Benstonea Callm. & Buerki (Pandanaceae): characterization, circumscription, and distribution of a new genus of screw-pines, with a synopsis of accepted species

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Abstract
Pandanaceae, a palaeotropical monocot family of c. 700 species, comprises four currently recognized genera: Freycinetia Gaudich., Martellidendron (Pic. Serm.) Callm. & Chassot, Pandanus Parkinson and Sararanga Helms. Within Pandanus (c. 500 spp.), species of sect. Acrostigma Kurz [one of four sections comprising subg. Acrostigma (Kurz) B. C. Stone] possess highly distinctive morphological features (viz. sharp spini-form, linear styles with the stigmatic groove on the abaxial side of the style and a staminate flower reduced to 1 to 3 stamens) shared with two other species (likewise belonging to subg. Acrostigma but originally placed in sect. Fusiforma B. C. Stone) that separate them from all other congeners. Based on morphology, biogeography, and recent inferences from plastid DNA sequence data, we place these distinctive species in a new genus, Benstonea Callm. & Buerki, making the necessary new combinations for the 50 recognized species, accompanied by six lectotypifications, one epitypification and two neotypifications, and placing seventeen names in synonymy. A generic key is provided to facilitate distinguishing Benstonea from the four other genera of Pandanaceae. Comments are provided on the distribution, ecology and typification of each accepted species.

Key-words

Résumé

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This article is dedicated to Benjamin Clemens Stone
Introduction

The screw-pine family, Pandanaceae, is a paleotropical group of arborescent or lianoid dioecious monocotyledonous plants, including c. 700 species traditionally assigned to four genera: Pandanus Parkinson (c. 500 species), Freycinetia Gaudich. (c. 200 species), Martellidendron (Pic. Serm.) Calm. & Chassot (six species) and Sararanga Hemsl. (two species) (Stone & al., 1998; Callmander & al., 2003; Buerki & al., 2012). Freycinetia occurs in SE Asia, the Pacific Islands and Australasia, and is characterized by its liana habit, multi-ovulate carpels and berry fruits (Stone, 1990). Martellidendron has a narrow range in Madagascar and the granitic Seychelles (Mahé and Praslin islands), and includes tree species characterized by potentially bisexual flowers (presence of carpelloidia and staminodia in the staminate and the pistillate flowers, respectively), drupaceous fruit (mesocarp extending between the seed locules) and distinctive pollen morphology (3-layered pollen exine with an incomplete tectum; see Callmander, 2000, 2001; Callmander & al., 2003). Sararanga is restricted to the Philippines, New Guinea and the Solomon Islands, and harbours large tree species that can be distinguished from other Pandanaceae by their paniculate inflorescences and flowers with a perianth (Huynh, 2001).

Finally, Pandanus has the broadest geographical distribution of the four genera, occurring in the paleotropics from West Africa eastward to Hawaii, and includes species of trees and shrubs. It is characterized by its pistillate flowers with one to several carpels, partially or entirely united; a stigma ranging from flat to spiniform, and arranged in various positions at the apex of the drupe; and staminate flowers with numerous stamens organized around a stemanophore or rarely free (see Huynh, 1982). To accommodate this wide morphological variability found within Pandanus and to simplify identification, an elaborate infra-generic classification system has been developed in which eight subgenera (Stone, 1974; Huynh, 1991; see Table 1 in Buerki & al., 2012) and 86 sections (Stone, 1974; St. John, 1975; Huynh, 1975, 1976, 1977, 1979, 1980; Callmander & al., 2001; Laivao & al., 2006) are currently recognized.

Despite decades of work by several specialists, including B. C. Stone and K.-L. Huynh, the taxonomy of Pandanaceae, and in particular of Pandanus, still presents many challenges. Relationships among and within the genera are not well understood, and species identification is often problematic, even for experienced botanists. The time has now come to incorporate evidence from molecular inferences and biogeography in an effort to refine generic and infra-generic delimitations, especially within Pandanus. Stone (1990) questioned whether this large, polymorphic genus represented a natural (i.e., monophyletic) assemblage, given the distinctive morphology of several groups he recognized as subgenera, in particular subg. Martellidendron (Pic. Serm.) B. C. Stone and subg. Acrostigma (Kurz) B. C. Stone. Subsequent work has confirmed that the species historically assigned to the subg. Martellidendron represented a distinct clade, which led to its recognition as a separate genus (Callmander & al., 2003). In the present paper we explore the phylogenetic relations of Pandanus subg. Acrostigma and consider the taxonomic and nomenclatural implications.


Pandanus sect. Acrostigma is currently divided into eight subsections based on various vegetative and reproductive characters, in particular habit (epiphytes or shrubs), presence or absence of prickles on the apical part of the ventral pleats, whether the distal part of pileus is smooth or scabrid, and the shape of the syncarp (cylindric to globose). Despite the diversity of the section, it nevertheless appears to form a natural group characterized by carpels that are consistently free (forming one-seeded drupes), a sharp, linear stigma always positioned on the abaxial side of the style, and staminate flowers reduced to a single stamen, or in triads, free or very slightly joined at the base.

Pandanus epiphyticus, the sole member of Pandanus sect. Epiphytica, is a massive epiphytic species (sometimes also growing on sandstone hills) found in Peninsular Malaysia and Borneo. Its morphology is unique, with a massive infructescence bearing up to nine sub-cylindric syncarps and small ovate stigmas (Fig. 1A, 1B). According to Stone (1971a: 143), “Its true relationship remains to be discovered”.

Pandanus sect. Pseudoacrostigma, the third section included in Pandanus subg. Acrostigma, was described by Stone (1971a) to accommodate P. platystigma and was later expanded to include a subsequently described species, P. ornithocephaulus B. C. Stone. The syncarp of P. platystigma (Fig. 1C) is dark red and fleshy, a character unknown elsewhere in Pandanus subg. Acrostigma, as circumscribed by Stone (1974). Furthermore, the stigmas are flat and reniform, which contrasts with other members of the subgenus. Pandanus ornithocephaulus, known only from one collection in the Indonesian part of New Guinea (West Papua), bears styles with a swollen base with an oblique stigma (Stone, 1978; Jebl, 1992: 30). Its taxonomic position remains unclear, but unlike P. platystigma, it does not seem to
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Fig. 1. – General habit, infructescences and details of stigmas of species of Pandanus sect. Epiphytica Martelli (A-B) and Pseudoacrostigma B. C. Stone (C-D). A-B. Pandanus epiphyticus Martelli; C. Pandanus platystigma Martelli; D. Pandanus pugnax B. C. Stone.

[Photos: M. W. Callmander]
bear fleshy fruits. Pandanus pugnax B. C. Stone, a species only tentatively assigned to Pandanus sect. Acrostigma as an incertae sedis entity by Stone (1978, 1993) because the fertile portion of its type (Meijer SAN 23289) appears to have been lost, was recently re-collected in Borneo by two of the authors of the present paper (SB and MWC; Callmander & al. 1035). This new material shows that P. pugnax bears a terminal sub-elliptic syncarp (c. 4.5 × 10 cm) on a very long (c. 85 cm) and narrow (c. 1.3 cm) peduncle, a distinctive combination of character in Pandanus. The fruit is dark red and fleshy (Fig. 1D) as in P. platystigma, and its placement in Pandanus sect. Pseudo-acrostigma thus seems appropriate.

Members of Pandanus sect. Fusiforma, the fourth component of Stone’s (1974) Pandanus subg. Acrostigma, have distinctive leaves, which are exceedingly hard, very long (up to 8 m) and wide (up to 8 cm), a caespitose soboliferous habit, and drupes that have a pyramidal tip with an acute, rostriform stigma. On the basis of their stigmatic structure, however, the five species originally placed in Pandanus sect. Fusiforma (viz., P. biplicatus H. St. John, P. dumerorum, P. pachyphyllos Merr., P. saint-johnii B. C. Stone and P. soboliferos B. C. Stone) may well be allied to Pandanus sect. Acrostigma given the position of their stigmatic groove, as seen particularly well in P. pachyphyllos, which was originally placed by Stone in Pandanus sect. Fusiforma (1968, 1974, 1978) but later transferred to Pandanus sect. Acrostigma (Stone, 1993). Pandanus biplicatus, also initially placed in Pandanus sect. Fusiforma by Stone (1968, 1974, 1978), may likewise be related to the members of Pandanus sect. Acrostigma considering its sharp, linear stigma.

One last species, Pandanus microglottis B. C. Stone, endemic to the Mulu National Park in Sarawak (Borneo), was surprisingly placed in Pandanus sect. Acrostigma by Stone (1982b, 1993). It stands out, however, because it bears short appressed styles that are ovate in shape (Stone, 1982b: 35, Tab. 7), a feature not found in any other member of the section. The relationships of this species, only known from the type collection, remain unclear, and additional gatherings, in particular of staminate material, will be needed to assess its taxonomic position.

Based on personal observations and familiarity with Pandanus throughout nearly all its geographic range, we have discerned that the group of species characterized by having the stigma consistently positioned on the abaxial side of a sharp, linear style stands out from all other Pandanus. This group corresponds to Pandanus sect. Acrostigma (with the exception of P. microglottis, which its relationship remains to be assessed) and also includes at least two species initially placed in Pandanus sect. Fusiforma sensu Stone (1968, 1974) (see above). This interpretation was supported by a recent plastid phylogenetic analysis of Pandanaceae (Buerki & al., 2012), which revealed five major clades within the family corresponding to Sararanga, Freycinetia, Martellidendron, Pandanus sect. Acrostigma, and the remaining species of Pandanus, including its type, P. tectorius Parkinson (Fig. 2) (Buerki & al., 2012). The distinctive nature of Pandanus sect. Acrostigma revealed by morphology and molecular data is further supported by the fact that the group exhibits a coherent biogeographic distribution ranging from India to the South Pacific, with high species richness in South East Asia (especially Borneo and Peninsular Malaysia; Fig. 3).

Based on these findings, we propose the new generic name Benstonea Calm. & Buerki to accommodate the group comprising Pandanus sect. Acrostigma, as defined by Stone (1974) and modified above. A new name is required because Acrostigma O. F. Cook & Doyle is a validly published genus of Arecaceae. Benstonea is defined by its sharp spiniform styles with stigmatic grooves consistently placed on the abaxial side of the style (vs always adaxial in Pandanus, as redefined by the exclusion of the species placed in our new genus), staminate flowers reduced to a single stamen or in triads that are free or very slightly joined at the base (vs connate, borne on a stemonophore, rarely free) and an epiphytic to mainly acaulescent shrubby habit (vs mainly small to large trees). A complete synopsis of Benstonea, including distribution, typification and synonymy of each of the 50 currently recognized species, is presented below. Nomenclatural notes are also provided for some species. Seventeen new synonymies are proposed and lectotypes are designated for six names, along with one epitype and two neotypes. We also provide an updated key to the five genera of Pandanaceae now recognized. Appendix 1 includes a complete list of synonyms for each of the accepted names in Benstonea.

Taxonomic treatment

Key to the genera of Pandanaceae (adapted from Stone, 1974; Stone & al., 1998)

1. Pistillate inflorescence (infructescence) a panicle; leaves in 4 spiral rows; flowers with a perianth-like cupule ............

2a. ... SARARANGA

1a. Pistillate inflorescence (infructescence) a cephaliom or a raceme or pseudo-umbel of cephaliom; leaves in 3 spiral rows; flowers without a perianth-like cupule .......... 2

2. Liana; fruit a berry; carpels multi-ovulate (ovules much more numerous than 3); seeds generally free and germinating outside the fruit ................. FREYCINETIA

2a. Acaulescent shrubs to large trees; fruit a drupe with a hard bony endocarp; carpels uni-ovulate, rarely 2-3 ovulate; seed bound to endocarp and always germinating within the fruit ..........
3. Drupes with endocarp not extending between the seed locules, but replaced by the mesocarp extending from the apex to the base; stigmas two, forming a cross at the apex of the pileus; staminodia present at the base of each drupe, each comprising a filament and an anther with four sterile pollen sacs ............................................. *Martellidendron*

3a. Drupes with endocarp extending between the seed locules surrounded by mesocarp; stigma(s) 1 to numerous, of various shapes but never two and forming a cross at the apex of the pileus; staminodia rarely and abnormally present........................................... 4

4. Carpels either free or connate into multicarpellate, several-seeded drupes; stigmas always on the adaxial side of the style, variable in shape but usually not sharp and linear (but if so with stigmas always on the abaxial side of the style); staminate flower with several connate stamens, i.e. borne on a stemonophore, rarely free (in *P. epipythicus* Martelli and *P. pentodon* Ridl.) ............................................. *Pandanus*

4a. Carpels always free, forming one-seeded drupes; stamens always positioned on abaxial side of the style, sharp, linear; staminate flower reduced to one stamen, or in triads, free or very slightly joined at the base............. *Benstonea*
**Benstonea** Callm. & Buerki, nom. & stat. nov.


**Type:** *Benstonea affinis* (Kurz) Callm. & Buerki (= *Pandanus affinis* Kurz) (lectotype designated by St. John 1960: 226).

Acaulescent or short-stemmed shrubs, often epiphytic, rarely tall trees. Leaves ligulate to linear-attenuate; leaf apex adaxially spinulose along the two main pleats (spines rarely absent). Inflorescences terminal or lateral on short side-branches, pistillate cephalia solitary, sometimes spicately disposed. Cephalia always of simple drupes, drupes never connate into phalanges; pileus usually distinct and calyptrate, grading upward into a hard, spini-form style; stigma linear, always positioned on abaxial side of the style. Endocarp usually with seed-chamber roofed by a thin cartilaginous partition above which is located a small more or less distinct supra-seminal chamber distinct from the rest of the apical mesocarp. Stamine inflorescence normally spicate. Stamineate flowers sessile, composed of free stamens with anthers much longer than the short or nearly obsolete filaments, apiculate, sometimes stamens arranged in pauci-staminate dyads, phalanges or triads.

**Etymology.** – This genus is named in honour of Benjamin Clemens Stone (1933-1994) to whom we dedicate this article. Ben contributed immensely to the taxonomy of *Pandanaceae* and was the leading authority on the family for several decades; his work will remain fundamental to the study of the group for many years to come.

**Observations.** – As suggested above, our current understanding of relationships indicates that the entity recognized by Stone (1974) as *Pandanus* subg. *Acrostigma* is probably not monophyletic, and that the group treated here as *Benstonea* should be limited to include only the members historically assigned to *Pandanus* sect. *Acrostigma* (excluding *P. microglottis*), along with two clearly related species originally placed in sect. *Fusiforma* (*P. pachyphyllus* and *P. biplicatus*). The other species

![Fig. 3. Distribution map of Benstonea Callm. & Buerki showing the number of species and the level of endemicity per geographical region.](image-url)
assigned to *Pandanus* subg. *Acrostigma* by Stone (1974), viz. the members of sects. *Epiphytica* and *Pseudoacrostigma*, along with the remaining species of sect. *Fisiforma*, are morphologically distinct and currently remain in *Pandanus* (as redefined here), although their taxonomic affinities within the family remain to be elucidated.

*Benstonea* is the third largest genus of *Pandanaceae*, with 50 currently accepted species (see below). It ranges from India to Australia with its centre of diversity in Borneo (21 spp. [17 of which are endemic]) and Peninsular Malaysia (14 spp. [6 endemic]), where two third of the species are found (Fig. 3). Most members of the genus are acaceous or short-stemmed shrubs, or facultative or true epiphytes, rarely tall trees [e.g. *B. atrocarpus* (Griff.) Callm. & Buerki]. Species occur in a variety of habitats including lowland rainforest, swamps, mangrove fringes and montane forests on various soil types (granitic, sandstone and limestone) (Stone, 1978). *Benstonea* can be easily recognized in the field by its: 1) staminate flowers bearing single (sometimes 2 or 3 connate) stamens with a short filament and a narrow anther; and 2) pistillate drupes always monocarpellate, with a sharp spiniform style and an abaxial stigmatic groove (Figs. 4-6). When fertile, the only taxa with which *Benstonea* can possibly be confused are some species of *Pandanus* sect. *Solmsia* B. C. Stone from subg. *Ryokia* (de Vriese) B. C. Stone, which also bear simple spiniform styles, but which have a stigmatic groove that is always adaxial on the style. The presence of teeth along the two ventral pleats of the leaf apex can also help to recognize *Benstonea* when sterile, although some *Pandanus* species found in regions where *Benstonea* is present (i.e. *Pandanus echinodermos* Holtum & H. St. John and *P. pentodon* Ridley., both occurring in Peninsular Malaysia) also bear ventral apical teeth (Stone, 1968a).

A Synopsis of the genus *Benstonea*

The following synopsis of the currently recognized species placed in *Benstonea* is based on observations of herbarium specimens deposited at key herbaria [Berlin (B), Berkeley (UC), Geneva (G), Firenze (FI), Harvard (A), Honolulu (BISH), Kew (K), Kuala-Lumpur (KLU), Leiden (L), Sabah (SAN), Sarawak (SAR), Saint-Louis (MO), Singapore (SING) and Washington (US)] and previous taxonomic revisions, supplemented with collections and observations made during fieldwork recently conducted in Fiji and Borneo (Sabah and Sarawak). A total of 50 species are provisionally accepted. Taxa from Peninsular Malaysia (Beentje, unpubl. data), Indonesia (incl. Sulawesi, Sumatra, Papua and adjacent Islands; Keim, 2009a, 2009b, 2012) and Thailand (MWC & SB) are currently being revised, and as a consequence the number of species assigned to the genus will likely change in the coming years.

   
   = *Pandanus adinobotrys* Merr. & L. M. Perry in J. Arnold Arbor. 21: 175, 1940.
   
   
   

   **Distribution and ecology.** – *Benstonea adinobotrys* occurs from (400-)1400-2250 m in humid forest (Jebb, 1992). It is known in Indonesia (Sulawesi, West Papua) and Papua New Guinea.

   **Observations.** – This taxon comprises a complex that includes several “morpho-species” that have been described based on slight variations in leaf length and width, and the dimensions and number of syncarps. As stated by Stone (1983c), the “limits of variation within members of this group are still not very well understood, and further field study of them is desirable”. The taxonomic revision of *Pandanaceae* for the region currently being undertaken by Ary Keim and collaborators will hopefully clarify this matter. Some of the names placed in synonymy above may represent entities that justify recognition at the species level, in which case new combinations in *Benstonea* will be required.
2. **Benstonea affinis** (Kurz) Callm. & Buerki, **comb. nova.**
   = *Pandanus affinis* Kurz in J. Bot. 5: 101. 1867.
   **Typus:** **INDONESIA. Bangka Isl.: Kurz** (lecto-: BO) (designated by **STONE**, 1978: 13).

**Distribution and ecology.** – **Benstonea affinis** is found in peat swamps and gallery forest/river edges from sea level to c. 500 m. It is a widespread species, distributed from Peninsular Malaysia to the Philippines, including Vietnam, Sumatra, Singapore, and Borneo.

**Observations.** – This species is characterized by its 3 to 9 ovoid fruit heads crowded at the apex of an erect peduncle (Fig. 4A). **STONE** (1972, 1978, 1983a, 1993a), mentioning some differences in dimensions of the fruit, recognized the two species placed in synonymy above, albeit with doubt. He wrote: “*Pandanus merrillii* Warb. is so similar to *P. affinis* Kurz that, on the basis of herbarium material alone, discrimination is virtually impossible” (**STONE**, 1983a: 208). *Pandanus sarawakensis* was described by **MARTELLI** (1904) on the basis of two syntypes: Beccari 350 and 1895. The first of these, misprinted as 550 in **MARTELLI** (1904: 303), is designated here as the lectotype because it comprises a sheet with a leaf and an infructescence deposited in the Beccari herbarium and a spirit collection of one syncarp in the associated carpollical collection. Further taxonomic work is clearly needed for a better understanding of *Benstonea affinis* with respect to its relatives, especially *B. ellipsoidea* (Warb.) Callm. & Buerki (see below).

3. **Benstonea alticola** (Holttum & H. St. John) Callm. & Buerki, **comb. nova.**
   **Typus:** **MALAYSIA. Johore (Peninsular Malaysia):** Sungei Kayu, Mawai-Jemaluang rd., II.1935, Corner s.n. (holo-: SING [SING0169801]).

**Distribution and ecology.** – **Benstonea alticola** is found in montane forest and is an epiphyte growing to 12 m above ground, or a terrestrial shrub on limestone domes in Peninsular Malaysia (Bukit Takun, Selangor; Gua Musang, Kelantan) and Borneo (Sarawak) at an altitude of c. 700-1500 m.

4. **Benstonea andersonii** (H. St. John) Callm. & Buerki, **comb. nova.**
   **Typus:** **MALAYSIA. Sarawak (Borneo):** Lawas, XI.1960, Anderson s.n. (holo-: SAR!).

**Distribution and ecology.** – **Benstonea andersonii** is known from freshwater swamp forests of Borneo (Sabah and Sarawak) (**STONE**, 1993).

5. **Benstonea ashtonii** (B. C. Stone) Callm. & Buerki, **comb. nova.**
   **Typus:** **BRUNEI:** Gunong Pagon Periok, IV.1958, P. S. Ashton 283 (holo-: K [K000781334!]; iso-: PH [PH960512] image seen).

**Distribution and ecology.** – **Benstonea ashtonii** is known from tropical forest understorey of North Borneo (Brunei and Sabah) (**STONE**, 1993).

6. **Benstonea atrocarpa** (Griff.) Callm. & Buerki, **comb. nova.**

**Typus:** **MALAYSIA. Malacca:** Griffith s.n. (holo-: K).

**Distribution and ecology.** – **Benstonea atrocarpa** occurs in lowland swamp forests in Peninsular Malaysia, Singapore and Sumatra (**STONE**, 1978).

7. **Benstonea beccata** (B. C. Stone) Callm. & Buerki, **comb. nova.**

**Typus:** **MALAYSIA. Sarawak (Borneo):** Mt. Kinabalu, Marai Parai ridge, 17.I.1983, Ansow, Kulip & Tan SNP (holo-: SNP!).

**Distribution and ecology.** – **Benstonea beccata** is endemic to the montane forests around Mt. Kinabalu in Borneo (Sabah) (**STONE**, 1993).
Fig. 4. – Inflorescences and details of stigmas of species of Benstonea Callm. & Buerki. A. Benstonea affinis (Kurz) Calim. & Buerki; B. Benstonea gibbsiana (Martelli) Calim. & Buerki; C. Benstonea ornata (Solms) Calim. & Buerki; D. Benstonea pachyphylla (Merr.) Calim. & Buerki.

[Photos: M. W. Callmander]


**Distribution and ecology.** – *Benstonea biplicata* is restricted to southern Thailand, close to the Malaysian border (STONE, 1968b).

**Observations.** – This species was placed in *Pandanus* sect. *Fusiforma* by STONE (1968b), a section that we have not included in *Benstonea* (see above). Careful examination of the type in SING showed that its leaves (c. 4 × 100 cm) and styles (sharp and narrow) are similar to those in all the other species of *Benstonea*. *Benstonea biplicata* is therefore excluded from *Pandanus* sect. *Fusiforma* and transferred here to *Benstonea*. It is morphologically similar to *B. nana* (Martelli) Callm. & Buerki, but differs in possessing a larger syncarp. Pending taxonomic revisions in the region should help clarify the status of this taxon.


**Typus:** MALAYSIA. Sabah (Borneo): Beaufort Dist., Lumat, V.1961, J. Singh SAN 24235 (holo-: SAN!; iso-: K [K000781344]!).

**Distribution and ecology.** – *Benstonea brevistylis* is endemic to lowland tropical forest understorey in Borneo (eastern Sabah) (STONE, 1993).


**Typus:** MALAYSIA. Sarawak (Borneo): Miri, Sg. Dalam Forest Reserve, S.V.1959, E. F. Brunig S17492 (holo-: SAR!).

**Distribution and ecology.** – *Benstonea brunigii* is endemic to lowland tropical forest understorey in Borneo (Sarawak) (STONE, 1993).


**Typus:** MALAYSIA. Sarawak (Borneo): Baram Dist., Gunong Api, 12.VII.1961, Anderson 4720 (holo-: SAR!).

**Distribution and ecology.** – *Benstonea calcinata* (B. C. Stone) Callm. & Buerki is endemic to limestone hills in Gunung Mulu National Park in Borneo (Sarawak) (STONE, 1993).

12. **Benstonea celebica** (Warb.) Callm. & Buerki, comb. nova.
    = *Pandanus celebicus* Warb. in Engl., Pflanzenr. 3(IV , 9): 80. 1900.

**Typus:** INDONESIA. Sulawesi: s.d., Warburg s.n. (holo-: B [B100279969] image seen; iso-: FI [FI003942] image seen).

**Distribution and ecology.** – *Benstonea celebica* is restricted to Sulawesi (Indonesia) (STONE, 1978).

**Observations.** – The delimitation of this taxon remains challenging. The fruiting material deposited at B was apparently destroyed, but a photograph is deposited at FI. According to WARBURG’S description (1900), *B. celebica* is morphologically very similar to *B. pachyphylla* (Merr.) Callm. & Buerki. STONE (1978) has suggested that these two entities may be conspecific, but in the absence of fruiting material we have opted to maintain them as distinct until new collections are available.

13. **Benstonea copelandii** (Merr.) Callm. & Buerki, comb. nova.

**Typus:** PHILIPPINES. Negros: Gimagong River, 5.I.1904, Copeland 140 (PNG destroyed; iso-: FI not located).


**Distribution and ecology.** – *Benstonea copelandii* is endemic to the Philippines (ranging from Luzon to Mindanao).
**Observations.** – The holotype, deposited at the herbarium in Manila (PNG), was destroyed during World War II, but a fragment has been located in FI. The original collection was rather incomplete, comprising only a few drupes, which were illustrated in Martelli (1914: Tab. 31, Fig. 5-7) and St. John (1969: 357, Fig. 295). We have not been able to locate the duplicate material at FI despite an extensive search. A neotype (Elmer 15267) is therefore designated here. This collection is complete and well represented in several herbaria. Pandanus copelandii var. panchoi is considered as a synonym. It was described on the basis of a collection bearing only a single syncarp (vs 3-8 crowded, spicate syncarp in the remaining collections of *Benstonea copelandii*), but is considered to fall within the morphological variation of the species, even though it is rather atypical and is documented only by a single collection.

14. *Benstonea ellipsoidea* (Warb.) Callm. & Buerki, **comb. nova.**

= Pandanus ellipsoidea Warb. in Engl., Pflanzenr. 3(IV, 9): 81. 1900.


**Distribution and ecology.** – *Benstonea ellipsoidea* is confined to the mountain rainforests of the island of Sulawesi in Indonesia (Stone, 1978).

**Observations.** – This taxon was described on the basis of an immature infructescence (Warburg 16151), which is almost impossible to distinguish from Beccari s.n., type of *Pandanus dipsaceus*. In his revision, Stone (1978) maintained these two as separate species, albeit with much doubt. *Benstonea ellipsoidea* is indeed very similar to *B. affinis*, but it differs in the shape and dimensions of its drupes and the syncarps. Moreover, *B. ellipsoidea* is found at high altitude on limestone substrate in Sulawesi (Keim, pers. comm.), whereas *B. affinis* is found in lowlandpeat swamp forests from Vietnam to Peninsular Malaysia, Borneo and Indonesia (Bangka, Sumatra). Given the strong ecological differences between these taxa, we tentatively follow the treatment of Stone (1978).

15. *Benstonea elostigma* (Martelli) Callm. & Buerki, **comb. nova.**


**Typus:** **Malaysia. Perak (Peninsular Malaysia):** Larut, IX.1884, King’s Collector (Kunstler) 6559 (lecto-: CAL; isoneo-: SING [SING0059007]) (designated by St. John, 1965: 224).

**Distribution and ecology.** – *Benstonea elostigma* occurs in lowland rainforests at c. 30-700 m in Peninsular Malaysia.

16. *Benstonea foetida* (Roxb.) Callm. & Buerki, **comb. nova.**

= Pandanus foetidus Roxb., Fl. Ind. ed. 1832, 3: 742. 1832.

= Pandanus wallichianus Martelli in Webbia 4: 36. 1913 [nomen nudum].

**Neotypus** (designated here): **Burma:** Amherst, 1827, Cat. Wallich 8588 (K [K000781275]; isoneo-: K [K000781270], M [M0175808, M0175809, M0175813] images seen).

**Distribution and ecology.** – *Benstonea foetida* is found in lowland and swamp forests around the Bay of Bengal in Bangladesh, Burma and India (Stone, 1978).

**Observations.** – Roxburg described this species in 1832 in his *Flora Indica*. He wrote that it grew wild in Bengal and was cultivated at the Royal Botanic Gardens in Calcutta. A careful search of various herbaria known to hold collections made by Roxburg failed to reveal any authentic material of *Benstonea foetida*. In Wallich’s catalogue (1831), published the year before the protologue, two collections can be attributed to *Pandanus foetidus*: *Wallich 8588 & 8591*. The latter of these represents a staminate inflorescence (E [E00567756] image seen; FI image seen; K image seen; M [M0175808, M0175809, M0175813] images seen).

**Distribution and ecology.** – *Benstonea foetida* is found in lowland rainforests (> 800 m) in Sabah (Borneo) (Fig. 4B).

17. *Benstonea gibbsiana* (Martelli) Callm. & Buerki, **comb. nova.**


**Typus:** **Malaysia. Sabah (Borneo):** between Tambunan and Korikut, II.1930, S. L. Gibbs 1417 (holo-: BM [BM00958510]!).

**Distribution and ecology.** – *Benstonea gibbsiana* is known only from lowland rainforests (> 800 m) in Sabah (Borneo) (Fig. 4B).
Fig. 5. - Inflorescences and details of stigmas of species of Benstonea Callm. & Buerki. A. Benstonea parva (Ridl.) Callm. & Buerki; B. Benstonea pectinata (Martelli) Callm. & Buerki; C. Benstonea rupestris (B. C. Stone) Callm. & Buerki; D. Benstonea thomissophylla (B. C. Stone) Callm. & Buerki.

[Photos: M. W. Callmander]
18. **Benstonea glaucophylla** (Ridl.) Callm. & Buerki, **comb. nova.**


**Typus:** MALAYSIA. Perak (Peninsular Malaysia): Thaiping Hill, XII.1898, Ridley s.n. (holo-: SING [SING0059042]!).

**Distribution and ecology.** – *Benstonea glaucophylla* appears to be restricted to lowland rainforests (450-750 m) of Peninsular Malaysia (STONE, 1978).

19. **Benstonea herbacea** (Martelli) Callm. & Buerki, **comb. nova.**


**Lectotypus** (designated here): MALAYSIA. Perak (Peninsular Malaysia): Trang, III.1881, Kunstler 1397 (FI [FI003936] image seen).

**Distribution and ecology.** – *Benstonea herbacea* grows in lowland and mountain rainforests (600-1300 m) of northern Peninsular Malaysia and the southern part of Thailand (STONE, 1978).

**Observations.** – The collection locality for the type of *Pandanus herbaceus* Martelli was cited as “Irang, Penins. Malese (H. Calc.)” (MARTELLI, 1904: 303). STONE (1978: 37) later indicated “coll. ignot.”, but a fragment in Martelli’s herbarium (FI) clearly comes from the type locality cited by Martelli and was collected by H. H. Kunstler (Kunstler 1397), and should be considered as type material. Because the holotype in CAL was not located by B. C. Stone and appears to have been lost, the collection in FI is here designated as the lectotype.

20. **Benstonea humilis** (Lour.) Callm. & Buerki, **comb. nova.**

= *Pandanus humilis* Lour., Fl. Cochinch.: 603. 1790.


**Distribution and ecology.** – *Benstonea humilis* grows in rainforests from NE India to Peninsular Malaysia from sea level to c. 300 m (STONE, 1983b).

**Observations.** – *Benstonea humilis*, as circumscribed here, includes the types of many validly published names. A complete synonymy can be found in Appendix 1.

21. **Benstonea inquilina** (B. C. Stone) Callm. & Buerki, **comb. nova.**


**Typus:** MALAYSIA. Sabah (Borneo): Sandakan Dist., Ulu Dusun, 28.III.1977, Stone & al. 12890 (holo-: KLU!; iso-: K!, PH [PH00018271, PH00018272] image seen, SAN!).

**Distribution and ecology.** – *Benstonea inquilina* is only known by the type specimen, collected near Sandakan in lowland secondary rainforests.

22. **Benstonea korthalsii** (Solms) Callm. & Buerki, **comb. nova.**

= *Pandanus korthalsii* Solms in Linnaea 42: 12. 1878.


**Distribution and ecology.** – *Benstonea korthalsii* occurs in rainforests from Borneo to Sumatra (STONE, 1978).

23. **Benstonea kurzii** (Merr.) Callm. & Buerki, **comb. nova.**


**Typus:** INDONESIA. Java: Mt. Salak, 17.V.1863, Coll. ignot. (lecto-: BO) (designated by STONE, 1972: 29).

**Distribution and ecology.** – *Benstonea kurzii* is confined to the rainforests of Java (Indonesia) (STONE, 1978).

24. **Benstonea lauterbachii** (K. Schum. & Warb.) Callm. & Buerki, **comb. nova.**

= *Pandanus lauterbachii* K. Schum. & Warb. in Engl., Pflanzenr. 3(IV, 9): 81. 1900.

**Typus:** PAPUA NEW GUINEA. Madang Prov.: Gogol, 28.X.1890, Lauterbach 863 (holo-: B [B100216880] image seen).

**Distribution and ecology.** – *Benstonea lauterbachii* grows on wet soils, in swamps or near mangroves in New Guinea (West Papua, Papua and Papua New Guinea) and in northern Australia (Queensland) (WILSON, 2011).
25. **Benstonea lepatophila** (B. C. Stone) Callm. & Buerki, **comb. nova.**
   **Typus:** *Malaysia. Sarawak (Borneo):* Gunung Mulu NP, 14.IV.1978, Argent & Jermy 973 (holo-: E [E00318031] image seen; iso-: KL!; SARI!).

   **Distribution and ecology.** — *Benstonea lepatophila* is endemic to the limestone hills of Gunung Mulu National Park in Borneo (Sarawak) (Stone, 1993).

26. **Benstonea monticola** (F. Muell.) Callm. & Buerki, **comb. nova.**
   = *Pandanus monticola* F. Muell., Fragm. 5: 40. 1865.
   **Typus:** *Australia. Queensland:* around Rockingham Bay, 1864, Dallachy s.n. (holo-: MEL; iso-: P [P02138396, P02138397]).

   **Distribution and ecology.** — *Benstonea monticola* is restricted to the lowland rainforests (from sea level to 800 m) in northeastern Australia (Queensland) (Wilson, 2011).

27. **Benstonea nana** (Martelli) Callm. & Buerki, **comb. nova.**
   **Typus:** *Malaysia. Perak (Peninsular Malaysia):* Larut, IV.1883, Kunstler 4080 (holo-: FI [FI003936: 3 sheets] images seen; iso-: SING [SING0059057]).

   **Distribution and ecology.** — *Benstonea nana* is endemic to the lowland rainforests of Peninsular Malaysia (Perak and Pahang) and southern Thailand occurring at an altitude of 90-300 m (Stone, 1978).

28. **Benstonea odoardii** (Martelli) Callm. & Buerki, **comb. nova.**


   **Distribution and ecology.** — *Benstonea odoardii*, as currently circumscribed, is widely distributed in lowland and montane rainforests of New Guinea (from 100 to 2000 m) (Jebb, 1982).

   **Observations.** — The type collection of *B. odoardii* (*D’Albertis* s.n.), deposited in the Beccari herbarium (*Erbario Beccari della Malesia*) in FI, includes the holotype mounted on three sheets, two with leaves and one with the infructescence. Another possible fragment of the infructescence, considered here as an isotype, is also kept in Martelli’s herbarium. This species is a stemless shrub with long slender leaves (up to 250 cm) and a solitary sub-globose syncarp (c. 6-12 cm in diam.) borne on an erect peduncle (up to 60 cm) (Jebb, 1992). The range of variation of *B. odoardii* accepted here follows *Jebb* (1982), who gathered several specimens that cannot be distinguished from other material of this species, even though the styles have a rather variable morphology: either short and acute or more slender to recurved. All this material seems to fall within the currently accepted range of variability of the species (Jebb, 1982). Further collections and fieldwork are required to determine whether this circumscription is appropriate or whether it may include more than a single variable species (Jebb, 1982).

29. **Benstonea ornata** (Solms) Callm. & Buerki, **comb. nova.**
   = *Pandanus ornatus* Solms in Linnaea 42: 11. 1878.


   **Distribution and ecology.** — *Benstonea ornata* is distributed from Peninsular Malaysia to Borneo (through Sumatra and Singapore) and Thailand. It grows in forest understory on hilltops, often on poor soils, at an altitude of 300 to 1350 m (Stone, 1978).
Observations. – Pandanus ornatus was first illustrated by Gaudichaud (1841) in the invalidly published genus Fisquetia Gaudich. This name was then invalidly transferred by Kurz (1869) to Pandanus, without a description. Solms-Laubach (1878), while attempting to transfer it to Pandanus, in fact described it as new, designating two syntypes: Gaudichaud’s drawing and a Gaudichaud collection in the Delessert herbarium in G (Gaudichaud 108). His description thus validates the name as P. ornatus, even though he believed he was simply making a new combination. Gaudichaud 108 has both an infructescence and leaves, and is here designated as the lectotype. Benstonea ornata is characterized by a sub-cylindric cephalia (varying in length from 5 to 23 cm), pendent on a long peduncle (up to 50 cm) with sharp, proximally arcuate styles up to 5 mm in length (Fig. 4C). This species is wonderfully illustrated in Gaudichaud (1841: Tab. 5, Figs. 1, 8-9).

Martelli (1904) described Pandanus monotheca based on Ridley 10821. The holotype deposited at CAL was not found by Stone, neither in 1968 nor in 1974 (Stone, 1978), and this entity was therefore regarded by him as a poorly known species. Drupes of this collection (with neither leaves nor syncarps) were, however, subsequently found in both FL and G. The FL collection, here designated as lectotype, clearly belongs to Benstonea ornata, and Pandanus monotheca is therefore treated as a synonym.

30. Benstonea pachyphylla (Merr.) Callm. & Buerki, comb. nova.


Distribution and ecology. – Benstonea pachyphylla is endemic to the lowland rainforests of Borneo (Kalimatan, Sabah and Sarawak).

Observations. – This species is very characteristic, with its acaulescent habit and syncarp borne in the middle of a large clump of leaves growing directly from the ground (Fig. 4D). Its leaves are similar to those of the poorly known B. celebica, the latter only known by its leaves and a picture of the fruit (see above). These may represent a single species that occurs in both Sulawesi and Borneo.

31. Benstonea parva (Ridl.) Callm. & Buerki, comb. nova.


Distribution and ecology. – Benstonea parva grows in lowland to montane rainforests (from sea level to 1500 m) and is distributed from Peninsular Malaysia through Singapore to Borneo (Sabah).

Observations. – This small terrestrial herbaceous species is characterized by its short monocaulous habit (up to 60 cm high), its broad but small leaves that are abruptly caudate-acuminate in the distal part, glaucous on the abaxial surface, and its rather small globose terminal syncarp (Fig. 5A). It remains difficult to differentiate B. parva from B. unguiculata (Ridl.) Callm. & Buerki (with slightly narrower leaves and larger fruit), and further collections are needed to confirm whether they are distinct.


Typus: MALAYSIA. Sarawak (Borneo): Beccari s.n. (holo-: FL [FI003941, carpo.] image seen).

Distribution and ecology. – Benstonea pectinata occurs in the montane rainforests (900-2500 m) of Borneo and has been collected twice in Sumatra (Stone, 1975a, 1978).

Observations. – This species is strictly epiphytic and easily distinguished from other epiphytic members of the genus (e.g. B. alticola) by its lobed auricles at the base of the leaves. Benstonea pectinata has often been collected on fallen trees in montane rainforests, but seems to be a strict epiphyte (Fig. 5B).

33. Benstonea permicron (Kaneh.) Callm. & Buerki, comb. nova.

= Pandanus permicron Kaneh. in Bot. Mag. (Tokyo) 55: 258. 1940.


Distribution and ecology. – Benstonea permicron is found growing on clay between 100 to 1200 m in the rainforests of West Papua (New Guinea) (Kanehira, 1940; Stone, 1982a).
34. **Benstonea pilaris** (Ridl.) Callim. & Buerki, comb. nova.

   **Lectotypus** (designated here): **MALAYSIA. Negeri Sembilan (Peninsular Malaysia)**: Bukit Tangga, 10.XII.1920, Ridley s.n. (K [K00781286]!)

   **Epitypus** (designated here): **MALAYSIA. Selangor (Peninsular Malaysia)**: Pantai Valley, 13.IX.1967, Mahmud & Sharif s.n. (KLU image seen).

   **Distribution and ecology.** – *Benstonea pilaris* is endemic to the rainforests of Peninsular Malaysia (Stone, 1969).

   **Observations.** – The type collection (Ridley s.n.) has not been found in SING, but a sterile duplicate has recently been rediscovered by HB at Kew, which is here designated as the lectotype. In 1978, Stone designated a specimen at KLU (Mahmud & Sharif s.n.) as the neotype, but the rediscovery of the type revokes this nomenclatural act. As Mahmud & Sharif s.n. is a fertile collection including a complete syncarp, and clearly belongs to *B. pilaris*, we designate it as the epitype.


   **Typus**: **SOLOMON ISLANDS. Santa Isabel Isl.**: Totolu islet, X.1957, Stone 2468 (holo-: BISH!; iso-: K [K000781510, K000781511]).

   **Distribution and ecology.** – *Benstonea poronavila* is confined to the Solomon Islands (in Santa Ysabel and Guadalcanal).

   **Observations.** – The habit of *Benstonea poronavila* is very similar to that of *B. setistyla* (Warb.) Callim. & Buerki, which occurs in Papua New Guinea, a poorly-known species represented by only a few collections from lowland forests in Sepik and Morobe Prov. (Jebb, 1992). The very long styles seem to be distinctive to *B. setistyla* (Jebb, 1992: 34), and we therefore maintain these two species separate. Further fieldwork will be needed to clarify whether they are indeed distinct.

36. **Benstonea pseudosyncarpa** (Kaneh.) Callim. & Buerki, comb. nova.
   - *Pandanus pseudosyncarpus* Kaneh. in Bot. Mag. (Tokyo) 54: 258. 1940.

   **Typus**: **INDONESIA. West Papua (New Guinea)**: Nabire, 16.IV.1939, Inokuma 636 (holo-: FU).

   **Distribution and ecology.** – *Benstonea pseudosyncarpa* occurs in lowland tropical rainforests (from c. 100 to 400 m) (Jebb, 1992; Keim, 2009, 2012) in Indonesian New Guinea (in Papua and recently found in the island of Yapen; Keim, 2009).


   **Typus**: **MALAYSIA. Sarawak (Borneo)**: Gunung Pueh, 25.IX.1955, Purseglove 4799 (holo-: SING [SING0059062]!)

   **Distribution and ecology.** – *Benstonea pumila* is endemic to lowland rainforests of Sabah and Sarawak (Borneo).


   **Typus**: **MALAYSIA. Sarawak (Borneo)**: Bukit Pantu, Melinau, Kapit, 9.VIII.1967, Ilias Paie 25728 (holo-: SAR!) (designated here).

   **Distribution and ecology.** – *Benstonea rupestris* is endemic to the lowland rainforests of Sabah and Sarawak (Borneo).

   **Observations.** – Stone (1978) described *Pandanus scandens* based on a more mature infructescence than that of *P. rupestris*, which was described six years earlier. He distinguished these two taxa based on the number of syncarps (5 in *P. scandens* vs 7 to 9 in *P. rupestris*) and other minor morphological characters such as the leaf length (c. 3 × 105 cm vs 3-4 × 190 cm) and color (glaucescent vs not glaucescent beneath). Recent observations in the field by MWC and SB have, however, confirmed that populations corresponding to *Benstonea rupestris* are characterized by a long pendent infructescence with up to 9 oblong syncarps (sometimes 5 to 8) and that leaf length and width fall within the normal variation of *B. rupestris* as currently circumscribed (Fig. 5C).

   *Pandanus oresbios*, also described in 1978, is here considered as a synonym of *Benstonea rupestris*. It was described based on an immature infructescence, and despite its apparent narrower leaves (2 cm vs 3-4 cm in *B. rupestris*) and smaller syncarps (c. 3.5 cm in length vs 8 cm), it appears to represent the same entity as *B. rupestris*. Further field observations are needed to understand the relationship between *B. rupestris* and *B. calcinacta*, another species that may also be part of this group but is provisionally accepted here (see above).
39. **Benstonea rustica** (B. C. Stone) Callm. & Buerki, **comb. nova.**


   **Typus:** **MALAYSIA. Sarawak (Borneo):** Kalabat highlands, Bario, 15.IV.1970, Nooteboom & Chai 2108 (holo-: L [L0050638] image seen; iso-: SAR!).

   **Distribution and ecology.** – *Benstonea rustica* is endemic to the lowland rainforests of Sabah and Sarawak (Borneo).

40. **Benstonea setistyla** (Warb.) Callm. & Buerki, **comb. nova.**

   = *Pandanus setistylus* Warb. in Engl., Pflanzenr. 3(IV, 9): 81. 1900.


   **Distribution and ecology.** – *Benstonea setistyla* is restricted to lowland rainforests in Papua New Guinea (JEBB, 1982).

41. **Benstonea stenocarpa** (Solms) Callm. & Buerki, **comb. nova.**


   **Typus:** **INDONESIA. West Papua (New Guinea):** Mt. Arfak, ad Hatam, VI.1875, Beccari s.n. (holo-: FI-B [FI003937: Erbario Beccari 11486]; iso-: B [B100279929] image seen).

   **Typus:** **PANDANUS acicularis** H. St. John in Pacific Sci. 27: 44. 1973. **Typus:** **PAPUA NEW GUINEA. Morobe Dist.:** Satelberg, 30.VII.1938, M. S. Clemens 8578 (holo-: B [B10027996] image seen), **syn. nov.**


   **Distribution and ecology.** – *Benstonea stenocarpa* is endemic to lowland rainforests of Sarawak (Borneo).

42. **Benstonea sylvatica** (B. C. Stone) Callm. & Buerki, **comb. nova.**


   **Typus:** **MALSAY. Sarawak (Borneo):** Bau Dist., Bukit Jebong, 10.VII.1970, Anderson & Chai S29924 (holo-: KLU image seen; iso-: SAR!).

   **Distribution and ecology.** – *Benstonea sylvatica* is endemic to limestone hills of the Sarawak state in Borneo.

43. **Benstonea thomissophylla** (B. C. Stone) Callm. & Buerki, **comb. nova.**


   **Typus:** **MALSAY. Sarawak (Borneo):** Bau Dist., Bukit Jebong, 10.VII.1970, Anderson & Chai S29924 (holo-: KLU image seen; iso-: SAR!).

   **Distribution and ecology.** – *Benstonea thomissophylla* is endemic to limestone hills of the Sarawak state in Borneo.

   **Observations.** – This species has recently been reviewed by KEIM (2012), who adopted a broad species concept, including as synonyms several entities spanning from the Moluccas (Halmahera Isl.) through the Bismark Archipelago to the northern part of the Solomon Island (Bougainville) (see KEIM, 2012 and Appendix 1). Among those synonyms, *Pandanus misimaensis* was regarded as a *nomen nudum* by KEIM (2012), but in fact the name was validly published by STONE (1978: 54). Another species, *P. gladiator* B. C. Stone, not mentioned in Keim’s taxonomic review, shares all the morphological characters of *P. stenocarpus*, including its typical beaked styles (see STONE, 1983a: 210, Fig. 4), and is therefore considered as a synonym.

44. **Benstonea sylvatica** (B. C. Stone) Callm. & Buerki, **comb. nova.**


   **Typus:** **MALSAY. Sarawak (Borneo):** Bau Dist., Bukit Jebong, 10.VII.1970, Anderson & Chai S29924 (holo-: KLU image seen; iso-: PH [PH00018604, PH00018605] images seen).

   **Distribution and ecology.** – *Benstonea sylvatica* is endemic to lowland rainforests of Sarawak (Borneo).

   **Observations.** – This species has recently been reviewed by KEIM (2012), who adopted a broad species concept, including as synonyms several entities spanning from the Moluccas (Halmahera Isl.) through the Bismark Archipelago to the northern part of the Solomon Island (Bougainville) (see KEIM, 2012 and Appendix 1). Among those synonyms, *Pandanus misimaensis* was regarded as a *nomen nudum* by KEIM (2012), but in fact the name was validly published by STONE (1978: 54). Another species, *P. gladiator* B. C. Stone, not mentioned in Keim’s taxonomic review, shares all the morphological characters of *P. stenocarpus*, including its typical beaked styles (see STONE, 1983a: 210, Fig. 4), and is therefore considered as a synonym.

   **Observations.** – This species has recently been reviewed by KEIM (2012), who adopted a broad species concept, including as synonyms several entities spanning from the Moluccas (Halmahera Isl.) through the Bismark Archipelago to the northern part of the Solomon Island (Bougainville) (see KEIM, 2012 and Appendix 1). Among those synonyms, *Pandanus misimaensis* was regarded as a *nomen nudum* by KEIM (2012), but in fact the name was validly published by STONE (1978: 54). Another species, *P. gladiator* B. C. Stone, not mentioned in Keim’s taxonomic review, shares all the morphological characters of *P. stenocarpus*, including its typical beaked styles (see STONE, 1983a: 210, Fig. 4), and is therefore considered as a synonym.
44. **Benstonea thurstonii** (C. H. Wright) Callm. & Buerki, **comb. nova.**


**Typus:** Fiji. Viti Levu: V.1894, J. B. Thurston s.n. (holo-: K!; iso-: FI [FI003945]).

**Distribution and ecology.** – *Benstonea thurstonii* is endemic to Fiji and has been recorded on the islands of Viti Lev and Koro, and has recently been collected on Vanua Levu (Fig. 6).

45. **Benstonea thwaitesii** (Martelli) Callm. & Buerki, **comb. nova.**


**Distribution and ecology.** – *Benstonea thwaitesii* is endemic to the lowland rainforests of Sri Lanka (Stone, 1975b).

46. **Benstonea toei** (H. St. John) Callm. & Buerki, **comb. nova.**


**Typus:** Thailand: Krabi, 83 km from Huay Yawt, 28.I. 1958, Tem Smitinand 4143 (holo-: BKF [SN080179] image seen).

**Distribution and ecology.** – *Benstonea toei* is endemic to lowland evergreen forests in Thailand and Peninsular Malaysia.

**Observations.** – This species is morphologically similar to *B. humilis* but lacks the tessellate venation and armed pleats on the leaves that characterized the latter. Furthermore, *B. toei* has a syncarp with fewer and smaller drupes (160 drupes of 15-18 mm long vs 240-430 drupes of 20-25 mm in *B. humilis*). *Benstonea toei* was strangely omitted from Stone’s (1978) revision of *Pandanus* subg. Acrostigma.
47. **Benstonea tunicata** (B. C. Stone) Callm. & Buerki, **comb. nova.**


**Typus:** **MALAYSIA. Sabah (Borneo):** Mt Kinabalu, S slope, 11.IV.1973, Stone & al. 11437 (holo-: PH [PH000 18607] image seen; iso-: K [K000781395]!, SING [SING0 059102]!).

**Distribution and ecology.** – **Benstonea tunicata** is confined to montane rainforests of Mt. Kinabalu in Sabah (Borneo) (Stone, 1975a).

48. **Benstonea undulifolia** (Holtttum & H. St. John) Callm. & Buerki, **comb. nova.**


**Typus:** **MALAYSIA. Johore:** Sungei Kayu, Mawai-Jamalun rd., 11.X.1936, Corner 32477 (holo-: SING [SING0 59105], iso-: K [K000781312]!, SING [SING059104]!).

**Distribution and ecology.** – **Benstonea undulifolia** is known only from lowland swampy rainforest of Johore in Peninsular Malaysia (Stone, 1975b).

49. **Benstonea unguiculata** (Ridl.) Callm. & Buerki, **comb. nova.**


**Typus:** **MALAYSIA. Selangor (Peninsular Malaysia):** Gunung Kutu, V.1896, Ridley 7659 (holo-: SING [SING0 59105]!).

**Distribution and ecology.** – **Benstonea unguiculata** is endemic to lowland rainforests of Peninsular Malaysia from sea level to 1500 m (Stone, 1978).

50. **Benstonea vriensii** (Martelli) Callm. & Buerki, **comb. nova.**

\[ = Pandanus vriensii \] Martelli in Webbia 4: 433. 1914.

**Typus:** **INDONESIA. Sumatra:** Battakbergen, I.1905, De Vriens s.n. (holo-: FI [FI003944: 3 sheets] images seen).

**Distribution and ecology.** – **Benstonea vriensii** is confined to the lowland rainforests of Sumatra (Indonesia) (Stone, 1978).

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References

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### Appendix 1. Complete list of accepted names in Benstonea Callm. & Buerki with synonyms (incl. basionyms).

<table>
<thead>
<tr>
<th>Accepted taxon name</th>
<th>Synonyms (incl. Basionyms)</th>
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</table>
| 1 Benstonea adinobotrys (Merr. & L. M. Perry) Callm. & Buerki | P. adinobotrys Merr. & L. M. Perry  
P. angiensis Kaneh.  
P. congregatus H. St. John  
P. ketele B. C. Stone  
P. lustrorum B. C. Stone |
| 2 Benstonea affinis (Kurz) Callm. & Buerki | P. affinis Kurz  
P. aurantiacus Ridl.  
P. merrillii Warb.  
P. sarawakensis Martelli |
| 3 Benstonea alticola (Holttum & H. St. John) Callm. & Buerki | P. alticola Holttum & H. St. John |
| 4 Benstonea andersonii (H. St. John) Callm. & Buerki | P. andersonii H. St. John |
| 5 Benstonea ashtonii (B. C. Stone) Callm. & Buerki | P. ashtonii B. C. Stone |
| 6 Benstonea atrorcarpa (Griff.) Callm. & Buerki | P. atrorcarpus Griff. |
| 7 Benstonea beccata (B. C. Stone) Callm. & Buerki | P. beccatus B. C. Stone |
| 8 Benstonea biplicata (H. St. John) Callm. & Buerki | P. biplicatus H. St. John |
| 9 Benstonea brevistylin (B. C. Stone) Callm. & Buerki | P. brevistylin B. C. Stone |
| 10 Benstonea brunigii (B. C. Stone) Callm. & Buerki | P. brunigii B. C. Stone |
| 11 Benstonea calcinacta (B. C. Stone) Callm. & Buerki | P. calcinactus B. C. Stone |
| 12 Benstonea celebica (Warb.) Callm. & Buerki | P. celebicus Warb. |
| 13 Benstonea copelandii (Merr.) Callm. & Buerki | P. copelandii Merr.  
P. copelandii var. panchoi B. C. Stone  
P. muricatus Merr. |
| 14 Benstonea ellipsoidea (Warb.) Callm. & Buerki | P. ellipsoidea Warb.  
P. dipsaceus Martelli  
P. kjellbergii Fagerl. |
| 15 Benstonea elostigma (Martelli) Callm. & Buerki | P. elostigma Martelli |
| 16 Benstonea foetida (Roxb.) Callm. & Buerki | P. foetida Roxb.  
P. wallichianus Martelli, inval. name |
| 17 Benstonea gibbsiana (Martelli) Callm. & Buerki | P. gibbsianus Martelli |
| 18 Benstonea glaucophylla (Ridl.) Callm. & Buerki | P. glaucophyllus Ridl. |
| 19 Benstonea herbacea (Martelli) Callm. & Buerki | P. herbaceus Martelli  
P. collinus Ridl.  
P. collinus var. spinulosus Ridl.  
P. ingianus Martelli |
| 20 Benstonea humilis (Lour.) Callm. & Buerki | P. humilis Lour.  
Fisquetia ovata Gaudich., inval. name  
P. distans Craib  
P. leucocephalus Martelli  
P. ovatus Kurz, inval. name  
P. ovatus Warb.  
P. perakensis Ridl.  
P. pierrei Martelli  
P. pierrei var. bariensis Martelli  
P. pierrei var. constrictus Gagn.  
P. pseudofoetidus Martelli  
P. retroaculeatus H. St. John  
P. similis Craib  
P. toinu H. St. John |
| 21 Benstonea inquilina (B. C. Stone) Callm. & Buerki | P. inquillius B. C. Stone |
| 22 Benstonea korthalsii (Solms) Callm. & Buerki | P. korthalsii Solms |
| 23 Benstonea kurzii (Merr.) Callm. & Buerki | P. kurzii Merr.  
P. asper H. St. John |
| 26 Benstonea monticola (F. Muell.) Callm. & Buerki | P. monticola F. Muell.  
P. pluvisilvaticus H. St. John |
<table>
<thead>
<tr>
<th>Accepted taxon name</th>
<th>Synonyms (incl. Basionyms)</th>
</tr>
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</table>
| 27 **Benstonea nana** (Martelli) Callm. & Buerki | *P. nanus* Martelli  
*P. magnifibrosus* H. St. John |
| 28 **Benstonea odoardi** (Martelli) Callm. & Buerki | *P. odoardi* Martelli  
*P. eumeke* B. C. Stone  
*P. humicola* Kaneh.  
*P. ihuanus* Martelli  
*P. inokumae* Kaneh.  
*P. papanus* Ridl., illeg. name  
*P. pentagonos* H. St. John  
*P. rostellatus* Merr. & L. M. Perry |
| 29 **Benstonea ornata** (Solms) Callm. & Buerki | *P. ornatum* Solms  
*Fisquetia ornata* Gaudich., inval. name  
*P. monotheca* Martelli  
*P. ornatus* Kurz, inval. name  
*P. ornatus f. spicatus* Martelli  
*P. recurvatus* H. St. John |
| 30 **Benstonea pachyphylla** (Merr.) Callm. & Buerki | *P. pachyphyllum* Merr.  
*P. apicalis* H. St. John |
| 31 **Benstonea parva** (Ridl.) Callm. & Buerki | *P. parvus* Ridl.  
*P. flagellifer* Warb.  
*P. mollifoliaceus* H. St. John |
| 32 **Benstonea pectinata** (Martelli) Callm. & Buerki | *P. pectinatus* Martelli  
*P. papilio* B. C. Stone |
| 33 **Benstonea permicron** (Kaneh.) Callm. & Buerki | *P. permicron* Kaneh. |
| 34 **Benstonea pilaris** (Ridl.) Callm. & Buerki | *P. pilaris* Ridl. |
| 35 **Benstonea poronavila** (B. C. Stone) Callm. & Buerki | *P. poronavila* B. C. Stone |
| 36 **Benstonea pseudosyncarpa** (Kaneh.) Callm. & Buerki | *P. pseudosyncarpus* Kaneh. |
| 37 **Benstonea pumila** (H. St. John) Callm. & Buerki | *P. pumilus* H. St. John |
| 38 **Benstonea rupestris** (B. C. Stone) Callm. & Buerki | *P. rupestris* B. C. Stone  
*P. scandens* B. C. Stone  
*P. oresbios* B. C. Stone |
| 39 **Benstonea rustic** (B. C. Stone) Callm. & Buerki | *P. rustic* B. C. Stone |
| 40 **Benstonea setistyla** (Warb.) Callm. & Buerki | *P. setistyla* Warb. |
| 41 **Benstonea stenocarpa** (Solms) Callm. & Buerki | *P. stenocarpus* Solms  
*P. acicularis* H. St. John  
*P. arcuatus* H. St. John  
*P. dancellmannianus* K. Schum.  
*P. erinaceus* B. C. Stone  
*P. gladiator* B. C. Stone  
*P. jacobii* B. C. Stone  
*P. lictor* B. C. Stone  
*P. misimaensis* B. C. Stone  
*P. nigrifrons* B. C. Stone  
*P. verruculosus* B. C. Stone |
| 42 **Benstonea sylvatica** (B. C. Stone) Callm. & Buerki | *P. sylvaticus* B. C. Stone |
| 43 **Benstonea thomissophylla** (B. C. Stone) Callm. & Buerki | *P. thomissophyllus* B. C. Stone |
| 44 **Benstonea thurston** (C. H. Wright) Callm. & Buerki | *P. thurstonii* C. H. Wright  
*P. varawha* H. St. John |
| 45 **Benstonea thwaitesii** (Martelli) Callm. & Buerki | *P. thwaitesii* Martelli  
*P. foetidus var. racemosus* Trimen |
| 46 **Benstonea toei** (H. St. John) Callm. & Buerki | *P. toei* H. St. John |
| 47 **Benstonea tunicata** (B. C. Stone) Callm. & Buerki | *P. tunicatus* B. C. Stone |
| 48 **Benstonea undulifolia** (Holttum & H. St. John) Callm. & Buerki | *P. undulifolia* Holttum & H. St. John |
| 49 **Benstonea uguiculata** (Ridl.) Callm. & Buerki | *P. uguiculata* Ridl.  
*P. attenuatus* H. St. John  
*P. caudatifolius* H. St. John  
*P. globiferus* Ridl.  
*P. globulosus* H. St. John |
| 50 **Benstonea vriensii** (Martelli) Callm. & Buerki | *P. vriensii* Martelli |