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Update on the systematics of *Benstonea* (Pandanaceae): When a visionary taxonomist foresees phylogenetic relationships

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Abstract

The paleotropical monocot Pandanaceae family comprises c. 700 species distributed into five genera: *Benstonea* (c. 60 spp.), *Freycinetia* (c. 250 spp.), *Martellidendron* (6 spp.), *Pandanus* (c. 450 spp.) and *Sararanga* (2 spp.). *Benstonea* was circumscribed to include species previously placed in *Pandanus* section *Acrostigma* (one of the four sections of *Pandanus* subgenus *Acrostigma*). New phylogenetic data show that the six species of the remaining three sections of subgenus *Acrostigma* (sections *Epiphytica*, *Fusiforma* and *Platystigma*) and a seventh species doubtfully placed in section *Acrostigma* (*Pandanus microglottis*) also belonged to *Benstonea*. This genus is therefore characterized by a suite of morphological characters, viz. stigmatic groove on the adaxial side of the stigma and a staminate flower reduced to 1 to 3 free stamens (sometimes joined at base). We therefore make here the necessary seven new combinations accompanied by one lectotypification in *Benstonea*, a genus that now reflects the view of the visionary Benjamin Stone who had already grouped these species in *Pandanus* subgenus *Acrostigma* based solely on morphology.

Introduction

The arborescent or lianoid dioecious monocot family Pandanaceae has c. 700 species distributed throughout the paleotropics. Five genera have been recognized within the family: *Benstonea* Callmander & Buerki (in Callmander *et al.* 2012: 328) (c. 60 spp.), *Freycinetia* Gaudichaud (1824: 509) (c. 250 spp.), *Martellidendron* (Pichi-Sermolli in Martelli & Pichi-Sermolli 1951: 20) Callmander & Chassot (in Callmander *et al.* 2003) (6 spp.), *Pandanus* Parkinson (1773: 76) (c. 450 spp.) and *Sararanga* Hemsley (1894: 216) (2 spp.). The systematics of this family has puzzled generations of botanists due to the apparent convergence/homology of key morphological characters (especially in its largest genus *Pandanus*, see Buerki *et al.* 2012). A recent molecular analysis based on plastid data greatly contributed to our understanding of the evolution of this family and provided evidence to i) support new generic circumscriptions and ii) assess the infra-generic classification within *Pandanus* (Buerki *et al.* 2012). One of the main results of this study was to show the paraphyly of *Pandanus*: the species of *Pandanus* section *Acrostigma* Kurz (1867: 100) formed a distinct lineage, now described as the genus *Benstonea* (Buerki *et al.* 2012, Callmander *et al.* 2012). Only species from *Pandanus* section. *Acrostigma* were included in *Benstonea* (except *P. microglottis* Stone (1982: 34), doubtful sectional placement; see Stone, 1982, 1993) since only species belonging to this section were included in the phylogenetic inference. *Pandanus* subgenus *Acrostigma* (Kurz) Stone (1974: 521) included three other sections: *Epiphytica* Martelli (1904: 304), *Fusiforma* St. John (in Holttum & St. John 1962: 227) and *Pseudoacrostigma* Stone (1971: 146) in Stone's (1974, 1978, 1983) classification. This subgenus was based on the constant adaxial disposition of the stigmatic groove on the apex of each drupe and stamens solitary or in triads (where in triads, free or very slightly joined at the base). Callmander *et al.* (2012) did not transfer all four

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sections to *Benstonea* due to the high morphological heterogeneity of Pandanaceae and the frequent convergence of key characters. In this context, the new genus was characterised by a very distinctive sharp spiniform style with an adaxial disposition of the stigma groove. The three other sections possess blunter (*Pandanus* section *Fusiforma*) to flat elliptic-ovate stigmas (*Pandanus* section *Epiphytica* and section *Pseudoacrostigma*), but all with stigmatic grooves also placed on the adaxial side of the style.

Thanks to collaboration and recent fieldwork in Peninsular Malaysia and Borneo, the authors have been able to include the species belonging to the three sections of *Pandanus* subgenus *Acrostigma* missing from their previous molecular dataset (Booth *et al.* unpubl. data) and have confirmed that they resolve with the other species of *Benstonea*. This new finding was obtained by including at least one representative of each species in our previous plastid DNA matrix based on *matK*, *trnQ-rps16* and *trnL-trnF* (Buerki *et al.* 2012). To further improve our understanding of phylogenetic relationships between species of *Benstonea*, two additional plastid regions were sequenced (*ndhF-rpl32*, *trnV-ndhC*). Finally, a Bayesian phylogenetic inference was conducted following the approach described in Buerki *et al.* (2012) that strongly supported (with Bayesian posterior probabilities > 0.95) the placement of these species in *Benstonea* (Booth *et al.* unpubl. data). The newly sampled species are *Pandanus microglottis* B.C. Stone doubtfully placed in *Pandanus* section *Acrostigma* (see Stone 1982, 1993), *Pandanus epiphyticus* Martelli (1904: 304), the sole member of *Pandanus* section *Epiphytica*; *P. platystigma* Martelli (1904: 300), a member of *Pandanus* section *Pseudoacrostigma* and *P. dumetorum* Holttum & St. John (1962: 227), *P. saint-johnii* Stone (1968: 412) and *P. sobolifer* Stone (1968: 415), all three members of *Pandanus* section *Fusiforma*.

Benjamin Stone worked extensively for more then three decades (1960-1993) on the screw-pine family and remains a leading source for global understanding and reliable classification of the whole family. Our new results are in agreement with Stone's circumscription of *Pandanus* subgenus *Acrostigma*. He was certainly a visionary in combining characters from both staminate and pistillate plants in his classification (Stone, 1974).

When sterile, *Benstonea* is characterized by its leaves with generally armed apical ventral pleats. This character is also present in a few species of *Pandanus*, e.g. *P. discostigma* Martelli (1914: 427). The pistillate plants are characterized by their monocarpellate drupes with the stigmatic grooves consistently placed on the adaxial side of the stigma (never present in *Pandanus*). Finally, the staminate flowers of *Benstonea* are reduced to one stamen, or stamens in triads, free or very slightly joined at the base, a rare combination in *Pandanus*. A clear trend towards filament connation and fasciation of stamens can be observed throughout the latter genus with species showing an androecium represented by numerous stamens arranged in phalanges, often with a *stemonophore* (nearly all the species) but some species have flowers reduced to a single stamen attached to the axis (rarely, i.e. *P. discostigma*).

We here transfer the seven remaining species previously placed in *Pandanus* subgenus *Acrostigma* by Stone (1974, 1978, 1982) to *Benstonea*. These species were previously placed in *Pandanus* section *Acrostigma* (1 sp.), *Pandanus* section *Epiphytica* (1 sp.), *Pandanus* section *Fusiforma* (3 spp.) and *Pandanus* section *Pseudoacrostigma* (2 spp.). Based on the findings mentioned above, we therefore propose the following new combinations: *Benstonea dumetorum* (Holttum & H. St. John) Callm. & Buerki, *comb. nov.*, *B. epiphytica* (Martelli) Callm. & Buerki *comb. nov.*, *B. microglottis* (B.C. Stone) Callm. & Buerki *comb. nov.*, *B. ornithocephala* (B.C. Stone) Callm. & Buerki, *comb. nov.*, *B. platystigma* (Martelli) Callm. & Buerki, *comb. nov.*, *B. saint-johnii* (B.C. Stone) Callm. & Buerki *comb. nov.* and *B. sobolifer* (B.C. Stone) Callm. & Buerki, *comb. nov.* A lectotypification is also provided for *B. platystigma* where the most mature specimen is designated as lectotype (*Beccari 2050*).

Taxonomy

Benstonea dumetorum (Holttum & H. St. John) Callm. & Buerki, *comb. nov.*

Basionym: *Pandanus dumetorum* Holttum & St. John (1962: 227). Type:—MALAYSIA [PENINSULAR]. Trengganu, Ulu Bendong, 500 ft., 30 October 1935, fr., *Corner 30066* (holotype, SING [SING0059073, SING0059074]!; isotype, K [carpo.]!)

Benstonea epiphytica (Martelli) Callm. & Buerki, *comb. nov.*

Basionym: *Pandanus epiphyticus* Martelli (1904: 304). Lectotype (designated by Stone 1978: 65):—MALAYSIA [BORNEO]. Sarawak: Mt. Mattang, 6.1866, fr., *Beccari 1901* (lectotype, FI-B [FI003954]!; isolectotype, FI [FI003960] image seen). Paralectotypes:—MALAYSIA [BORNEO]. Sarawak: Kuching, November 1866, st. fl., *Beccari 2708* (paralectotype, FI-B [FI003956]!; isoparalectotype, FI [FI003961] image seen); ibid. loc., December 1867, st., *Beccari 3991* (paralectotype, FI-B [FI003955]!).

Benstonea microglottis (B.C. Stone) Callm. & Buerki, *comb. nov.*

Basionym: *Pandanus microglottis* Stone (1982: 34). Type:—MALAYSIA [BORNEO]. Sarawak: Mulu National Park, upper reaches of Sg. Melinau Paku, 5 April 1979, fr., *Stone 13694* (holotype, KLU [2 sheets]!; isotypes, BISH [BISH1011591]!, K [K000781348]!, PH [PH00018287, PH00018288, PH00018289, PH00018290] images seen, SAR!)

Benstonea ornithocephala (B.C. Stone) Callm. & Buerki, *comb. nov.*

Basionym: *Pandanus ornithocephalus* (1978: 64). Type:—INDONESIA [NEW GUINEA]. West Papua Prov.: Vogelkop Peninsula [Kepala Burung], Skendi (N of Teminaboean), c. 100 m, 21 May 1958, fr., *Versteegh BW7474* (holotype, L [L0050607]!)

Benstonea platystigma (Martelli) Callm. & Buerki, *comb. nov.*

Basionym: *Pandanus platystigma* Martelli (1904: 300). Lectotype (designated here):—MALAYSIA [BORNEO]. Sarawak: Mt. Mattang, July 1866, fr., *Beccari 2050* (lectotype, FI-B [FI003958] image seen). Paralectotype:—MALAYSIA [BORNEO]. Sarawak: Kuching, June 1865, y. fr., *Beccari 44* (paralectotype, FI-B [FI003957] image seen).

Benstonea saint-johnii (B.C. Stone) Callm. & Buerki, *comb. nov.*

Basionym: *Pandanus saint-johnii* Stone (1968: 412). Type:—MALAYSIA [PENINSULAR]. Johore: Kota Tinggi, Gunung Panti, W ridge, Panti Forest Reserve, c. 1 mile NE of Lombong, 500 ft., 14 April 1966, fr., *Stone, Chew & Hill 6231* (holotype, KLU [2 sheets, carpo.]!)

Benstonea sobolifer (B.C. Stone) Callm. & Buerki, *comb. nov.*

Basionym: *Pandanus sobolifer* Stone (1968: 415) [as soboliferus]. Type:—MALAYSIA [PENINSULAR]. Perak: Gunung Bubu, 19 August 1966, fr., *Whitmore FRI0694* (holotype, KEP!)

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