellow uncinate hairs, ridged when dry, more or less revealing the underlying reticulum of endocarp ridges. Mesocarp 70–200 µm when dry. Calyx persistent. Length 16.0–18.2 mm, width 9.0–10.8 mm, thickness 5–7 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 15.4 mm, width ca 10 mm, thickness ca 6.6 mm. Keel surrounding the endocarp in the plane of symmetry. Apex rounded-flattened, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits primarily elongate, 0.2–0.4 in length, arranged in longitudinal lines with 12–14 pits longitudinally and 8–9 pits transversally (ca 100–110 pits per face). Pits associated with peg-shaped tubercles protruding into the locule; tubercles 828–905 µm in length and 311–327 µm in diameter at the base, with ca 16 cells in width. Tubercle cells sclerotic, digitate and elongate. Ridges rounded and thin, more or less diffuse, faintly apparent. Endocarp wall 288–304 µm thick (excluding pits). Endocarp wall (excluding pits) with two cell layers: outermost layer with ca 12 rows of periclinally oriented cells, cells 14.7–32.3 µm in width; innermost layer with one row of periclinally oriented cells, cells 4.1–10.0 µm in width, lining the locule surface with inflated cells or regularly spaced and large papillate cells (generally at the apex of the tubercle), cells 12.5–20.0 µm in diameter. Locule not lacunate.

Pyrenacantha soyauxii (Engl.) Byng & Utteridge
Fig. 29.10–29.18

Material examined

Specimen used for endocarp and fruit description
GABON • 1899; *R.P. Klaine 1469*; P[MNHN-P-P04494736].

Description

Fruit. Elliptical, accrescent at the apex and forming an inflated cap (representing about half of the length). Epicarp pilose, with yellow long and thin hair. Mesocarp ca 100 µm thick when dry. Calyx persistent, separated from the fruit by a short gynophore. Length 33–50 mm, width 11.2–26.0 mm, thickness 8.6–12.0 mm.

Fig. 29. Fruits of Icacinaceae Miers. **1**–**9**. *Pyrenacantha rakotozafyi* Labat, El-Achkar & R.Rabev. (*F. Barthelat 1764*). **1**. Dried fruit, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing the pits. **3**. Dorsal view showing the keel. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the endocarp in transverse section showing peg-shaped tubercles. **8**. Detail showing the tubercle base and endocarp cells in transverse section. **9**. SEM image of the uncinate hairs on the epicarp. – **10**–**18**. *Pyrenacantha soyauxii* (Engl.) Byng & Utteridge (*R.P. Klaine 1469*). **10**. Dried fruit with a short gynophore (broken here) and an inflated cap at the apex, lateral view. **11**–**15**. Broken endocarp. **11**. Lateral view showing the pits and ridges. **12**. Dorsal view showing the keel. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of an elongate-flattened tubercle. **17**. SEM image of an elongate-flattened tubercle in its longitudinal section. **18**. Detail showing the endocarp wall in transverse section. – **19**–**27**. *Pyrenacantha staudtii* (Engl.) Engl. (*R.P. Tisserant 1737*). **19**. Dried fruit, lateral view. **19**–**24**. Endocarp. **20**. Lateral view showing the pits and ridges. **21**. Dorsal view showing the keel. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. SEM image of fruit in transverse section showing the cylindrical tubercles. **26**. Detail of a tubercle base and endocarp cells in transverse section. **27**. SEM image of the capitate tubercle apices. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–24 = 10 mm; 25 = 2 mm; 7 = 1 mm; 16–18, 26–27 = 500 µm; 8 = 300 µm; 9 = 100 µm.

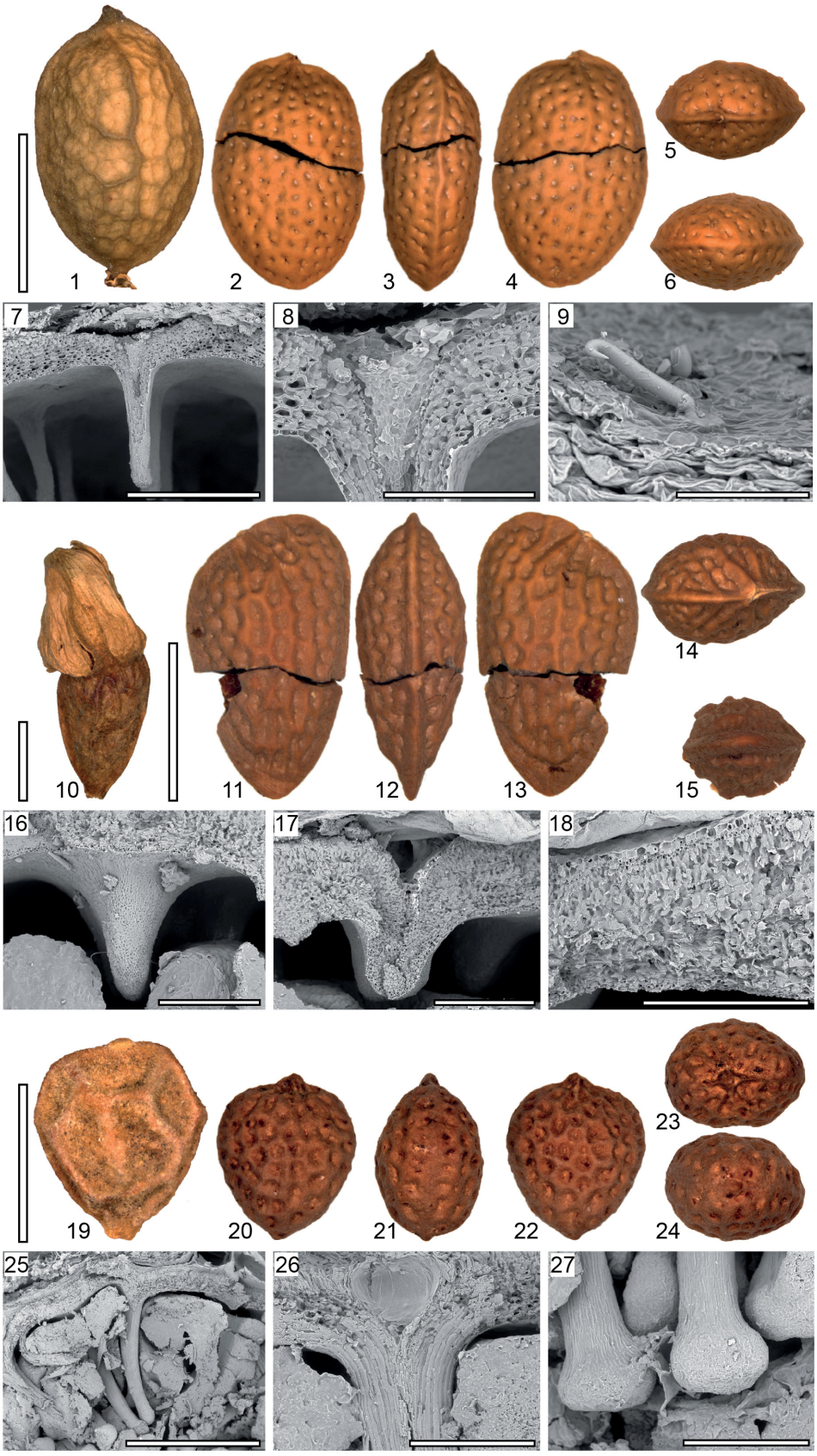

Fig. 29. (see full caption on page 90)

Endocarp. Cream, obovoid in lateral view, lenticular in transverse section, length ca 18.5 mm, width ca 10.5 mm, thickness ca 7 mm. Keel surrounding the endocarp in the plane of symmetry. Apex truncate and slightly asymmetrical, with protuberance; base rounded almost acute, symmetrical. Outer surface of the endocarp pitted and ridged. Pits primarily elongate, arranged in longitudinal lines with 10–11 pits longitudinally and 8–9 pits transversally (ca 60–70 pits per face). Pits associated with elongate-flattened tubercles protruding into the locule; tubercles 523–813 µm in length and 554–651 µm in diameter at the base, with 25–26 cells in width. Tubercle cells sclerotic, digitate and not elongate, more or less anticlinal-isodiametric. Ridges rounded, thin, delimiting a dense reticulum enclosing all pits in an areole. Endocarp wall ca 400 µm thick (excluding pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with 4–6 rows of anticlinally oriented to isodiametric cells, cells 20.5–37.0 µm in length, followed by a layer with 11–13 rows of periclinally oriented cells, cells 7.1–16.2 µm in width; innermost layer with one row of periclinally oriented cells, cells 5.1–9.0 µm in width, lining the locule surface with regularly spaced and rounded papillae or inflated cells, cells 9.1–23.7 µm (av. 13.9 µm) in diameter with ca 1300 papillae / inflated cells per 0.25 mm^2. Locule not lacunate.

Pyrenacantha staudtii (Engl.) Engl.
Fig. 29.19–29.27

Material examined

Specimen used for endocarp and fruit description

CENTRAL AFRICAN REPUBLIC • Boukoko; 10 May 1950; *R.P. Tisserant 1737*; P[MNHN-P-P04472207].

Other material

CAMEROON • 1982; *J.N. Asonganyi 448*; P[MNHN-P-P05279462] • 1962; *F.J. Breteler 2968*; WAG[WAG.1399253].

Description

Fruit. Obovoid, slightly accrescent at the apex. Epicarp puberulent, with yellow simple hairs with granular ornamentation, shriveled when dry. Mesocarp 350–410 µm thick when dry. Calyx persistent. Length 12–20 mm, width 10–12 mm, thickness 7–9 mm.

Endocarp. Brown, elliptical to obovoid in lateral view, lenticular in transverse section, length ca 10.8 mm, width ca 9 mm, thickness ca 6.7 mm. Trace of keel present in the upper part. Apex with acute protuberance, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits primarily elongate, arranged in longitudinal lines with 5–7 pits longitudinally and 7–8 pits transversally (ca 38–43 pits per face). Pits associated with cylindrical tubercles protruding into the locule; tubercles ca 1.8 mm in length and 0.6 mm in diameter at the base, capitate at the apex, with ca 30 cells in width. Tubercle cells sclerotic, digitate and elongate. Ridges rounded and large, delimiting a dense reticulum enclosing all pits in an areole. Endocarp wall 244–295 µm thick (excluding pits). Endocarp wall (excluding pits) with two cell layers: outermost layer with 12 rows of periclinally oriented cells, cells 14.7–21.8 µm in width; innermost layer with one row of periclinally oriented cells, cells 7.3–9.0 µm in width, lining the locule surface. Locule not lacunate.

Pyrenacantha sylvestris S.Moore
Fig. 30.1–30.9

Material examined

Specimen used for endocarp and fruit description

GABON • 1964; *N. Hallé 3598*; P[MNHN-P-P04472269].

Other material

GABON • 1979; *J. Florence 2002*; P[MNHN-P-P04472191].

Description

Fruit. Elliptical, acuminate and accrescent at the apex, brown when mature. Epicarp puberulent, with yellow simple hairs with granular ornamentation and yellow-red uncinate hairs, shriveled when dry, revealing the underlying reticulum of endocarp ridges. Mesocarp 170–300 µm thick when dry. Calyx persistent. Length 10.2–12.0 mm, width 8.5–12.0 mm, thickness 3.5–5.6 mm.

Endocarp. Brown, elliptical in lateral view, lenticular in transverse section, length ca 9 mm, width ca 7.4 mm, thickness ca 5 mm. Sharp keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical and acute in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits elongate and thin, ca 0.1–0.5 mm in length, randomly arranged with 6–7 pits longitudinally and 5–8 pits transversally (ca 44–54 pits per face). Pits associated with cylindrical tubercles protruding into the locule; tubercles ca 1307–1549 µm in length and 488–604 µm in diameter at the base, capitate or bifid at the apex, with ca 28 cells in width. Tubercle cells sclerotic, digitate and elongate. Ridges rounded and thin, more or less diffuse, faintly apparent, with a median ridge running longitudinally from the base up to the apex. Endocarp wall 189–228 µm thick (excluding pits). Endocarp wall (excluding pits) with three cell layers: outermost layer with 2–3 rows of anticlinally oriented to isodiametric cells, cells 11.8–18.5 µm in length, followed by a layer with 9–10 rows of periclinally oriented thick cells, cells 13.1–17.9 µm in width; innermost layer with one row of periclinally oriented cells, cells 8.4–14.7 µm in width, lining the locule surface with inflated to papillate cells. Locule not lacunate.

Pyrenacantha thomsoniana (Bail.) Byng & Utteridge
Fig. 30.10–30.18

Material examined

Specimen used for endocarp and fruit description

GABON • 1907; *M. Le Testu 1038*; P[MNHN-P-P04494723].

Other material

CENTRAL AFRICAN REPUBLIC • Boukoko; 10 Dec. 1947; *Equipe ?*; P[MNHN-P-P04494725] • Boukoko; 27 Jan. 1949; *Equipe ?*; P[MNHN-P-P04494720].

Description

Fruit. Elliptical, accrescent elongate at the apex (representing ⅕ of the fruit length). Epicarp pilose, with yellow long and thin hairs. Mesocarp thin when dry. Calyx persistent, separated from the fruit by an elongate gynophore. Length 45–80 mm, width 14–18 mm, thickness 7–12 mm.

Endocarp. Brown, elliptical in lateral view, lenticular in transverse section, length ca 14.8 mm, width ca 11.5 mm, thickness ca 6.8 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits circular, occasionally elongate, 0.3–0.6 mm in diameter, randomly arranged with 7–12 pits longitudinally and 9–11 pits transversally (ca 74–83 pits per face). Pits associated with elongate-flattened tubercles protruding into the locule; tubercles 634–761 µm in length and ca 670 µm in diameter at the base, with ca 20 cells in width. Tubercle cells sclerotic, digitate and not elongate, more or less anticlinal-isodiametric. Ridges rounded and thin, with 5–6 ridges longitudinally; the median ridge runs from the base up to the apex. Ridges delimiting a reticulate pattern enclosing 5–7 areoles. Secondary ridges delimiting small areoles more or less enclosing each pit. Endocarp wall 376–433 µm

thick excluding ridges (520–590 µm thick including ridges). Endocarp wall (excluding pits) with three cell layers: outermost layer with 3–6 rows of anticlinally oriented cells, cells 11.9–35.3 µm in length, followed by a layer with 5–9 rows of periclinally oriented cells, cells 9.7–18.6 µm in width; innermost layer with one row of periclinally oriented cells, cells 6.9–9.9 µm in width, lining the locule surface with regularly spaced and rounded papillae; papillae 7.1–11.2 µm (av. 9.1 µm) in diameter, 650–920 papillae per 0.25 mm^2. Locule not lacunate.

Pyrenacantha tropophila Labat, El-Achkar & R.Rabev.
Fig. 30.19–30.26

Material examined

Specimen used for endocarp and fruit description
MADAGASCAR • 1904; *H. Perrier de la Bâthie 1746*; P[MNHN-P-P00441092].

Other material
MADAGASCAR • s.d.; *H. Perrier de la Bâthie 1621*; P[MNHN-P-P00440610].

Description

Fruit. Elliptical to globose, accrescent at the apex, brown-orange when mature. Epicarp puberulent with yellow long and thin hairs and yellow simple hairs with granular ornamentation, shriveled when dry. Length 25–32 mm, width 17–25 mm, thickness 16–18 mm.

Endocarp. Brown, elliptical to ovoid in lateral view, globose in transverse section, length ca 20 mm, width ca 14.1 mm, thickness ca 12 mm. Trace of keel present in the upper part. Apex with acute protuberance, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted. Pits circular, occasionally elongate longitudinally, 0.7–1.3 mm in length, randomly arranged with 9–12 pits longitudinally and 8–10 pits transversally (ca 80–93 on each face). Pits associated with spiny-cylindrical tubercles protruding into the locule; tubercles 2290–2702 µm in length and 992–1264 µm in diameter at the base, capitate at the apex, with ca 33 cells in width. Tubercle cells sclerotic, digitate and elongate. Endocarp wall 374–394 µm thick (excluding pits). Endocarp wall (excluding pits) with

Fig. 30. Fruits of Icacinaceae Miers. **1**–**9**. *Pyrenacantha sylvestris* S.Moore (*N. Hallé 3598*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing the pits and ridges. **3**. Dorsal view showing the keel. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the fruit in transverse section showing cylindrical tubercles. **8**. Detail of a tubercle base and endocarp cells in transverse section. **9**. Detail of the pericarp showing endocarp bellow the mesocarp and epicarp covered by dense simple hairs. – **10**–**18**. *Pyrenacantha thomsoniana* (Bail.) Byng & Utteridge (*M. Le Testu 1038*). **10**. Dried fruit with short gynophore and a cap ending in a very long tip, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing the pits and ridges. **12**. Dorsal view showing the keel. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of the pericarp in transverse section showing the elongate-flattened tubercles. **17**. SEM image of pericarp showing the long and thin hairs on the epicarp. **18**. SEM image of the endocarp wall in transverse section bearing the tubercules. – **19**–**26**. *Pyrenacantha tropophila* Labat, El-Achkar & R.Rabev. (*H. Perrier de la Bâthie 1746*). **19**–**23**. Endocarp. **19**. Lateral view showing the pits. **20**. Dorsal view. **21**. Opposite lateral view. **22**. Apical view. **23**. Basal view. **24**. SEM image of the endocarp and seed in transverse section showing the spiny tubercles. **25**. Detail of longitudinal section of a tubercle base. **26**. Detail showing inner layers of the endocarp and the papillae emerging from the locule surface. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–23 = 10 mm; 7, 17, 24 = 2 mm; 16, 18 = 1 mm; 9 = 500 µm; 8, 25 = 300 µm; 26 = 50 µm.

Fig. 30. (see full caption on page 92)

three cell layers: outermost layer with 2–5 rows of isodiametric to periclinally oriented cells, cells 7.5–13.0 µm in width, followed by a layer with ca 18 rows of periclinally oriented cells, cells 10.8–21.0 µm in width; innermost layer with one row of periclinally oriented cells, cells 10.7–16.5 µm in width, lining the locule surface with regularly spaced and rounded papillae; papillae 11.8–27.0 µm (av. 16.9 µm) in diameter. Locule surface not lacunate.

Pyrenacantha vogeliana Baill.
Fig. 31.1–31.9

Material examined

Specimen used for endocarp and fruit description
AFRICA • "Côte orientale d'Afrique"; s.d.; *R.P. Sacleux 1873*; P[MNHN-P-P04472242].

Other material
GABON • 1900; *R.P. Klaine 1803*; P[MNHN-P-P04472246].

Description

Fruit. Elliptical, accrescent at the apex, red when mature. Epicarp strigose, with yellow simple hairs with granular ornamentation. Mesocarp 141–170 µm thick when dry. Calyx persistent. Length ca 17.4 mm, width ca 9.2 mm, thickness ca 7.2 mm.

Endocarp. Cream, elliptical in lateral view, lenticular in transverse section, length ca 14.6 mm, width ca 8.3 mm, thickness ca 6.6 mm. Keel surrounding the endocarp in the plane of symmetry. Apex with acute protuberance, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp pitted and ridged. Pits exclusively circular, 0.1–0.2 mm in diameter, more or less longitudinally arranged with 12–18 pits longitudinally and 13–14 pits transversally (ca 200–210 pits per face). Pits associated with peg-shaped tubercles protruding into the locule; tubercles ca 852–1057 µm in length and 273–286 µm in diameter at the base. Endocarp wall 300–477 µm thick (excluding pits). Endocarp wall (excluding pits) with two cell layers: outermost layer with ca 19 rows of periclinally oriented cells, cells 9.0–59.7 µm in width; innermost layer with one row of periclinally oriented cells, cells 5.7–8.5 µm in width, lining the locule surface with regularly spaced and rounded papillae; papillae 10.0–19.4 µm (av. 15 µm) in diameter. Locule surface not lacunate.

Fig. 31. Fruits of Icacinaceae Miers. **1**–**9**. *Pyrenacantha vogeliana* Baill. (*R.P. Sacleux 1873*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing pits and faintly marked ridges. **3**. Dorsal view showing the keel. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the endocarp in a transverse section showing peg-shaped tubercles. **8**. SEM image of a longitudinal section of the peg-shaped tubercle showing cells and central lacuna. **9**. SEM image of the endocarp in transverse section. – **10**–**17**. *Rhyticaryum elegans* G.Schellenb. (*R. Schlechter 18681*). **10**. Dried fruit, lateral view. **11**–**14**. Broken endocarp. **11**. Lateral view showing a reticulate pattern of ridges. **12**. Opposite lateral view. **13**. Basal view. **14**. Magnification of the lateral view showing the pore at the apex (arrow). **15**. SEM image of the pericarp in transverse section showing a ridge. **16**. SEM image of the endocarp and mesocarp in transverse section. **17**. Detail of the inner layers of the endocarp with papillae lining the locule surface. – **18**–**25**. *Rhyticaryum fasciculatum* Becc. (*Heu Her 4*). **18**–**22**. Endocarp. **18**. Lateral view showing a reticulate pattern of ridges. **19**. Dorsal view showing the keel. **20**. Opposite lateral view. **21**. Apical view. **22**. Basal view. **23**. SEM image of the endocarp wall in transverse section. **24**. Detail showing the cell arrangement. **25**. Other detail of inner part of the endocarp showing the papillae lining the locule surface. Images taken from Del Rio (2018). Scale bars: 1–6, 10–13, 18–22 = 10 mm; 7, 14, 23 = 1 mm; 15–16, 24 = 500 µm; 9 = 300 µm; 8 = 200 µm; 25 = 100 µm; 17 = 50 µm.

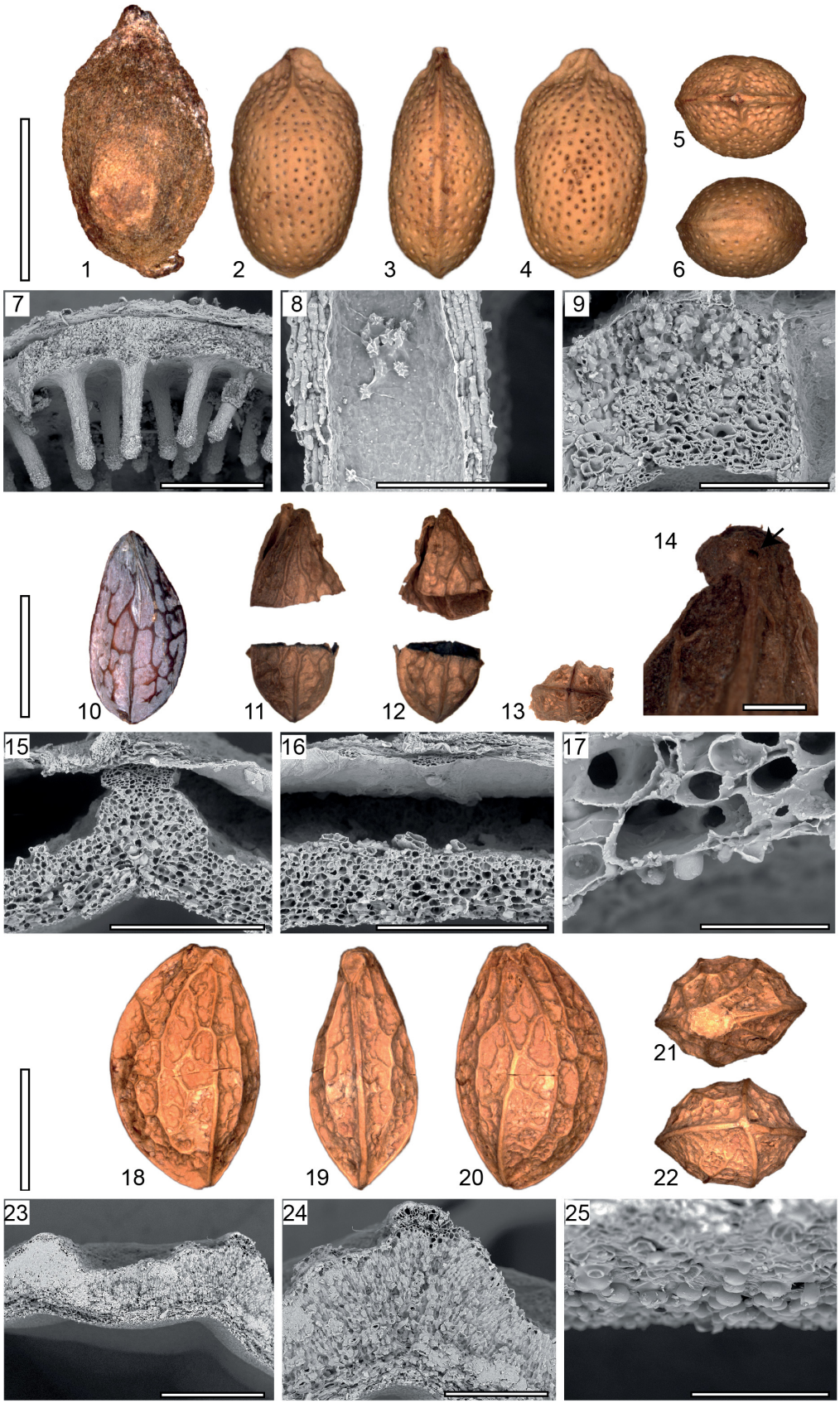

Fig. 31. (see full caption on page 96)

Genus ***Rhyticaryum*** Becc.
Figs 31.10–31.25, 32, 33.1–33.18

Description

Fruit. Elliptical, asymmetrical at the apex, laterally compressed, red when mature. Epicarp strigose, with simple hairs with granular ornamentation or glabrous, shriveled when dry, revealing the underlying reticulum of endocarp ridges. Calyx persistent.

Endocarp. Brown-cream, elliptical in lateral view, lenticular in transverse section. Keel surrounding the endocarp in the plane of symmetry. Apex asymmetrical in lateral view, with pair of subapical pores, occasionally absent; base symmetrical. Outer surface of the endocarp ridged, rarely rugose; ridges diffuse or delimiting a reticulate pattern enclosing polygonal areoles with freely ending ridgelets. Ridges rounded, occasionally sharp. Vasculatures of the endocarp resting on the ridges. Endocarp primary vascular bundle outside the endocarp wall or in a channel on the keel. Endocarp wall at least with one layer with rows of periclinally oriented cells and another with rows of anticlinally oriented cells. Locule surface covered with large to rounded and regularly spaced papillae. Locule lacunate.

Key to the genus *Rhyticaryum*

1. Endocarp 28.8–36.3 mm in length, endocarp wall 800–950 µm thick .....***R. macrocarpum*** Becc.
– Endocarp less than 23.6 mm in length, endocarp wall less than 600 µm thick 2

2. Endocarp primary vascular bundle in a channel .....***R. novoguineense*** (Warb.) Sleumer
– Endocarp primary vascular bundle outside the endocarp wall 3

3. Endocarp ridging reticulate 4
– Endocarp ridging not reticulate ..... ***R. oleraceum*** Becc.

4. Subapical pores present, endocarp wall less than 250 µm thick .....***R. elegans*** G.Schellenb.
– Subapical pores absent, endocarp wall more than 300 µm thick 5

5. Areoles 15–21 on each face, endocarp wall 514–575 µm thick ..... ***R. fasciculatum*** Becc.
– Fewer than 15 areoles on each face, endocarp wall less than 500 µm thick 6

6. Fruit strigose, endocarp width ca 10 mm .....***R. longifolium*** K.Schum. & Lauterb.
– Fruit glabrous, endocarp width ca 13 mm .....***R. racemosum*** Becc.

Rhyticaryum elegans G.Schellenb.
Fig. 31.10–31.17

Material examined

Specimen used for endocarp and fruit description

MELANESIA • "Papouasie" [Papuasia]; 1908; *R. Schlechter 18681*; P[MNHN-P-P04513302].

Description

Fruit. Epicarp strigose, with yellow simple hairs with granular ornamentation; mesocarp 50–72 µm thick when dry. Length 16.3–18.0 mm, width 8.2–9.0 mm, thickness 5–7 mm.

Endocarp. Brown, length ca 15.2 mm, width ca 7.2 mm, thickness ca 5.8 mm. Keel surrounding the endocarp in the plane of symmetry. Apex acute, asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp ridged, with 2–4 main longitudinal ridges; the median ridge reaching the

point of the base. Ridges rounded and thin, with a median channel, almost diffuse but enclosing ca 6 longitudinal polygonal areoles with freely ending ridgelets. Endocarp possessing a symmetrical pair of pores positioned eccentrically and subapically on the median ridge. Primary vascular bundle positioned outside the endocarp wall. Endocarp wall 174–246 µm thick excluding ridges (280–370 µm thick including ridges). Endocarp wall with three cell layers: outermost layer with 0–2 row(s) of isodiametric to anticlinally oriented cells, cells 15.9–23.5 µm in length; middle layer with 8–10 rows of anticlinally oriented cells, cells 18.0–20.9 µm in length; innermost layer with one row of periclinally oriented cells, cells 6.7–11.0 µm in width, lining the locule surface with regularly spaced and large papillae; papillae 9.1–20.7 µm (av. 15.1 µm) in diameter, 500–900 papillae (av. 637 papillae) per 0.25 mm^2.

Rhyticaryum fasciculatum Becc.
Fig. 31.18–31.25

Material examined

Specimen used for endocarp and fruit description
INDONESIA • 12 Oct. 2004; *Heu Her 4*; K[K000271837].

Description

Fruit. Epicarp sparsely strigose, with yellow simple hairs with granular ornamentation. Mesocarp thin. Length 13.0–20.5 mm, width 10–15 mm, thickness 7–9 mm.

Endocarp. Brown, length ca 20.5 mm, width ca 12.3 mm, thickness ca 9 mm. Keel surrounding the endocarp in the plane of symmetry. Apex truncate, slightly inflated and asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp ridged, with ca four ridges longitudinally, the median ridge reaching the point of the base. Ridges rounded and thin, with a median channel, enclosing 15–21 polygonal areoles. Areols elongate longitudinally, with freely ending ridgelets, some ridgelets arbuscular. Primary vascular bundle positioned outside the endocarp wall. Endocarp wall 514–575 µm thick excluding ridges (751–989 µm thick including ridges). Endocarp wall with three cell layers: outermost layer with ca 14 rows of anticlinally oriented cells, cells 24.6–54.4 µm in length, followed by a layer with ca 8 rows of periclinally oriented cells, cells 18.1–25.1 µm in width; innermost layer with one row of periclinally oriented cells, cells 8.7–11.9 µm in width, lining the locule surface with regularly spaced and large papillae; papillae 7.2–21.0 µm (av. 13.9 µm) in diameter, 710 papillae per 0.25 mm^2.

Rhyticaryum longifolium K.Schum. & Lauterb.
Fig. 32.1–32.9

Material examined

Specimen used for endocarp and fruit description
PAPUA NEW GUINEA • 21 Nov. 1973; *Jacobs 9671*; L[L.229211] • 1962; *Bowers 84*; L[L.2292735].

Other material
PAPUA NEW GUINEA • 1996; *W. Takeuchi & J. Kulang 11657*; P[MNHN-P-P05279704].

Description

Fruit. Epicarp strigose, with red simple hairs with granular ornamentation. Mesocarp 110–130 µm thick when dry. Length 18.2–25.0 mm, width 11.4–17.0 mm, thickness 7.6–10.0 mm.

Endocarp. Cream, length 16.8–17.0 mm, width 10.7–11.9 mm, thickness 7.6–8.1 mm. Keel surrounding the endocarp in the plane of symmetry. Apex truncate, slightly inflated and asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp ridged, with ca five longitudinal ridges; the

median ridge reaching the point of the base. Ridges sharp to slightly rounded and thin, with a median channel, enclosing 7–11 polygonal areoles with small freely ending ridgelets. Primary vascular bundle positioned outside the endocarp wall. Endocarp wall 312–445 µm thick excluding ridges (740–840 µm thick including ridges). Endocarp wall with three cell layers: outermost layer with 2–3 rows of anticlinally oriented cells, cells 14.1–20.5 µm in length, followed by a layer with ca13 rows of periclinally oriented cells, cells 15.6–40.3 µm in width; innermost layer with one row of periclinally oriented cells, cells 10.1–17.4 µm in width, lining the locule surface with regularly spaced and rounded papillae; papillae 9.5–18.8 µm (av. 12.7 µm) in diameter, 550 papillae per 0.25 mm^2.

Rhyticaryum macrocarpum Becc.
Fig. 32.10–32.18

Material examined

Specimen used for endocarp and fruit description
NEW GUINEA • 1961; *W. Vink 11381*; L[L.2293146].

PAPUA NEW GUINEA • 17 Feb. 1972; *Katik 46856*; L[L.2293142].

Description

Fruit. Epicarp glabrous, mesocarp thick, leather-like in texture. Calyx not persistent. Length 35–43 mm, width 25–30 mm, thickness ca 15 mm.

Endocarp. Brown, length 28.8–36.3 mm, width 21.5–28.0 mm, thickness 13.7–14.6 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly flattened, asymmetrical in lateral view; base rounded-truncate or cleft at the base, or slightly asymmetrical. Outer surface of the endocarp sparsely rugose and ridged, with ca 2–5 longitudinal ridges; the median ridge spanning from the base to the apex. Ridges rounded and large, enclosing ca 0–5 polygonal areoles, occasionally without transversal ridges. Endocarp possessing a symmetrical pair of pores positioned eccentrically and subapically on the median ridge. Primary vascular bundle positioned outside the endocarp wall. Endocarp wall 800–950 µm thick excluding ridges (ca 1300 µm thick including ridges). Endocarp wall with three cell layers: outermost layer with ca 17 rows of anticlinally oriented cells, cells 16.4–47.7 µm in length, followed by a layer with ca 14 rows of periclinally oriented cells, cells 16.4–27.1 µm in width; innermost layer with one row of periclinally oriented cells, lining the locule surface with regularly spaced and large papillae; papillae 19.4–32.7 µm (av. 25.0 µm) in diameter, 400 papillae per 0.25 mm^2.

Fig. 32. Fruits of Icacinaceae Miers. **1**–**9**. *Rhyticaryum longifolium* K.Schum. & Lauterb. (*Jacobs 9671*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing a reticulate pattern of ridges. **3**. Dorsal view showing the keel. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the keel in transverse section. **8**. SEM image of the pericarp in transverse section showing the ridges and endocarp wall. **9**. SEM image of papillae lining the locule surface. – **10**–**18**. *Rhyticaryum macrocarpum* Becc. **10**. Dried fruit, lateral view (*W. Vink 11381*). **11**–**15**. Endocarp (*W. Vink 11381*). **11**. Lateral view showing the ridges. **12**. Dorsal view showing the keel. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. Lateral view of other specimen showing the reticulum of ridges (*Katik 46856*). **17**. SEM image of the endocarp wall in transverse section (*W. Vink 11381*). **18**. SEM image of papillae lining the locule surface (*W. Vink 11381*). – **19**–**26**. *Rhyticaryum novoguineense* (Warb.) Sleumer. (*A. Millar, NGF 40764*). **19**. Dried fruit, lateral view. **20**–**24** . Endocarp. **20**. Lateral view showing a reticulate pattern of ridges. **21**. Dorsal view showing the keel. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. SEM image of the pericarp in transverse section. **26**. SEM image of the papillae lining the locule surface. Images taken from Del Rio (2018). Scale bars: 1–6, 10–16, 19–24 = 10 mm; 7–8, 17, 25 = 1 mm; 18, 26 = 100 µm; 9 = 50 µm.

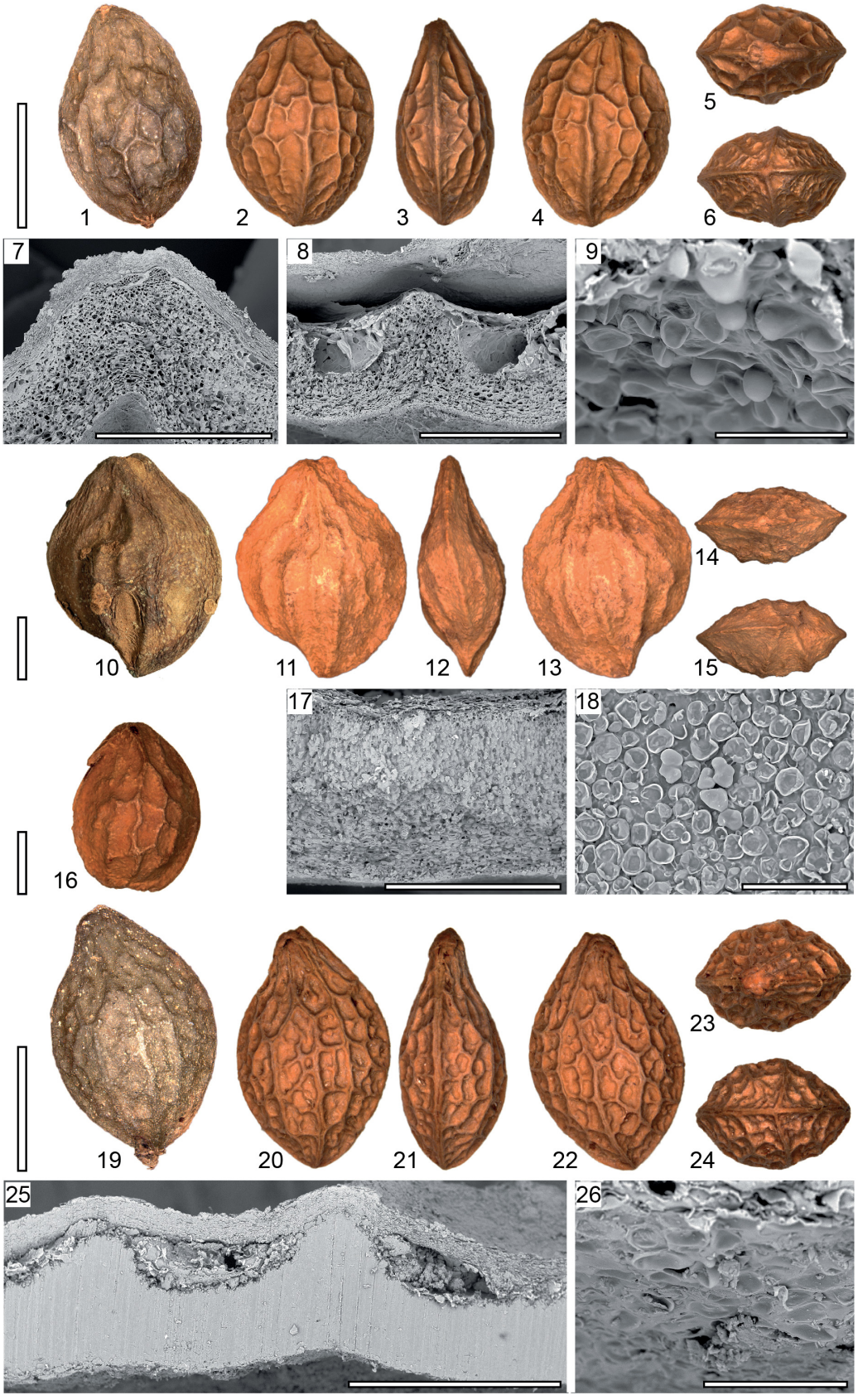

Fig. 32. (see full caption on page 100)

Rhyticaryum novoguineense (Warb.) Sleumer
Fig. 32.19–32.26

Material examined

Specimen used for endocarp and fruit description
PAPUA NEW GUINEA • 1968; *A. Millar NGF 40764*; L[L.2293149].

Description

Fruit. Epicarp strigose, with yellow simple hairs with granular ornamentation; mesocarp 120–340 µm thick when dry. Length 17.0–21.1 mm, width 13.2–15.0 mm, thickness 5.0–9.2 mm.

Endocarp. Cream, length ca 19.8 mm, width 12.4–12.5 mm, thickness ca 8.7 mm. Keel surrounding the endocarp in the plane of symmetry, with a central channel. Apex slightly inflated and asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp ridged, with 5–6 ridges longitudinally; the median ridge running from the base to the apex. Ridges rounded and thin, with a median channel, enclosing ca 22 polygonal areoles with small freely ending ridgelets. Endocarp possessing a symmetrical pair of pores positioned eccentrically and subapically on the median ridge. Primary vascular bundle positioned inside the channel on the keel. Endocarp wall 391–405 µm thick excluding ridges (624–654 µm thick including ridges). Endocarp wall structure unknown.

Remarks

The structure of the wall was crushed in the process of material preparation, rendering the anatomy unobservable (see Discussion for preservation issues).

Rhyticaryum oleraceum Becc.
Fig. 33.1–33.9

Material examined

Specimen used for endocarp and fruit description
INDONESIA • Moluccas isl.; 1938; *P. Buwalda 4471*; L[L.2293162].

Fig. 33. Fruits of Icacinaceae Miers. **1**–**9**. *Rhyticaryum oleraceum* Becc. (*P. Buwalda 4471*). **1**. Dried fruit, lateral view. **2**–**6**. Broken endocarp. **2**. Lateral view showing the ridges. **3**. Dorsal view showing the keel. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the keel in transverse section. **8**. SEM image of the endocarp wall in transverse section. **9**. SEM image of papillae lining the locule surface. – **10**–**18**. *Rhyticaryum racemosum* Becc. (*Royen 3448*). **10**. Dried fruit, lateral view. **11**–**15**. Broken endocarp. **11**. Lateral view showing a reticulate pattern of ridges. **12**. Dorsal view showing the keel. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of a ridge in transverse section. **17**. SEM image of the endocarp wall in transverse section. **18**. SEM image of papillae lining the locule surface. – **19**–**24**. *Sarcostigma kleinii* Wight & Arn. (*King's Collector s.n.*). **19**–**21**. Broken endocarp. **19**. Lateral view showing the faint ornamentation. **20**. Dorsal view. **21**. Opposite lateral view. **22**. Apical view. **23**. Basal view. **24**. SEM image of the endocarp wall in transverse section. – **25**–**31**. *Sarcostigma paniculata* Pierre; E. (*Poilane 6677*). **25**. Dried fruit, lateral view. **26**–**30**. Broken endocarp. **26**. Lateral view showing the indistinct ornamentation. **27**. Dorsal view showing the keel. **28**. Opposite lateral view. **29**. Apical view. **30**. Basal view. **31**. SEM image of the endocarp wall in transverse section. 32. SEM image of the papillae lining the locule surface. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–23, 25–30 = 10 mm; 16 = 1 mm; 7, 17, 24, 31 = 500 µm; 8 = 200 µm; 18, 32 = 100 µm; 9 = 50 µm.

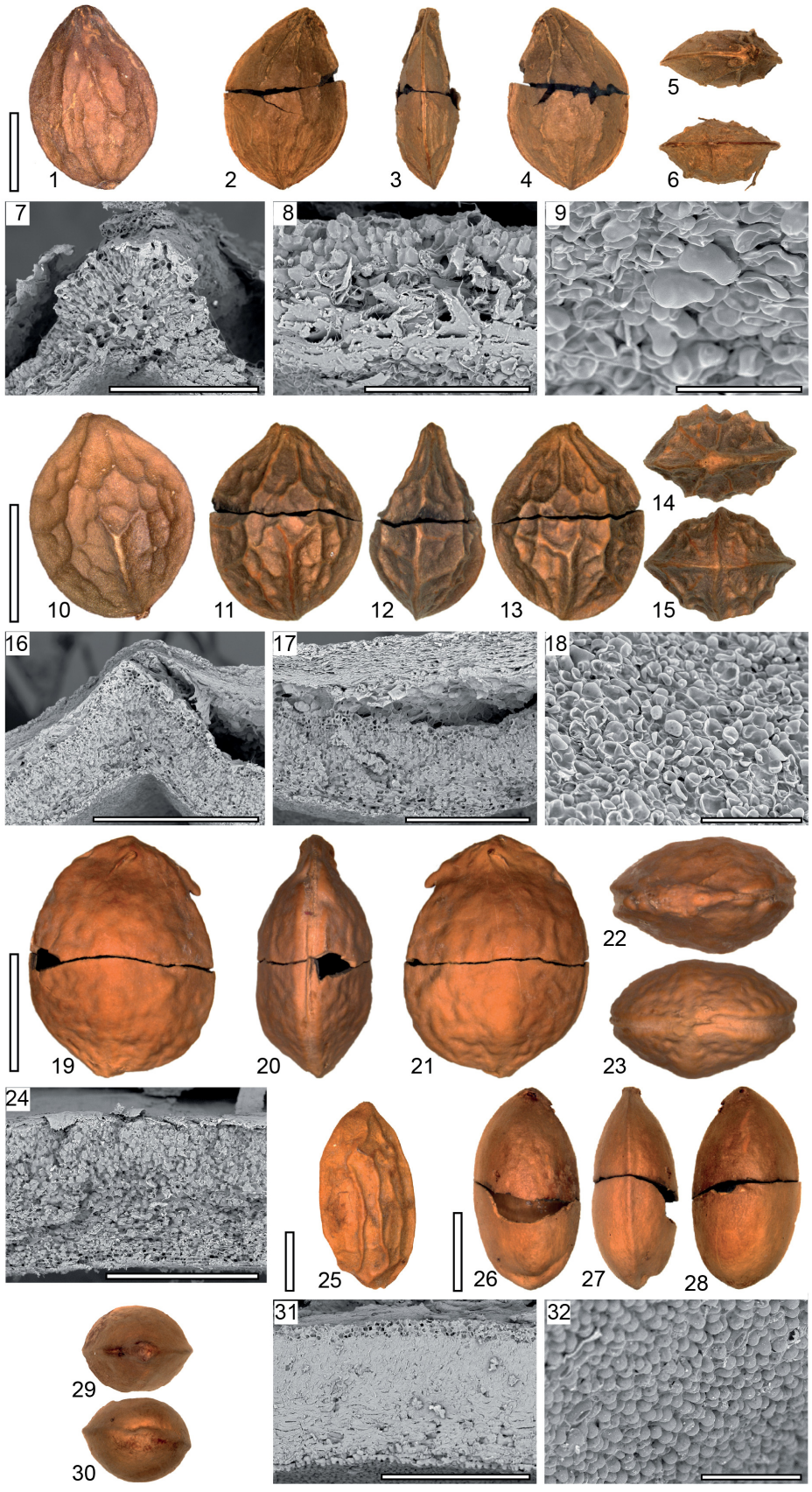

Fig. 33. (see full caption on page 102)

Description

Fruit. Epicarp glabrous; mesocarp 260–270 µm thick when dry. Length 17–26 mm, width 10.0–15.7 mm, thickness 7.4–10.0 mm.

Endocarp. Cream, length ca 23.6 mm, width ca 15.7 mm, thickness ca 8.7 mm. Keel surrounding the endocarp in the plane of symmetry. Apex slightly inflated and asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp ridged with three main ridges longitudinally. Ridges rounded and thin, forming a diffuse pattern, with two ridges spanning from the apex to nearly the base and a median ridge spanning from the base to nearly the apex. Primary vascular bundle positioned outside the endocarp wall. Endocarp wall 157–188 µm thick excluding ridges (ca. 420 µm including ridges). Endocarp wall with three cell layers: outermost layer with 5–7 rows of anticlinally oriented cells, cells 17.2–29.4 µm in length, followed by a layer with 2–3 rows of periclinally oriented cells, cells 15.4–24.0 µm in width; innermost layer with one row of periclinally oriented cells, cells 4.3–6.0 µm in width, lining the locule surface with regularly spaced and large papillae; papillae 8.9–28.3 µm (av. 15.0 µm) in diameter.

Rhyticaryum racemosum Becc.
Fig. 33.10–33.18

Material examined

Specimen used for endocarp and fruit description
NEW GUINEA • 1954; *Royen 3448*; L[L.2293115].

Description

Fruit. Epicarp glabrous; mesocarp 70–200 µm thick when dry. Length 15–18 mm, width 10.0–13.8 mm, thickness 8–10 mm.

Endocarp. Cream, length ca 17.1 mm, width ca 13.3 mm, thickness ca 10 mm. Keel surrounding the endocarp in the plane of symmetry. Apex asymmetrical in lateral view; base rounded, symmetrical. Outer surface of the endocarp ridged, with three longitudinal ridges; the median ridge spanning from the base to the apex. Ridges sharp and thin, with a median channel, delimiting a reticulate pattern enclosing ca 10 irregular areoles, each with freely ending ridgelets more or less branched. Endocarp primary vascular bundle outside the endocarp wall. Endocarp wall 363–391 µm thick excluding ridges (520–686 µm thick including ridges). Endocarp wall with three cell layers: outermost layer with ca 8 rows of anticlinally oriented to isodiametric cells, cells 15.7–28.7 µm in length, followed by a layer with ca 11 rows of periclinally oriented cells, cells 8.1–20.0 µm in width; innermost layer with one row of periclinally oriented cells, cells 5.9–7.4 µm in width, lining the locule surface with regularly spaced and large papillae; papillae 8.0–27.0 µm (av. 16.4 µm) in diameter, ca 790 papillae per 0.25 mm^2.

Genus ***Sarcostigma*** Wight & Arn.
Fig. 33.19–33.32

Description

Fruit. Elliptical, slightly asymmetrical or symmetrical, laterally compressed, red-black when mature. Epicarp puberulent, with simple hairs with granular ornamentation or uncinate hairs, occasionally shriveled when dry. Calyx persistent.

Endocarp. Cream, elliptical in lateral view, lenticular to globose in transversal view. Keel or channel surrounding the endocarp in the plane of symmetry. Apex asymmetrical in lateral view, with a pair of subapical pores with a central pit; base symmetrical. Outer surface of the endocarp rugose, irregular,

almost smooth. Vasculature of the endocarp free. Primary vascular bundle outside the endocarp wall or in a channel on the keel. Endocarp wall with at least one layer with row(s) of periclinally oriented cells and another with rows of anticlinally oriented cells. Locule surface covered by rounded and regularly spaced papillae. Locule lacunate.

Key to the genus *Sarcostigma*

1. Endocarp globose in transverse section, ca 13 mm in width, endocarp primary vascular bundle positioned outside the endocarp wall ..... ***S. paniculata*** Pierre
– Endocarp lenticular in transverse section, ca 16 mm in width, endocarp primary vascular bundle lying in a channel ..... ***S. klenii*** Wight & Arn.

Sarcostigma kleinii Wight & Arn.
Fig. 33.19–33.24

Material examined

Specimen used for endocarp and fruit description
INDIA • 1890; *King's Collector s.n.*; K.

Other material
VIETNAM • 2008; *DDS_14043*; P[MNHN-P-P06807860].

Description

Fruit. Red when mature. Epicarp puberulent, with yellow simple hairs with granular ornamentation. Mesocarp 313–343 µm thick when dry. Length 22–35 mm, width 16–23 mm, thickness 10–15 mm.

Endocarp. Lenticular in transverse section, length ca 21 mm, width ca 16 mm, thickness ca 9.9 mm. Channel surrounding the endocarp in the plane of symmetry, with thin median ridge. Apex rounded. Primary vascular bundle lying in the channel surrounding the endocarp. Endocarp wall 496–513 µm thick excluding rugosities (614 µm thick including rugosities). Endocarp wall with three cell layers: outermost layer with ca 13 rows of anticlinally oriented cells, cells 17.6–35.8 µm in length; middle layer with 10 rows of periclinally oriented cells, cells 13.0–17.2 µm in width; innermost layer with one row of periclinally oriented cells, cells 5.8–6.1 µm in width, lining the locule surface. Detail of the locule surface unknown.

Remarks

The surface of the locule was decayed by a fungi (see Discussion for preservation issues).

Sarcostigma paniculata Pierre
Fig. 33.25–33.32

Material examined

Specimen used for endocarp and fruit description
VIETNAM • 1923; *E. Poilane 6677*; P[MNHN-P-P05279454].

Other material
VIETNAM • 2008; *DDS_14047*; P[MNHN-P-P06807857].

Description

Fruit. Slightly asymmetrical at the apex, brown-black when mature. Epicarp strigose, with yellow uncinate hairs, shriveled when dry. Mesocarp 200–250 µm thick when dry. Length 30–38 mm, width 15–23 mm, thickness 9.0–13.4 mm.

Endocarp. Globose in transverse section, length 26.1–27.6 mm, width 12.9–14.0 mm, thickness 10.5–10.8 mm. Keel surrounding the endocarp in the plane of symmetry. Apex acute. Primary vascular bundle positioned outside the endocarp wall. Endocarp wall 474–490 µm thick. Endocarp wall with three cell layers: outermost layer with ca 14 rows of anticlinally oriented cells, cells 20.3–40.5 µm in length, followed by a layer with ca 7 rows of periclinally oriented cells, cells 16.1–22.4 µm in width; innermost layer with one row of periclinally oriented cells, cells 6.7–8.7 µm in width, lining the locule surface with regularly spaced and rounded papillae; papillae 12.8–20.6 µm (av. 15.7 µm) in diameter, ca 1020–1070 papillae per 0.25 mm^2. Locule surface not lacunate.

Genus ***Stachyanthus*** Engl.
Fig. 34

Description

Fruit. Elliptical, acute-acuminate at the apex, laterally compressed, yellow or blue when mature. Epicarp strigose to pubescent, with simple hairs with granular ornamentation and / or uncinate hairs, rugose-ridged or smooth when dry. Calyx persistent.

Endocarp. Cream to brown, elliptical in lateral view, lenticular in transverse section. Keel surrounding the endocarp in the plane of symmetry. Apex asymmetrical; base symmetrical. Outer surface of the endocarp pitted and ridged. Pits more or less circular, associated with bullate tubercles. Ridges forming a diffuse pattern, faintly apparent. Vasculature of the endocarp free. Primary vascular bundle positioned outside the endocarp wall. Endocarp wall with at least one layer with rows of periclinally oriented cells. Locule surface smooth and lacunate.

Fig. 34. Fruits of Icacinaceae Miers. **1**–**9**. *Stachyanthus donisi*i (Boutique) Boutique (*J.H. Laurent 423*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing the pits and ridges. **3**. Dorsal view showing the keel. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the bullate tubercle from the locule side. **8**. SEM image of the endocarp in transverse section, showing arrangement of the bullate tubercle cells. **9**. Detail showing the central tubercle cells. – **10**–**18**. *Stachyanthus occidentalis* (Keay & É. Miège) Boutique (*A. Chevalier 23794*). **10**. Dried fruit, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing the pits and ridges. **12**. Dorsal view showing the keel. **13**. Opposite lateral view. **14**. Apical view. **15**. Basal view. **16**. SEM image of the bullate tubercles from the locule side. **17**. SEM image of the pericarp in transverse section showing bullate tubercles. **18**. Detail of the endocarp wall. – **19**–**27**. *Stachyanthus zenkeri* Engl. (*Carvalho 3626*). **19**. Dried fruit, lateral view. **20**–**24**. Broken endocarp. **20**. Lateral view showing the pits and ridges. **21**. Dorsal view showing the keel. **22**. Opposite lateral view. **23**. Apical view. **24**. Basal view. **25**. SEM image in transverse section of the pericarp showing the ridges and bullate tubercles. **26**. Detail on the pericarp in transverse section. **27**. Detail showing the endocarp wall. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 19–24 = 10 mm; 25 = 2 mm; 26 = 1 mm; 8, 17, 27 = 500 µm; 7 = 300 µm; 16, 18 = 200 µm; 9 = 50 µm.

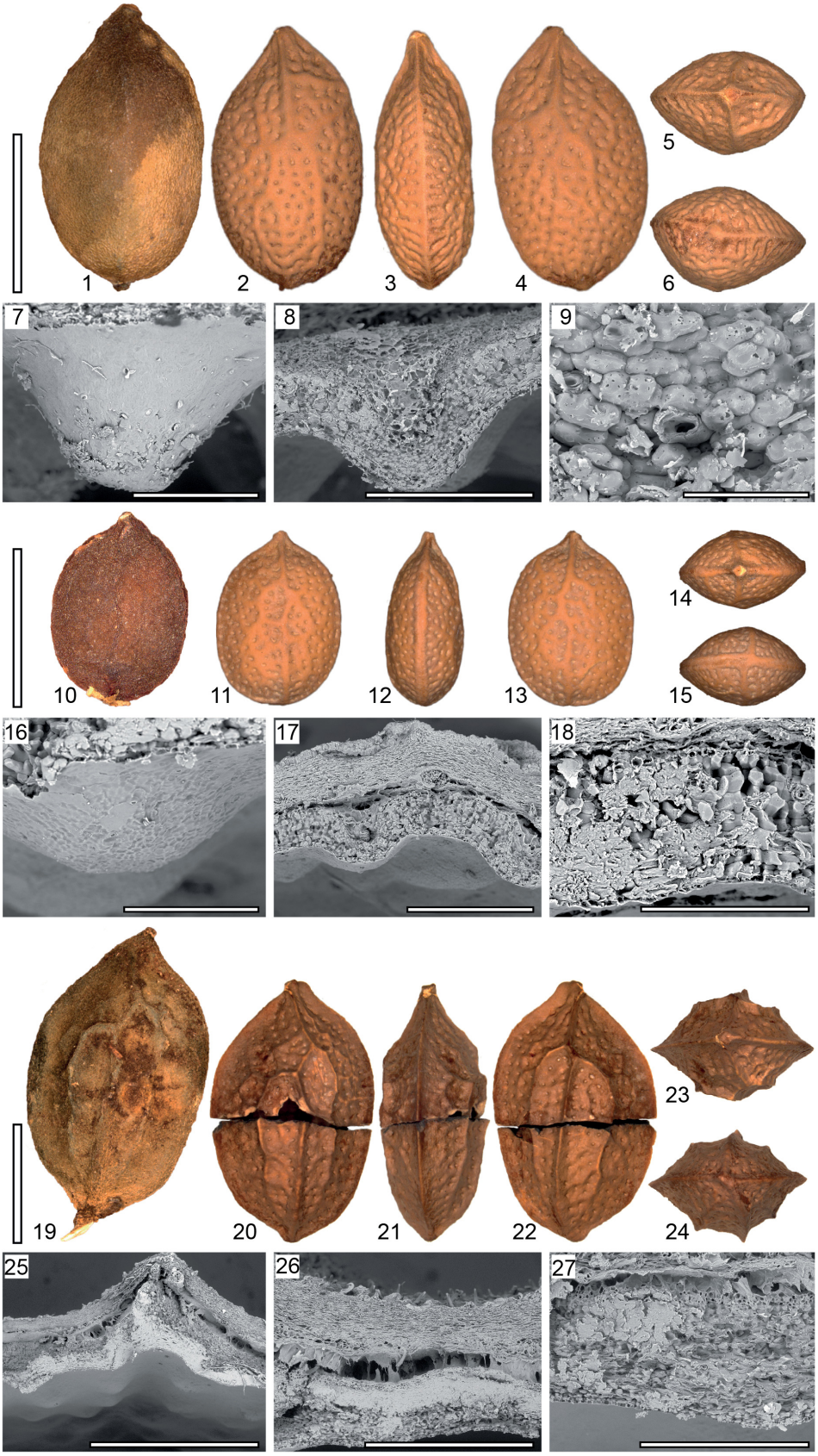

Fig. 34. (see full caption on page 106)

Key to the genus *Stachyanthus*

1. Endocarp ca 22 mm in length, ridges sharp ..... ***S. zenkeri*** Engl.
– Endocarp ≤ 17 mm in length, ridges rounded 2

2. Endocarp length ca 17 mm, pits per face 150–160 ..... ***S. donisii*** (Boutique) Boutique
– Endocarp length ca 11 mm, pits more than 180 ..... ***S. occidentalis*** (Keay & É.Miège) Boutique

Stachyanthus donisii (Boutique) Boutique
Fig. 34.1–34.9

Material examined

Specimen used for endocarp and fruit description
DEMOCRATIC REPUBLIC OF THE CONGO • Gimbi; 4 Apr. 1948; *J.H. Laurent 423*; BR[BR0000005850273].

Description

Fruit. Slightly asymmetrical at the apex, yellow-blue when mature. Epicarp strigose, with yellow simple hairs with granular ornamentation and yellow uncinate hairs, rugose when dry. Mesocarp ca 200 µm thick when dry. Length 17.0–18.6 mm, width 10.0–10.4 mm, thickness ca 7 mm.

Endocarp. Cream, length ca 16.9 mm, width ca 9.8 mm, thickness ca 6.3 mm. Pits circular in the center, more elongate laterally, 0.2–0.6 mm (av. 0.3 mm) in diameter, randomly arranged with 12–16 pits longitudinally and 9–11 pits transversally (ca 153–155 pits per face). Pits associated with bullate tubercles protruding into the locule; tubercles ca 364–418 µm in length and 768–819 µm in diameter at the base. Tubercle cells sclerotic, digitate and periclinal. Ridges rounded and thin, faintly apparent, with the median ridge spanning from the apex to the ⅓ of the base. Reticulum forming a diffuse pattern of ridges interconnecting the median ridge with the keel, arbuscle-like shaped. Endocarp wall 110–216 µm thick excluding ridges (ca 220 µm thick including ridges). Endocarp wall with two cell layers: outermost layer with ca 10–11 rows of periclinally oriented cells, cells 8.3–26.4 µm in width; innermost layer with one row of periclinally oriented cells, cells 7.7–9.7 µm in width, lining the locule surface.

Stachyanthus occidentalis (Keay & É.Miège) Boutique
Fig. 34.10–34.18

Material examined

Specimen used for endocarp and fruit description
BENIN • "Dahomey"; 28 May 1910; *A. Chevalier 23794*; P[MNHN-P-P04495077].

Other material
IVORY COAST • 1955; *Aké Assi ? 3104*; P[MNHN-P-P04495080].

Description

Fruit. Acuminate and asymmetrical at the apex. Epicarp puberulent, with yellow simple hairs with granular ornamentation. Mesocarp 201–216 µm thick when dry. Length 9.0–12.4 mm, width 6.0–8.5 mm, thickness 3.0–5.4 mm.

Endocarp. Cream, length ca 11.3 mm, width ca 8.1 mm, thickness ca 5.1 mm. Pits circular in the center, more elongate laterally, 0.1–0.3 mm (av. 0.2 mm) in diameter, randomly arranged with 12–14 pits longitudinally and 11 pits transversally (ca 184 pits per face). Pits associated with bullate tubercles protruding into the locule; tubercles ca 244–248 µm in length and 377–382 µm in diameter at the base.

Tubercle cells sclerotic, digitate and periclinal. Ridges rounded and thin, faintly apparent, with one median ridge running from the apex to the base. Reticulum forming a diffuse pattern of ridges running from the median ridge. Endocarp wall 145–165 µm thick (excluding ridges). Endocarp wall with two cell layers: outermost layer with 9–10 rows of periclinally oriented (or occasionally isodiametric) cells, cells 6.3–24.7 µm in width; innermost layer with one row of periclinally oriented cells, cells 6.0–11.5 µm in width, lining the locule surface.

Stachyanthus zenkeri Engl.
Fig. 34.19–34.27

Material examined

Specimen used for endocarp and fruit description
EQUATORIAL GUINEA • Bioko; 26 Sep. 1988; *Carvalho 3626*; P[MNHN-P-P05030978].

Description

Fruit. Acute at the apex. Epicarp strigose, with yellow uncinate hairs, ridged when dry, revealing the underlying endocarp ridges. Mesocarp 204–264 µm thick when dry. Length 24–30 mm, width 14–18 mm, thickness 9–12 mm.

Endocarp. Brown, length ca 22.3 mm, width ca 13.8 mm, thickness ca 8.8 mm. Pits exclusively circular, 0.2–0.3 mm in diameter, more or less organized in longitudinal lines with 14–18 pits longitudinally and 9–10 pits transversally (ca 162–164 pits per face). Pits associated with bullate tubercles protruding into the locule; tubercles ca 320 µm in length and ca 701 µm in diameter at the base. Tubercle cells sclerotic, digitate and periclinal. Ridges sharp and thin, with three longitudinal ridges; the median ridge running from the base to the apex, the two lateral ridges running subbasally up to the top third of the endocarp length, where they merge with the median ridge. Endocarp wall 277–477 µm thick excluding ridges (800–960 µm thick including ridges). Endocarp wall with three cell layers: outermost layer with 3–4 rows of isodiametric to anticlinally (mesocarp?) oriented cells, cells 13.5–19.2 µm in width, followed by a layer with 11–12 rows of periclinally oriented cells, cells 18.0–21.4 µm in width; innermost layer with one row of periclinally oriented cells, cells 6.3–10.0 µm in width, lining the locule surface.

Fruit descriptions of Icacinaceae *s. lat. sensu Sleumer*

Class Magnoliopsida Brongn.
Subclass Lamiidae
Order Metteniusales Takht.
Family **Metteniusaceae** H.Karst. ex Schnizl.
Figs 35, 36.1–36.8

Apodytes dimidiata E.Mey. ex Arn.
Fig. 35.1–35.9

Material examined

Specimen used for endocarp and fruit description
MADAGASCAR • 1997; *R. Ranaivojaona et al.* 114; P[MNHN-P-P05279728].

Other material
MADAGASCAR • 1992; *S.T. Malcomber et al. 1212*; P[MNHN-P-P00379386] • 1933; *H. Perrier de la Bâthie 19254*; P[MNHN-P-P00440680] • 2009; *M.Y. Ammann, M.C. Madiomanana & A.J. Tahinarivo MYA495*; P[MNHN-P-P05279690].

KENYA • 2000; *G. Simon, L. Festo & G. Massawe 527*; P[MNHN-P-P04499342].

Description

Fruit. Black when dry, laterally compressed and elongate dorsally. Ventrally truncate, with a fleshy appendage (red but black in dry condition) attached at the truncate part. Epicarp glabrous, shriveled when dry, revealing the underlying endocarp ridges. Mesocarp ca 80–100 µm thick when dry. Calyx persistent. Length ca 6 mm, width ca 10 mm, thickness ca 3 mm.

Endocarp. Brown, bilaterally symmetrical, unilocular, single-seeded, globose-truncate in lateral view, length ca 5.5 mm, width ca 7.6 mm. Outer surface of the endocarp ridged with rounded diffuse and thin ridges, with ca 10 lateral ridges. Vasculature of the endocarp free; primary vascular bundle positioned outside the endocarp wall. Endocarp wall 177–266 µm thick (excluding ridges). A sclerotic mass, ca 1.3 mm thick, is developed from the wall in the truncate part of the endocarp. Endocarp wall with sclerotic cells, with two cell layers: outermost layer with 4–7 rows of anticlinally oriented cells, cells 29–86 µm in length; innermost layer with one row of periclinally oriented cells, cells 13.0–16.5 µm in width, lining the locule surface, forming ripples (the cells have a triangular shape).

Remarks

The sclerotic mass in the truncate part could be a mechanical reinforcement due to the connection of this part with the fleshy appendage.

Dendrobangia boliviana Rusby
Fig. 35.10–35.17

Material examined

Specimen used for endocarp and fruit description
FRENCH GUIANA • Maripasoula; 2015; *O. Poncy 2800*; P[MNHN-P-P00784576].

Fig. 35. Fruits of Metteniusaceae H.Karst. ex Schnizl. **1**–**9**. *Apodytes dimidiata* E.Mey. ex Arn. (*R. Ranaivojaona et al. 114*). **1**–**5**. Asymmetrical fruit with calice and style. **1**. Lateral view. **2**. Dorsal view. **3**. Opposite lateral view. **4**. Apical view. **5**. Basal view. **6**. Lateral view of the endocarp showing lateral ridges. **7**. SEM image of the sclerotic mass in the ventral part of the fruit. **8**. SEM image of the endocarp wall in transverse section. **9**. Detail showing the layer of elongate cells lining the locule. – **10**–**18**. *Dendrobangia boliviana* Rusby (*O. Poncy 2800*). **10**. Dried fruit, lateral view. **11**–**15**. Endocarp. **11**. Lateral view showing the inconspicuous roughness. **12**. Dorsal view showing the enlarged channel. **13**. Opposite lateral view. **14**. Apical view showing the enlarged channel on the left side. **15**. Basal view. **16**. SEM image of the endocarp wall in transverse section. **17**. Detail of another part of the endocarp in transverse section. – **18**–**27**. *Emmotum nitens* (Benth.) Miers (*R.M. Harley & R. Souza 10028*). **18**. Dried fruit, lateral view. **19**–**24**. Endocarp. **19**. Lateral view showing the coarse expansions. **20**. Dorsal view showing the keel. **21**. Opposite lateral view. **22**. Transverse section of the endocarp in apical view. **23**. Apical view. **24**. Basal view. **25**. SEM image of a detail of the outer endocarp wall showing porate cell wall with thorn expansions. **26**. SEM image of pores on the outer endocarp wall. **27**. SEM image of the inner endocarp wall in transverse section. Images taken from Del Rio (2018). Scale bars: 1–6, 10–15, 18–24 = 10 mm; 7 = 2 mm; 26, 27 = 500 µm; 8 = 300 µm; 25 = 200 µm; 9 = 50 µm.

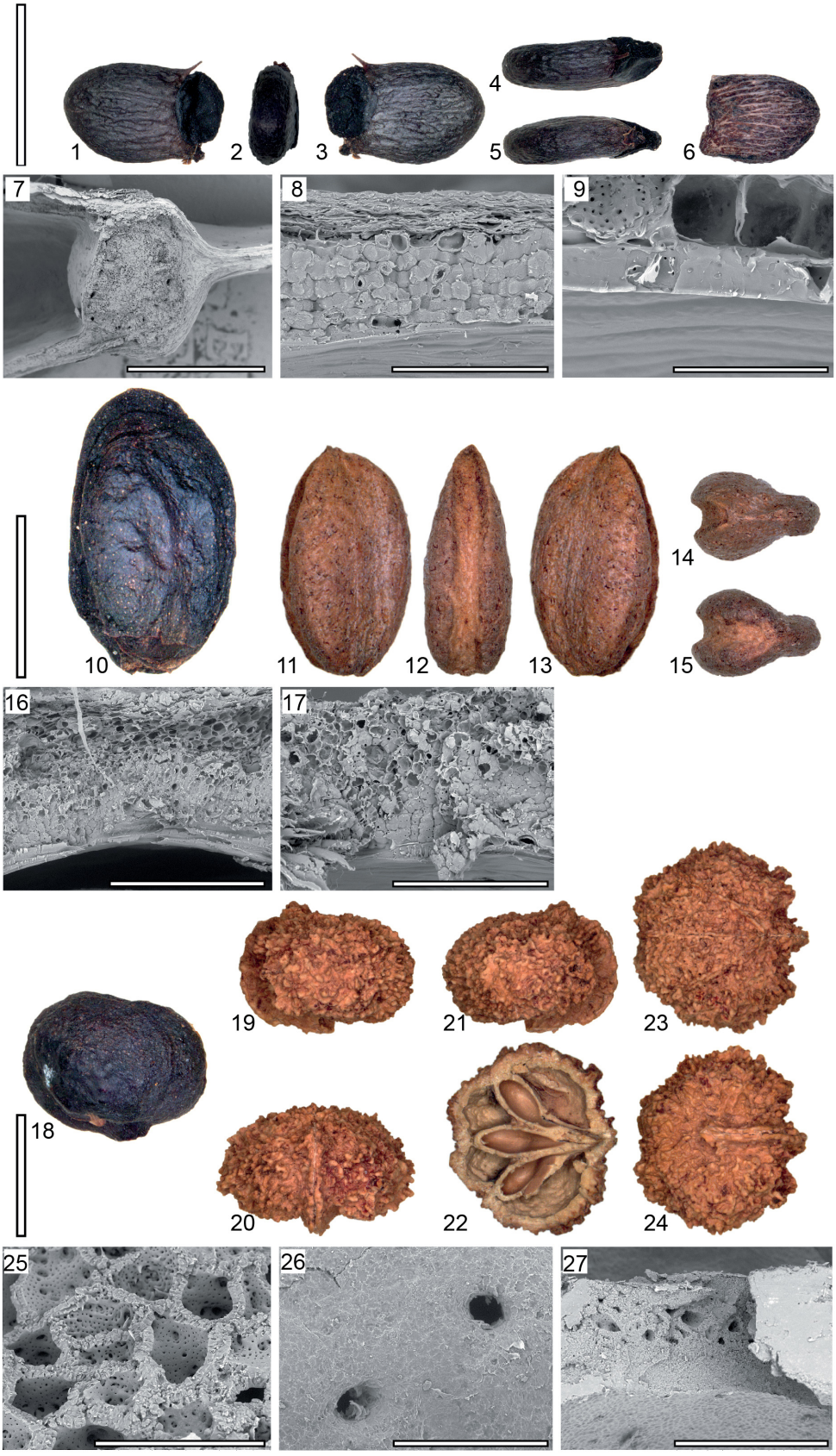

Fig. 35. (see full caption on page 110)

Description

Fruit. Laterally compressed, black when dry, elliptical. Epicarp glabrous. Mesocarp ca 190 µm thick when dry. Calyx persistent. Length 15–20 mm, width 6.0–10.4 mm, thickness ca 6.1 mm.

Endocarp. Cream, bilaterally symmetrical, unilocular, single-seeded, elliptical in lateral view, triangular or pyriform in transverse section, length ca 14.5 mm, width ca 8.1 mm, thickness ca 5.9 mm. Large channel present on dorsal side, ca 2mm wide, mirrored by a keel on ventral side. Apex and base slightly asymmetrical in lateral view. Outer surface of the endocarp rugose-granulate, homogeneous. Vasculature of the endocarp free; primary vascular bundle positioned outside the endocarp wall. Endocarp wall 300–320 µm thick. Endocarp wall with sclerotic cells, with two cell layers: outermost layer with 6–8 rows of anticlinally oriented to isodiametric cells, cells 27.4–38.4 µm in width; innermost layer with 1-5 rows of periclinally oriented cells, cells 23.8–35.2 µm width, cells tunnel-shaped (very elongate cells).

Emmotum nitens (Benth.) Miers
Fig. 35.18–35.27

Material examined

Specimen used for endocarp and fruit description
BRAZIL • 1968; *R.M. Harley & R. Souza 10028*; P[MNHN-P-P05279304].

Other material
BRAZIL • 1969; *M. Claussen 1838*; P[MNHN-P-P04513313] • 1974; *R.M. Harley et al. 15081*; P[MNHN-P-P04513269] • 1894; *A. Glaziou 22041*; P[MNHN-P-P04513276].

BOLIVIA • 1993; *R. Quevedo 927*; P[MNHN-P-P04513320].

Description

Fruit. Black when dry, globose. Epicarp glabrous. Calyx persistent. Length 10–15 mm, width 10–15 mm, thickness 15–18 mm.

Endocarp. Cream, bilaterally symmetrical, trilocular, three-seeded, globose in lateral view and transverse section, flattened in the apex-base axis, length ca 10.4 mm, width ca 14.9 mm, thickness ca 15 mm. Keel surrounding the endocarp on dorsal side only. Apex and base flattened in lateral view. Outer surface of the endocarp rugose with long and brittle rugosities. Endocarp wall of two parts: the outer part, ca 400 µm thick (930–1230 µm with rugosities), surrounds the three inner locule walls (350–390 µm thick), which surround the seeds. The outer surface of the endocarp with circular pores piercing the wall, ca 110 µm in diameter. Endocarp wall with sclerotic, isodiametric and homogeneous cells (inner and outer walls), 59.4–111.9 µm in diameter. Cells pitted and with spikes inside.

Remarks

The pores piercing the outer part of the wall might offer a means of gas exchange between the outer and inner parts of the locules. The significance of the spikes inside the endocarp cells is currently unclear.

Platea parvifolia Merr. & Chun
Fig. 36.1–36.8

Material examined

Specimen used for endocarp and fruit description
CHINA • 1936; *W.T. Tsang 27299*; P[MNHN-P-P04518074].

Fig. 36. Fruits of Metteniusaceae H.Karst. ex Schnizl. and Oncothecaceae Kobuski ex Airy Shaw. **1**–**8**. *Platea parvifolia* Merr.& Chun (*W.T. Tsang 27299*). **1**. Dried fruit, lateral view. **2**–**6**. Endocarp. **2**. Lateral view showing the mounds. **3**. Dorsal view. **4**. Opposite lateral view. **5**. Apical view. **6**. Basal view. **7**. SEM image of the endocarp wall in transverse section. **8**. Detail showing the endocarp cell walls and their organization. – **9**–**14**. *Oncotheca balansae* Baill. (*H.S. Mackee 37671*). **9**–**11**. Dried fruit **9**. Lateral view. **10**. Apical view. **11**. Basal view. **12**. SEM image of the outer and inner endocarp wall. **13**. SEM image of the inner endocarp wall showing prismatic crystal. **14**. SEM image of the locule surface lined by elongate cells. Images taken from Del Rio (2018). Scale bars: 1–6, 9–11 = 10 mm; 12= 1 mm; 7 = 500 µm; 13 = 300 µm; 14 = 200 µm; 8 = 100 µm.

Description

Fruit. Laterally compressed, black when dry, ovoid-elongate, acute at the apex. Epicarp glabrous. Mesocarp thin when dry. Length 30–34 mm, width 13.5–15.0 mm, thickness 13.7 mm.

Endocarp. Brown, slightly elliptical in lateral view, globose in transverse section, length ca 33.2 mm, width ca 12.2 mm, thickness ca 12.5 mm. Apex acute and asymmetrical; base rounded and symmetrical. Outer surface of the endocarp rugose with ca 62–65 mounds, more or less square-polygonal in shape, with freely ending channels inside, more or less branched. Mounds organized in 3–4 longitudinal lines separated by 2–3 main longitudinal channels. The main channel on each face reaches a pore positioned subapically. Vasculature of the endocarp positioned in the channels between mounds and in the channel of the mounds. Endocarp wall 500–550 µm thick. Endocarp wall with 11–21 rows of sclerotic, periclinally oriented, elongated and homogeneous cells, cells 18.0–44.8 µm in width. Inner endocarp surface smooth, not lacunate.

Class Magnoliopsida Brongn.
Subclass Lamiidae
Order Icacinales Tiegh.
Family **Oncothecaceae** Kobuski ex Airy Shaw
Fig. 36.9–36.14

Oncotheca balansae Baill.
Fig. 36.9–36.14

Material examined

Specimen used for endocarp and fruit description
NEW-CALEDONIA • 1979; *H.S. Mackee 37671*; P[MNHN-P-P00180992].

Description

Fruit. Brown-black when dry, more or less globose but flattened in the apex-base axis. Epicarp glabrous. Calyx persistent. Length ca 10.4 mm, width ca 16.7 mm, thickness ca 16.7 mm.

Endocarp. Brown, with five locules and five seeds, globose in transverse section. Outer surface of the endocarp smooth. Endocarp wall with two parts, the outer part surrounding the inner locule walls, but outer and inner walls fused and difficult to dissociate. All walls ca 2 mm thick, inner endocarp wall (locule) ca 200 µm thick, with crystalliferous cells. Endocarp wall with sclerotic cells, with two stratified cell layers: outermost layer with numerous rows of isodiametric cells, cells 28.3–44.0 µm in diameter; innermost layer with one row of periclinally oriented cells, cells 2.4–3.3 µm in width, lining the locule surface with inflated, elongate and semi-triangular cells.

Remarks

The mesocarp is strongly attached to the endocarp wall. The structure of the endocarp is difficult to break due to the thickness of the endocarp wall.

Discussion

Use of the Xper^3 database

The interactive identification part includes the descriptors on the left (Fig. 4.1) and the remaining taxa in the table on the right (Fig. 4.2). The user can begin the identification of the specimen with any descriptor. When the user clicks on a descriptor, the different character states appear, among which the user can choose.

The choice of a character state induces removal of taxa in the table (Fig. 4.2). The user can click on names of the remaining taxa (Fig. 4.2, arrow) and obtain all the available information for the species in one sheet (Fig. 5): the species name (Fig. 5.1), all associated pictures (Fig. 5.2), the specimens studied (Fig. 5.3) and all associated character states. Thus, the user can check the accuracy of the identification. A history of characters used is available (Fig. 4.1) in case the user needs to revise the characters if an error occurs during the identification. This interactive identification is available online, but it is also possible to transfer the database in the Xper^2 software.

Diversity of Icacinaceae endocarps

Across all genera of Icacinaceae, great diversity is shown here in the epicarp hairs, mesocarp thickness, endocarp ornamentation, tubercle shape (if present), endocarp structure and thickness, and microtomography of the locule lining. These characters and others permit the distinction, in most cases, of genera as well as species (see below and the keys above for more details).

However, members of Icacinaceae s. str. also share endocarp traits that permit differentiation from the genera of Metteniusaceae (formerly placed in Icacinaceae s. lat.). In particular, the structure of the endocarp wall offers a means of anatomical differentiation. Cells in endocarp walls of Icacinaceae s. str. are small with periclinal to anticlinal orientation. The Mettenuisaceae species studied here do not show these features in their endocarp cells. Instead, we see a great diversity of shapes, with more or less sinuous cells, very elongate cells (e.g., *Platea parvifolia* Merr. & Chun and *Dendrobangia boliviana* Rusby), or very large cells with thick cell walls (*Emmotum nitens* (Benth.) Miers). The endocarp wall of *Apodytes dimidiata* might be the most similar to that of Icacinaceae s. str., but in this species, the last cell row ripples inside the endocarp locule. Therefore, we are able to define criteria based on the endocarp anatomy for diagnosing members of Icacinaceae s. str.

In Icacinaceae s. str., the endocarp length varies from 6 to 58 mm. This disparity might be due to differences in niche / habitat, life history and habit (tree, shrub, or liana), and / or frugivore syndrome (Tiffney 1984), because at least some species of Icacinaceae s. str. are eaten by birds and primates, including human beings (Fay 1993; Ganesh & Davidar 2001). In the fossil record, there are several taxa with endocarps smaller than in all modern species included in this survey, e.g., *Iodes sinuosa* Del Rio, Thomas & De Franceschi, *Iodes parva* Del Rio, Thomas & De Franceschi (Del Rio *et al.* 2019b), *Iodes germanica* Knobloch & Mai (Knobloch & Mai 1986), and *Palaeophytocrene hammenii* Stull (Stull *et al.* 2012). For the three fossil *Iodes* species mentioned, taphonomic processes could alter the endocarp length. However, this small size might also represent an adaption to a particular paleohabit (perhaps with no modern analogs) and / or an early diversification without selection by frugivorous dispersers. There is a trend of increasing of fruit size into the Eocene (Tiffney 1984). Many of the smaller fossil specimens mentioned above are quite old (from the Cretaceous or Paleocene), and thus *Iodes* and *Palaeophytocrene* Reid & Chandler might be following this general trend, especially in light of the larger fruits observed for these genera in the Eocene (e.g., Manchester 1994).

Surprising shapes and structures of Icacinaceae fruits and endocarps indicate that the family has diversified considerably in fruit morphology across its evolutionary history. Some examples are listed in this part. In the most diverse genus, *Pyrenacantha*, we found an accrescent structure at the apex of the fruits in some species formerly assigned to *Chlamydocarya* Baill., in particular in *Pyrenacantha gossweileri* (Exell) Byng & Utteridge, *P. soyauxii* (Engl.) Byng & Utteridge, *P. macrocarpa* (A.Chev. ex Hutch. & Dalziel) Byng & Utteridge and *P. thomsoniana* (Bail.) Byng & Utteridge. In the flora of Cameroon (Villiers 1973) and a preceding developmental study (Villiers 1971), this structure (an inflated or tubular cap) was interpreted as an extension of the ovary, whereas a study from the 19th century interpreted it as derived from the perianth (Baillon 1874). This structure deserves additional developmental study. The cap is often longer than the endocarp, especially in *P. thomsoniana*. The potential function of the

cap has yet to be explored. During fruit preparation for this survey, fruits of *P. soyauxii* remained at the surface when placed in water, with the cap providing buoyancy. This species, along with other species of *Pyrencantha*, is a quite common liana along streams. We therefore hypothesize that this structure aids in the dispersal of this species by water. The hairs on some *Phytocrene* Wall. species, particularly *Phytocrene borneensis* Becc., *P. bracteata* Wall., *P. hirsuta* Blume and *P. oblonga* Wall., are long, thin and grouped in clusters. These hairs are sharp and irritating, easily penetrating the skin (Sleumer 1971 and personal observation). These hairs might act as a repellent to all or some frugivorous species. Endocarps of *Pleurisanthes flava* Sandwith possess a distinctive hairs-like upper layer. This trait is apparently not mentioned in literature. Baillon (1874) did not have any *Pleurisanthes* Baill. fruit to examine. This layer might be a diagnostic character for the species or for the genus; however, we have too few specimens to determine the taxonomic significance of this character. Endocarps of *Cassinopsis ciliata* are broader dorsoventrally than wide transversely. In dorsal view (Fig. 7.12), we show the distinct difference in size compared to the lateral view (Fig. 7.13). This fruit was illustrated previously (Perrier de la Bâthie 1952), but it seems that there was a confusion between the dorsal and the lateral view. We found hairs on the locule surface in *Leretia* Vell., *Lavigeria* Pierre and *Cassinopsis madagascariensis* Baill. In the latter, the hairs are different from those of the two other genera in being thick; the hairs in *Leretia* and *Lavigeria* are quite long and thin. In the description of *C. madagascariensis* (Baillon 1874), and in the flora of Madagascar (Perrier de la Bâthie 1952), there is no mention of these hairs. These hairs seem unique within *Cassinopsis* and may be used as a diagnostic character for this species; additional work is needed to confirm this hypothesis. For *Leretia*, the hairs inside the locule were mentioned previously in the literature (Jansen-Jacobs 1979; Duno de Stefano 2013), as is the case for *Lavigeria* (Villiers 1973). *Casimirella*, not studied here, also has hairs on the locule surface (De Roon 1994). Several phylogenetic studies show that *Casimirella*, *Lavigera* and *Leretia* are closely related, forming a clade along with the genus *Icacina* A.Juss. (Angulo *et al.* 2013; Byng *et al.* 2014; Stull *et al.* 2015). Locule hairs might be synapomorphic for this clade, implying a loss of this feature in *Icacina* based on the current phylogenetic framework. A gynophore, more or less elongate, is present in the genera *Miquelia* Meisn. and *Pyrenacantha*, but often this structure is broken on fruits placed in herbarium fragment packets. These two genera are closely related, but not sister groups; most analyses support a sister relationship between *Miquelia* and *Phytocrene* (e.g., Byng *et al.* 2014; Stull *et al.* 2015). These structures therefore might represent a case of parallel evolution in *Miquelia* and *Pyrenacantha*, unless this trait evolved deeper within Phytocreneae Engler and was subsequently lost by several genera (e.g., *Phytocrene*, *Sarcostigma* Wight & Arn.).

Among all genera of Icacinaceae s. str., *Desmostachys* s. lat. is the most variable in endocarp morphology. During the completion of this survey, a new study splits this genus in two: *Desmostachys* Planch. ex Miers, including only *Desmostachys planchonianus* Miers, and *Vadensea* Jongkind & O.Lachenaud, including all other species (Jongkind & Lachenaud 2019). We fully support this view. In fact, considering endocarp characters only, it seems unlikely that *Desmostachys* s. lat. is natural; most species appear to have a bulge or a complex apex, but the diversity of endocarp ornamentation and size across the genus is surprising. The original description of *Desmostachys*, emphasizing floral traits, was based entirely on specimens from Madagascar (representing *D. planchonianus*). Villiers (1973) subsequently noted that the position of the flowers in the inflorescences is diagnostic for the genus. Although there have been no published phylogenetic studies including the type species (*D. planchonianus*) in addition to other species from Africa, the likely polyphyly of *Desmostachys* s. lat. can be extrapolated from previous results (Byng *et al.* 2014; Stull *et al.* 2015). The analyses of Byng *et al.* (2014) included two African species of *Desmostachys* s. lat. (*D. brevipes* (Engl.) Sleumer and *D. vogelii* (Miers) Stapf), and these were found to form a clade with *Alsodeiopsis* Oliv. in Benth. and several other genera (*Mappianthus* Hand.-Mazz. and *Pleurisanthes*), with low support; the analyses of Stull *et al.* (2015) included only *D. planchonianus* from *Desmostachys* s. lat., but this species was found to be sister to *Natsiatum herpeticum* with strong support. More recent analyses (Stull *et al.*, in prep.), based on numerous chloroplast and nuclear genes

across a greater diversity of taxa, show that *Desmostachys* s. lat. is clearly polyphyletic, with the African species of *Desmostachys* s. lat. (e.g., *D. brevipes*, *D. oblongifolius* (Engl.) Villiers, *D. tenuifolius* Oliv., and *D. vogelii*) sister to *Alsodeopsis* while the malagasy taxon *D. planchoniana* forms a distant clade with *Natsiatum* Buch.-Ham. ex Arn., *Natsiatopsis* and *Sleumeria*. These phylogenetic results are consistent with the fruit morphological data presented here in suggesting that *Desmostachys* s. lat. is polyphyletic. Thus, our survey fully supports the new taxonomic work of Jongkind & Lachenaud (2019).

Diversity of *Iodes* endocarps

Iodes is the only genus in Icacinaceae possessing the following three characters: papillae on the inner endocarp surface, ridged ornamentation on the endocarp and the primary vascular bundle embedded within the endocarp wall. However, *Iodes seguinii* (H.Lév.) Rehder lacks these characters. Nevertheless, the placement of this species in *Iodes* is confirmed by other morphological features (e.g., opposite leaves, tendrils) and new molecular data (Stull *et al.*, in prep.). The Flora of China (Peng & Howard 2008) describes the endocarp of this species as "smooth, slightly grooved or reticulate". We did not observe any reticulate endocarps for this species. This absence of classical traits could be simply due to a lack of sclerotization of the ovary in comparison with other *Iodes* species during fruit development, which could explain the channel for the vascular bundle and the lack of ridges. However, developmental studies are necessary to test this hypothesis. This particular endocarp might also represent an instance of reversion to plesiomorphic states.

The presence of the vascular bundle inside the endocarp wall is rare in Icacinaceae and frequently used for identification of *Iodes* endocarps in the fossil record. We also found this character in *Icacina*, *Cassinopsis*, *Lavigeria* and *Leretia*. *Icacina* species can have a ridged pattern on the endocarp surface, similar to the genus *Iodes*, but *Icacina* species do not have papillae on the locule lining. Thus, all three characters are necessary for confident assignation to *Iodes*. However, we note that endocarps of *Icacina* species are generally longer and wider than those of *Iodes* species and more globose in transverse section. Thus, aspects of shape might also be useful for the assignment of fossil species to *Iodes* when papillae are absent (possibly due to degradation) or unobservable given the mode of preservation.

Iodes species from Asia differ from African species in several characters. Asian species usually possess a pair of horn-like protrusions or pores, are typically larger (12.4–33.8 mm in length vs 10.4–12.1 mm in length for the African species), and the surface ridging is generally less reticulate than that of the African species. The reticulation of fossil *Iodes* is somewhat variable, including representatives both with and without freely ending ridgelets inside areoles. In modern *Iodes* species, a reticulate pattern without freely ending ridgelets is rare. Therefore, the fossil species of *Iodes* that lack freely ending ridgelets are perhaps distinct from modern lineages and, overall, add to the morphological diversity observed in this group.

Value of the endocarp in species recognition

Some fossil sites consist almost entirely of fruits, endocarps and seed remains. Such sites offer important information about species diversity, floral composition and paleoenvironment parameters. For Icacinaceae, most of the fossil records are endocarps (Del Rio & De Franceschi 2020). Therefore, endocarp characters are crucial for genus and species recognition in the fossil record.

The different keys proposed in this survey show that in almost all cases, the endocarps of living species are differentiable. However, *Pyrenacantha ambrensis* Labat, El-Achkar & R.Rabev., *Pyrenacantha andapensis* Labat, El-Achkar & R.Rabev., and *Pyrenacantha tropophila* Labat, El-Achkar & R.Rabev. are identical in almost all characters. They are documented in the same study (Labat *et al.* 2006) and are very similar in shape. The main character in the Labat *et al.* (2006) key for differentiating *P. ambrensis* from *P. andapensis* is the texture of the leaves (papyrus-like vs coriaceous), and the shape of the fruit was

used to differentiate *P. andapensis* and *P. tropophila*. Additional systematic work, including molecular sampling of multiple accessions, will be necessary to clarify the status of these three species from Madagascar. *Pyrenacantha lebrunii* Boutique and *P. puberula* Boutique are very similar in endocarp shape and differ mostly by their size, although our endocarp sampling was limited for these species, meaning that endocarps of these taxa might be difficult to distinguish if they exhibit overlapping variation in size.

In *Pyrenacantha*, it is common for different species to have similar endocarp shape. However, the tubercle shape allows differentiation of most species. Therefore, with only endocarp material, it is possible to differentiate a large proportion of species, but not all of them; this indicates that studies of fossil endocarps in some cases might underestimate the number of species. However, this pattern for *Pyrenacantha* is not completely applicable for other genera. For example, species of *Phytocrene* and *Iodes* are all highly differentiable, whereas species of *Rhyticaryum* Becc. are more homogeneous in endocarp morphology.

The ridge ornamentation of the endocarp seems to be an important character in the species recognition. In particular, *Alsodeiopsis* shows that the shape of ridges can be a key feature to differentiate some species. The structure of the ridges can also be useful for differentiating modern as well as fossil species of *Iodes*, especially in the recognition of the African (reticulate) vs Asian (diffuse) species (already discussed above).

We encountered only one case where one species has two distinct types of endocarps. *Rhyticaryum macrocarpum* can have endocarps with diffuse ridging and a basal cleft on one side (or at least strongly asymmetrical) (Fig. 32.10–32.13) as well as endocarps showing a reticulate pattern of ridging and a rounded base (Fig. 32.16). In fossil remains, these two shapes might be interpreted as representing two closely related species. We did not encounter any similar case in other species where two or more specimens were examined.

In conclusion, endocarps are valuable organs for differentiating Icacinaceae genera and species, based on both distinct characters and slight variations in the morphology of structures. Size is useful for distinguishing species when distinct gaps are present (i.e., there is no overlap in the size ranges of related species). Based on endocarp morphology alone, there is a greater risk of underestimating than overestimating species diversity, which has important implications for paleobotanical diversity assessments of Icacinaceae, whose fossil record consists primarily of endocarp remains.

Stomata and papillae on the locule lining

During our observations, we found stomata on the endocarp locule lining of the following species: *Pyrenacantha malvifolia* Engl. (Fig. 37.1), *Rhyticaryum macrocarpum* (Fig. 37.2), *Stachyanthus donisii* (Boutique) Boutique (Fig. 37.3) and *Stachyanthus occidentalis* (Keay & É.Miège) Boutique (Fig. 37.3). The occurrence of stomata has previously been noted (Potgieter & van Wyk 1994) for *Pyrenacantha kaurabassana* and *Pyrenacantha grandiflora* Baill. Our observations indicate that two additional genera (*Rhyticaryum* and *Stachyanthus* Engl.) also share this feature. Potgieter & van Wyk (1994) speculate that these stomata act as gas exchange apparatuses between the outer and inner part of the endocarp. The stomata also seem to be denser at the apex of the tubercles, which is in contact with the seed.

Papillae are often present on the locule lining of *Pyrenacantha*, especially at the tubercle apices, and they are also present in *Hosiea* Hemsl. & E.H.Wilson, *Iodes* and *Rhyticaryum*. These papillae make direct contact with the testa of the seed, increasing the contact surface area between the seed and the endocarp. They might therefore facilitate gas exchange (like the stomata) or transfer of nutrients through the testa.

Preservation issues

Among the 88 Icacinaceae s. str. endocarps sectioned for anatomical studies (one per species), 15 (or 17%) showed fungal degradation of the endocarp wall and locule lining. Of the 19 genera studied here, 10 included species with fungal degradation: *Vadensea*, *Hosiea*, *Icacina*, *Iodes*, *Miquelia*, *Natsiatum*, *Phytocrene*, *Pyrenacantha*, *Rhyticaryum* and *Sarcostigma*. This relatively large proportion of degraded specimens poses challenges for anatomical studies owing to the limited availability of endocarps for this family. For example, the endocarp of *Pyrenacantha glabrescens* (Engl.) Engl. (Fig. 25.16) had atrophied tubercles and a highly degraded endocarp wall (with a cardboard-like texture) as a result of fungal attack, highly limiting the number of complete characters we were able to score for this taxon. Another case of catastrophic degradation was found in the endocarp of *Natsiatum herpeticum*; here, the endocarp wall structure was preserved, but not the outer and inner ornamentations (Figs 19.19–19.26, 38.3). The inner surface of the locule, which carries important anatomical information, was not observable in most cases (Fig. 38.1–38.3).

In the past three decades, there has been considerable discussion about the best methods for collecting plant tissue for DNA preservation (Chase & Hills 1991; Gaudeul & Rouhan 2013; Rouhan & Gaudeul 2014). Similar discussions should be made about collecting fruits in the future to ensure high-quality preservation for anatomical and morphological studies. Fixation in an ethanol solution might be a simple

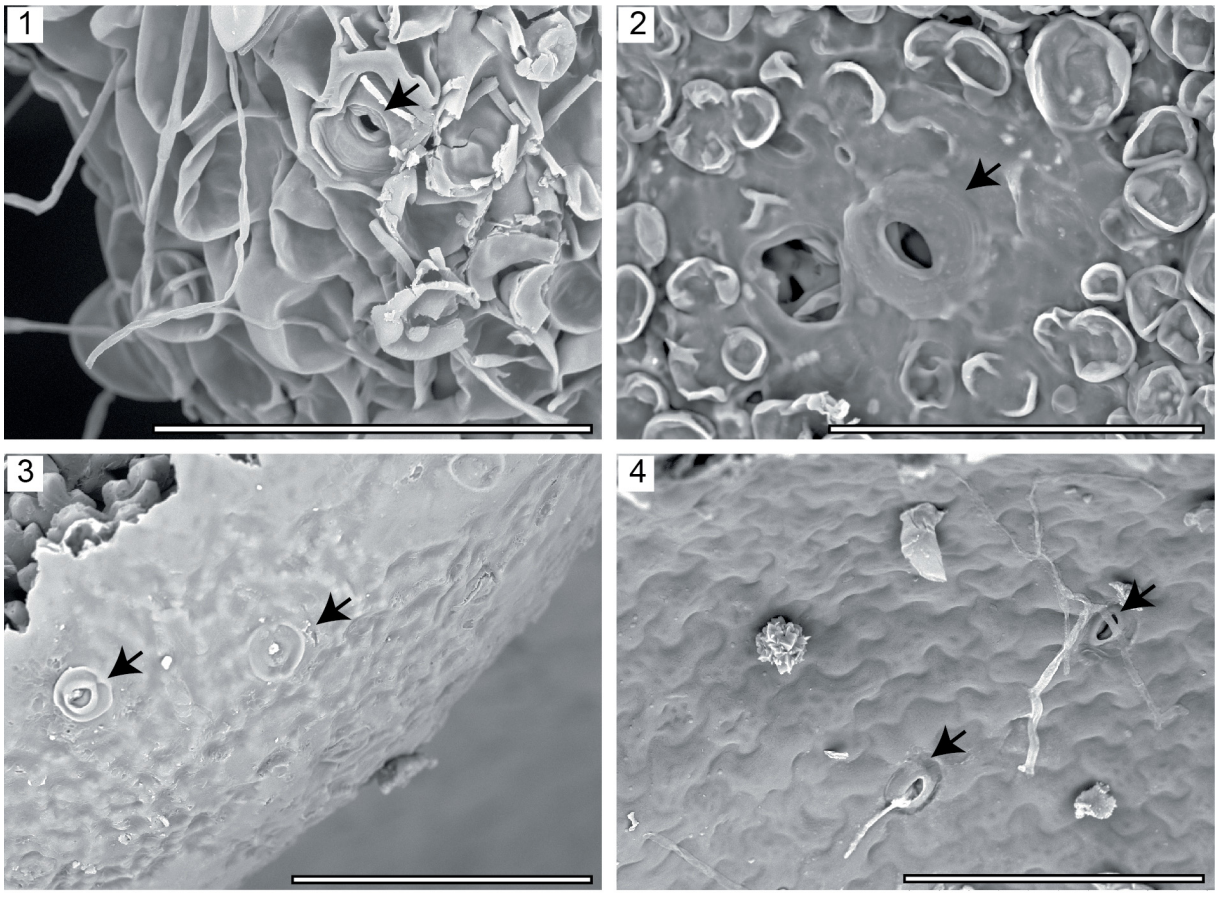

Fig. 37. SEM image of stomata on the locule surface (arrow). **1**. *Pyrenacantha malvifolia* Engl. (*P. Polill 475*). **2**. *Rhyticaryum macrocarpum* Becc. (*W. Vink 11381*). **3**. *Stachyanthus donisii* (Boutique) Boutique. **4**. *Stachyanthus occidentalis* (Keay & É.Miège) Boutique (*J.H. Laurent 42*3). Images taken from Del Rio (2018). Scale bars: 100 μm.

and effective mean of ensuring quality preservation (by preventing fungal degradation), but this is not always easy to do in the field.

Another problem, less frequently encountered in this study, is the sampling of immature fruit. We examined one immature specimen of *Iodes vitiginea* (Hance) Hance (voucher: *J.F. Maxwell 92-328*; MNHN-P-P04504884) as the fruit showed no superficial indications of immaturity (Fig. 38.4). However, the anatomical study revealed poorly differentiated layers in the pericarp (Fig. 38.5) and underdeveloped papillae (Fig. 38.6). Thus, we decided to not include this species in our survey. Ambiguity about the maturation level of fruits could be resolved in two ways: (1) the collector of the sample could specify

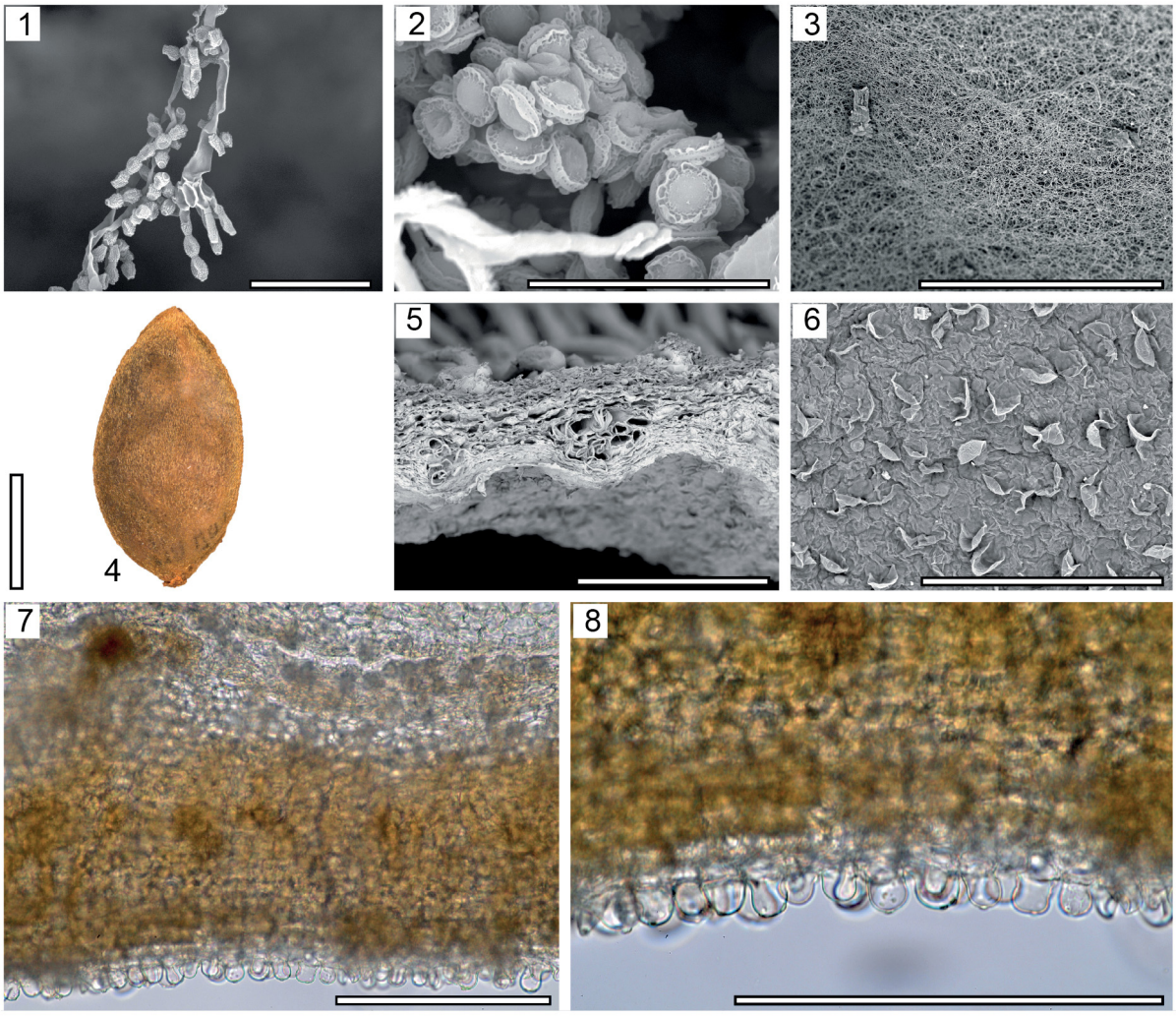

Fig. 38. Preservation issues. **1**. Fungal mycelium and echinate spore from *Vadensea vogelii* (Miers) Jongkind & O.Lachenaud (*Service forestier 364*). **2**. Fungal rounded spore from *Pyrenacantha glabrescens* (Engl.) Engl. (*A. Chevalier 17326*). **3**. Dense mycelium on the locule lining of *Natsiatum herpeticum* Buch.-Ham. ex Arn. (*H.B. Cale s.n.*). – **4**–**6**. *Iodes vitiginea* (Hance) Hance (*J.F. Maxwell 92-328*) **4**. Fruit, lateral view. **5**. SEM image of the undifferentiated pericarp in transverse section **6**. SEM image showing the papillae on the locule lining. **7**. *Iodes africana* Welw. Ex Oliv. (*R.P. Tisserant s.n.*), cross section of the endocarp under light microscope. 8. Same with magnification. Images taken from Del Rio (2018). Scale bars: 4 = 10 mm; 3 = 500 µm; 5–8 = 200 µm; 1–2 = 20 µm.

the fruit maturity and color on the specimen label and/or (2) the collector could cut a single fruit in transverse section. Several scientists (personal observation) have adopted the latter solution.

The process of studying endocarps anatomically is partially destructive. Commonly, cell walls are damaged when the endocarp is sectioned (for example, see *Phytocrene hirsuta* Blume, Fig. 21.23–21.24). This depends on the endocarp texture and the organization of the cell wall. Some genera such *Iodes* or *Alsodeiopsis* are easy to cut correctly, whereas *Phytocrene* or *Miquelia* are very difficult. We preliminarily tested a technique using a microtome after embedding the inclusion of specimens in epoxy resin (finaly not used for this survey). The result for an *Iodes africana* Welw. ex Oliv. fruit shows the cell layers and the papillae in transverse section (Fig. 38.7–38.8). However, the endocarp wall is a hard structure, and we could only make samples around 50 µm thick for *Iodes africana*. Moreover, the wall of *I. africana* is on the smaller side for Icacinaceae, suggesting that many species would be more difficult to cut. Several cell rows were overlapped in our *I. africana* sample. Additional studies using this technique can improve the results. Another major issue is that we destroyed at least half of the specimen in the process. When we have only one specimen representing a species, this technique does not allow the preparation of the transverse view of the pericarp as well as a view of the overall endocarp morphology. Furthermore, this technique for preparing specimens is slow, requiring several weeks of work. In contrast, using SEM to study specimens is less laborious and offers the additional advantage of producing similar images to those that would be obtained from anatomical analyses of fossil specimens, making the material more directly comparable. Although we suspect that cryosectionning would improve the quality of fruit sections, we were unable to test this possibility owing to resource limitations.

Limitations and prospects

This study aims to provide a survey of Icacinaceae fruits and endocarps. This survey should prove useful for paleocarpological studies as well as taxonomic investigations of modern species. Over the history of taxonomic studies on Icacinaceae, the fruit has been neglected as a source of diagnostic characters for species and broader groups. However, we show here that fruits offer important information for discriminating species, genera and the family as a whole. Despite the extensive data underlying this survey, the lack of more comprehensive sampling, including multiple accessions per species for assessing intraspecific variation, is a clear limitation of this study. These sampling deficiencies are a consequence of limited availability of fruit material.

To remedy these shortcomings, current and future field work on Icacinaceae should prioritize the collection and preservation of fruit material, in addition to samples for DNA analyses. Furthermore, the survey covers only half of the species in Icacinaceae; the work presented here could be extended in the future to include complete sampling of all accepted species of Icacinaceae. This study shows the value of anatomy in carpological studies, and the survey methods used here (in terms of both morphological methods and data organization using Xper3) could be used as a model for future studies focusing on fruit morphology in other families or major clades.

Conclusion

This study documents the extensive diversity of fruit and endocarp morphologies found in Icacinaceae, particularly in terms of hairs type, endocarp ornamentation, tubercle morphology (when present), apex configuration, and pattern of vascularization. These characters and others permit nearly all species we examined to be distinguished. The digitate cells in the endocarp wall seem to be a good character for differentiating Icacinaceae s. str. from genera of Metteniusaceae that were formerly placed in Icacinaceae s. lat. Some particularities are also noted and discussed, such as the presence of hairs in the locules of *Leretia*, *Lavigeria* and *Cassinopsis*; the presence of caps on the fruit apices of some *Pyrenacantha* species; unique hairs-like unit on the surface of *Pleurisanthes* endocarps; and the presence of gynophores in *Miquelia* and *Pyrenacantha*.

Species of *Iodes* can be easily identified using a combination of three characters: ridges on the endocarp surface, a vascular bundle inside the endocarp wall, and papillae on the locule surface. Because genera share one or two of these characters, only the presence of all three characters seems to be diagnostic for *Iodes*. However, in the case of poorly preserved endocarps (fossil or modern), the overall shape of the endocarp might be useful for identifying *Iodes* when information about one of the three main characters is not available.

Stomata, papillae and tubercles were found on the locule surfaces of some taxa. These three structures might have a similar (and in some cases coordinated) function: allowing gas exchange between the fruit exterior and the seed.

Some specimens examined in this study were degraded by fungi. It is likely that greater attention to fruit collection and preservation during botanical expeditions could limit fungal contamination and degradation, as has been the case for tissue collections for DNA over the last ca 20 years.

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References

Allen S.E., Stull G.W. & Manchester S.R. 2015. Icacinaceae from the Eocene of western North America. *American Journal of Botany* 102: 725–44. https://doi.org/10.3732/ajb.1400550

Angulo D.F., De Stefano R.D. & Stull G.W. 2013. Systematics of *Mappia* (Icacinaceae), an endemic genus of tropical America. *Phytotaxa* 116 (1): 1–18. https://doi.org/10.11646/phytotaxa.116.1.1

Baillon H.E. 1874. Deuxième étude sur les Mappiées (cont.). *Adansonia* 11: 187–203.

Boutique R. 1960. Icacinaceae. *In*: Robyns W. (ed.) *Flore du Congo belge et du Ruanda-Urundi*: 237–278. INEAC, Bruxelles.

Byng J.W., Bernardini B., Joseph J.A., Chase M.W. & Utteridge T. 2014. Phylogenetic relationships of Icacinaceae focusing on the vining genera. *Botanical Journal of the Linnean Society* 176 (3): 277–294. https://doi.org/10.1111/boj.12205

Chase M.W. & Hills H.H. 1991. Silica gel: an ideal material for field preservation of leaf samples for DNA studies. *Taxon* 40 (2): 215–220. https://doi.org/10.2307/1222975

Collinson M.E., Manchester S.R. & Wilde V. 2012. *Fossil Fruit and Seeds of the Middle Eocene Messel Biota*, *Germany*. Abh. Senckenb. Ges. Naturforsch, Stuttgart.

De Roon A.C. 1994. Icacinaceae. *In*: Görts-Van Rijn A.R.A. (ed.) *Flora of the Guianas*: 82–109 Koeltz Scientific Books, Koenigstein.

De Roon A.C. 2003. Icacinaceae. *In*: Buck W.R. (ed.) *Guide to the Vascular Plants of Central French Guiana Part 2 Dicotyledone*: 358–362. The New York Botanical Garden Press, New York.

Del Rio C. 2018. The Icacinaceae from the Paleogene of the Paris Basin. PhD thesis, Muséum national d'histoire naturelle, France. Available from https://tel.archives-ouvertes.fr/tel-02366974/document [accessed 23 Mar. 2020].

Del Rio C., De Franceschi D. 2020. Fossil record of the Icacinaceae and its paleogeographic implications. *Review of Palaeobotany and Palynology* 273 (104135): 1–16. https://doi.org/10.1016/j.revpalbo.2019.104135

Del Rio C., Stull G.W. & De Franceschi D. 2019a. New species of *Iodes* fruits (Icacinaceae) from the early Eocene Le Quesnoy locality, Oise, France. *Review of Palaeobotany and Palynology* 262: 60–71. https://doi.org/10.1016/j.revpalbo.2018.12.005

Del Rio C., Thomas R. & De Franceschi D. 2019b. Fruits of Icacinaceae Miers from the Palaeocene of the Paris Basin (Oise, France). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 108 (4): 459–469. https://doi.org/10.1017/S1755691018000221

Duno de Stefano R. 2013. Icacinaceae. *In*: Persson C. & Stahl B. (eds) *Flora of Ecuador*: 6–43. Herbarium CICY, Mexico.

Ellis B., Daly D.C., Hickey L.J., Mitchell J.D., Johnson K.R., Wilf P., Wing S.L. 2009. *Manual of Leaf Architecture*. Cornell University Press, Ithaca.

Engler A. 1893. Icacinaceae. *In*: Engler A. & Prantl K. (eds). 1896. *Die natürlichen Pflanzenfamilien*. Vol. 3 (5): 233–257, 459–460. Wilhelm Engelmann, Leipzig.

Fay J.M. 1993. *Icacina oliviformis* (Icacinaceae): A close look at an underexploited food plant. III. Ecology and production. *Economic Botany* 47 (2): 163–170. https://doi.org/10.1007/BF02862019

Ganesh T. & Davidar P. 2001. Dispersal modes of tree species in the wet forests of southern Western Ghats. *Current Science* 80 (3): 394–399.

Gaudeul M. & Rouhan G. 2013. A plea for modern botanical collections to include DNA-friendly material. *Trends in Plant Science.* 18 (4): 184–185. https://doi.org/10.1016/j.tplants.2012.12.006

Heintzelman C.E. & Howard R.A. 1948. The comparative morphology of the Icacinaceae. V. The pubescence and the crystals. *American Journal of Botany* 35 (1): 42–52. https://doi.org/10.1002/j.1537-2197.1948.tb05186.x

Holmgren P., Holmgren N. & Barnett L. 1990. *Index Herbariorum, Part I: The herbaria of the world*. New York Botanical Garden, New York.

Howard R.A. 1940. Studies of the Icacinaceae. I. Preliminary taxonomic notes. *Journal of the Arnold Arboretum* 21: 461–489.

Howard R.A. 1942a. Studies of the Icacinaceae. II. *Humirianthera*, *Leretia*, *Mappia*, and *Nothapodytes*, valid genera of the Icacineae. *Journal of the Arnold Arboretum* 23: 55–78. https://doi.org/10.5962/bhl.part.18680

Howard R.A. 1942b. Study of the Icacinaceae IV. Considerations of the new world genera. *Harvard University Herbaria* 142: 3–60.

Index Herbariorum online. Available from http://sweetgum.nybg.org/science/ih [accessed 16. Mar. 2020].

InsideWood. 2004–onwards. Available from http://insidewood.lib.ncsu.edu/search [accessed 16. Mar. 2020].

Jacques F.M.B. 2009. Survey of the Menispermaceae endocarps. *Adansonia* 31 (1): 47–87. https://doi.org/10.5252/a2009n1a4

Jansen-Jacobs M.J. 1979. Icacinaceae. *In*: Stoffers A.L. & Lindeman J.C. (eds) *Flora of Suriname.* Vol. 5: 344–355. Foundation Van Eedenfonds, Leiden.

Jongkind C.C. & Lachenaud O. 2019. *Vadensea* (Icacinaceae), a new genus to accommodate continental African species of *Desmostachys*. *Phytotaxa* 405 (5): 237–247. https://doi.org/10.11646/phytotaxa.405.5.2

Kårehed J. 2001. Multiple origin of the tropical forest tree family Icacinaceae. *American Journal of Botany* 88: 2259–2274. https://doi.org/10.2307/3558388

Kerr A.F.G. 1911. Contributions to the flora of Siam. I.: Sketch of the vegetation of Chiengmai. *Bulletin of Miscellaneous Information of the Royal Botanic Gardens Kew* 1911 (1): 1–60. https://doi.org/10.2307/4119550

Knobloch E. & Mai D.H. 1986. *Monographie der Fruchte und Samen in der Kreide von Mitteleuropa*. Rozpravy Ústředního ústavu geologického 47, Ústřední ústav geologický, Praha.

Labat J.N., El-Achkar E. & Rabevohitra R. 2006. Révision synoptique du genre *Pyrenacantha* (Icacinaceae) à Madagascar. *Adansonia* 28 (2): 389–404. Available from http://sciencepress.mnhn.fr/fr/periodiques/adansonia/28/2/revision-synoptique-du-genre-pyrenacantha-icacinaceae-madagascar [accessed 5 May 2020].

Leaf Architecture Working Group. 1999. *Manual of Leaf Architecture: Morphological Description and Categorization of Dicotyledonous and Net-veined Monocotyledonous Angiosperms*. Smithsonian Institute, Washington DC.

Manchester S.R. 1994. *Fruits and seeds of the Middle Eocene nut beds flora*, *Clarno Formation*, *Oregon*. Palaeontolographica Americana 58, Paleontological Research Institution, New York.

Peng H. & Howard R.A. 2008. Icacinaceae. *In*: Zhengyi W. & Raven P.H. (eds) *Flora of China*: 505–513. Science Press. Beijing / Missouri Botanical Garden. St. Louis.

Perrier de la Bâthie H. 1952. Icacinacées (Icacinaceae). *In*: Humbert H. (ed.) *Flore de Madagascar et des Comores*: 119. Firmin-Didot and Cie., Paris.

Potgieter M.J. & van Wyk A.E. 1993. Fruit structure of the genus *Cassinopsis* Sond. (Icacinaceae) in Africa. *South African Journal of Botany* 60 (2): 117–122. https://doi.org/10.1016/S0254-6299(16)30642-1

Potgieter M.J. & van Wyk A.E. 1994. Fruit structure of the genus *Pyrenacantha* Hook. (Icacinaceae) in southern Africa. *Botanical Bulletin of Academia Sinica* 35: 105–113.

Rasband W.S. 2016. ImageJ website. Available from https://imagej.nih.gov/ij/ [accessed 3 Dec. 2019].

Reid E.M. & Chandler M.E. 1933. *The London Clay Flora*. The British Museum (Natural History), London. https://doi.org/10.5962/bhl.title.110147

Rouhan G. & Gaudeul M. 2014. Plant taxonomy: a historical perspective, current challenges, and perspectives. *In*: Besse P. (ed.) *Molecular Plant Taxonomy*: 1–37. Methods in Molecular Biology 1115, Humana Press, Totowa. https://doi.org/10.1007/978-1-62703-767-9_1

Sarmiento C., Détienne P., Heinz C., Molino J.F., Grard P. & Bonnet P. 2011. Pl@ntWood: a computer-assisted identification tool for 110 species of Amazon trees based on wood anatomical features. *IAWA Journal* 32 (2): 221–232. https://doi.org/10.1163/22941932-90000053

Sleumer H. 1971. Icacinaceae. *In*: van Steenis C.G.G.J. (ed.) *Flora Malesiana.* Vol. 7 (1): 1–87. Noordhoff, Leiden.

Stull G.W., Herrera F., Manchester S.R., Jaramillo C. & Tiffney B.H. 2012. Fruits of an "Old World" tribe (Phytocreneae; Icacinaceae) from the Paleogene of North and South America. *Systematic Botany* 37 (3): 784–794. https://doi.org/10.1600/036364412X648724

Stull G.W., Moore B.R., Manchester S.R., 2011. Fruits of Icacinaceae from the Eocene of southeastern North America and their biogeographic implications. *International Journal of Plant Sciences* 172 (7): 935–947. https://doi.org/10.1086/660877

Stull G.W., Duno de Stefano R., Soltis D.E. & Soltis P.S. 2015. Resolving basal lamiid phylogeny and the circumscription of Icacinaceae with a plastome-scale data set. *American Journal of Botany* 102(11): 1794–1813. https://doi.org/10.3732/ajb.1500298

Thomas R. 2011. *Palm-ID, a database to identify the palm stem anatomy with an expert system (Xper2)*. PhD Thesis, Université Paris, France.

Thomas R. & De Franceschi D. 2013. Palm stem anatomy and computer-aided identification: The Coryphoideae (Arecaceae). *American Journal of Botany* 100 (2): 289–313. https://doi.org/10.3732/ajb.1200242

Tiffney B.H. 1984. Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. *Annals of the Missouri Botanical Garden* 71 (2): 551–576. https://doi.org/10.2307/2399037

Ung V., Dubus G., Zaragueta-Bagils R. & Vignes-Lebbe R. 2010. Xper^2: introducing e-taxonomy. *Bioinformatics* 26 (5): 703–704. https://doi.org/10.1093/bioinformatics/btp715

Utteridge T.M.A. & Schori M. 2011. Updating Malesian Icacinaceae. *Gardens' Bulletin Singapore* 63 (1–2): 105–118.

Villiers J.-F. 1971. Origine et développement de l'accrescence dans les genres *Chlamydocarya* Baill. et *Polycephalium* Engl. (Icacinacées). *Bulletin de la Société botanique de France* 118 (9): 659–666. https://doi.org/10.1080/00378941.1971.10838933

Villiers J.-F. 1973. Icacinaceae. *In*: Aubréville A. & Leroy J-F. (eds) *Flore Du Cameroun*: 3–100. Muséum national d'histoire naturelle, Paris.

Wheeler E.A. 2011. InsideWood – A web resource for hardwood anatomy. *IAWA Journal* 32 (2): 199–211. https://doi.org/10.1163/22941932-90000051

Wheeler E.A., Baas P. & Gasson P.E. 1989. IAWA list of microscopic features for hardwood identification. *IAWA Bulletin* 10 (3):219–332. https://doi.org/10.1163/22941932-90000496

Zuquim G., Tuomisto H. & Prado J. 2017. A free-access online key to identify Amazonian ferns. *PhytoKeys* 78: 1–15. https://doi.org/10.3897/phytokeys.78.11370

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Appendix 1. List of characters used in the Xper^3 database, generated by Xper^2.

Base : E-identification Icacinaceae – Del Rio *et al.*

93 Items
56 Descriptors
24 children descriptors

1. Fruit : type : { 1. Drupe, 2. Other }

2. Fruit : color : { 1. Green, 2. Red, 3. Brown, 4. Black, 5. Yellow, 6. Blue }

3. Fruit : length (unit: mm)

4. Fruit : width (unit: mm)

5. Fruit : thickness (unit: mm)

6. Epicarp : indumentum type : { 1. Glabrous, 2. Pilose, 3. Puberulent, 4. Strigose }

+ 8. Epicarp hair : color : { 1. Red, 2. White, 3. Yellow } Conditions for inapplicability (Glabrous)

+ 7. Epicarp hair : type : { 1. Papillae like hairs, 2. small ovoid hairs with an acuminate apex, 3. Uncinate, 4. Simple, 5. Long and thin, 6. Cluster of hairs } Conditions for inapplicability (Glabrous)

9. Epicarp : additional structure : { 1. None, 2. Apex elongate, 3. Cap at the apex elongate, 4. Cap at the apex inflated }

10. Endocarp : presence of a keel : { 1. Yes, 2. No }

11. Endocarp : shape in lateral view : { 1. Elliptical, 2. Globose, 3. Obovoid, 4. Triangular, 5. Oblong }

12. Endocarp : shape in transverse section : { 1. Lenticular, 2. Globose, 3. Triangular }

13. Endocarp : apex structure : { 1. Absent, 2. Horns, 3. Pores, 4. Bulge }

14. Endocarp : base morphology : { 1. Symmetrical (no basal cleft), 2. Cleft on one side }

15. Endocarp : length (unit: mm)

16. Endocarp : width (unit: mm)

17. Endocarp : thickness (unit: _)

18. Endocarp wall : thickness (unit: _)

19. Endocarp : surface structures : { 1. Ridged, 2. Pitted, 3. Rugose, irregular, 4. Smooth }

+ 20. Endocarp : ridging pattern : { 1. Reticulate, 2. Not reticulate } Conditions for inapplicability (Pitted, Rugose, irregular, Smooth)

+ 27. Areoles : freely ending ridgelets : { 1. Yes, 2. Rare or No } Conditions for inapplicability (Diffuse)

+ 36. Areoles : number closed by ridges (unit: _) Conditions for inapplicability (Diffuse)

+ 40. Endocarp Wall : Thickness with ridges/rugosity (unit: µm) Conditions for inapplicability (Pitted, Smooth)

+ 22. Pits : arrangement : { 1. In longitudinal lines, 2. Random } Conditions for inapplicability (Ridged, Rugose, irregular, Smooth)

+ 25. Pits : diameter (unit: µm) Conditions for inapplicability (Ridged, Rugose, irregular, Smooth)

+ 41. Pits : number per faces (unit: _) Conditions for inapplicability (Ridged, Rugose, irregular, Smooth)

+ 23. Pits : number longitudinally (unit: _) Conditions for inapplicability (Ridged, Rugose, irregular, Smooth)

+ 24. Pits : number transversally (unit: _) Conditions for inapplicability (Ridged, Rugose, irregular, Smooth)

+ 21. Pits : shape : { 1. Mainly circular, 2. Primarily elongate } Conditions for inapplicability (Ridged, Rugose, irregular, Smooth)

+ 50. Ridges : secondary : { 1. Yes, 2. No } Conditions for inapplicability (Pitted, Smooth, Rugose, irregular)

+ 37. Ridges : shape : { 1. Rounded, 2. Sharp, 3. Angular } Conditions for inapplicability (Pitted, Rugose, irregular, Smooth)

+ 29. Tubercles : presence : { 1. Yes, 2. No } Conditions for inapplicability (Ridged, Rugose, irregular, Smooth)

+ 32. Tubercles : morphology : { 1. Bullate, 2. Elongate-flattened, 3. Peg-shaped, 4. Cylindrical, 5. Spiny, 6. “Shallow mound” not protruding beyond wall } Conditions for inapplicability (No)

+ 33. Tubercle apex : morphology : { 1. Not elaborated (more or less rounded or pointed), 2. Capitate (Swollen head), 3. Biphid } Conditions for inapplicability (“Shallow mound” not protrude beyond wall)

+ 34. Tubercle : length (unit: µm) Conditions for inapplicability (“Shallow mound” not protrude beyond wall)

+ 51. Shallow mound invagination : shape : { 1. narrow, 2. broad, concave } Conditions for inapplicability (Elongate-flattened, Cylindrical, Spiny, Peg-shaped, Bullate)

+ 56. Tubercle : number of cells in cross section (unit: count) Conditions for inapplicability (“Shallow mound” not protrude beyond wall, Bullate)

+ 35. Tubercle : diameter (unit: _) Conditions for inapplicability (No)

26. Endocarp surface : vasculature : { 1. Resting on ridges, 2. Resting between ridges / mounds, 3. In the channel of endocarp, 4. Free }

28. Endocarp primary vascular bundle : position : { 1. Outside endocarp wall, 2. In a channel, 3. Inside endocarp wall }

30. Locule : microtomography : { 1. Smooth, 2. Papillate, 3. Inflated }

+ 44. Papillae : density (unit: mm) Conditions for inapplicability (Smooth, Inflated)

+ 43. Papillae : diameter (unit: µm) Conditions for inapplicability (Smooth, Inflated)

+ 42. Papillae : shape : { 1. Rounded, 2. Elongate } Conditions for inapplicability (Smooth, Inflated)

31. Locule : hairs : { 1. Yes, 2. No }

38. Ridges : number reaching the base : { 1. 0, 2. 1, 3. 2, 4. 4, 5. 6 }

39. Vertical ridges : number : { 1. 0, 2. 1, 3. 2, 4. 3, 5. 4, 6. 5, 7. > 5 }

45. Endocarp wall : layers : { 1. Divided into distinctive units, 2. Homogeneous }

46. Endocarp wall cells : orientation : { 1. Periclinal, 2. Anticlinal, 3. Isodiametric }

47. Locule : number : { 1. One, 2. Three, 3. Five }

48. Locule : lacunate : { 1. Yes, 2. No }

49. Geographical sampling : { 1. Africa, 2. Asia, 3. South America, 4. Oceania, 5. Madagascar }

52. Endocarp : thicker than wide : { 1. Yes, 2. No }

53. Fruit : fleshy appendage : { 1. Yes, 2. No }

54. Fruit : gynophore : { 1. Yes, 2. No }

55. Endocarp : hairs : { 1. Yes, 2. No }

Appendix 2 (continued on next page)**.** The discriminative power of all descriptors.

	XPER	Sokal & Michener	Jaccard
1. Fruit : type	0/4278 (0.0)	0/4278 (0.0)	0/4278 (0.0)
2. Fruit : color	1231/4278 (0.29)	1848/4278 (0.43)	2754/4278 (0.64)
3. Fruit : length	2930/4278 (0.68)	4181/4278 (0.98)	4181/4278 (0.98)
4. Fruit : width	2836/4278 (0.66)	4181/4278 (0.98)	4181/4278 (0.98)
5. Fruit : thickness	2794/4278 (0.65)	3734/4275 (0.87)	3734/4275 (0.87)
6. Epicarp : indumentum type	2813/4278 (0.66)	1714/4278 (0.4)	3132/4278 (0.73)
7. Epicarp hair : type	1090/2701 (0.4)	722/2701 (0.27)	1604/2701 (0.59)
8. Epicarp hair : color	128/2701 (0.05)	437/2701 (0.16)	558/2701 (0.21)
9. Epicarp : additional structure	2034/4278 (0.48)	1108/4278 (0.26)	2104/4278 (0.49)
10. Endocarp : presence of a keel	1650/4278 (0.39)	1741/4278 (0.41)	1741/4278 (0.41)
11. Endocarp : shape in lateral view	1412/4278 (0.33)	691/4278 (0.16)	1679/4278 (0.39)
12. Endocarp : shape in transverse section	1388/4278 (0.32)	986/4278 (0.23)	1478/4278 (0.35)
13. Endocarp : apex structure	2234/4278 (0.52)	1117/4278 (0.26)	2234/4278 (0.52)
14. Endocarp : base morphology	348/4278 (0.08)	439/4278 (0.1)	439/4278 (0.1)
15. Endocarp : length	4075/4278 (0.95)	4079/4263 (0.96)	4079/4263 (0.96)
16. Endocarp : width	4147/4278 (0.97)	4149/4242 (0.98)	4149/4242 (0.98)
17. Endocarp : thickness	3849/4278 (0.9)	3853/4216 (0.91)	3853/4216 (0.91)
18. Endocarp wall : thickness	3438/4278 (0.8)	4183/4278 (0.98)	4183/4278 (0.98)
19. Endocarp : surface structures	1767/4278 (0.41)	1538/4278 (0.36)	2589/4278 (0.61)
20. Endocarp : ridging pattern	759/1953 (0.39)	955/1953 (0.49)	955/1953 (0.49)
21. Pits : shape	312/666 (0.47)	312/666 (0.47)	312/666 (0.47)
22. Pits : arrangement	322/666 (0.48)	322/666 (0.48)	322/666 (0.48)
23. Pits : number longitudinally	483/666 (0.73)	629/666 (0.95)	629/666 (0.95)
24. Pits : number transversally	530/666 (0.8)	663/664 (1.0)	663/664 (1.0)
25. Pits : diameter	243/666 (0.36)	593/666 (0.89)	593/666 (0.89)
26. Endocarp surface: vasculature	2430/4278 (0.57)	1626/4278 (0.38)	2842/4278 (0.66)
27. Areoles : freely ending ridgelets	374/780 (0.48)	393/780 (0.5)	393/780 (0.5)
28. Endocarp primary vascular bundle : position	1944/4278 (0.45)	1387/4278 (0.32)	2040/4278 (0.48)
29. Tubercles : presence	0/666 (0.0)	0/666 (0.0)	0/666 (0.0)
30. Locule : microtomography	1985/4278 (0.46)	1828/4278 (0.43)	2489/4278 (0.58)
31. Locule : hairs	270/4278 (0.06)	270/4278 (0.06)	270/4278 (0.06)
32. Tubercles : morphology	559/666 (0.84)	186/666 (0.28)	559/666 (0.84)
33. Tubercle apex : morphology	187/435 (0.43)	153/435 (0.35)	205/435 (0.47)
34. Tubercle : length	359/435 (0.83)	405/435 (0.93)	405/435 (0.93)
35. Tubercle : diameter	351/666 (0.53)	405/666 (0.61)	405/666 (0.61)
36. Areoles : number closed by ridges	606/780 (0.78)	665/780 (0.85)	665/780 (0.85)
37. Ridges : shape	844/1953 (0.43)	776/1953 (0.4)	1081/1953 (0.55)

Appendix 2 (continued)**.** The discriminative power of all descriptors.

	XPER	Sokal & Michener	Jaccard
38. Ridges : number reaching the base	2456/4278 (0.57)	1037/4278 (0.24)	2552/4278 (0.6)
39. Vertical ridges : number	3189/4278 (0.75)	1201/4278 (0.28)	3401/4278 (0.8)
40. Endocarp Wall : thickness with ridges/rugosity	1352/3003 (0.45)	1539/3003 (0.51)	1539/3003 (0.51)
41. Pits : number per faces	585/666 (0.88)	629/666 (0.95)	629/666 (0.95)
42. Papillae : shape	243/1225 (0.2)	495/1225 (0.4)	495/1225 (0.4)
43. Papillae : diameter	138/1225 (0.11)	559/1225 (0.46)	559/1225 (0.46)
44. Papillae : density	180/1225 (0.15)	189/1225 (0.16)	189/1225 (0.16)
45. Endocarp wall : layers	1140/4278 (0.27)	1231/4278 (0.29)	1231/4278 (0.29)
46. Endocarp wall cells : orientation	312/4278 (0.07)	1575/4278 (0.37)	1863/4278 (0.44)
47. Locule : number	183/4278 (0.04)	122/4278 (0.03)	183/4278 (0.04)
48. Locule : lacunate	1989/4278 (0.46)	2124/4278 (0.5)	2124/4278 (0.5)
49. Geographical sampling	2883/4278 (0.67)	1153/4278 (0.27)	2883/4278 (0.67)
50. Ridges : secondary	612/1953 (0.31)	612/1953 (0.31)	612/1953 (0.31)
51. Shallow mound invagination : shape	10/21 (0.48)	10/21 (0.48)	10/21 (0.48)
52. Endocarp : thicker than wide	356/4278 (0.08)	356/4278 (0.08)	356/4278 (0.08)
53. Fruit : fleshy appendage	92/4278 (0.02)	92/4278 (0.02)	92/4278 (0.02)
54. Fruit : gynophore	1332/4278 (0.31)	1378/4278 (0.32)	1378/4278 (0.32)
55. Endocarp : hairs	92/4278 (0.02)	92/4278 (0.02)	92/4278 (0.02)
56. Tubercle : number of cells in cross section	168/276 (0.61)	170/276 (0.62)	170/276 (0.62)