European Journal of Taxonomy 943: 1–23
https://doi.org/10.5852/ejt.2024.943.2583
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2024 · Lagrange F. *et al.*

This work is licensed under a Creative Commons Attribution License (CC BY 4.0).

Research article

Seed morphology of the paleotropical tribe Paropsieae (Passifloraceae, Malpighiales), and paleobotanical implications

Flavien LAGRANGE [1], Camila MARTÍNEZ [2] & Cédric DEL RIO [3,*]

[1,3] CR2P – Centre de Recherche en Paléontologie – Paris, MNHN – Sorbonne Université – CNRS, 43 Rue Buffon, 75005 Paris, France.
[2] Área de Sistemas Naturales y Sostenibilidad, Universidad EAFIT, Medellín, Colombia.
[2] Center for Tropical Paleoecology and Archaeology, Smithsonian Tropical Research Institute, Panama City, Panama.

[*] Corresponding author: cedric.del-rio@mnhn.fr
[1] Email: flagrange@edu.mnhn.fr
[2] Email: cmartinez2@eafit.edu.co

Abstract. The fossil record of the diverse subfamily Passifloroideae (>750 species and 17 genera) is relatively poor. Despite the distinctiveness of its leaves (glandular and often emarginate), most of the fossils from this group have been described from seeds. Fossil seeds have been recovered from Europe, and North and South America. A lack of information on seed morphology for all the genera and tribes of this subfamily has prevented a tribe-level identification of the fossils and a better understanding of their biogeographic patterns. The Passifloroideae is divided into three tribes: Passifloreae with 10 genera, Paropsieae with six genera and the monotypic Jongkindieae. This study provides new descriptions for 15 species from 5 genera from the mostly Afrotropical tribe Paropsieae based on herbarium material, and introduces an online seed database and a key for 100 species of Passifloroideae compiled from literature and direct observations. Our study shows a low morphological diversity among the seeds of Paropsieae in comparison to a much larger diversity within Passifloreae. Some rare morphologies are only present in Passifloreae and can be used to assign seeds to this tribe. Within the Paropsieae, *Androsiphonia* has seed that are very distinct from those in the other genera in the tribe and also from the rest of the subfamily. The genus *Paropsia* exhibits two main morphotypes, while the genera *Barteria*, *Paropsiopsis* and *Smeathmannia* have very similar seeds with a highly conserved morphology. These results suggest that living or fossil Paropsieae cannot be identified confidently based solely on seed characters.

Keywords. Seeds, taxonomy, anatomy, paleobotany, botany.

Lagrange F., Martínez C. & Del Rio C. 2024. Seed morphology of the paleotropical tribe Paropsieae (Passifloraceae, Malpighiales), and paleobotanical implications. *European Journal of Taxonomy* 943: 1–23. https://doi.org/10.5852/ejt.2024.943.2583

Introduction

The passion fruit family Passifloraceae Juss. ex. Roussel comprises four subfamilies: Passifloroideae Burnett (Angiosperm Phylogeny Group 2003), historically considered Passifloraceae s. str. (Angiosperm

Phylogeny Group 1998); Turneroideae Eaton and Malesherbioideae Burnett previously recognized as independent families (Stevens 2001 onwards; Angiosperm Phylogeny Group 2009; Tokuoka 2012); and a recently been added subfamily Pibirioideae M.W.Chase & Christenh (Maas *et al.* 2019). This redefined family contains approximately 27 genera and over 1000 species (Stevens 2001 onwards). The family Passifloraceae belongs to the order Malpighiales Martius, according to the APG IV classification (Angiosperm Phylogeny Group 2016).

The subfamily Passifloroideae has a widespread geographical distribution, including South America, Africa, Asia and Oceania (Feuillet & MacDougal 2007; Hermsen 2021). This subfamily comprises 17 genera and 700–750 species (Feuillet & MacDougal 2007; Krosnick *et al.* 2009; Breteler *et al.* 2022). Leaf shape varies greatly within the subfamily, sometimes with bi- or trilobed leaves, and stipules that have variable development and forms (Feuillet & MacDougal 2007). A characteristic feature of the group is the presence of extrafloral glands at the apex, margin or base of the leaves, on the petioles or on the stipules. The flowers are pentamerous, with two whorls of perianth and a whorl of stamens, the stamens are, sometimes connate and often fused with the carpels to form an androgynophore (Feuillet & MacDougal 2007). The flower has a large corona around the stamens, which can be highly complex and composed of several series of extensions around the stamens and nectar pits (e.g., Jørgensen *et al.*1984; Bonilla Morales *et al.* 2015). The fruits are berries or capsules containing seeds that are almost always arillate. The seeds have diagnostic characteristics for the subfamily, including a compressed shape, a seed coat formed by a palisade tissue of columnar cells, and ruminate endosperm (Feuillet & MacDougal 2007; Martínez 2017). Passifloroideae is divided into the tribes Passifloreae, mainly found in South America, Paropsieae, mainly found in Africa (de Wilde 1971; Feuillet & MacDougal 2007; Tokuoka 2012) and the new and monotypic tribe Jongkindieae from Liberia (Breteler *et al.* 2022).

The tribe Passifloreae comprises 10 genera, including the genus *Passiflora* L., with over 500 species (Feuillet & MacDougal 2007; Krosnick *et al.* 2009, 2013). The tribe is morphologically characterized by climbing herbaceous plants with tendrils (Feuillet & MacDougal 2007; Tokuoka 2012). The passion fruit is part of this clade and mainly corresponds to the fruit of *Passiflora edulis* Sims (Morton 1987). The genus *Passiflora* is by far the most extensively studied genus due to its significant economic and ecological importance (e.g., Ulmer & MacDougal 2004). Plants from this tribe can be found in both paleotropical and neotropical environments, but only the genus *Passiflora* is present in both geographic areas (Krosnick *et al.* 2013; Hermsen 2021).

The Paropsieae comprises 6 genera and 22 species: *Paropsia* Noronha ex Thouars (12 species, 11 in Africa and Madagascar, one in Malaysia), *Paropsiopsis* Engl. (two species, both in West Africa), *Viridivia* J.H.Hemsl. & Verdc (one species, *V. suberosa* J.H.Hemsl. & Verdc, in East Africa), *Androsiphonia* Stapf (one species, *Androsiphonia adenostegia* Stapf, in West Africa), *Smeathmannia* Sol. ex R.Br. (two species, in West Africa) and *Barteria* Hook.f. (four species, throughout tropical Africa) (Feuillet & MacDougal 2007; POWO 2023). With the exception of a single species, *Paropsia vareciformis* (Griff.) Mast. from Asia, all species of Paropsieae occur in Africa or Madagascar (POWO 2023). The genus *Barteria* is notable because three of its four species have a symbiotic relationship with ants, which inhabit the hollow stems of the plant (Sleumer 1970; Feuillet & MacDougal 2007). The members of the tribe are morphologically characterized as robust shrubs or bushes with axillary flowers or inflorescences (Feuillet & MacDougal 2007; Tokuoka 2012).

The fossil record of the Passifloroideae is poor (Martínez 2017). Some fossils are difficult to identify and could belong to other groups (Martínez 2017; Hermsen 2021). Fossilized leaves dating back to the Cretaceous period have been considered as belonging to the Passifloroideae, but they lack the diagnostic petiolar gland, and their familial identification has recently been questioned (Martínez 2017; Hermsen 2021, 2023). Similarly, attribution of fossilized pollen to the Passifloraceae is considered ambiguous

(Martínez 2017; Hermsen 2021) except for those reported from the Miocene of South America (Palazzesi *et al.* 2014; D'Apolito *et al.* 2021; Hermsen 2023). Fortunately, fossilized seeds can be confidently identified as belonging to Passifloroideae thanks to the palisade structure of the seed coat and the ruminate ornamentation of the surface (Martínez 2017). Apart from *Passiflora appalachiana* Hermsen (4.5 Ma), *Passiflora bulgarica* (Palamarev) Hermsen (15.9–11.6 Ma) and *Passiflora sulcatasperma* Hermsen (4.5 Ma) (Hermsen 2021, 2023), all species of fossilized seeds of Passifloroideae that cannot be assigned to a particular extant genus of seeds have all been grouped under the fossil genus *Passifloroidesperma* Martínez (Martínez 2017; Hermsen 2021). The oldest member of *Passifloroidesperma*, *P. sogamosense* Martínez, dates back to the late Eocene (45–34 Ma; Martínez 2017). Therefore, fossilized seeds are the most numerous remains that are unambiguous, making these organs particularly important for understanding the biogeography and evolutionary history of the group. However, as demonstrated by the establishment of the genus *Passifloroidesperma*, their taxonomic resolution below the genus level is often insufficient (Martínez 2017).

The seed morphology of the extant Passifloreae has been extensively studied for the genus *Passiflora*, particularly representatives from South America (e.g., MacDougal 1994; Mezzonato-Pires *et al.* 2017; Pérez-Cortéz *et al.* 2002; Pérez-Cortéz 2007) while the seed morphology of other genera of the tribe (e.g., *Adenia* Forssk. with 100 species) has not been the subject of much research (e.g., Perrier de la Bathie 1945; Ngumbau *et al.* 2017). Although the seed morphology is not used to define modern genera or species (Feuillet & MacDougal 2007), it appears to be of great importance in the diagnosis of certain subgenera of the genus *Passiflora* (Mezzonato-Pires *et al.* 2017; Hermsen 2021). Indeed, seeds of *Passiflora* can differ in ornamentation, size, apex shape, and base shape (e.g., Mezzonato-Pires *et al.* 2017). On the other hand, the seeds of Paropsieae have been poorly studied, with only the seed of *Paropsia gabonica* Breteler being illustrated (Breteler 2003). Up to now, Martínez (2017) provided the most complete overview of the seed morphology in the Paropsieae, but mostly based on incomplete descriptions of seeds from the literature and not providing illustrations of them. Martínez (2017) concluded that there are probably no differences between the seeds of the two tribes. However, given the current state of knowledge, it is still difficult to determine whether it is feasible to attribute fossil seeds of *Passifloroidesperma* to one tribe rather than another, or if it is simply impossible to distinguish them based solely on the seed morphology. A distinction between the seed morphology of the tribes would help clarify affinities of the fossils with extant Passifloroideae.

The aim of this study is to remedy this lack of information on the morphology of the seeds of the tribe Paropsieae. The objectives are: (1) to assess whether it is possible to distinguish the seeds of Paropsieae from those of the Passifloreae, (2) to study whether the seeds can be used in the diagnoses of the genera of Paropsieae and (3) to distinguish the species within the genera on the basis of the seeds.

Material and methods

Material sampled

Specimens were collected from the Paropsieae collection at the Herbarium of Paris in the Muséum national d'Histoire naturelle. A total of 892 herbarium sheets belonging to the subfamily were examined. Among these sheets, only 75 included seeds. Floras and taxonomic revisions of the tribe were used to validate the identifications of these specimens (Olivier 1871; Perrier de la Bathie 1945; Hutchinson & Dalziel 1952; Sleumer 1970; Breteler 1999, 2003; de Vos & Breteler 2009). In total, 16 sheets were selected based on the quality of seed preservation, covering 5 out of 6 genera and 15 out of the 22 species in the tribe. Two seeds were selected per sampled sheet. The species *Paropsia gabonica*, described in 2003 (Breteler 2003), was not present in the collection but is still mentioned in the online database (see below) because there is an illustration of the seed (Breteler 2003).

The following species are studied: *Androsiphonia adenostegia* Stapf (*A.J.B. Chevalier 17461*, *21194*, Supp. file 1), *Barteria dewevrei* De Wild. & T.Durand (*Guignonis 1938*), *B. fistulosa* Mast. (*H. Jacques-Félix 4802*), *B. nigritana* Hook.f. (*A. Walker s.n.*), *Paropsia brazzaeana* Braill. (*E. Dekindt 564*), *P. edulis* Thouars (*G. Cours 3424*), *P. grandiflora* Sleumer (*H. Humbert 32553*), *P. grewioides* Welw. ex Mast. (*R. Letouzey 5589*), *P. humblotii* H.Perrier (*Ragauaparany 8040*), *P. madagascariensis* (Baill.) H.Perrier (*R. Bernard 120*), *P. obscura* O.Hoffm. (*Madiomanana et al. 108*), *P. vareciformis* (Griff.) Mast. (*H. Schaller & L.E. Teo 3826*), *Paropsiopsis decandra* (Baill.) Sleumer (*T.J. Klaine 194*), *Smeathmannia laevigata* Sol. ex R.Br. (*Heudelot 655*) and *S. pubescens* Sol. ex R.Br (*A.J.B. Chevalier 17306*).

Methods of study and descriptive nomenclature

The selected seeds were photographed using a Canon EOS 5DS camera equipped with an MPE65mm lens. The seeds were placed flat under multidirectional lighting. Each seed was photographed from four aspects: a view of each face, a side view, and a basal view. The focal stacking was done using the stackshot device and Affinity Photo and Designer software (ver. 1.10) to combine the photographs. The seeds were then embedded in resin and cut to create thin sections in the laboratory following the protocol by Benedict (2015). The thin sections were observed under a Nikon Eclipse 80i optical microscope and a Hirox RH-2000 digital microscope, and photographs were taken at 4 × to 20 × magnifications.

The methodology for measuring the seeds and establishing the characteristics of ornamentation, shape, and structure of the margin, apex and base is based on Pérez-Cortéz *et al.* (2002) and Mezzonato-Pires *et al.* (2017), with modifications based on the descriptions by Hermsen (2021, 2023). All measurement were performed using ImageJ software (Rasband 2016).

The morphological data were recorded in an online database Xper3 (Ung *et al.* 2010; Kerner *et al.* 2021). The key based on this database is available at: https://app.xper3.fr:443/xper3GeneratedFiles/publish/identification/-5560928563158630166/.The database contains 116 species. In order to have a means of comparing the morphologies and diversity of Paropsieae to Passifloreae, we have added in the database selected descriptions from the literature of the Passifloreae genera *Passiflora*, *Deidamia* Noronha ex Thouars, *Ancistrothyrsus* Harms and *Adenia* (Perrier de la Bathie 1945; de Wilde 1972; Jørgensen *et al.* 1987; MacDougal 1994, 2001; Gilbert & MacDougal 2000; Pérez-Cortéz *et al.* 2002, 2005, 2009; Pérez-Cortéz 2007; Jørgensen & Vásquez 2009; Vanderplank & Zappi 2011; Lozada-Pérez & Gutiérrez 2016; Mezzonato-Pires *et al.* 2017; Ngumbau *et al.* 2017; Espinoza *et al.* 2018; Feuillet 2020; Vanderplank & Ochoa 2020). In total, 100 species (91 species of *Passiflora*, one species of *Ancistrothyrsus*, one species of *Deidamia* and seven species of *Adenia*) of the Passifloreae were entered into the database. Another 15 species came from our study and one species from Breteler (2003). The database utilizes 15 descriptors: the degree of compression of the seed, general shape, ornamentation, appendage on the apex, base shape, mucro presence, margin, length, width, thickness, width/thickness ratio, number of reticulations per mm^2, reticulation diameter, reticulation depth, totaling 23 character states. We converted the average and deviation values from the study of Pérez-Cortéz *et al.* (2002) to ranges. The literature is inconsistent in describing the general shape, calling the same shape as "elliptical", "oblong", or "obovoid". We consider these differences as insignificant for our purpose and describe the general shape in such cases as "elliptic to oblong". The descriptors for reticulation dimensions and reticulation number are dependent on the ornamentation and are not applicable to the smooth ornamentation state. The database comprehensively covers the Paropsieae (Supp. file 2) but the Passifloreae are less complete because the reticulation dimensions and wall thickness are mostly not specified in the literature.

Results

An overview of the morphological diversity of the Paropsieae studied here is given in Table 1.

The palisade seed coat structure is the same for all the following seeds except for *Androsiphonia*, and we have illustrated the character only once in Fig. 1F.

Table 1. Comparisons of the 5 genera belonging to the tribe Paropsieae studied herein.

	Androsiphonia **Stapf**	***Barteria*** **Hook.f.**	***Paropsia*** **Noronha ex Thouars**	***Paropsiopsis*** **Engl.**	***Smeathmannia*** **R.Br.**
General shape	oblong to circular	oblong	oblong or cordate	oblong	oblong
Apex appendage	absent or reduced	absent or reduced	present, absent or reduced	absent or reduced	absent or reduced
Surface ornamentation	smooth	coarsly reticulate	coarsly reticulate or reticulate foveolate	reticulate foveolate	reticulate foveolate
Margin	entire	entire	striate or entire	entire	entire
Mucro	absent	present	present or absent	present	present
Average reticulation per mm²	NA	4	5.6	6.1	9.5
Length (mm)	6.0–9.0	4.6–7.0	4.9–8.1	5.9–6.1	4.6–5.2
Width (mm)	6.0–8.0	3.0–4.0	2.9–7.0	2.6–2.9	3.0–3.7
Thickness (mm)	5.0–5.5	1.8–2.2	1.3–2.7	1.6–1.9	1.6–1.8
Seed coat width (mean, µm)	negligible	135	230	103	155

Class Magnoliopsida Brongn.
Order Malpighiales Juss. ex Bercht. & J.Presl
Family Passifloraceae Juss. ex. Roussel
Tribe Paropsieae

Genus ***Androsiphonia*** Stapf
Figs 1A, 2

Remark

This genus is represented by a single species.

Androsiphonia adenostegia Stapf
Figs 1A, 2

Material examined

IVORY COAST • Province de l'Attié, Alépé; 1907; *A.J.B. Chevalier 17461*; P [P04772166]! • Bassin du Haut-Nuon, Pays des Diolas, entre Kuankoulé et Danané; 7 Apr. 1909; *A.J.B. Chevalier 21194*; P [P04772168]!.

Seed description

Seeds are ca 6.0–9.0 mm long, 6.0–8.0 mm wide and 5.0–5.5 mm thick, oblong to nearly circular, wider than thick. The surface is completely smooth, dark brown, with visible hairy tegument. The apex is blunt, rounded with a small depression. The base is rounded. The margin is entire. The integuments are reduced to a single cellular layer.

Genus ***Barteria*** Hook.f.
Figs 1B, F, 3

Seed description

Seeds compressed, 4.6–7.0 mm long, 3.0–4.0 mm wide and 1.8–2.2 mm thick, curved oblong. The surface is coarsely reticulate, with an average of 4.00 reticulations per mm^2. The reticulations have an average diameter of 630 µm and a depth of 170 µm. The margin is entire. The apex lacks a prominent appendage. The base is acute and truncate, bearing a mucro. The palisade seed coat is on average 135 µm thick.

Remark

The genus is represented by 4 species, 3 are studied here.

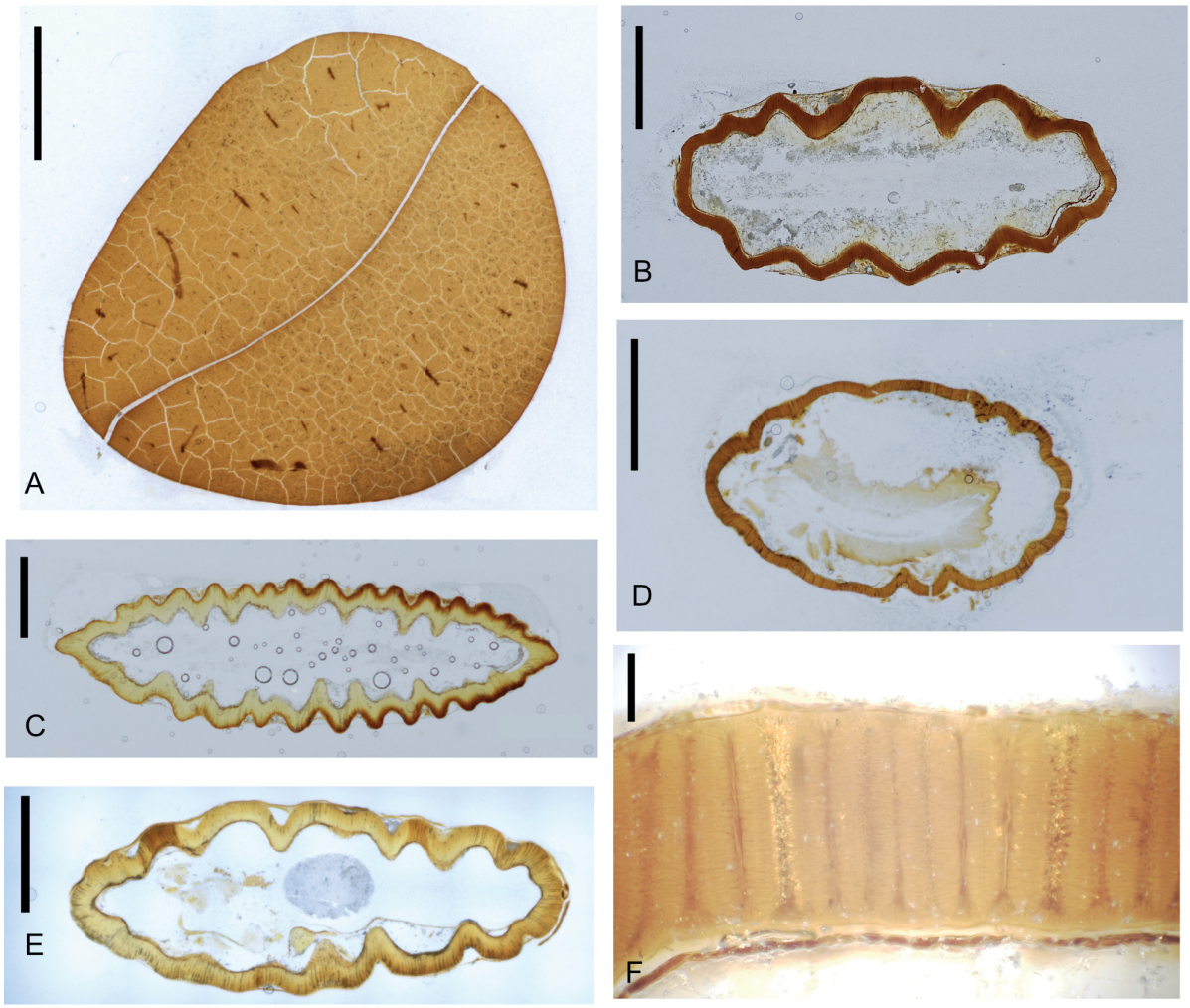

Fig. 1. Cross-sections of seeds from each genus. **A**. *Androsiphonia adenostegia* Stapf (P04772168). **B**. *Barteria fistulosa* Mast. (P04772344). **C**. *Paropsia edulis* Thouars (P04767996). **D**. *Paropsiopsis decandra* (Baill.) Sleumer (P04772112). **E**. *Smeathmannia pubescens* Sol. ex R.Br. (P04772722). **F**. Seed coat of *Barteria fistulosa* (P04772344). Scale bars: A = 1.5 mm; B–D = 1 mm; E = 0.8 mm; F = 1.1 mm.

Barteria dewevrei De Wild. & T.Durand
Fig. 3A–H

Material examined

CENTRAL AFRICAN REPUBLIC • Forêt de la Seriki près Kembe, Oubangu; Oct. 1960; *Guignonis 1938*; P [P04772304]!.

Fig. 2. Seeds of *Androsiphonia adenostegia* Stapf. **A–D**. From specimen *A.J.B. Chevalier 17461* (P04772166). **E–H**. From specimen *A.J.B. Chevalier 21194* (P04772168). **A, E**. Face view. **B, F**. Side view. **C, G**. Second face view. **D, H**. Basal view. Scale bar = 5 mm.

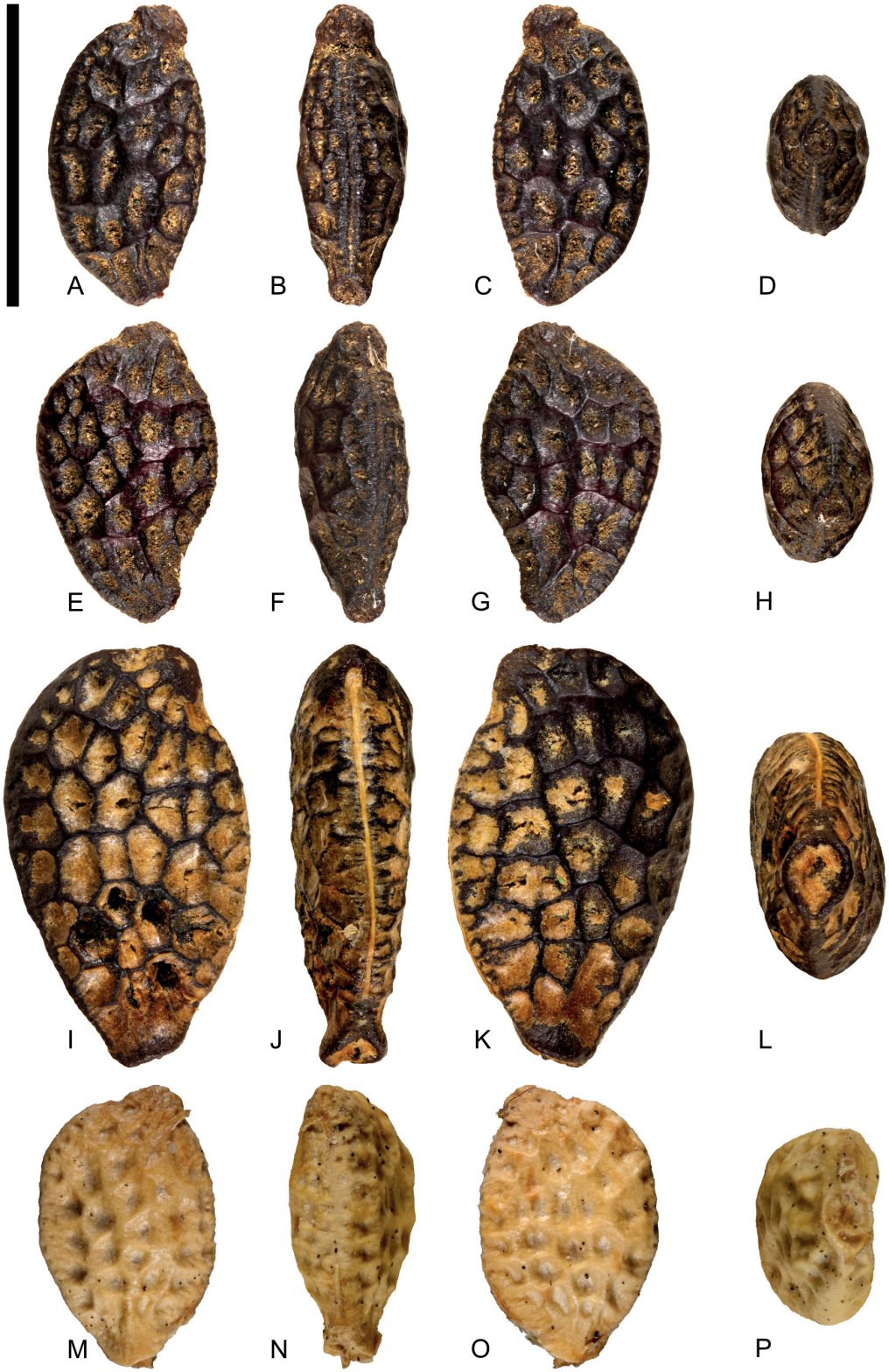

Fig. 3. Seeds of the genus *Barteria* Hook.f. **A–D**. *Barteria dewevrei* De Wild. & T.Durand (*Guignonis 1938*; P04772304) seed. **E–H**. *Barteria dewevrei* second seed. **I–L**. *Barteria fistulosa* Mast. (*H. Jacques-Félix 4802*; P04772344). **M–P**. *Barteria nigritana* Hook.f. (*A. Walker s.n.*; P04772081). **A, E, I, M**. Face view. **B, F, J, N**. Side view. **C, G, K, O**. Second face view. **D, H, L, P**. Basal view. Scale bar = 5 mm.

Seed description

Seeds compressed, 5.0 mm long, 3.0 mm wide and 2.0 mm thick, curved oblong. The surface is coarsely reticulate and black, with an average of 4.50 reticulations per mm^2. The reticulations have an average diameter of 634 µm and a depth of 159 µm. The margin is entire with a fold. The apex lacks prominent appendages. The base is acute and truncate, with a mucro. The palisade seed coat is 135 µm thick on average.

Barteria nigritana Hook.f.
Fig. 3M–P

Material examined

GABON • Aug.–Sep. 1938; *A. Walker s.n.*; P [P04772081]!.

Seed description

Seeds compressed, 4.7 mm long, 3.0 mm wide and 1.8–2.2 mm thick, curved oblong. The surface is coarsely reticulate and cream, with an average of 4.75 reticulations per mm^2. The reticulations have an average diameter of 634 µm and a depth of 159 µm. The margin is entire with a lateral fold. The apex lacks a prominent appendage. The base is acute and truncate, with a mucro. The palisade seed coat is 105 µm thick on average.

Barteria fistulosa Mast.
Figs 1B, F, 3I–L

Material examined

CAMEROON • Yaoundé; Aug. 1939; *H. Jacques-Félix 4802*; P [P04772344]!.

Seed description

Seeds compressed, 7.0 mm long, 4.0 mm wide and 2.0 mm thick, curved oblong. The surface is coarsely reticulate and black, with an average of 3.68 reticulations per mm^2. The reticulations have an average diameter of 818 µm and a depth of 231 µm. The margin is entire. The apex lacks a prominent appendage. The base is acute and truncate, with a mucro. The palisade seed coat is 161 µm thick on average.

Genus ***Paropsia*** Noronha ex Thouars
Figs 1C, 4–5

Seed description

Seeds compressed, 4.9–8.1 mm long, 2.9–7.0 mm wide and 1.3–2.7 mm thick, oblong or cordate, sometimes curved. The surface is reticulate-foveolate or coarsely reticulate, with an average of 5.60 reticulations per mm^2. The reticulations have an average diameter of 487 µm and a depth of 190 µm. The margin is striate or entire, sometimes with a lateral fold. The apex may have a prominent appendage. The base is obtuse or acute, sometimes truncate, and may have a mucro. The palisade seed coat is on average 230 µm thick.

Remark

The genus is represented by 12 species, 8 are studied here.

Paropsia brazzaeana Baill.
Fig. 4A–D

Material examined

ANGOLA • Huilla; Feb. 1899; *E. Dekindt 564*; P [P04772425]!.

Seed description

Seeds compressed, 7.5 mm long, 5.2 mm wide and 2.6 mm thick, oblong. The surface is reticulate-foveolate and orange-brown, with 3.87 reticulations per mm^2. The reticulations have an average diameter of 720 µm and a depth of 213 µm. The margin is entire and very thick. The reticulations bordering the margin are open laterally. The apex has a hooked prominent appendage. The base is obtuse, without a mucro. The palisade seed coat is 275 µm thick.

Paropsia edulis Thouars
Figs 1C, 4E–H

Material examined

MADAGASCAR • d'Ambolavoanio à Mataninina au bord rivière Andronomadio; 2 Sep. 1949; *G. Cours 3424*; P [P04767996]!.

Seed description

Seeds compressed, 7.1 mm long, 5.8 mm wide and 2.4 mm thick, cordate. The surface is coarsely reticulate and light brown, with 7.12 reticulations per mm^2. The reticulations have an average diameter of 414 µm and a depth of 188 µm. The margin is striate. The apex has a prominent appendage. The base is obtuse and truncate, with a mucro. The palisade seed coat is 281 µm thick.

Paropsia grandiflora Sleumer
Fig. 4M–P

Material examined

MADAGASCAR • Collines et palteaux calcaires de l'Ankarana du Nord (prov. de Diego-Suarez); Jan.–Feb. 1960; *Humbert 32553*; P [P04767592]!.

Seed description

Seeds compressed, 5.3 mm long, 3.0 mm wide and 1.5 mm thick, cordate. The surface is coarsely reticulate and brown, with 6.25 reticulations per mm^2. The reticulations have an average diameter of 268 µm and a depth of 99 µm. The margin is striate. The apex lacks prominent appendages. The base is obtuse and truncate, with a mucro. The palisade seed coat is 122 µm thick.

Paropsia grewioides Welw. ex Mast.
Fig. 4I–L

Material examined

CAMEROON • 8 km N de Ntam (80 km ENE de Lomié); 8 Aug. 1963; *R. Letouzey 5589*; P [P04772193]!.

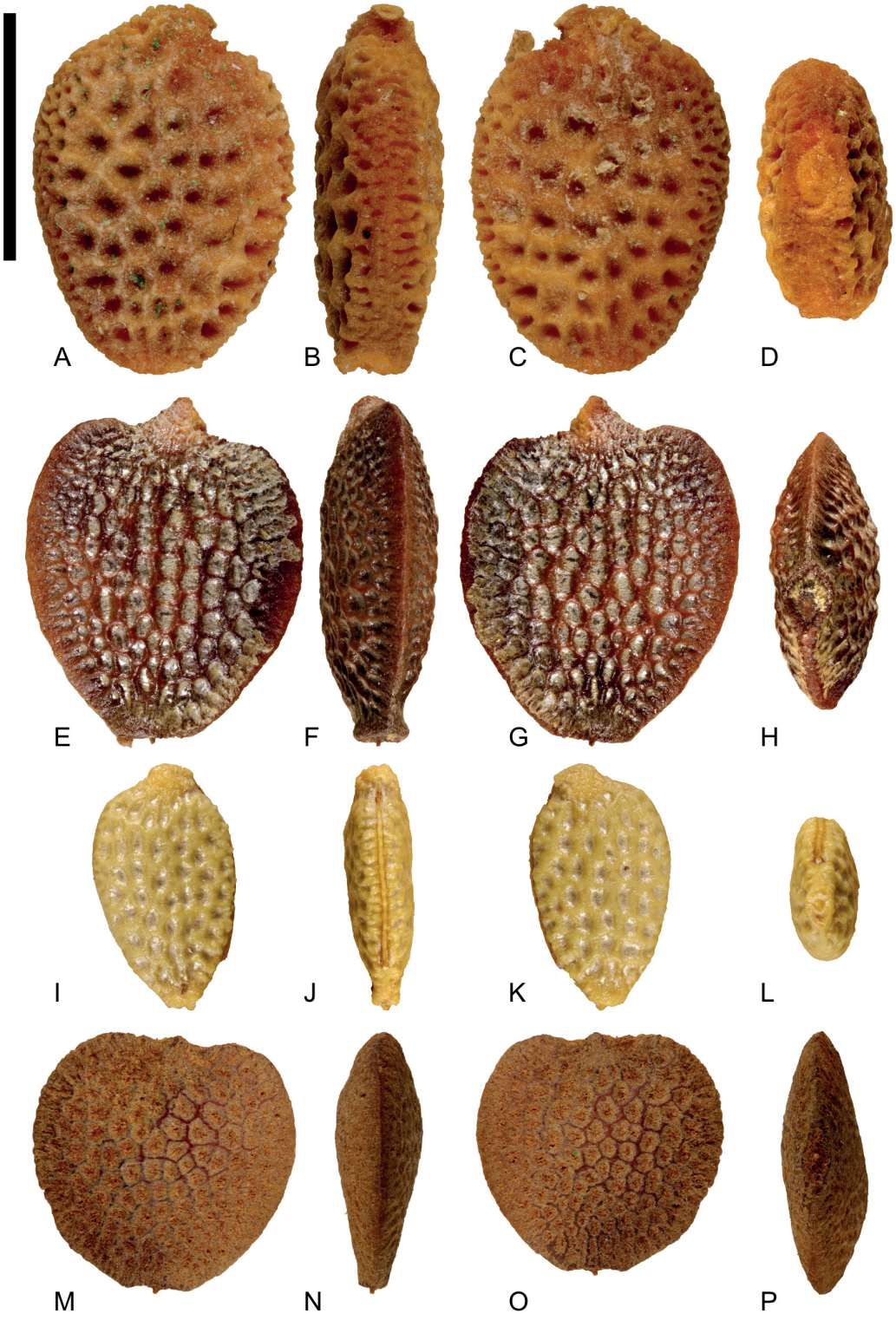

Fig. 4. Seeds of the genus *Paropsia* Noronha ex Thouars. **A–D**. *Paropsia brazzaeana* Braill. (*E. Dekindt 564*; P04772425). **E–H**. *Paropsia edulis* Thouars (*G. Cours 3424*; P04767996). **I–L**. *Paropsia grewioides* Welw. ex Mast. (*R. Letouzey 5589*; P04772193). **M–P**. *Paropsia grandiflora* Sleumer (*H. Humbert 32553*; P04767592). **A, E, I, M**. Face view. **B, F, J, N**. Side view. **C, G, K, O**. Second face view. **D, H, L, P**. Basal view. Scale bar = 5 mm.

Seed description

Seeds compressed, 5.0 mm long, 2.9 mm wide and 1.4 mm thick, oblong. The surface is reticulate-foveolate and light cream, with 6.12 reticulations per mm^2. The reticulations have an average diameter of 458 µm and a depth of 173 µm. The margin is entire with a very pronounced fold. The apex lacks a prominent appendage. The base is acute, with a mucro. The palisade seed coat is 221 µm thick.

Paropsia humblotii H.Perrier
Fig. 5A–D

Material examined

MADAGASCAR • Distr. Tamatave, canton Ambodonana; 16 Dec. 1956; *Ragauaparany 8040*; P [P04766828]!.

Seed description

Seeds compressed, 7.5 mm long, 6.9 mm wide and 2.0 mm thick, cordate. The surface is coarsely reticulate and light cream, with 7.62 reticulations per mm^2. The reticulations have an average diameter of 589 µm and a depth of 277 µm. The margin is striate. The apex lacks any appendages. The base is obtuse, without a mucro. The palisade seed coat is 243 µm thick.

Paropsia madagascariensis (Baill.) H.Perrier
Fig. 5E–H

Material examined

MADAGASCAR • Antsiranana, env. 6 km S d'Ambohimahery, forêt littorale sur sable, Antalaha, Masoala PN; 12 May 1995; *R. Bernard 120*; P [P04766852]!.

Seed description

Seeds compressed, 7.0 mm long, 5.5 mm wide and 2.4 mm thick, cordate. The surface is coarsely reticulate and light cream, with 4.62 reticulations per mm^2. The reticulations have an average diameter of 361 µm and a depth of 238 µm. The margin is striate with a lateral fold. The apex has a prominent appendage. The base is obtuse, with a mucro. The palisade seed coat is 234 µm thick.

Paropsia obscura O.Hoffm.
Fig. 5I–L

Material examined

MADAGASCAR • Diego-Suarez/Antsiranana: Presqu'île d'Ampasindava, Ampasindiva, forêt de Bongomihiravavy; 10 Nov. 2008; *M.C. Madiomanana et al. 108*; P [P05470672]!.

Seed description

Seeds compressed, 7.7 mm long, 6.3 mm wide and 2 mm thick, cordate. The surface is coarsely reticulate and light cream, with 3.75 reticulations per mm^2. The reticulations have an average diameter of 675 µm and a depth of 188 µm. The margin is striate. The apex has a prominent appendage. The base is obtuse, without a mucro. The palisade seed coat is 214 µm thick.

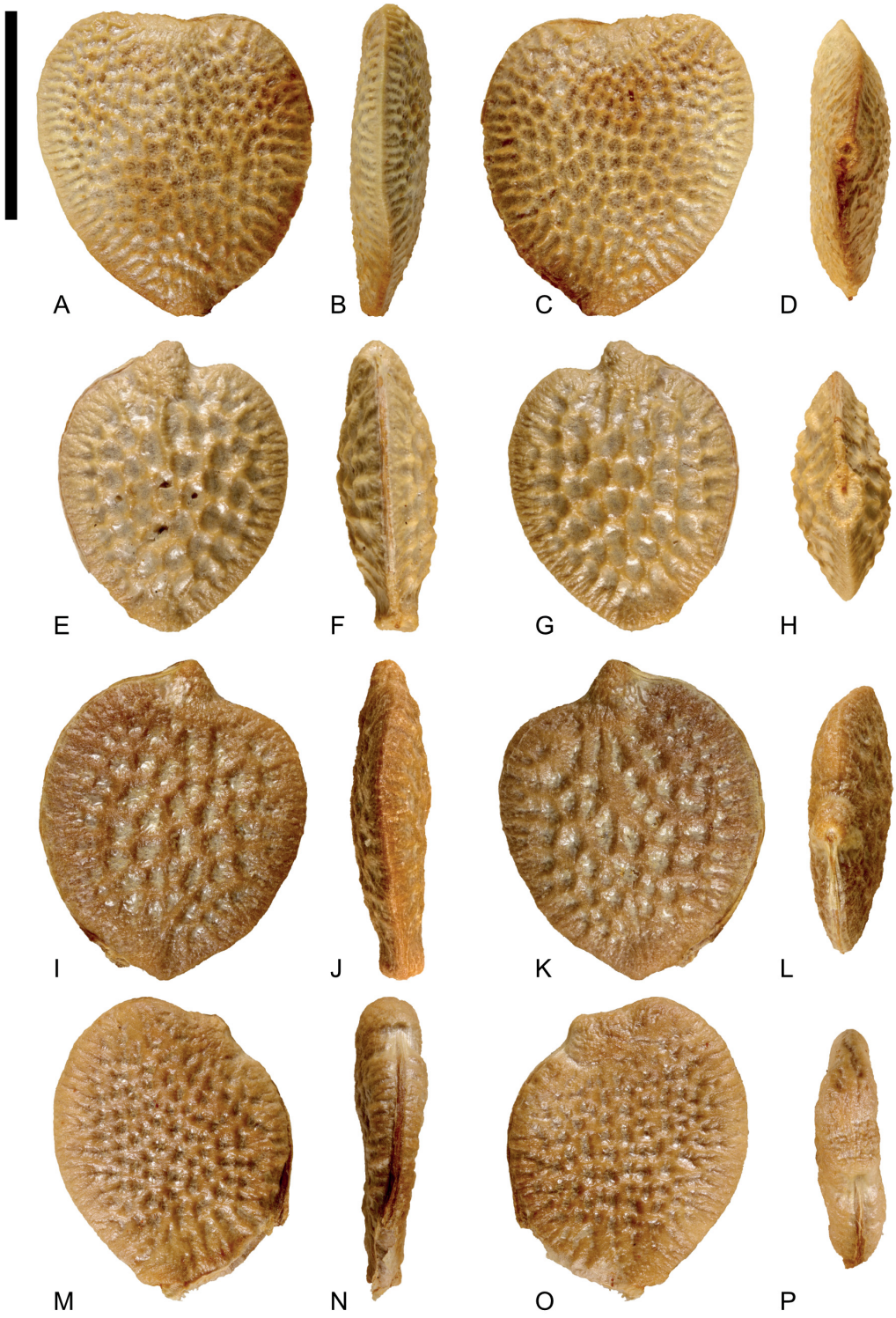

Fig. 5. Seeds of the genus *Paropsia* Noronha ex Thouars. **A–D**. *Paropsia humblotii* H.Perrier (*Ragauaparany 8040*; P04766828). **E–H**. *Paropsia madagascariensis* H.Perrier (*R. Bernard 120*; P04766852). **I–L**. *Paropsia obscura* O.Hoffm (*Madiomanana et al. 108*; P05470672). **M–P**. *Paropsia vareciformis* (Griff.) Mast. (*H. Schaller & L.E. Teo 3826*; P05538484). **A, E, I, M**. Face view. **B, F, J, N**. Side view. **C, G, K, O**. Second face view. **D, H, L, P**. Basal view. Scale bar = 5 mm.

Paropsia vareciformis (Griff.) Mast.
Fig. 5M–P

Material examined

MALAYSIA • Lumut, Hutan Simpan Segari Melintang; 10 Jan. 1990; *H. Schaller & L.E. Teo 3826*; P [P05538484]!.

Seed description

Seeds compressed, 7.3 mm long, 6.4 mm wide and 1.8 mm thick, curved cordate. The surface is coarsely reticulate and light cream, with 5.37 reticulations per mm^2. The reticulations have an average diameter of 411 µm and a depth of 164 µm. The margin is striate with a lateral fold. The apex has a prominent appendage. The base is obtuse and truncate. The palisade seed coat is 228 µm thick.

Genus ***Paropsiopsis*** Engl.
Figs 1D, 6A–D

Remark

The genus is represented by 2 species, 1 is studied here.

Paropsiopsis decandra (Baill.) Sleumer
Figs 1D, 6A–D

Material examined

GABON • 1906?; *T.J. Klaine 194*; P [P04772112]!.

Seed description

Seeds compressed, 5.9–6.1 mm long, 2.6–2.9 mm wide and 1.6–1.9 mm thick, oblong. The surface is reticulate foveolate and brown, with an average of 6.12 reticulations per mm^2. The reticulations have an average diameter of 195 µm and a depth of 106 µm. The margin is entire. The apex lacks a prominent appendage. The base is acute and truncate, with a mucro. The palisade seed coat is 103 µm thick.

Genus ***Smeathmannia*** Sol. ex R.Br.
Figs 1E, 6E–L

Seed description

Seeds compressed, 4.6–5.2 mm long, 3.0–3.7 mm wide and 1.6–1.8 mm thick, oblong. The surface is reticulate foveolate, with an average of 9.50 reticulations per mm^2. The reticulations have an average diameter of 236 µm and a depth of 121 µm. The margin is entire. The apex lacks prominent appendages. The base is obtuse, truncate, and has a mucro. The palisade seed coat is on average 155 µm thick.

Remark

The genus is represented by 7 species, 2 are studied here.

Smeathmannia laevigata Sol. ex R.Br.
Fig. 6E–H

Material examined

SENEGAL-GAMBIA • Sénégambie; 1837; *Heudelot 655*; P [P04772782]!.

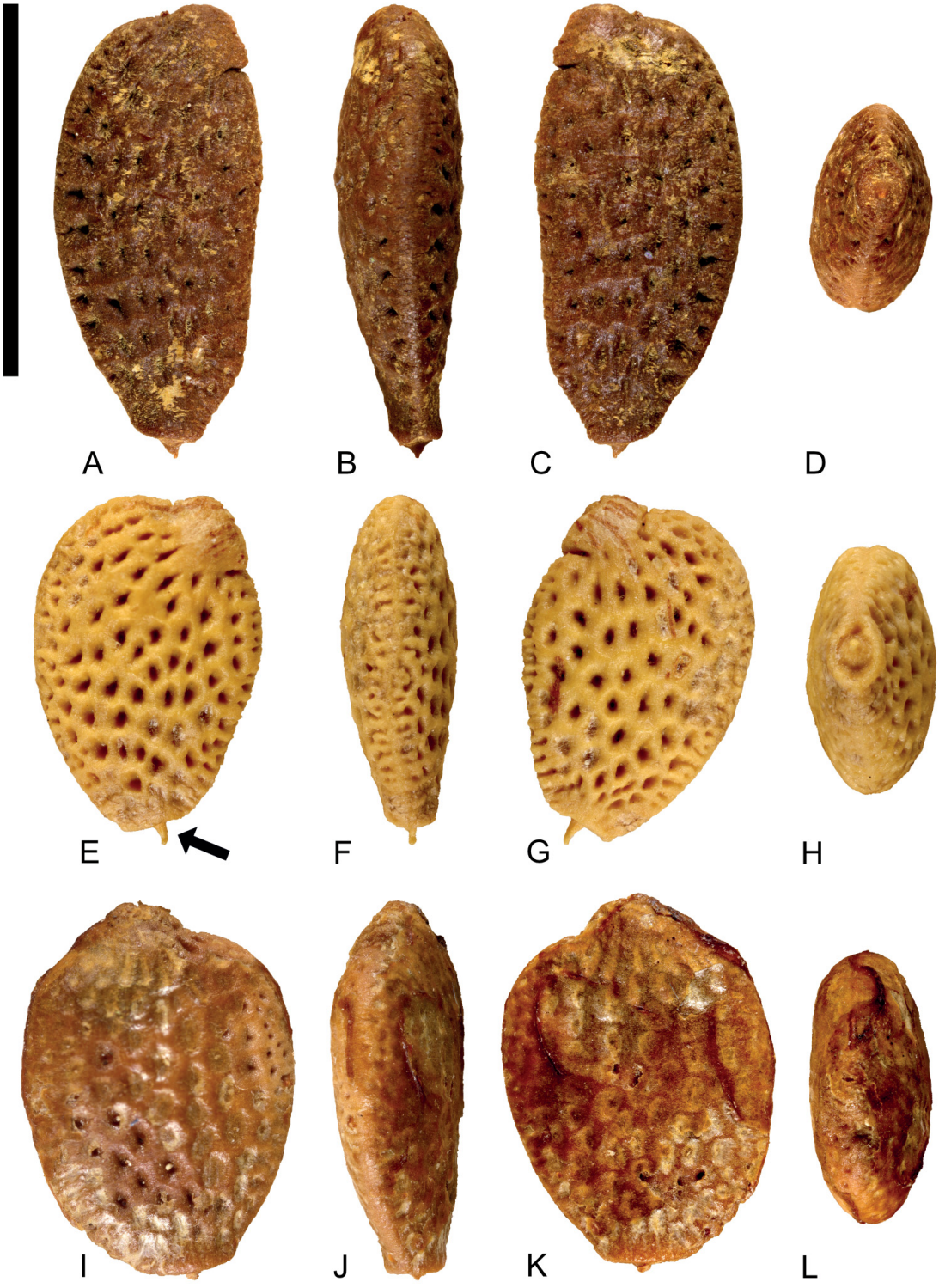

Fig. 6. Seeds of the genera *Paropsiopsis* Engl. and *Smeathmannia* R.Br. **A–D**. *Paropsiopsis decandra* (Baill.) Sleumer (*T.J. Klaine 194*; P04772112). **E–H**. *Smeathmannia laevigata* Sol. ex R.Br. (*Heudelot 655*; P04772782). **I–L**. *Smeathmannia pubescens* Sol. ex R.Br. (*A.J.B. Chevalier 17306*; P04772722). **A, E, I**. Face view. **B, F, J**. Side view. **C, G, K**. Second face view. **D, H, L**. Basal view. Scale bar = 5 mm. Arrow: mucro.

Seed description

Seeds compressed, 4.7 mm long, 3.1 mm wide, and 1.6 mm thick, curved oblong. The reticulate-foveolate surface is yellow-brown, with 7.62 reticulations per mm^2. The reticulations have an average diameter of 245 µm and a depth of 108 µm. The margin is entire with a lateral fold. The reticulations bordering the margin are open laterally. The apex lacks prominent appendages. The base is obtuse and truncate, with a mucro. The palisade seed coat is 156 µm thick.

Smeathmannia pubescens Sol. ex R.Br.
Figs 1E, 6I–L

Material examined

IVORY COAST • Bingerville; 14–18 Dec. 1906; *A.J.B. Chevalier 17306*; P [P04772722]!.

Seed description

Seeds compressed, 5.1 mm long, 3.6 mm wide, and 1.7 mm thick, oblong. The reticulate-foveolate surface is light brown, with 8.50 reticulations per mm^2. The reticulations have an average diameter of 231 µm and a depth of 135 µm. The margin is entire. The apex lacks prominent appendages. The base is obtuse and truncate, with a mucro. The palisade seed coat is 154 µm thick.

Discussion

Position of *Androsiphonia*

The seed morphology in the genus *Androsiphonia* differs from the other genera of the tribe Paropsieae and is also very distinct among all other seeds of Passifloroideae. As the only non-compressed seed, it is completely smooth, without reticulation, and has a wide oblong shape, almost circular. Its surface is covered with a hairy tegument that is absent in all other seeds of the family. The appearance of the apex is very distinctive: it is recessed, and the rest of the seed folds over it. The seed coat structure is also completely different. While all other genera have seeds with a palisade seed coat, *Androsiphonia* is covered with a single layer of isodiametric cells. *Androsiphonia* seems to be the only genus in Passifloroideae that has lost the palisade structure. Even though its seed does not resemble a Passifloroideae seed, the genus *Androsiphonia* is confidently placed within the Passifloroideae in phylogenies and studied floras (Stapff 1904; Feuillet & MacDougal 2007; Tokuoka 2012). Schmelzer & Gurib-Fakim (2008) described the seed of *Androsiphonia* as "Seed with pitted wall, surrounded by pulpy aril". This succinct description was not supported by any illustration. There seems to be no misidentification in the herbarium of Paris (see Supp. file 1), which includes most of the vegetative characters we expected to find. The leaves have a pair of glands in the basal part, are broad and toothed with six to eight pairs of secondary veins (Hutchinson & Dalziel 1952), and the fruit is characteristic of Passifloroideae (Supp. file 1). The studied plates are also very consistent with the collection of plates associated with this genus, which can be consulted via the GBIF aggregator (https://www.gbif.org/fr/occurrence/gallery?taxon_key=7313531). Until now, the seed has never been illustrated. It is therefore conceivable that *Androsiphonia* has extremely derived seeds among the Passifloraceae. Pollen of *Androsiphonia* is also very distinct compared to the other types of pollen present in the Passifloroideae (Mezzonato-Pires *et al.* 2022). Thus, *Androsiphonia* appears to be a particularly derived genus within the Passifloroideae.

Comparison of the tribes Passifloreae and Paropsieae

The tribes Passifloreae and Paropsieae are separated by molecular and vegetative morphological criteria (Feuillet & MacDougal 2007; Tokuoka 2012). The tribe Passifloreae is highly diverse and exhibits several seed morphological characters that are absent in the tribe Paropsieae (Supp. file 2). For example, seeds with sulcate or scrobiculate ornamentation are only found in *Passiflora* (Supp. file 2). Similarly, the

seed of *Passiflora microstipula* L.E.Gilbert & J.M.MacDougal is unique in having the winged margin (Gilbert & MacDougal 2000). Several species of *Passiflora* also have dentate, crested or fractioned margin, very different to what we find in the Paropsieae (Supp. file 1). The genus *Dilkea* Mast. also has seeds distinguishable from others: the seeds are large with a smooth to pustulate surface (Hermsen 2021). The tribe Paropsieae exhibits much lower morphological diversity compared to the Passifloreae. Excluding the genus *Androsiphonia*, only two forms (oblong and cordate), two types of ornamentation (reticulate-foveolate and coarsely reticulate), and two types of margin (entire and striate) are present in Paropsieae. These are also the most common morphologies in the Passifloreae (Supp. file 2). It appears that the morphological diversity of the Paropsieae is contained within the morphological space of the Passifloreae, as previously stated by Martínez (2017). Thus, it is not possible to identify a seed as belonging to the tribe Paropsieae, as its morphological equivalent will be found in Passifloreae, except for the genus *Androsiphonia*.

Comparison of the genera within the Paropsieae

Within the Paropsieae, the seeds of different genera have relatively similar morphologies but with some marked differences (Table 1). Two major morphological categories can be distinguished: one with an elongated oblong seed, entire margin, and apex without an appendage (morphotype 1), and one with a wide and flat cordate seed, coarsely reticulate ornamentation, striate margin, and obtuse base (morphotype 2). Morphotype 1 is present in the genera *Barteria*, *Paropsia*, *Paropsiopsis*, and *Smeathmannia*. Morphotype 2 is only found in *Paropsia*, representing the majority (six out of eight) of the studied species. The genera other than *Paropsia* each have only one morphology, meaning that, apart from *Paropsia*, all seeds within the same genus have the same ornamentation. Only in *Paropsia* do we find coarsely reticulate and reticulate-foveolate seeds. The genera *Barteria*, *Paropsiopsis*, and *Smeathmannia* have very similar morphologies and all bear a basal mucro (Table 1). The genera *Smeathmannia* and *Barteria* are sometimes considered synonymous (POWO 2023) and are phylogenetically sister taxa (Tokuoka 2012). The phylogeny by Tokuoka (2012) separates *Paropsia* from the rest of the Paropsieae and places *Smeathmannia* and *Barteria* together in one clade, along with *Androsiphonia*. However, the study did not include *Paropsiopsis* due to a lack of available specimens (Tokuoka 2012). *Smeathmannia* and *Barteria* are also grouped together in a clade in the morphological classification by Feuillet & MacDougal (2007). The study of the seed morphology suggests that *Paropsiopsis* is part of the *Smeathmannia-Barteria-Androsiphonia* clade and confirms the close relationship between *Smeathmannia* and *Barteria*, as, apart from ornamentation, the seeds are very similar in their shape (curved oblong), margin (entire with a fold) and base with a mucro.

No trends linking the genera to the seed size could be observed, as they are all within the same order of magnitude. The genera (except *Androsiphonia*) do not possess unique diagnostic characters, but certain species of *Paropsia* have unique combinations of characters that allow them to be separated from other genera. Since the genera of this tribe often occur in the same geographical areas (Olivier 1871; Perrier de la Bathie 1945; Hutchinson & Dalziel 1952; Sleumer 1970, Breteler 1999, 2003; de Vos & Breteler 2009), knowledge of the seed morphology can, in some cases (e.g., cordate shape), indicate the genus within the tribe.

Comparison at the species level

The genus *Barteria* exhibits particularly conserved morphology. All studied seeds of the genus are oblong, slightly curved, with reticulation of crests and an entire margin with a pronounced fold on one side, as well as very similar apex and base shapes. This is the only genus with more than two species where there are no variations in seed morphology among species. Therefore, it is impossible to distinguish species within this genus based on the seed shape.

The genus *Paropsia* is the only one that comprises two morphotypes. *Paropsia brazzaeana* and *P. grewioides* belong to morphotype 1 and exhibit reticulate foveolate and coarsely reticulate ornamentation, respectively.

All other seeds belong to morphotype 2. *Paropsia brazzaeana* displays an atypical morphology of its seed with a very thick, almost vertical margin and a hooked-horn apex. Its resemblance to other seeds of morphotype 1 is purely superficial and primarily based on its shape. On the other hand, *P. grewioides* stands out for its strong resemblance to a *Barteria* seed with its reticulate-foveolate ornamentation. They share the same characteristics of the shape, apex, base, and margin. The cordate morphotype seeds resemble each other greatly, with *P. edulis*, *P. obscura*, and *P. madagascariensis* being particularly similar and distinguishable only by their dimensions and the number of reticulations. Apart from the apex, all seeds of morphotype 2 share the same characteristics, except for *P. vareciformis* which has a highly curved cordate shape. It is also the only Asian species in the tribe, found in Malaysia (Kiew *et al.* 2018). Therefore, it is possible to distinguish two morphotypes within *Paropsia*, but it remains challenging to differentiate species based on seed morphology.

The genus *Smeathmannia* comprises only two species: *Smeathmannia laevigata* and *S. pubescens*. The seeds of both species have very similar morphology and only differ in their curvature. Due to the limited number of samples, we cannot exclude that this difference can be due to intra-specific variation.

Paleobotanical implications

The genus *Passifloroidesperma* contains fossil seeds that can only be confidently identified at the sub-family level (Martínez 2017). There are three extant tribes: Jongkindieae is at the base of the sub-family and is a sister group of both Passifloreae + Paropsieae (Breteler *et al.* 2022). The tribe Jongkindieae has seeds very distinct from those of *Passifloroidesperma*. The seed surface of Jongkindieae is tuberculate and the seed wall has a corrugated testa (Breteler *et al.* 2022). *Passifloroidesperma* is characterized by a seed surface foveolate, coarsely foveolate, reticulate-foveolate or transversally grooved, and the seed coat made of prismatic palisade cells (Martínez 2017; Hermsen 2021). These characteristics, although very different from Jongkindieae, are found in the Passifloreae and Paropsieae as shown in this study. Thus, *Passifloroidesperma* should be placed at the node that includes Passifloreae and Paropsieae and excludes Jongkindieae.

Fossil seeds with the morphological characteristics of the Paropsieae should be placed in *Passifloroidesperma* as their definitive attribution to an existing tribe is impossible based solely on their morphology. On the contrary, fossil seeds possessing characters such as sulcate or scrobiculate ornamentation and winged, dentate, crested or fractioned margin should be at least placed in the Passifloreae. Within Passifloreae, some combinations of characters allow fossils to be placed at the genus or subgenus level (Hermsen 2021, 2023), but the lack of knowledge of some genera (e.g., *Adenia*, *Basananthe* Peyr, *Crossostemma* Planch. ex. Benth., *Efulensia* C.H.Wright, *Mitostemma* Mast. and *Schlechterina* Harms, POWO 2023) remains an unresolved obstacle to a better taxonomic accuracy in this tribe.

Conclusion

This study has documented several seed morphologies in the tribe Paropsieae, thereby filling a gap in the taxonomic knowledge of the subfamily Passifloroideae. We have found that the separation between Passifloreae and Paropsieae is challenging to accomplish based solely on the seed morphology because the morphological space occupied by seeds of the Passifloreae includes the less diversified morphospace occupied by the Paropsieae. Only the seed of the genus *Androsiphonia* is distinctive enough to be assigned to the Paropsieae. Therefore, in certain cases, it is possible to assign a fossil seed to the tribe Passifloreae or a genus rather than to just the subfamily. At the level of the tribe Paropsieae, it is practically impossible to differentiate between the genera *Paropsiopsis* and *Smeathmannia* based on seed characteristics. Within the genus *Barteria*, it is impossible to distinguish between different species based on seeds. *Paropsia* is the only species-rich genus where it is possible to identify particular morphotypes and potentially identify a species based on the seed morphology. The genus *Androsiphonia* is particularly atypical, and its seeds are very distinct from the others in the tribe.

As a perspective, it should be noted that the vast majority of Passifloreae seeds come from the study of the genus *Passiflora*, while the other genera (e.g., *Adenia*, *Basananthe*, *Crossostemma*, *Efulensia*, *Mitostemma* and *Schlechterina*; POWO 2023) which have an African or African-Asian distribution are poorly documented. The absence of a detailed phylogeny of the tribe is also a limitation to our study. It has been impossible to link the different morphotypes to the evolutionary history of the group and determine the plesiomorphic state of seed morphology in the Paropsieae. While it can be assumed that the oblong seed with an entire margin found in Passifloreae represents the plesiomorphic condition, a complete phylogenetic study of Paropsieae is needed to draw definitive conclusions.

Declaration of competing interest

The authors declared that they have no conflicts of interest to this work.

Acknowledgments

We would like to thank Germinal Rouhan for granting us access to the Passifloraceae collections at the Paris Herbarium, as well as Myriam Gaudeul for allowing us to collect the seeds for this study. We also extend our gratitude to Vincent Rommevaux for preparing the thin sections of the seeds and Olivier Bethoux for providing the camera and camera lens. We would also like to thank the reviewers, Elizabeth Hermsen and Steven Manchester, for their great improvements to the article, and the editor, Marie-Béatrice Forel. This study benefited from the Hirox RH-2000 equipment funded by the DIM PAMIR (MIRCoV project).

References

Angiosperm Phylogeny Group 1998. An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden* 85 (4): 531–53. https://doi.org/10.2307/2992015

Angiosperm Phylogeny Group 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* 141 (4): 399–436. https://doi.org/10.1046/j.1095-8339.2003.t01-1-00158.x

Angiosperm Phylogeny Group 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161 (2): 105–121. https://doi.org/10.1111/j.1095-8339.2009.00996.x

Angiosperm Phylogeny Group 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181 (1): 1–20. https://doi.org/10.1111/boj.12385

Benedict J.C. 2015. A new technique to prepare hard fruits and seeds for anatomical studies. *Applications in Plant Sciences* 3 (10): Art. 1500075. https://doi.org/10.3732/apps.1500075

Bonilla Morales M.M., Aguirre Morales A.C. & Agudelo Varela O.M. 2015. Morfología de Passiflora: una guía para la descripción de sus especies. *Revista de Investigación Agraria y Ambiental* 6: 91–109. https://doi.org/10.22490/21456453.1266

Breteler F.J. 1999. *Barteria* Hook f. (Passifloraceae) revised. *Adansonia* 21 (2): 307–318.

Breteler F.J. 2003. Novitates Gabonenses 48. A new species of *Paropsia* (Passifloraceae) from Gabon. *Adansonia* 25 (2): 247–249.

Breteler F.J., Breman F.C., Lei D. & Bakker F.T. 2022. Wrong flowers? The evolutionary puzzle of *Jongkindia* (Passifloraceae s.l.), a new monotypic genus and tribe from Liberia, West Africa. *Webbia* 77: 229–246. https://doi.org/10.36253/jopt-13470

D'Apolito C., Jaramillo C. & Harrington G. 2021. Miocene palynology of the Solimões Formation (Well 1-AS-105-AM), western Brazilian Amazonia. *Smithsonian Contributions to Paleobiology* 105: 1–134. https://doi.org/10.5479/si.16803493

de Vos J. & Breteler F.J. 2009. A revision of the African genera *Paropsiopsis* and *Smeathmannia* (Passifloraceae – Paropsieae), including a new species of *Paropsiopsis* from Cameroon. *Edinburgh Journal of Botany* 66 (1): 27–49. https://doi.org/10.1017/S0960428609005174

de Wilde W.J.J.O. 1971. The systematic position of tribe Paropsieae, in particular the genus *Ancistrothyrsus*, and a key to the genera of Passifloraceae. *Blumea: Biodiversity, Evolution and Biogeography of Plants* 19 (1): 99–104.

de Wilde W.J.J.O. 1972. Passifloraceae. *Flora Malesiana – Series 1, Spermatophyta 7*: 405–434.

Espinoza T.E.B., Jørgensen P.M. & MacDougal J.M. 2018. A taxonomic revision of *Passiflora* sect. *Xerogona* (Passifloraceae) using principal component analysis. *Annals of the Missouri Botanical Garden* 103: 258–313. https://doi.org/10.3417/2017055

Feuillet C. 2020. *Ancistrothyrsus scopae* (Passifloraceae), a new species from Amazonian Brazil and Guyana, with keys to the genus and species. *Phytotaxa* 438 (3): 207–212. https://doi.org/10.11646/phytotaxa.438.3.5

Feuillet C. & MacDougal J.M. 2007. Passifloraceae. *In*: Kubitzki K. (ed.) *The Families and Genera of Vascular Plants, Vol. 9, Flowering Plants. Eudicots*: 270–281. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-32219-1_35

Gilbert L.E. & MacDougal J.M. 2000. *Passiflora microstipula*, a new species of Passifloraceae from Southeast Mexico. *Lundellia* 3: 1–5. https://doi.org/10.25224/1097-993X-3.1.1

Hermsen E. 2021. Review of the fossil record of *Passiflora*, with a description of new seeds from the Pliocene Gray Fossil Site, Tennessee, USA. *International Journal of Plant Sciences* 182 (6): 533–550. https://doi.org/10.1086/714282

Hermsen E. 2023. Pliocene seeds of *Passiflora* subgenus *Decaloba* (Gray Fossil Site, Tennessee) and the impact of the fossil record on understanding the diversification and biogeography of *Passiflora*. *American Journal of Botany* 110 (3): e16137. https://doi.org/10.1002/ajb2.16137

Hutchinson J. & Daziel J.M. 1952. *Flora of West tropical Africa, Vol. 1*. Crown Agents for Overseas Governments and Administrations, London.

Jørgensen P.M., Lawesson J.E. & Holm-Nielsen L.B. 1984. A guide to collecting passionflowers. *Annals of the Missouri Botanical Garden* 71: 1172–1174. https://doi.org/10.2307/2399250

Jørgensen P.M., Holm-Nielsen L.B. & Lawesson J.E. 1987. New species of *Passiflora* subg. *Plectostemma* and subg. *Tacsonia* (Passifloraceae). *Nordic Journal of Botany* 7: 127–133. https://doi.org/10.1111/j.1756-1051.1987.tb00925.x

Jørgensen P. & Vásquez R. 2009. A revision of *Passiflora* sections *Insignes* and *Inkea* (Passifloraceae). *Anales del Jardín Botánico de Madrid* 66: 35–53. https://doi.org/10.3989/ajbm.2204

Kerner A., Bouquin S., Portier R. & Vignes Lebbe R. 2021. The 8 years of existence of Xper3: State of the art and future developments of the platform. *Biodiversity Information Science and Standards* 5: e74250. https://doi.org/10.3897/biss.5.74250

Kiew R., Chung R.C.K., Saw L.G. & Soepadmo E. 2018. Flora of peninsular Malaysia. Series II: Seed plants. Volume 7. *Malayan Forest Records* 49: 1–321.

Krosnick S.E., Ford A.J. & Freudenstein J.V. 2009. Taxonomic revision of *Passiflora* subgenus *Tetrapathea* including the monotypic genera *Hollrungia* and *Tetrapathea* (Passifloraceae), and a new species of *Passiflora*. *Systematic Botany* 34 (2): 375–385. https://doi.org/10.1600/036364409788606343

Krosnick S.E., Porter-Utley K.E., MacDougal J.M., Jørgensen P.M. & McDade L.A. 2013. New insights into the evolution of *Passiflora* subgenus *Decaloba* (Passifloraceae): phylogenetic relationships and morphological synapomorphies. *Systematic Botany* 38 (3): 692–713. https://doi.org/10.1600/036364413X670359

Lozada-Pérez L. & Gutiérrez J.F.R. 2016. A new species of *Passiflora* L. (Passifloraceae) from Guerrero and Oaxaca, México. *Phytotaxa* 263 (3): 3 June 2016. https://doi.org/10.11646/phytotaxa.263.3.11

Maas P.J.M., Baas P., Christenhusz M.J.M., Clarkson J.J., Koek-Noorman J., Mennega A.M.W., Tokuoka T., Van Der Bank M., Van Der Ham R.W.J.M., Van Marle E.-J., Westra L.Y.TH. & Chase M.W. 2019. "Unknown yellow": *Pibiria*, a new genus of Passifloraceae with a mixture of features found in Passifloroideae and Turneroideae. *Botanical Journal of the Linnean Society* 189 (4): 397–407. https://doi.org/10.1093/botlinnean/boz003

MacDougal J.M. 1994. Revision of *Passiflora* Subgenus *Decaloba* Section *Pseudodysosmia* (Passifloraceae). *Systematic Botany Monographs* 41: 1–146. https://doi.org/10.2307/25027834

MacDougal J.M. 2001. Two new species of passionflower (*Passiflora*, Passifloraceae) from Southwestern Mexico. *Novon* 11 (1): 69–75. https://doi.org/10.2307/3393211

Martínez C. 2017. Passifloraceae seeds from the late Eocene of Colombia. *American Journal of Botany* 104 (12): 1857–1866. https://doi.org/10.3732/ajb.1700224

Mezzonato-Pires A.C., Mendonça C.B.F., Milward-de-Azevedo M.A. & Gonçalves-Esteves V. 2017. The taxonomic significance of seed morphology in the *Passiflora* subgenus *Astrophea* (Passifloraceae). *Acta Botanica Brasilica* 31 (1): 68–83. https://doi.org/10.1590/0102-33062016abb0414.

Mezzonato-Pires A.C., de Souza Freitas G.H.G., Mendonça C.B.F. & Gonçalves-Esteves V. 2022. The systematic value of pollen morphology in the tribe Paropsieae (Passifloraceae sensu stricto). *Review of Palaeobotany and Palynology* 299: Art. 104606. https://doi.org/10.1016/j.revpalbo.2022.104606

Morton J.F. 1987. Passion fruit. *In*: Morton J.F. (ed.) *Fruits of Warm Climates*: 320–328. Florida Flair Book, Miami, FL.

Ngumbau V., Nyange M., Dai C., Zhong Z-X., Wei N., Malombe I., Hu G.-W. & Wang Q.-F. 2017. *Adenia angulosa* (Passifloraceae), a new species from coastal forests of Kenya and Tanzania. *Phytotaxa* 313 (1): 137–142. https://doi.org/10.11646/phytotaxa.313.1.10

Olivier D. 1871. *Flora of Tropical Africa, Vol II*. L. Reeve and co., London.

Palazzesi L., Barreda V.D., Cuitiño J.I., Guler M.V., Tellería M.C. & Ventura Santos R. 2014. Fossil pollen records indicate that Patagonian desertification was not solely a consequence of Andean uplift. *Nature Communications* 5: Art. 4558. https://doi.org/10.1038/ncomms4558

Pérez-Cortéz S. 2007. *Atlas morfológico de Semillas en Especies del Género Passiflora L. Presentes en Venezuela*. Fundación Instituto Botánico de Venezuela, Caracas, Venezuela.

Pérez-Cortéz S., Tillett S. & Escala M. 2002. Estudio Morfológico de la semilla de 51 especies del género *Passiflora* L. *Acta Botánica Venezuelica* 25 (1): 67–96.

Pérez-Cortéz S., Escala M. & Tillett S. 2005. Anatomia de la cubierta seminal en ocho especies de *Passiflora* L., subgénero *Passiflora*. *Acta Botánica Venezuélica* 28: 337–348.

Peréz-Cortéz S., Escala M. & Tillett S. 2009. Morfoanatomia de la cubierta seminal en siete especies de *Passiflora* L., subgénero *Passiflora* (Passifloraceae). *Hoehnea* 36: 131–137. https://doi.org/10.1590/S2236-89062009000100007

Perrier de la Bathie H. 1945. Passifloracées. *In*: Humbert H. (ed.) *Flore de Madagascar et des Comores*. Tananarive Imprimerie officielle, Madagascar. https://doi.org/10.5962/bhl.title.6600

POWO 2023. Plants of the world online. Facilitated by the Royal Botanic Gardens, Kew. Available from https://powo.science.kew.org/ [accessed 3 May 2024].

Rasband W.S. 2016. ImageJ. US National Institutes of Health, Bethesda, MD. Available from https://imagej.nih.gov/ij/ [accessed 3 May 2024].

Schemelzer H.H. & Gurib-Fakim A. 2008. *Plant Resources of Tropical Africa 11 (1): Medicinal Plants 1*. PROTA Foundation, Wageningen, Netherlands.

Sleumer H. 1970. Le genre *Paropsia* Noronha ex Thouars (Passifloraceae). *Bulletin du Jardin botanique National de Belgique / Bulletin van de National Plantentuin van België* 40 (1): 49–75. https://doi.org/10.2307/3667544

Stapff O. 1904. Contribution to the flora of Liberia. *Botanical Journal of the Linnean Society* 61: 79–115. https://doi.org/10.1111/j.1095-8339.1905.tb00826.x

Stevens P.F. 2001 onwards. Angiosperm Phylogeny Website. Ver. 14, July 2017. Available from http://www.mobot.org/MOBOT/research/APweb/ [accessed 3 May 2024].

Tokuoka T. 2012. Molecular phylogenetic analysis of Passifloraceae sensu lato (Malpighiales) based on plastid and nuclear DNA sequences. *Journal of Plant Research* 125: 489–497. https://doi.org/10.1007/s10265-011-0472-4

Ulmer T. & MacDougal J.M. 2004. *Passiflora: Passionflowers of the World*. Timber Press, Portland, USA

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

Vanderplank J. & Ochoa J. 2020. *Passiflora insoliti*. *Curtis's Botanical Magazine* 37 (1): 131–138. https://doi.org/10.1111/curt.12325

Vanderplank J. & Zappi D. 2011. *Passiflora cristalina*, a striking new species of *Passiflora* (Passifloraceae) from Mato Grosso, Brazil. *Kew Bulletin* 66: 149–153. https://doi.org/10.1007/s12225-011-9255-2

Manuscript received: 21 September 2023
Manuscript accepted: 4 January 2024
Published on: 25 June 2024
Topic editor: Marie-Béatrice Forel
Desk editor: Radka Rosenbaumová

Printed versions of all papers are deposited in the libraries of four of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France; Meise Botanic Garden, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium. The other members of the consortium are: Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.

Supplementary files

Supp. file 1. Plates of *Androsiphonia adenostegia* Stapf used in this study.
https://doi.org/10.5852/ejt.2024.943.2583.11757

Supp. file 2. Database of Passifloraceae seeds extracted from Xper3.
https://doi.org/10.5852/ejt.2024.943.2583.11759