Otto Warburg and His Contributions to the Screw Pine Family (Pandanaceae)

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Abstract: Otto Warburg (1859–1938) had a great interest in tropical botany. He travelled in South-East Asia and the South Pacific between 1885 and 1889 and brought back a considerable collection of plant specimens from this expedition later donated to the Royal Botanical Museum in Berlin. Warburg published the first comprehensive monograph on the family *Pandanaceae* in 1900 in the third issue of *Das Pflanzenreich* established and edited by Adolf Engler (1844–1930). The aim of this article is to clarify the taxonomy, nomenclature and typification of Warburg’s contributions to the *Pandanaceae*. Considerable parts of Warburg’s original material was destroyed in Berlin during World War II but duplicates survived, shared by Engler and Warburg with Ugolino Martelli (1860–1934). Martelli was an expert on the family and he assembled a precious herbarium of *Pandanaceae* that was later donated to the Museo di Storia Naturale dell’Università degli Studi di Firenze. Warburg published 86 new names in *Pandanaceae* between 1898 and 1909 (five new sections, 69 new species, five new varieties, two new combinations and five replacement names). A complete review of the material extant in B and FI led to the conclusion that 38 names needed a nomenclatural act: 34 lectotypes, three neotypes and one epitype are designated here. Twenty new synonyms are also proposed. One *Freycinetia* name and six *Pandanus* names are considered as *incertae sedis*. A total of 21 names published by Warburg are accepted: 11 in *Freycinetia* and ten in *Pandanus*. In addition, four names published in *Pandanus* by Warburg serve as the basionyms of accepted names in the genus *Benstonea*.

Key words: *Benstonea*, epitype, *Freycinetia*, lectotype, neotype, new synonym, nomenclature, Otto Warburg, *Pandanaceae*, *Pandanus*, screw pine, taxonomy, typification, Ugolino Martelli

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Introduction

Otto Warburg (1859–1938) was born on 20 July 1859 in Hamburg (Germany). He studied Natural Sciences and Philosophy at the Universities of Bonn, Berlin and finally Strasbourg, where he completed in 1883 a PhD under the guidance of the renowned Heinrich Anton de Bary (1831–1888) with a wood morphological dissertation “Über Bau und Entwicklung des Holzes von *Caulopteris heterophyllus*” (Warburg 1883). In the years 1884 to 1885, postdoctoral studies in München and Tübingen followed where Warburg pursued chemical and plant physiological issues with Adolph von Baeyer (1835–1882) and Wilhelm Pfeffer (1845–1920) respectively (Leimkugel 2005). Influenced by Adolf Engler’s (1844–1930) research on plant geography and enthusiastic about the theories and work of the British naturalists Charles Darwin (1809–1882) and Alfred Russel Wallace (1823–1913), Warburg began to focus more and more on issues of plant evolution and plant geography. He was specially fascinated by Wallace’s book *Island Life* (Wallace 1880) and it was the theory of the so-called Wallace’s line, a hypothetical line that separates the Malay archipelago into two distinct parts with different – Indian and eastern Australian – animal and plant origins (Wallace 1880), which inspired him on a four-year research trip to South-East Asia. Otto Warburg came from an extremely wealthy family, was financially independent by inheritance and...
financed the trip from his own assets (Leimkugel 2005). He started in Bombay in December 1885, visited Peninsular Malaysia, Java, Singapore, China, Korea, Japan, the Philippines, the Moluccas islands, German New Guinea and the Bismarck archipelago (now the northern region of Papua New Guinea), and ended up in Australia in June 1889 (see Warburg 1900a). From this four-year expedition, Warburg brought back a collection of more than 25 000 plant specimens (c. 22 000 phanerogams, mosses and fungi and several thousands of wood, fruit and seed samples as well as material conserved in alcohol) later donated to the Royal Botanical Museum in Berlin (Urban 1916).

Warburg settled down in Berlin and worked intensively on his collections, and in a paper on phytogeographic considerations and the rejection of the theory of Wallace’s line he included a first, annotated list of the spermatophytes that he gathered in South-East Asia (Warburg 1891). Some years later, he published the first volume of Monsunia: Beiträge zur Kenntniss der Vegetation des süd- und ostasiatischen Monsungebietes (Warburg 1900a) summarizing part of the scientific results of his four-year expedition and including fungi, algae, bryophytes, ferns and lycophytes, conifers, Cycadaceae and Gnetaceae.

As he was now well known as an expert in tropical flora, Warburg was invited to take over the treatments for several plant families in the handbook Die natürlichen Pflanzenfamilien established and edited by Adolf Engler (with Karl Anton Eugen Prantl [1849–1925]) until his early death, and in the year 1900 he published his monograph of the Pandanaceae in Das Pflanzenreich (Warburg 1900b). Das Pflanzenreich was established by Engler to furnish a full and comparative account of all known species by plant families (Anonymous 1902). Warburg’s interest in the screw pine family started in 1898 when he treated the family in Franz Reinecke’s (1866–unknown) Die Flora der Samoa-Inseln including first descriptions of new species in Freycinetia Gaudich. and Pandanus Parkinson (Warburg 1898). By 1909, Warburg had named 79 taxa of Pandanaceae, most of those described in Das Pflanzenreich (62 spp., Warburg 1900b), the remaining in treatments for Africa (three spp., Warburg 1904a; Volkens 1909a, 1909b), the Philippines (one sp., Warburg 1904b), the German colonies in the Pacific area (four spp., Warburg 1905), and New Caledonia (five spp., Warburg 1906). Warburg’s (1900b) Pandanaceae treatment is the first comprehensive monograph on the family. In this work, he published 19 new names in Freycinetia (two new sections and 17 new species) and introduced 50 new names in Pandanus (three new sections, 35 new species, five new varieties, two new combinations and five replacement names, including several validations of pre-Linnaean or previously not validly published names). The five new sections were: Freycinetia sect. Oligostigma Warb., F. sect. Pleiostigma Warb., Pandanus sect. Fouliyoya Warb., P. sect. Sussea Warb. and P. sect. Vinsonia Warb.

At the time of Warburg’s (1900b) monograph, about 180 Pandanaceae species were known (Stone 1976), among which 79 (c. 43%) were newly named by Warburg. Today the family includes c. 750 species (Pandanaceae Project 2020). Warburg (1900b) was the first to present a coherent infrageneric classification at sectional level for both Freycinetia and Pandanus including identification keys at this taxonomic level. This infrageneric classification started to receive more attention in the mid-20th century and was subsequently improved and developed by several taxonomists, e.g. St. John (1960) and Stone (1974). The relatively low number of accepted Pandanaceae names introduced by Warburg (24 out of 79; 30%) is certainly because he “apparently seldom if ever used specimens from other herbaria on loan for study” and this was “a major drawback in his work” (Stone 1973: 267). Most of the material on which Warburg based his studies originated from German New Guinea, from which he had access, in addition to his own gatherings, to further material in the Berlin Botanical Museum collected by botanists who joined the expeditions to this area, e.g. Udo Max Hollrung (1858–1937) and Carl Adolf Georg Lauterbach (1864–1937). He also extensively used available literature in validating several Pandanus names. Examples can be found in the validation by Warburg of the numerous not validly published names of Gaudichaud-Beaupré (1841) in his Botanical Atlas of the Voyage autour du monde exécuté pendant les années 1836 et 1837 sur la corvette la Bonite commandée par M. Vaillant. Warburg was aware only of Gaudichaud’s illustrations and overlooked the Gaudichaud collections kept mainly in P (see, e.g., under P. delessertii Warb.).

Warburg’s interest shifted gradually to plants of economic importance, in particular those of relevance for the colonies of the Deutsches Reich and he acted for many years as a private lecturer for tropical agriculture at the “Seminar für Orientalische Sprachen” [Seminar for Oriental Languages] at the Royal Friedrich-Wilhelms-Universität and as a member of the Kolonialwirtschaftliches Komitee [Colonial Economic Committee] in Berlin. He wrote a highly regarded monograph on the nutmeg family, i.e. the Myristicaceae (Warburg 1897), for which he was awarded the “Prix de Candolle” in Geneva. Warburg founded, and edited for 25 years, Der Tropenpflanzer, a journal dedicated to tropical agriculture; he published his three-volume standard work Die Pflanzenwelt (Warburg 1913–1922) and was increasingly engaged in the World Zionist Congress acting as its president between 1911 and 1920 (Leimkugel 2005; Reichert 1938). Otto Warburg died on 10 January 1938 in Berlin.

In the early 20th century, Ugolino Martelli (1860–1934), an Italian botanist, became interested in the family Pandanaceae. Martelli was the student of the notable Italian naturalist Odoardo Beccari (1843–1920), who introduced him to the systematics of Arecaceae and Pandanaceae (Moggi 2009). Beccari travelled extensively in South-East Asia (Beccari 1877–1889, 1902) and be-
queathed his impressive Herbarium palmarum to Martelli in 1920 (Cucuini & Nepi 1999). Martelli also assembled a precious herbarium of Pandanaceae that was later donated along with Beccari’s Herbarium palmarum to the Museo di Storia Naturale dell’Università degli Studi di Firenze (Italy) following his will (Moggi 2009). Martelli wrote his first observations on the genus Pandanus in 1902 in the Bullettino della Società Botanica Italiana (Martelli 1902; see Moggi & al. 2009) and described his first new Pandanus species in the same journal (Martelli 1904). Later, he published most of his new taxa in Webbia, a journal that he founded in 1905 on the occasion of the 50th anniversary of the death of Philip Barker Webb (1793–1854) (Martelli 1905, 1907, 1910a, 1910b). Between 1904 and 1951 Martelli named 277 Pandanaceae taxa, including the posthumously published treatment on Pandanaceae from Madagascar, completed by Rodolfo E. G. Pichi-Sermolli (1912–2005) (Martelli & Pichi-Sermolli 1951), namely 54 Freycinetia taxa and 233 of Pandanus (including 30 varieties and nine forms) (Pandanaceae project 2020). Martelli corresponded with Engler and Warburg in Berlin (Unpublished sources: Corrispondenza di U. Martelli 29, 44). Reading this correspondence, one understands how keen Martelli was to receive Pandanaceae duplicates from the Museum in Berlin after the publication of Warburg’s monograph. Even if the material in the Botanical Museum in Berlin was sometimes very limited, Warburg and Engler were very generous in sending many duplicates to Martelli in Firenze (Fig. 1). While much of Warburg’s original material was destroyed in Berlin during World War II, duplicates survived thanks to the material shared with Martelli by Engler and Warburg.

The aim of this article is to clarify the taxonomy, nomenclature and typification of Warburg’s contribution to the Pandanaceae.

Material and methods

Original material of Warburg’s names was studied in B, FI, FI-B (Herbarium Beccarianum-Malesia) and FI-W (Her-
barium Webb) as well as in BM, G, K, L and P (herbarium codes follow the standard abbreviations of Index herbariorum; Thiers 2008+). The taxonomy of Warburg’s names in the present study is based on the fundamental work of Benjamin Clemens Masterman Stone (1933–1994), who was the authority on the family for several decades (Stone 1967, 1969a, 1969b, 1970a, 1970b, 1970c, 1971, 1972, 1973, 1976, 1978, 1982, 1983, 1992), and more recent work by the first author and colleagues (e.g. Beentje & Callmander 2014, in press; Callmander & Buerki 2013; Callmander & al. 2012, 2014; Keim 2009, 2012). For each of Warburg’s names listed, the currently accepted name is indicated in boldface. New synonyms proposed in the present study, as well as designations of lectotype, neotype or epitype, result from ongoing taxonomic revisions, mostly in Madagascar and New Caledonia, or were never published by Stone. Names involved in these taxonomic revisions, including names published by authors other than Warburg, are therefore provided with bibliographic references and type citations. They are associated with the following names: Freycinetia coriacea Warb., Freycinetia australiensis Warb., Freycinetia marantifolia Warb., Freycinetia marginata Blume.

Most of the original herbarium material cited was digitized and is available online, e.g. in the virtual herbaria of B (Curators Herbarium B 2000+), G (CHG 2020), FI (Parlatore database 2020+) and P (Sonnerat 2020). Specimens of Pandanaceae often necessarily consist of multiple preparations, e.g. one or more herbarium sheets plus material in a carpological, spirit or wood collection. Such a specimen, even though its parts may have separate barcodes, is nevertheless a single specimen and can serve as a nomenclatural type (Turland & al. 2018: Art. 8.3). In the present study, such specimens are cited as, e.g., “B barcodes B 10 0367708! + B 10 0367708 excluding leaf! + B 81 0000574 spirit! [3-part specimen]”. Carpological, spirit and wood collections are indicated by “carpol.”, “wood” and “spirit”.

Results

Among the 81 Pandanaceae names linked to Warburg, 38 names needed a nomenclatural act: 34 lectotypes, three neotypes and one epitype are designated here. Twenty new synonyms are also proposed. One Freycinetia name and six Pandanus names are considered as incertae sedis. A total of 21 names published by Warburg are accepted: 11 in Freycinetia and ten in Pandanus. In addition, four names published in Pandanus by Warburg serve as the basionyms of accepted names in the genus Benstonea Callm. & Buerki (Callmander & al. 2012).

In his Botanical Atlas of the Voyage autour du monde, Gaudichaud-Beaupré (1841) introduced a number of new generic and species names that were validated by an illustration with analysis. A monotypic genus and species can be validated simultaneously by a single illustration with analysis (Turland & al. 2018: Art. 38.5–38.9), e.g. Roussinia Gaudich. and R. indica Gaudich. on t. 21, fig. 1–4 of the Atlas. However, the new genus must be monotypic. On other plates in the Atlas, where Gaudichaud introduced a new generic name and illustrated more than one species in that genus, none of the names at either rank was validly published. These generic names are “Barrotia” (t. 13), “Dorystigma” (t. 13, 31), “Eydlouxia” (t. 18), “Fisquetia” (t. 4, 5), “Fouliloydia” (t. 26), “Sesseia” (t. 24, 25, 38) and “Vinsonia” (t. 17, 23, 31). For the same reason, these generic and species names were not validated by the later-published accompanying text (Alleizette 1866: 113–134). Kurz (1869) and Balfour (1878) unsuccessfully attempted new combinations in Pandanus based on some of Gaudichaud’s not validly published species names. However, when Warburg (1900b) attempted such new combinations, or adopted those of Kurz and Balfour, he provided Latin diagnoses, thereby validly publishing names of new species.

Taxonomy and nomenclature

Genus Freycinetia

Freycinetia australiensis Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 32. 1900. – Holotype: Australia, Daintree river, 1886, Pentzke s.n. (B barcode B 10 0367714!: isotypes: MEL barcodes 2270801, 2270802, 2270803 [images!).

= Freycinetia marginata Blume

Remarks — A single specimen of original material collected by Theodor Pentzke is extant in B. This specimen is considered here as the holotype. Three duplicates are extant in MEL, but none in FI.

According to Stone (1982), Freycinetia australiensis is a synonym of the New Guinean F. marginata.


= Freycinetia marantifolia Hemsl.

Remarks — A single specimen of original material is extant in B. This specimen is considered here as the holotype. A photograph of the holotype and a fragment packet containing part of an infructescence are extant in FI.

The holotype has a determinavit from Stone (18 Jul 1975) as Freycinetia marantifolia. This synonymy is accepted here. Many forms of F. marantifolia have been described as new species.

Freycinetia candeliformis Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 39. 1900. – Holotype: Indonesia, Sulawesi,
Minahassa, s.d., Warburg s.n. (B barcode B 10 0367712; isotype: FI barcode FI017791!).

= Freycinetia celebica Solms

Remarks — A single specimen of original material collected by Warburg is extant in B. This specimen is considered here as the holotype. A fragment packet containing fragments of infructescence is extant in FI. Martelli’s handwriting on the packet indicates that it was sent by Warburg to Martelli.

Freycinetia candeliformis is considered as a synonym of F. celebica (Stone 1969a).

Freycinetia coriacea Warb. in Bot. Jahrb. Syst. 39: 17. 1906, syn. nov. – Holotype: New Caledonia, “auf den Bergen bei Oubachte”, 700 m, 20 Dec 1902, Schlechter 15529 (B barcode B 10 0057435; isotype: FI barcode FI015248!).

= Freycinetia cylindracea Solms in Linnaea 42: 97. 1878. syn. nov. – Lectotype (designated here): New Caledonia, Wagap, Vieillard 3268 (P barcode P00271416; isoleotypes: FI barcode FI015249!, P barcode P00271417!).


= Freycinetia subulata Huynh in Candollea 59: 177. 2004, syn. nov. – Holotype: New Caledonia, hauteurs de Yaté, 300 m, 8 Feb 1981, MacKee 38714 (NOU barcode NOU006026!; isotypes: P barcode P00262880!, PH barcode PH00087121!).

Remarks — A single specimen of original material of Freycinetia coriacea is extant in B. This specimen is considered here as the holotype. A duplicate in FI consists of a leaf, a packet containing a fragment of an infructescence and a photograph of the holotype in B.

Freycinetia spectabilis is a distinctive species in New Caledonia characterized by its coriaceous leaves with straight, terminal infructescences on thick peduncles (Fig. 2A). This species shows variations in leaf width and size of syncarps, which is common in Freycinetia. No significant morphological character was found to keep F. coriacea, F. cylindracea and F. subulata distinct, and they are placed here in synonymy with F. spectabilis.
Freycinetia cyldractea and F. spectabilis described by Hermann Graf zu Solms-Laubach (1842–1915) based on material collected by Eugène Vieillard (1819–1896) need lectotypification on specimens now deposited in P. The most complete specimens, i.e. Vieillard 3268 and Vieillard 1390, are designated as lectotypes for F. cylindracea and F. spectabilis respectively.

Freycinetia ferox Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 33. 1900. – Holotype: Philippines, “Mittel Luzon”, s.d., Warburg s.n. (B barcodes B 10 0367707! + B 10 0367708 excluding leaf! + B 81 0000574 spirit! [3-part specimen]; isotype: FI barcode FI015206!).


Remarks — Original material of Freycinetia ferox has been located in B. This material consists of bracts and staminate inflorescences mounted on two sheets and in the spirit collection. The leaf mounted on B 10 0367708 belongs to the genus Pandanus and has to be excluded. The two sheets and spirit material comprise a single specimen and are considered here as the holotype.

Stone (18 Jul 1975) annotated B 10 0367708 with “Warburg’s description of the leaf is to be ignored”. Earlier, Stone (1969b) considered Freycinetia ferox as having leaves gradually attenuate to the apex, referring to Warburg’s description, which “is very different from the appearance of F. minahassae, whose leaves are quite abruptly acute-acuminate” (Stone 1969b: 605) and he did not know “what F. ferox is”. After visiting B in 1975 and studying the type specimen, Stone (1982) considered F. ferox as having very abruptly caudate leaf apices and considered F. maxima Merr., also from Luzon, as a synonym. Freycinetia maxima was described by Merrill based on two syntypes: Forestry Bureau [leg. Curran] 10754 and Forestry Bureau [leg. Curran] 12381, both destroyed in PNH. Forestry Bureau [leg. Curran] 10754 has been found in B and the US duplicate is designated here as the lectotype.

Keim (2012) considered a much larger species concept with both Freycinetia ferox and F. maxima as synonyms of F. marginata. The latter species would have the largest distribution in the genus from northern Queensland to Borneo. We are not accepting this species concept here.


= Freycinetia beccarii Solms

Remarks — Freycinetia globiceps was described based on two gatherings: Lauterbach 2119 and Hollrung 857, both cited in the protologue and therefore syntypes. A single specimen of both gatherings is present in B. The most complete specimen is that of Lauterbach, which is therefore designated here as the lectotype. Both type gatherings have duplicates in FI.

Freycinetia globiceps is considered as a synonym of F. beccarii following Keim (2009).


Remarks — Warburg provided a replacement name for Freycinetia beccarii Hemsl., which is a later homonym of F. beccarii Solms.


= Freycinetia scandens Gaudich.

Remarks — Freycinetia hollrungii was described based on three gatherings: Hollrung 218, Lauterbach 1522 and Warburg 20997, all cited in the protologue and therefore syntypes. Specimens of the three gatherings are extant in B. The most complete specimen is Hollrung 218, which is therefore designated here as the lectotype. The two sheets in B comprise a single specimen, which is designated here as the lectotype. A duplicate has been located in FI.

Freycinetia hollrungii is considered as a synonym of F. scandens (Stone 1969a).

Freycinetia jagorii Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 39. 1900. – Holotype: Philippines, “Insel Samar”, 1861, Jagor s.n. (B barcodes B 10 0367702! + B 10 0367703! [2-part specimen]; isotype: FI barcode FI017742!).

Remarks — Original material of Freycinetia jagorii has been located in B. This original material is mounted
on two sheets representing a single specimen, which is considered here as the holotype. A duplicate is extant in FI.

*Freycinetia jagorii* is listed as an accepted species by Stone (1969a) but a critical taxonomic revision of *Pandanaeae* is required for the Philippines.

*Freycinetia lagenicarpa* Warb. in Schumann & Lauterbach, Fl. Schutzgeb. Südsee Nachtr.: 52. 1905. – *Lectotype (designated here)*: Papua New Guinea, Toricelli-Gebirge, 100 m, Apr 1902, Schlechter 14572 (B barcode B 10 0367701!; isotype: FI barcode FI017781!). – Synotypes: Papua New Guinea, Toricelli-Gebirge, Apr 1902, Schlechter 14571 (B barcode B 10 0367701!, FI barcode FI017780!).

**Remarks** — A single specimen of original material is present in B. This specimen is considered here as the holotype. A duplicate is extant in FI.

The holotype has a determinavit from Stone (18 Jul 1975) as *Freycinetia marantifolia*. This synonymy is accepted here.

*Freycinetia novo-caledonica* Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 37. 1900. – *Holotype*: New Caledonia, Prony, s.d., Bougier s.n. (B barcode B 10 0352289!; isotype: FI barcode FI015219 photograph!).

**Remarks** — A single specimen of original material is present in B. This specimen is considered here as the holotype. A photograph of the holotype is extant in FI.

*Freycinetia novo-guineensis* Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 34. 1900. – *Lectotype (designated here)*: Papua New Guinea, Sattelberg, s.d., Warburg 21000 (B barcode B 10 0673249 excluding leaves!; isotype: FI barcode FI017774 fragment packet!).

≡ *Freycinetia funicularis* (Savigny) Merr.

**Remarks** — As already stated by Martelli (1910c: 313), the original material of *Freycinetia novo-guineensis* is a mixed gathering. The leaves are from *F. pseudoinsignis* and the fertile material from *F. funicularis*.

We designate here the fertile material of Warburg 21000 as the lectotype.

*Freycinetia novo-guineensis* is considered as a synonym of *F. funicularis* (Stone 1969a).

*Freycinetia papuana* Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 42. 1900. – Holotype: Papua New Guinea, *sine loco*, s.d., Hollrung 218a (B barcode B 10 0673220!; isotype: FI barcode FI017770!).

≡ *Freycinetia funicularis* (Savigny) Merr.

**Remarks** — The extant material in B represents a fragment packet with Warburg’s handwriting “*Freycinetia papuana* Warb.” Despite the fact that *Hollrung 218a* is not mentioned, we do consider this material as original. This specimen is considered here as the holotype. A duplicate is extant in FI.

*Freycinetia papuana* is considered as a synonym of *F. funicularis* (Stone 1969a).

*Freycinetia pseudoinsignis* Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 33. 1900. – Holotype: Papua New Guinea, *sine loco*, s.d., Hollrung 278 (B barcode B 10 0367693!; isotype: FI barcode FI0177709!).

**Remarks** — A single specimen of original material is present in B. This specimen is considered here as the holotype. A duplicate is extant in FI.

*Freycinetia reineckei* Warb. in Bot. Jahrb. Syst. 25: 578. 1898. – *Lectotype (designated here)*: Samoa, Upolu,
Freycinetia reineckei was described based on four gatherings: Reinecke 255, 255a, 255b and 362, all cited in the protologue and therefore syntypes. Only Reinecke 255a is still extant in B, mounted on two sheets. B 10 0367684 is wrongly labelled both as 255a and 355a, the latter clearly a typographical error. The two sheets in B comprise a single specimen, which is designated here as the lectotype. Other syntypes have been found in G (Reinecke 255) and FI (Reinecke 362). A sheet is present in B (B 10 0673256) with a copy of the illustration published in Warburg (1898: t. 8, fig. B).

Remarks — A single specimen of original material is present in B (Fig. 3). This specimen is considered here as the holotype. Two duplicates are extant in FI.


Remarks — A single specimen of original material is present in B. This specimen is considered here as the holotype. A duplicate is extant in FI.


= Freycinetia storkii Seem.

Remarks — Warburg described Freycinetia samoensis based on two gatherings: Reinecke 355c and 362a, both cited in the protologue and therefore syntypes. A single specimen of original material is extant in B and bears three labels: two as 362a and one as 355c. We consider the correct collecting number to be 362a. A fragment packet in FI, which Martelli most likely received from Berlin, bears collecting number 355, but with the locality of 355c. This should be considered as a typographical error for 355c. B 10 0673226 bears the original pencil drawing published in Warburg (1898: t. 8, fig. A). A copy of this drawing is also extant on another sheet in B (B 10 0673248).

Freycinetia samoensis is considered as a synonym of F. storkii Seem. (Stone 1969a).

Freycinetia sarasinorum Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 35. 1900. – Holotype: Indonesia, Sulawesi, 10 Feb 1895, Sarasin 904 (B barcode B 10 0367689!).

Remarks — A single specimen of original material is present in B. This specimen is considered here as the holotype. No original material has been located in FI.

Freycinetia scabripes Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 41. 1900. – Holotype: Philippines, Luzon, s.d., Warburg s.n. (B barcode B 10 0673227; isotypes: FI barcode FI0176898 excluding fragment packet on upper left!, FI017690!).

Remarks — A single specimen of original material is present in B (Fig. 3). This specimen is considered here as the holotype. Two duplicates are extant in FI.

Fig. 3. Holotype of *Freycinetia scabripes* Warburg s.n. (B 10 0673227). – Image © Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin.
des Roussettes, Nov 1977, Veillon 3366 (NOU barcode NOU006027!).

Remarks — A single specimen of original material is present in B. This specimen is considered here as the holotype. A duplicate is extant in FI.

Freycinetia involuta shows no morphological differences from F. sulcata, an endemic species from New Caledonia (Fig. 2C), and is considered here as a synonym.


= Freycinetia delicata Huynh in Candollea 59: 175. 2004, syn. nov. — Holotype: New Caledonia, forêt de Thy, 22°11’S, 166°32’E, 400 m, 24 Jun 1979, McPherson 1699 (MO accession number 3229824!).

Remarks — A single specimen of original material is present in B. This specimen is considered here as the holotype. A duplicate is extant in FI.

Freycinetia delicata shows no morphological distinction from F. verruculosa, a distinctive endemic species from New Caledonia (Fig. 2D), and has to be considered as a synonym.

Freycinetia incertae sedis

Freycinetia polystigma Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 42. 1900. — Holotype: Papua New Guinea, “Golf Aird river”, 1887, Bevan s.n. (B barcode B 10 0673247!; isotypes: FI barcodes FI017711!, FI017712!).

Remarks — The original material of this name in B and FI is very fragmentary. It consists of a bract, part of a syncarp and a leaf. Based on the limited available material, it is not possible to define the taxon to which this specimen represents.

Genus Pandanus

Pandanus amboinensis Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 83. 1900. — Holotype: Indonesia, Moluccas, Ambon, 1857, de Vriese s.n. (B barcode B 10 0367675!; isotypes: L barcodes L0050446!, L0050447!, L0050448!, L0050449!).


Remarks — Stone (1992: 53) considered the holotype of Pandanus amboinensis to be deposited in L. This could have been treated as an error to be corrected to lectotype (Turland & al. 2018: Art. 9.10), but original material is still extant in B and that specimen should be considered as the holotype.

The original material of Pandanus krauelianus considered here as the holotype consists of a single specimen mounted on three sheets.

Pandanus amboinensis is a synonym of P. krauelianus (Jebb 1992; Keim 2009).


Remarks — Pandanus bakeri was published by Warburg for the misapplied name P. montanus sensu Baker (1887: 527) [non Bory 1804]. The original material was cited by Warburg as “Rev. Rowlands, Baron n. 4931”, which is the same gathering cited by Baker and which is represented by a specimen still extant in K. This specimen is considered here as the holotype, with duplicates in FI and P.

Pandanus cyaneoglaucescens was described by Martelli based on Perrier de la Bâthie 12406, also collected in the southern part of the highlands of Madagascar. Careful study of original material and recent collections have shown that these represent the same species as P. bakeri and the name is therefore considered here as a synonym.

Pandanus boninensis Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 45. 1900. — Lectotype (designated here): Japan, Bonin Islands, Warburg s.n. (FI barcode FI017168!).

Remarks — No original material is extant in B. A fragment packet consisting of several phalanges is extant in FI. This packet was sent by Warburg to Martelli in 1903. This specimen is designated here as the lectotype. An original pencil drawing is extant in B (B 10 0673234). It represents the illustration published in Warburg (1900b: 47, fig. 13A–C).

Pandanus borneensis Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 78. 1900. — Lectotype (designated here): Malaysia, Borneo, s.d., Korthals s.n. (FI barcode FI014665!).

Remarks — No original material is extant in B. A duplicate in FI consists of a fragment packet with a single
Pandanus borneensis is distributed in Peninsular Malaysia and Indonesia (Sumatra, Borneo) (Fig. 4A).

Pandanus canaranus Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 75. 1900. – Holotype: India, “Mangalore in Canara [Karnataka]”, 1858, Hohenacker 2301 (B barcode B10 0460305!; isotypes: G barcode G00368276!, FI barcode FI017176!, P barcodes P00733273!, P00733274!).

= Pandanus unipapillatus Dennst.

Remarks — A single specimen of original material is present in B. This specimen is considered here as the holotype. Duplicates are extant in G, FI and P.

Pandanus canaranus was described with doubts by Warburg. He wrote: “Ad speciem forsan pertinent Perin Kaida Taddi Rheede […] ob iconem et descriptionem mancam dubia autem planta Rheedeana remanet”, which represents the pre-Linnaean name validated as P. unipapillatus by Dennstedt (1818: 27).

A complete description of Pandanus unipapillatus accompanied with illustrations can be found in Nadaf & Zanan (2012: 35–39).

Pandanus celebicus Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 80. 1900 = Benstonea celebica (Warb.) Callm.
Callmander & al.: Otto Warburg and his contributions to the Pandanaceae

& Buerki in Candollea 67: 332. 2012. – Holotype: Indonesia, Sulawesi, Minahassa, s.d., Warburg s.n. (B barcode B 10 0279969!; isotype: FI barcode FI003942 excluding leaves!). – Epitype (designated by Callmander & al. 2014: 162): Indonesia, Sulawesi, Mt Roroka Timbu, W slope, 80 km SSE of Palu, 01°16’S, 120°18’E, c. 1050 m, 11 May 1979, Vogel 5287 (L barcode L0332713!; isoepitypes: KLU accession number KLU-36404 [2 sheets] [images!], PH barcode PH00018268!).

Remarks — The original material still extant in B consists of a single leaf. A duplicate in FI consists of two fragment packets with drupes and two small leaves that must be excluded from the original material as they do not belong to Benstonea celebica (Callmander & al. 2012: 332). A photograph of a syncarp located in B, now destroyed, is extant in FI.

The taxonomic identity of this species has been resolved and was presented in Callmander & al. (2014: 162–163), where an epitype was designated.

Pandanus dammannii Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 49. 1900. – Lectotype (designated here): Australia, Batavia river [Wenlock river], 1894, Damman s.n. (FI barcode FI017171!).

= Pandanus spiralis R. Br.

Remarks — No original material is extant in B. A fragment packet consisting of a single phalange has been located in FI and is designated here as the lectotype.

Pandanus dammannii is considered as a synonym of P. spiralis (Wilson 2011: 222).


= Pandanus eydouxia Balf. f.

Remarks — Pandanus delesserti was based on “Eydouxia ? delesserti” of Gaudichaud-Beaupré (1841), which was not validly published (see above). A single phalange originating from Mauritius [not Réunion] that served for Gaudichaud’s drawing is extant in P (P00867902 carpol.). This specimen cannot be considered as original material because Warburg clearly specified “nur aus der Abbildung im Atl. Bon. bekannt” [known only from the illustration in Atl. Bon.]. Gaudichaud’s illustration is therefore considered as the holotype. According to Boss & Guého (2003: 38), this phalange is morphologically closely related to P. eydouxia. This phalange is nevertheless clearly an immature phalange of the latter species endemic to Mauritius. No collections are known from the nearby island of Reunion and this specimen is clearly from Mauritius.

Gaudichaud’s epithet probably refers to Adolphe Delessert (1809–1869) and not to his renowned uncle Benjamin Delessert (1773–1847). Gaudichaud stayed in Calcutta in April 1837 with A. Delessert in Nathaniel Wallich’s (1786–1854) residence (Unpublished sources: Correspondance d’Adolphe Delessert). On this occasion, A. Delessert may have given some of his own botanical specimens collected in 1835 in Mauritius (Delessert 1843) to Gaudichaud, including this phalange. A few botanical collections of A. Delessert are known from the Mascarenes.

Pandanus ellipsoideus Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 81. 1900 = Benstonea ellipsoidea (Warb.) Callm. & Buerki in Candollea 67: 333. 2012. – Lectotype (designated by Stone 1978: 15): Indonesia, Sulawesi, S Celebes, Tjamba, s.d., Warburg 16151 (B barcode B 10 0279961!). – Syntypes: Indonesia, Sulawesi, S Celebes, Moros, Schlucht von Bantimurong, s.d., Warburg 16152 (B barcode B 10 0673213!; FI barcode FI014675); Indonesia, Sulawesi, S Celebes, Manipi, s.d., Warburg 16150 (B barcode B 10 0673212!). Indonesia, Sulawesi, S Celebes, W[awo] Kraeng Bergwald, s.d., Warburg 16887 (B barcode B 10 0673401!).

Remarks — Pandanus ellipsoideus was described based on four gatherings: Warburg 16150, 16151, 16152 and 16887, all cited in the protologue and therefore syntypes. One syntype of each gathering is extant in B, of which Warburg 16151 was designated as the lectotype by Stone (1978: 22). Warburg 16152 is the only original material located in FI.

Pandanus ellipsoideus is the basionym of Benstonea ellipsoidea (Callmander & al. 2012).

Pandanus engleri Warb. in Bot. Jahrb. Syst. 34: 151. 1904. – Holotype: Tanzania, west Usambara, Sakare, 1800 m, 25 Sep 1902, Engler 981 (B barcode B 10 0167990!).

= Pandanus rhabaiensis Rendle

Remarks — A single specimen of original material of Pandanus engleri is present in B. This specimen is considered here as the holotype. No duplicate has been located in FI.

Pandanus engleri is considered as a synonym of P. rhabaiensis (see Beentje & Callmander 2014).

Pandanus flagellifer Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 80. 1900. – Holotype: Singapore, Jurong, 10 Jan 1889, Ridley 92 (B barcodes B 10 0279949! + B 10 0279950! [2-part specimen]; isotypes: FI barcode FI017931!, K barcode K000697924!).

= Benstonea parva (Ridl.) Callm. & Buerki

Remarks — St. John (1963: 334) cited the type gathering as Flora of Singapore 92, but this is undoubtedly from Henry Nicholas Ridley (1855–1956) and should be cited as Ridley 92.

Pandanus flagellifer is considered as a synonym of Benstonea parva (Ridl.) Callm. & Buerki (= P. parvus
Pandanus forbesii Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 78. 1900. — Lectotype (designated here): Sumatra, lice loco, s.d., Forbes s.n. (BM!; isotype: FI barcode FI003587!).

Remarks — Original material of Pandanus forbesii is not extant in B. The first author annotated FI017300 as the lectotype (Jun 2016), but much better original material has since been located in BM. The BM material is therefore designated here as the lectotype. Other duplicates are extant in G, L and LE.

Pandanus goetzii Warb. in Bot. Jahrb. Syst. 28: 350. 1900. — Holotype: Tanzania, Lofia river, 600 m, 6 Jan 1899, Goetz 437 (Tanzania B 10 016799! + B 10 0167992! [2-part specimen]; isotype: FI barcode FI003587!).

= Pandanus rabaiensis Rendle

Remarks — Original material has been located in B. This single specimen mounted on two sheets is considered here as the holotype. A duplicate has been located in FI. Pandanus goetzii is considered as a synonym of P. rabaiensis (Beentje 1993).


= Pandanus rabaiensis Rendle

Remarks — No original material of P. hahnii has been traced. This species was not illustrated in Warburg’s (1900b) monograph. An illustration is extant in FI, which served Martelli to illustrate this species in his Enumerazione delle Pandanaceae (Martelli 1913b: t. 24, fig. 4, 5). This drawing shows a side view and a top view of a phalange and is annotated in Martelli’s hand “In herb. Berolinense, communicavit Engler 1904”. This drawing is designated here as the neotype of P. hahnii because it represents the only link to the original material.

Pandanus hahnii is considered as a synonym of P. rabaiensis (Beentje & Callmander 2014).

Pandanus heddei Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 46. 1900. — Lectotype (designated here): Tanzania, Dar es Salaam, 1900, Hedde 31 (FI barcode FI017923!).

= Pandanus kirkii Rendle

Remarks — No original material of Pandanus heddei has been traced in B. The FI duplicate is therefore designated here as the lectotype. Pandanus heddei is considered as a synonym of P. kirkii (Beentje 1993).

Pandanus hollrungii Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 71. 1900, syn. nov. — Holotype: Papua New Guinea, sine loco, 1887, Hollrung 168 (B barcodes B 10 0525667! + B 10 0525668! + B 10 0525669! [3-part specimen]; isotype: FI barcode FI017928 excluding fragment packet at top right!).


Remarks — Original material of Pandanus hollrungii has been located in B and FI. A single specimen mounted on three sheets is extant in B. This material consists of parts of leaves, bracts and a fragment packet with loose drupes. This specimen is considered here as the holotype. The duplicate in FI consists of a fragment packet with drupes and a photograph of the now destroyed complete infructescence in B. The fragment packet at the top right is not part of the original material. This latter material belongs to a duplicate of Kaernbach s.n. received by Martelli from Berlin and determined by Warburg (1900b: 69) as P. subumbellatus. This fragment packet is attached to the sheet because of a later determination by Harold St. John (1892–1991) in 1967 as P. hollrungii. Finally, a copy of the drawing published in Warburg (1900b: 70, fig. 19E–J) is also extant in B (B 10 0673240).

Pandanus hollrungii was tentatively put in synonymy of P. cominsii Hemsl. by Kanehira (1936: 544). The same author later questioned his decision by listing P. hollrungii as an accepted species but writing “this is possibly a syno-

nym of Pandanus cominsii Hemsl. but we have no authen-
tic material for comparison” (Kanehira 1940: 253). Merrill & Perry (1939) and Stone (1982) accepted P. hollrungii.

Study of the original material shows that Pandanus hollrungii has large leaves and a flattened pileus, with a scarcely raised stigma, which is characteristic of P. sub-

umbellatus (Jebb 1992). Pandanus hollrungii is therefore considered as a synonym of P. subumbellatus. Finally, P. cominsii has much narrower leaves and infructescence and is therefore considered as a different taxon (Jebb 1992).

Pandanus indicus (Gaudich.) Warb. in Engler, Pflanzen-

reich IV. 9 (Heft 3): 56. 1900, syn. nov. = Roussinia in-

= Pandanus leram Jones ex R. Millar
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Fig. 5. Lectotype of *Roussinia indica* (≡ *Pandanus indicus*): copper engraving in Gaudichaud-Beaupré, Voy. Bonite, Bot. 3: t. 21, fig. 1–4. 1841 (only the parts numbered 1–4). – Image courtesy of Peter H. Raven Library, Missouri Botanical Garden.
Remarks — Balfour (1878: 66) rightly underlined that Gaudichaud-Beaupré (1841) mixed two species under his t. 21: *Roussinia indica* for fig. 1–4 and *Pandanus palastris* Thouars for figs. 5–9. The phalanges that served for the illustration of *R. indica* (fig. 5–9) are extant in P (P00867954, P00867955) and belong to *P. palastris*. The lectotype designated here is Gaudichaud’s t. 21, fig. 1–4 (Fig. 5). This illustration is a copy of the original illustrations in Fontana (1792) designated as the lectotype of *P. leram* by Turner (2013: 167). A copy is also extant in P (P01183280).

*Pandanus indicus* is therefore a synonym of *P. leram*.


Remarks — *Pandanus kaernbachii* was described based on two gatherings: Hollrung s.n. and Kaernbach s.n., both cited in the protologue and therefore syntypes. Only material of Hollrung s.n. has been located in the spirit collection in B. This specimen is designated here as the lectotype. A reproduction of the drawing published in Warburg (1900b: fig. 13D) is also extant in B (B 10 0673255). The sheet in FI bears two fragment packets and a reproduction of the drawing published by Martelli (1913b: t. 6, fig. 3, 4). Only the fragment packet on the lower part of the specimen has an annotation in Martelli’s handwriting “ex Museo botanico Berolinensis, leg Kaernbach, da Warburg 1903” and clearly represents a syntype. The fragment packet on the upper left has no indication and could represent either the Hollrung or Kaernbach gathering.

*Pandanus kamerunensis* Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 66. 1900. – Lectotype (designated here): Cameroon, sine loco, s.d., Schran 68 (FI barcode FI000998 + carpol.). = *Pandanus candelabrum* P. Beauv.

Remarks — No original material of *Pandanus kamerunensis* has been traced in B. The FI duplicate is therefore designated as the lectotype.

A staminate specimen determined by Warburg as *Pandanus kamerunensis* and mentioned in Warburg (1900b: 67) is still extant in B (Deistle 108, B barcode B 10 0715939).

*Pandanus kamerunensis* is considered as a synonym of *P. candelabrum* (Beentje & Callmander 2014).


Remarks — Original material has been located in B. This material consists of two gatherings: Kersting 52 in the wood collection and Kersting 693 in the herbarium. Kersting 693, a single specimen is mounted on three sheets, is designated here as the lectotype. There is a duplicate in FI.

*Pandanus kerstingii* was mentioned in the first part of Volken’s treatment of the economic plants of Togo (Volkens 1909a). The poor wood of *Pandanus kerstingii* Warb. was mentioned on p. 3 “Das lichtgelbliche Holz […] ist nur als Brennholz verwertbar” [the light-yellowish wood […] is only exploitable as firewood]. The species was formally described in the second part of Volken’s treatment on the economic plants of Togo (Volkens 1909b).

Volkens (1909b) ascribed the name *Pandanus kerstingii* to Warburg, but the latter was not mentioned as being an author of the treatment of Pandanaceae. We therefore consider the author of this name to be “Warb. ex Volken” (see also *P. togoensis*).

*Pandanus kerstingii* is considered as a synonym of *P. candelabrum* (Beentje & Callmander 2014), but see notes under *P. togoensis*.


Remarks — Original material has been located in B and is considered here as the holotype. Duplicates have been located in FI and WRSL.

*Pandanus lauterbachii* is the basionym of *Benstonea lauterbachii* (Callmander & al. 2012).


Remarks — Balfour (1878: 52) had previously attempted to transfer “Dorystigma madagascariense” illustrated in Gaudichaud-Beaupré (1841) to Pandanus, but neither name was validly published. Warburg (1900b) validated the name P. madagascariensis by providing a Latin diagnosis, which was based on Gaudichaud’s illustration. Warburg had no specimen in B: “Man kennt nur die canthus” of an original material seen by Warburg. It is received by Martelli from Engler in 1904 and undoubtedly represents original material seen by Warburg, having all the available material, we conclude that these differences do not justify recognizing different species along the eastern coast of Madagascar and they are considered here as synonyms.

Pandanus merrillii Warb. in Perkins, Fragm. Fl. Philipp.: 50. 1904. – Holotype: Philippines, Palawan Isl., Island of Paragua, San Antonio Bay, Feb 1903, Merrill 840 (B barcode B 10 0279959!; isotypes: FI barcode FI003946!, NY NY00307567! [image!], US barcode USA0086602 [image!]).

= Benstonea affinis (Kurz) Callm. & Buerki.

Remarks — Original material has been located in B and is considered here as the holotype. Duplicates have been located in FI, NY and US. Pandanus merrillii is considered as a synonym of Benstonea affinis (Callmander & al. 2012).

Pandanus micracanthus Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 83. 1900. – Lectotype (designated here): Malaysia, Borneo, s.d., Anon. s.n. (FI barcode FI017913 fragment packet on lower right!).

= Benstonea korthalsii (Solms) Callm. & Buerki.

Remarks — No original material of Pandanus micracanthus is extant in B. A fragment packet containing immature drupes has been located in FI. This packet was received by Martelli from Engler in 1904 and undoubtedly represents original material seen by Warburg. It is designated here as the lectotype. Pandanus micracanthus most likely represent a synonym of Benstonea korthalsii.

Pandanus microstigma Balf. f. ex Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 67. 1900, syn. nov. – Lectotype (designated here): Seychelles [not Madagascar], sine loco, s.d., Pervillé s.n. (P barcode P01728635!; isolec- totyp: FI barcode FI017888 excluding fragment packet on lower right!).

= Pandanus multispicatus Balf. f.

Remarks — Balfour (1878: 53) had previously attempted to transfer “Sussea microstigma” illustrated in Gaudichaud-Beaupré (1841: t. 38) to Pandanus, but
neither name was validly published. Warburg (1900b) validated the name *P. microstigma* by providing a Latin diagnosis.

Original material of *Pandanus microstigma* has been located in FI and P. The FI material consists of a photograph of the *Pervillé s.n.* specimen in P, a syncarp and a fragment packet received from P with a few loose drupes and another fragment packet that Martelli received from Berlin with a fragment of a staminate inflorescence.

The complete specimen in P that served for the good engraving of “*Sussea microstigma*” in Gaudichaud-Beaupré (1841) is designated here as the lectotype of *Pandanus microstigma*. The fragment packet in FI originating from Berlin with fragment of a staminate inflorescence is not considered as original material.

*Pandanus microstigma* is a synonym of *P. multisepiatus*, endemic to the Seychelles.

*Pandanus militaris* Ball, f. ex Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 79. 1900. – Lectotype (designated here): Singapore, 1837, Gaudichaud 110 (P barcode P00733282!; isotypes: FI barcode FI014757!, G barcode G00164428!, SING!).

= *Pandanus yvani* Solms

Remarks — Balfour (1878: 53) had previously attempted to transfer “*Fisqueta militaris*” illustrated in Gaudichaud-Beaupré (1841: t. 5, fig. 2–7) to *Pandanus*, but neither name was validly published. Warburg (1900b) validated the name *P. militaris* by providing a Latin diagnosis.

No original material is extant in B. Original material has been located in several herbaria, and *Gaudichaud militaris* in P is designated here as the lectotype.

*Pandanus militaris* is a synonym of *P. yvani* (Beentje & Callmander in press).

*Pandanus ovatus* Kurz ex Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 80. 1900. – Holotype: [icon] “*Fisqueta ovata*” in Gaudichaud-Beaupré, Voy. Bonite, Bot. 3: t. 4, fig. 1. 1841.

= *Benstonea humilis* (Lour.) Callm. & Buerki

Remarks — Kurz (1869: 147) had previously attempted to transfer “*Fisqueta ovata*” illustrated in Gaudichaud-Beaupré (1841) to *Pandanus*, but neither name was validly published. Warburg (1900b) validated the name *P. ovata* by providing a Latin diagnosis.

St. John (1965: 231) cited as the holotype “the illustration in Bot. Voy. La Bonite, Atlas, t. 4, fig. 1, 1843 [sic] which was drawn from the specimen, Malacca, *Gaudichaud* (P). Also there is a clastotype of 12 loose drupes (FI). Specimens examined! Also an isotype (G)!”. *Gaudichaud 44* (FI017821, G00164429, P02138415, P02138416), on which Gaudichaud’s illustration was based, cannot be considered as original material, because Warburg wrote “Man kennt nur die Abbildung” [One knows only the illustration]. Therefore the illustration in Gaudichaud-Beaupré (1841: t. 4, fig. 1) is considered here as the holotype. Gaudichaud’s gathering originated from Pulo (Pulau) Pinang (Malacca) in Malaysia.

*Pandanus ovatus* is a synonym of *Benstonea humilis* (Stone 1978; Callmander & al. 2012).

*Pandanus peterisi* Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 66. 1900. – Lectotype (designated here): Mozambique, s.d., Peters s.n. (FI barcode FI001032!).

= *Pandanus livingstonianus* Rendle

Remarks — Beentje & Callmander (2014: 321) cited a specimen in K (KEBC00000056) as the holotype of *Pandanus peterisi*. This was an error because this specimen is the holotype of *P. livingstonianus* Rendle cited correctly by Beentje & Callmander (l.c.).

No original material is extant in B (as mentioned by Beentje 2009), but a duplicate has been located in FI. This specimen is designated here as the lectotype.

*Pandanus platycarpus* Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 50. 1900. – Lectotype (designated here): Tanzania, Zanzibar, s.d., Krauss s.n. (FI barcode FI001052!).

= *Pandanus kirkii* Rendle

Remarks — The original material in B was destroyed and the FI duplicate is designated here as the lectotype.

*Pandanus platycarpus* is considered as a synonym of *P. kirkii* (see Beentje & Callmander 2014). Martelli (1933) considered *P. platycarpus* as originating from Java and cultivated in Zanzibar. The Javanese *P. odorifer* (Forssk.) Kuntze is cultivated in Zanzibar, but pistillate plants seem to be absent; only staminate plants are cultivated for their fragrant inflorescences (Stone 1973).

*Pandanus pseudolais* Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 76. 1900. – Lectotype (designated here): Indonesia, Java, s.d., Junghuhn s.n. (L barcode L0819041!).

Remarks — *Pandanus pseudolais* was described based on two gatherings: Hasskarl s.n. and Junghuhn s.n., both cited in the protologue and therefore syntypes. No original material has been traced in B and FI. Rahayu (2011) mentioned that original material of both gatherings is extant in BO. Despite a thorough search, we could not locate any original material in BO. The only original material we could trace is a sterile specimen of *Junghuhn s.n.* in L. This specimen is designated here as the lectotype.

*Pandanus pseudolais* is part of a complex of species of the taxonomically difficult *Pandanus sect. Rykiia* (de Vries) Kurz. Backer & Bakhuizen van den Brink (1968) did not recognize *P. pseudolais* and considered it as a synonym of *P. furcatus* Roxb. This synonymy is not accepted.
here, because *P. furcatus* is endemic to the western coast of India (Nadaf & Zazan 2012). Further taxonomic work on this section is needed in Java. A recent study on this section showed that three species should be accepted: *P. bantamensis*, *P. pseudolais* and *P. scabrolius* (Rahayu & al. 2011). This taxonomy is in agreement with Stone (1972) and is followed here.

**Pandanus radula** Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 76. 1900. – **Lectotype (designated here):** Indonesia, Java, s.d., Forbes 3253 (FI barcode FI017865!); isolecotypes: FI barcode FI017864 + carpol.!, L barcodes L0627768 carpol., L0628111 carpol.1).

= **Pandanus helicopus** Kurz

**Remarks** — No original material is extant in B, but duplicates of original material have been located in FI and L. Martelli received the material in FI from Leiden (two sheets) and from BM (two fruits in the carpological collection). The material in FI received from Leiden is the most complete. FI017865 bears a label “Java n°3253 Forbes” and FI017864 “Borneo, leg. Forbes”. We designate here FI017865 as the lectotype. FI017864 is considered as a duplicate and the locality “Borneo” on the label is certainly an error because all specimens in L are labelled as Forbes 3253 from Java.

**Pandanus radula** is considered as a synonym of *P. helicopus* (Stone 1972).


**Remarks** — The original material of *Pandanus reinecke* in B consists of a single drupe in a fragment packet. It is considered here as the holotype. No material has been traced in FI.

This very characteristic species is endemic to the American Samoa islands and has been collected on the summits of several ranges in Savaii, Upolu and Tutuila (Stone 1967) (Fig. 4D).


= **Pandanus krauelianus** K. Schum.

**Remarks** — Warburg published *Pandanus rumphii* citing as a synonym *P. ceramicus* var. *sylvestris* Kunth (1841: 98). Warburg’s species name can therefore be treated as a replacement name for Kunth’s varietal name. Warburg also cited as a synonym “*P. montanus* Rumph.” with a reference to Rumphius (1743: 145, t. 77), where two entities were recognized: “*Pandanus sylvestris sive terrestris*” or “keker wassi” (to which t. 77 belongs) and “*Pandanus montanus*” or “keker ewan” (not illustrated, see under *P. terrestris*). Kunth cited “*P. sylvestris*” and the same illustration from Rumphius and mentioned Rumphius after the validating description; he gave no indication that he knew the species from any source except Rumphius. Therefore we consider the Rumphius illustration to be the holotype. Warburg’s name is illegitimate because it is a later homonym of *P. rumphii* Gaudich. (Gaudichaud-Beaupré 1841: t. 22, fig. 11) (= *P. tectorius*).

**Pandanus rumphii** Warb. is a synonym of *P. krauelianus*.

**Pandanus samoensis** Warb. in Bot. Jahrb. Syst. 25: 580. 1898, syn. nov. – **Lectotype (designated here):** Samoa, sine loco, Reinecke s.n. (B barcode B 10 0673231!).

= **Pandanus tectorius** Parkinson

**Remarks** — *Pandanus samoensis* was described by Warburg based on both staminate and pistillate individuals. The locality mentioned in the protologue is “Upulu: Vaiele Mai 1894”. Only a single specimen of original material is extant in B, representing staminate material together with a sketch of an immature infructescence, which was published by Warburg (1898: t. 8, fig. C). This specimen is therefore designated here as the lectotype.

Martelli (1934: 23) wrote “I saw the type specimen in the Botanical Museum in Berlin, and I am sure that no confusion took place there. For male and female flowers belong to the same species.” Martelli nevertheless left left *P. samoensis* as an undefinable name due to the immature pistillate original material, but stated that the staminate material “probably [belongs] to *P. tectorius*”. Earlier, Martelli (1913a: 30) had considered *P. samoensis* as a synonym of *P. tectorius* var. *upolensis* Martelli. Both *P. samoensis* and *P. tectorius* var. *upolensis* are synonyms of the widespread and morphologically variable *P. tectorius*.

**Pandanus sarasinorum** Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 78. 1900. – **Lectotype (designated here):** Indonesia, Sulawesi, “Celebes, Minahassa, Fuss des So-putanstockes”, s.d., Sarasin 1099 (FI barcode FI015048!); isolecotype: B barcode B 10 0279932!.

**Remarks** — A single specimen of original material is present in B and represents a single leaf. A duplicate is extant in FI and represents two photographs of the leaf extant in B with two fragment packets containing parts of an infructescence received by Martelli from Warburg. The FI specimen (Fig. 6) is designated here as the lectotype as it is more complete than the original material deposited in B.

Fig. 6. Lectotype of *Pandanus sarasinorum*: Sarasin 1099 (FI015048). – Image © Università degli Studi di Firenze, Museo di Storia Naturale, Collezioni Botaniche.
Yaouhé, 400 m, 1902, *Schlechter* 15053 (B barcode B 10 0352291!; isotype: FI barcode FI015017!).

= **Pandanus decumbens** (Brongn.) Solms

**Remarks** — A single specimen of original material is present in B. This specimen is considered here as the holotype. A duplicate has been located in FI.

**Pandanus schlechteri** is a synonym of *P. decumbens* (see Callmander & Buerki 2013).


**Remarks** — The description of *Pandanus setistyla* was based on two gatherings: *Lauterbach* 2505 and *Hollrung* 175, both cited in the protologue and therefore syntypes. Specimens of both gatherings are extant in B. *Hollrung* 175 (B) was designated as the lectotype by Stone (1978: 22). It consists of a single specimen mounted on two sheets with additional material in the spirit collection. Duplicates of both gatherings have been located in FI.

**Pandanus setistyla** is the basionym of *Benstonea setistyla* (Callmander & al. 2012).

**Pandanus spinifer** Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 57. 1900. – Lectotype (designated here): Madagascar, *sine loco*, [1880], Hildebrandt s.n. (FI barcode FI017950 + carpol.); isolecotytes: BM carpol.!


**Remarks** — No original material of *Pandanus spinifer* is extant in B but original material has been located in BM and FI. The material in FI consists of a herbarium sheet with a fragment packet containing loose drupes and three syncarps and parts of leaves in the carpological collection. This original material representing a single specimen is designated here as the lectotype. Three syncarps have also been located in the carpological collection in BM.

The material in FI served for Martelli to describe *Pandanus sect. Acanthostyloa* Martelli (Martelli 1933). This section, endemic to Madagascar, is characterized by its distinctive “coniferoid” habit (see Stone 1970b).

**Pandanus fetosus** from the highlands of Madagascar (where *P. spinifer* has certainly been collected by Johann Maria Hildebrandt [1847–1881]) shows no discriminant morphological characters and is considered here a synonym of *P. spinifer*.

**Pandanus stuhlmannii** Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 57. 1900. – Holotype: Tanzania, Magodani, Usaramo, Dar es Salaam, 7 Jan 1894, *Stuhlmann* 6072 (B barcode B 10 0167989!; isotype: FI barcode FI003586).

= **Pandanus rabaiensis** Rendle

**Remarks** — A single specimen of original material of *Pandanus stuhlmannii*, *Stuhlmann* 6072, is present in B and is considered here as the holotype. Another specimen, *Stuhlmann* 8/1460 (B 10 0673282), was annotated by the first author as a syntype (Apr 2016), but it does not bear the locality “Dar es Salam”, as indicated in Warburg’s protologue and cannot be considered as original material.

The specimen in FI (barcode FI003586) consists of two fragment packets with loose drupes and two photographs of a now destroyed infructescence in B. Another fragment packet on the lower right of the same sheet in FI (barcode FI003585) is not considered as original material.

**Pandanus stuhlmannii** is considered as a synonym of *P. rabaiensis* (Stone 1973; Beentje & Callmander 2014).


**Remarks** — Warburg intended to publish a new combination at varietal rank based on *Pandanus laevis* sensu Kunth (1841: 100) [non Lour. 1790]. Warburg validly published the varietal name by providing a Latin diagnosis, as already mentioned by St. John (1965). Warburg did not cite any specimen and based his concept on earlier names and publications (St. John 1965). A specimen in B annotated by Warburg as “*Pandanus fasicularis* Lam var *laevis* Warb” is designated here as the neotype. Warburg (1900b: 46) considered *P. fasicularis* Lam. as a synonym of *P. tectorius*. A duplicate has been located in Philip Barker Webb’s (1793–1854) herbarium in FI. This gathering was collected by Gaudichaud in the Calcutta Botanic Garden and sent to Carl Sigismund Kunth (1788–1850) for study in 1841 in B (St. John 1965). Several Gaudichaud specimens in P possibly represent isoneotypes (P02131259, P02131262, P02131263, P02131264), but none bears the number “33”, which may represent a numbering within the Gaudichaud material sent to Kunth and Webb.
This cultivated species with unarmed leaves originated from the Moluccas (named by Rumphius [1743: 147–148, 1744: 147–148] as “Pandanus moschatus seu laevis”). Roxburgh (1832: 744) already mentioned its cultivation in the Calcutta Botanic Garden and its origin in Amboyna (Ambon) and named it P. inermis Roxb. St. John (1965: 232) described the new cultivar P. sparus ‘Putat’ and considered Warburg’s varietal name as a synonym. St. John’s view is certainly right that this taxon should be considered as an old cultivar of P. tectorius.


= Pandanus odorifer (Forssk.) Kunze

Remarks — The original material of Pandanus tectorius var. liukiuensis is a mixed gathering. The leaves represent an undetermined Freycinetia that should be excluded. Only the phalanges are considered as original material of P. tectorius var. liukiuensis. Therefore, the lectotype designated here in B is the fragment packet containing the fertile material. The specimen in Fl is mounted on three sheets: FI017955 consists of one sheet bearing a fragment packet containing a single phalange, while FI015204 consists of two sheets: one with a fragment packet containing three phalanges and with a drawing of the excluded leaf material, and the other with the excluded Freycinetia leaf mounted on it.

Pandanus tectorius var. liukiuensi is considered a synonym of P. odorifer.


= Pandanus tectorius Parkinson

Remarks — No original material is extant in B, but duplicates of original material have been located in Fl. The Fl material consists of four fragment packets and a glued phalange mounted on three sheets. The material on two sheets (FI014765, FI015004) originated from Berlin. The third sheet (FI017932) bears a fragment packet annotated by Martelli: “Pandanus tectorius var. pulposum Warb. det. Warburg. Con questo nome trovansi nelle collezioni di Berlino misto ad altre forme sembra tutte con la stessa determinazione. Fra quelle forme vi è pure il mio P. Fischeri. U. M.” [Under this name it is located in the Berlin collections mixed with other forms maybe all with the same identification. Among them my P. Fischeri as well]. This specimen also originated from Berlin but it is uncertain whether it is original material. We therefore consider only the four phalanges mounted on FI014765 and FI015004 as belonging to the same gathering and comprising a single specimen, and these are designated here as the lectotype.

Pandanus tectorius var. pulposus represents a synonym of the widespread and morphologically variable P. tectorius (see Wagner & al. 2020a).

Pandanus tectorius var. samak (Hassk.) Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 48. 1900, syn. nov. = Pandanus samak Hassk. in Flora 25(2, Beibl.): 13. 1842. – Neotype (designated here): Indonesia, Java, Buitenzorg, Soedinara, s.d., Heyne s.n. (L barcode L.1196018 [image!]: isoneotypes: B barcode B 10 0279957!, BO accession number BO-1567798 [image!]).

= Pandanus odorifer (Forssk.) Kunze

Remarks — No original material of Justus Carl Hasskarl (1811–1894) has been located. A specimen collected by Heyne in Java, Buitenzorg, Soedinara is designated here as the neotype.

Pandanus samak Hassk. was described based on the Javanese vernacular name “Pandan samak” (Rahayu & al. 2008). This name is used for a cultivated plant, the leaves of which are used for weaving, especially mats. The cultivated species was derived from P. odorifer (Stone 1972), of which P. samak is here considered a synonym (see Rahayu & al. 2008 for an illustration of the cultivated species).


= Pandanus tectorius Parkinson

Remarks — No original material is extant in B, but duplicates of original material have been located in Fl. The Fl material was received by Martelli from Berlin and represents both staminate and pistillate plants (Hillebrand s.n.). The fragment packets with loose phalanges received from Berlin (FI017961), Warburg in 1902 (FI017962) and Engler in 1904 (FI017863) originate from a single gathering and are mounted on the same sheet; they comprise a single specimen and are designated here as the lectotype. The fragment packet on the same herbarium sheet with staminate material (FI017960) is also considered to be original material.

Pandanus tectorius var. sandvicensis represents a synonym of the widespread and morphologically variable P. tectorius (see Wagner & al. 2020a).

Pandanus tectorius var. sinensis Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 48. 1900 = Pandanus sinensis
Remarks — St. John (1967) carefully studied the original material of Pandanus tectorius var. sinensis in B. He designated the only pistillate material as the lectotype: “It is from Hainan, 1889, A. Henry. One sheet bears two young pistillate inflorescences. A second bear a packet with several very young phalanges, and one mature phalange but, since it is the only fruiting one in the series, it is designated here as the lectotype of the var. sinensis.” Other syntypes are either sterile (Naumann s.n. and Warburg 5482) or represent staminate material (Henry 8290).

Pandanus tectorius var. sinensis is a synonym of P. odorifer (Stone 1983, under P. odoratissimus).


= Pandanus krauelianus K. Schum.

Remarks — Merrill (1917: 82) accepted Warburg’s species but excluded the synonymy with Pandanus montanus Miq. Merrill’s interpretation is not accepted here, because Warburg is considered to have published a replacement name for Miqüel’s (1855: 161) later homonym. Warburg cited as a synonym “P. sylvestris sive terrestris Rumph.” with a reference to Rumphius (1743: 145). Miqüel, on the other hand, cited “Pandanus sylvestris altera species s. Keker ewan (i. e. montanus)” also referring to Rumphius (I.c.). Rumphius recognized two entities: “Pandanus silvestris sive terrestris” or “keker wassi” (illustrated by his t. 77, see under P. rumphi) and “Pandanus montanus” or “keker ewan” (not illustrated, the plant described by Miqüel). No original material for P. montanus is known.

Both of Warburg’s names, Pandanus terrestris (= P. montanus Miq., “Pandanus montanus” or “keker ewan”) of Rumphii) and P. rumphi (= P. ceramicus var. sylvestris Kunth, “Pandanus silvestris sive terrestris” or “keker wassi” of Rumphius), represent the same species and are synonyms of P. krauelianus (Keim 2009, 2012).

Pandanus teuszii Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 67. 1900. – Lectotype (designated here): Gabon, sine loco, s.d., Teusz s.n. (FI barcode FI003584!).

= Pandanus candelabrum P. Beauv.

Remarks — The original material in B has been destroyed. The FI duplicate is designated here as the lectotype.

Pandanus teuszii is considered as a synonym of P. candelabrum (Beentje & Callmander 2014).


= Pandanus candelabrum P. Beauv.

Remarks — Original material of Pandanus togoensis has been located in B. This original material is mounted on two sheets comprising a single specimen and is considered here as the holotype. The material is sterile and represents only young leaves. A leaf is not sufficient to determine a Pandanus species, and therefore the fertile specimen Grüner s.n., collected at the type locality and described in detail by Huynh (1987: 15), is designated here as the epitype.

Volkens (1909b) ascribed the name Pandanus togoensis to Warburg, but the latter was not mentioned as being an author of the treatment of Pandanaceae. We therefore consider the author of this name to be “Warb. ex Volkens” (see also P. kerstingii).

Pandanus togoensis is currently considered as a synonym of P. candelabrum (Beentje & Callmander 2014). Further taxonomic work is needed in Togo to determine if more than a single species can be recognized. Recent field work at the type localities of P. kerstingii and P. togoensis tend to confirm that more than a single species is present in Togo (Ton Rulkens, pers. comm.).

Pandanus incertae sedis


Remarks — This species was described based on a leaf collected from a plant introduced by William Bull (1828–1902) originating from New Caledonia and described by Karl Koch (1809–1879). Koch (1872) named it Pandanus ceramicus K. Koch, which is an illegitimate later homonym of P. ceramicus Kunth (= P. conoideus Lam.), which was first described by Georg Everhard Rumphius (1627–1702) in his Herb. amboinense (Rumphius 1743: 149, t. 79). The descriptions of both Koch and Warburg mention a leaf with a midrib unarmed, which may represent P. tectorius Parkinson, but in the absence of any original material P. bullii will remain doubtful.

Remarks — Balfour (1878: 50) had previously attempted to transfer “Sussea lagenaeformis” illustrated in Gaudichaud-Beaupré (1841) to Pandanus, but neither name was validly published. Warburg (1900b) validated the name Pandanus lageniformis by providing a Latin diagnosis.

No specimen that is original material has been traced for Pandanus lageniformis. Gaudichaud’s drawing consists of an old drupe without its epicarp and pileus, the same drupe cut in the middle showing the seed locale, and possibly a seed. This is not sufficient to link P. lageniformis with certainty to any Pandanus and it will therefore remain a doubtful species. Kurz (1869) hypothesized that P. lageniformis is morphologically closely related to P. littoralis (Gaudich.) Kurz (= P. polypephalum Lam.).


Remarks — Warburg (1900b) treated Pandanus ornatus W. Bull in two places. On p. 58 he considered it a synonym of the later-published name P. heterocarpus Balf. f. (Balfour 1877), while on p. 88 he published Pandanus lindenii as an illegitimate superfluous replacement name for P. ornatus W. Bull, writing “nec Kurz”, i.e. explicitly excluding the later homonym published by Kurz (1869).

Pandanus ornatus W. Bull was based on a cultivated plant displayed on 23 January 1866 by William Bull (1828–1902) at the Royal Horticultural Society of London and described as “a species, of elegant drooping habit, with narrowish dark-green glossy leaves margined with short white spines; it was considered to be a very pretty subject for room-decoration, especially in the small state.” (Anonymous 1866: i). Édouard-François André (1840–1911) provided an illustration accompanied by two pages of detailed description (André 1872). This species originated from the Mascarenes (Rodrigues island) and was sent to Jean Jules Linden (1817–1898) in Ghent, Belgium. No original material of this horticultural species has been traced. This horticultural species is very likely a synonym of P. tectorius or one of its cultivars. A proposal to conserve the well-known and universally used name P. ornatus Kurz, now accepted as Benstonea ornata (Kurz) Callm. & Buerki, against the ignored and virtually unknown earlier homonym P. ornatus W. Bull has been submitted to the General Committee (Callmander & al. 2020).


Remarks — Warburg (1900b) validated Pandanus mauritianus as the name of a new species with a Latin diagnosis, although he intended it as a new combination based on the not validly published “Dorystigma mauritianum” of Gaudichaud-Beaupré (1841). The latter is a doubtful name that Balfour (1878: 38) associated with P. conglomeratus Balf. f. Gaudichaud’s illustration is the only available original material, and Bosser & Guého (2003: 39) already considered it to be the “type”. Pandanus mauritianus Warb. is an illegitimate later homonym of P. mauritianus Lem. (= P. utilis Bory).


Remarks — Édouard-Christophe Pynaert (1835–1900), a Belgian horticulturist, received a living Pandanus plant from the Botanical Garden of Corsi-Salviati in Italy. Pynaert (1881: 148) related this communication with the reproduction of a copper engraving and named the species “Pandanus microcarpus” [non P. microcarpus Balf. f. 1877]. The horticulturist did not provide any distinctive character and was just questioning if his Pandanus was the same as P. ornatus W. Bull: “les deux espèces – pour autant qu’il en ait deux – sont d’un parentage très rapproché [the two species – as long as there are two – are very closely related]”. Therefore, “P. microcarpus” is considered to be a nomen nudum and not validly published.

By providing a Latin diagnosis, Warburg (1900b) validated Pynaert’s name as P. pynaertii. No original material has been traced except for the illustration in Pynaert (1881: t. 11), which is designated here as the lectotype. The illustration represents an immature living Pandanus with a first crown of leaves. Warburg (1900b: 88) compared it to P. graminifolius Miq., but we conclude that it is probably the same horticultural species as P. ornatus W. Bull, most likely a synonym of P. tectorius or one of its cultivars.

Pandanus scopula Warb. in Engler, Pflanzenreich IV. 9 (Heft 3): 76. 1900. – Syntype: “Burma”, sine loco, s.d., Jagor s.n. (B not traced).

Remarks — A specimen is extant in FI determined by Martelli as Pandanus scopula. However, this specimen was received from the British Museum in 1904 and not from Berlin, and there is no indication that it is part of the original material. The FI specimen consists of a fragment packet with a few old drupes that have lost the epicarp and stigmas and are therefore indeterminable.
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