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The genus *Pandanus* Parkinson (Pandanaeae) on Halmahera Island (Moluccas, Indonesia) with descriptions of three new species and a key to the species on the island

Martin W. Callmander, Ary P. Keim, Sven Buerki & Peter B. Phillipson

Abstract

CALLMANDER, M. W., A. P. KEIM, S. BUERKI & P. B. PHILLIPSON (2015). The genus *Pandanus* Parkinson (Pandanaeae) on Halmahera Island (Moluccas, Indonesia) with descriptions of three new species and a key to the species on the island. *Candollea* 70: 179-195. In English, English abstract. DOI: <http://dx.doi.org/10.15553/c2015v702a2>

Halmahera is the largest (c. 18,000 km²) island of the Moluccan archipelago, but naturalists have only sporadically visited Halmahera and it has remained very poorly explored botanically. However, an intensive botanical inventory project was undertaken between 2012 and 2014 in part of the island to inform flora biodiversity management for certain proposed mining activities. This effort has contributed over 3600 plant collections and nearly doubled the number of *Pandanus* Parkinson (Pandanaeae) specimens (bringing the total to 55) available for Halmahera. After careful examination of all available material and comparison with other material from the region, we are able to present the first overview of the genus for the island. We have identified ten species from the island of which three are new to science and not known elsewhere, while the other seven are all representatives of species already described from other localities. The new species are formally described here as *Pandanus beguinii* Callm. & A. P. Keim, *Pandanus benstoneoides* Callm., Buerki & Phillipson and *Pandanus halmaherensis* Callm. & A. P. Keim. The new species are provided with notes on their respective morphology and known distributional and ecological ranges, line drawings. Those three new species are assigned a preliminary status of Endangered following IUCN Red List Categories and Criteria. All ten species are illustrated with colour photographs and a key to the species is provided.

Keywords

PANDANACEAE – *Pandanus* – Moluccas – Halmahera – Taxonomy – New Species – IUCN Red List

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Introduction

Halmahera is the largest (c. 18,000 km²) island within an archipelago of approximately 2896 islands in Indonesia collectively known as the Moluccas. Administratively the Moluccas are now divided into two provinces: North Maluku, which includes Halmahera, and Maluku, which includes the islands of Ambon and Seram to the south. The Moluccas, together with Sulawesi to the east and a long chain of islands to the south, form the biogeographic region known as Wallacea (Fig. 1), which is a biodiversity hotspot lying between Borneo and New Guinea (MYERS et al., 2000). After Sulawesi, Halmahera is the second largest island of Wallacea. Halmahera has a complex geological history situated at the interference of tectonic plates associated with past and active volcanic arcs (see HALL et al., 1988). The geology of the island consisting now of a mixture of sedimentary rocks resulting from raised coral reefs, intrusive igneous rocks and fragments of continental crust (see HALL, 2001). The coastline of Halmahera is just 13.5 kilometres away from the small, but economically dominant island of Ternate, one of the so-called “Spice Islands”, which is particularly known for the cultivation of cloves (RICKLEFS, 2008). Historically, botanical exploration of the region focused on Ternate, while the flora of Halmahera, despite it being the largest island of the Moluccas, was largely ignored and has remained very poorly known. Among the more extensive collections from the island were those made by Victor E. Beguin, a Dutch planter based in Java, who was hired by the Museum and Inquiry Office for Economic Botany in Buitenzorg (now Bogor) to make extensive travels to the Moluccas (VAN STEENIS, 1950). He visited different parts of Halmahera (see BACKER, 1936) and Ternate between 1920 and 1923 and left a legacy of more than 1750 herbarium collections from these travels, including 640 from Halmahera (VAN STEENIS, 1950). During the second half of the XXth Century only a handful of botanists have made more than a hundred collections each on Halmahera, but among these the contribution of Eduard (“Ed”) de Vogel (682 collections) is certainly the most important. The better-known fauna of Halmahera is however characterized by exceptional species-level endemism but is only moderately diverse (SETIADI et al., 2010).

Rumphius was the first to publish some information about the flora of Halmahera (then known by its indigenous name “Gelolo”) in his legendary six volumes series of “Herbarium Amboinense” (RUMPHIUS, 1741-1755). However, Rumphius probably never visited Halmahera himself despite his numerous visits to other islands adjacent to Ambon where he was based. Rumphius first mentioned *Pandanus ceramicus* Rumph. [nom. inval.] (= *P. conoideus* Lam.) as being present on Halmahera, presumably on the basis of reported observations. The earliest *Pandanaeae* specimens known from Halmahera were collected by Johannes E. Teijsmann and Willem H. de Vriese in their “Herb. Itineris

in Insulas Moluccanas” series in 1859 (VAN STEENIS, 1950). They twice collected *P. polycephalus* Lam. (Vriese & Teijsmann 18; Teijsmann 87; see Table 1), when they briefly visited Halmahera in the vicinity of Sidangolie (now Sidangoligam) on the coast facing Ternate (TEIJSMANN, 1861). Surprisingly, the Italian naturalist Odoardo Beccari, who travelled extensively in the region between 1870 and 1875, never visited Halmahera (BECCARI, 1924). No other records of *Pandanaeae* are known from Halmahera prior to the collections of Victor Beguin, who clearly had an interest in the family and made ca. 50 collections of *Pandanaeae* from Halmahera. A few additional *Pandanus* Parkinson collections were made during the second half of the XXth and early XXIst Century, notably by several ethnologists who visited Halmahera for their studies (YOSHIDA, 1980; TAYLOR, 1990; PURWANTO, 2009).

In 2012, the Missouri Botanical Garden, in collaboration with Herbarium Bogoriense and the National Herbarium of the Netherlands, was engaged by Weda Bay Nickel (WBN) to undertake a botanical inventory on the company’s Contract of Work (CoW), an extensive area spanning the Central and Eastern Halmahera Regencies (Fig. 1) to inform the process of flora biodiversity management in relation to their proposed mining project. This work built on earlier baseline studies undertaken for an impact assessment, which resulted in the identification of several *Pandanaeae* species, but unfortunately no voucher specimens were preserved. Between September 2012 and December 2014, a locally-based inventory team was trained and more than 3600 botanical collections were made on the CoW, and critical identification of the material is being undertaken by specialists. The collections include 65 *Pandanaeae* in three genera: *Benstonea* Callm. & Buerki [1 collection], *Freycinetia* Gaudich. [39 collections] and *Pandanus* [25 collections]. *Benstonea* is morphologically distinct by its one-seeded drupes with its stigma always positioned on the abaxial side of the its acutely-pointed, linear style. This genus is represented by only a single species: *B. verruculosa* (B. C. Stone) Callm., Buerki & Phillipson, which is endemic to Halmahera and which was the subject of a previous publication (CALLMANDER et al., 2014). *Freycinetia*, on the other hand, is characterized by its lianescent habit, multi-ovulate carpels and berry fruits and will be the subject of a forthcoming publication on the diversity of the genus on Halmahera. CALLMANDER et al. (2012) provide a key to the genera of *Pandanaeae* and BUERKI et al. (2012) and GALLAHER et al. (2015) report on molecular phylogenetic studies for the family.

The 25 newly collected *Pandanus* specimens together with Beguin’s legacy of 25 *Pandanus* specimens and the five other available collections allow us to present here a first overview of the genus for Halmahera. In this article we document 10 species of *Pandanus* that we have identified from Halmahera. These include seven species that are already known to

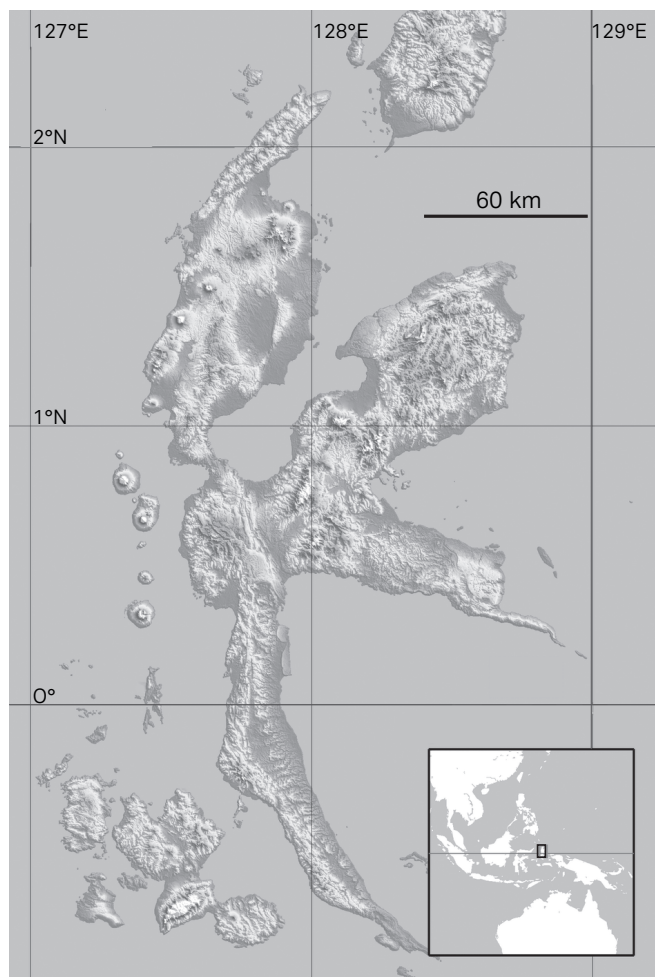


Fig. 1. – General Map of Halmahera Island and its localisation: west of New Guinea and east of Sulawesi (framed).

science and also occur in other parts of South-East Asia, and for which we provide descriptive notes. In addition, our studies have revealed the presence of three species that are new to science and which are, based of current knowledge, endemic to Halmahera. In this article we formally describe the three new species: *P. beguinii* Callm. & A. P. Keim, *P. benstoneoides* Callm., Buerki & Phillipson and *P. halmaherensis* Callm. & A. P. Keim and each of them are provided with notes on their morphology, relationships, conservation assessments and line drawings. We also provide an identification key to the ten species currently known from Halmahera, together with colour photographs for each species (Fig. 2, 3).

The genus *Pandanus* in Halmahera

The coastal *P. dubius* Spreng., *P. polycephalus* and *P. tectorius* Parkinson are widespread in littoral and lowland forest in swampy or sandy ground. *Pandanus dubius* is distrib-

uted from the Andaman Sea (Andaman Nicobar islands) to the western Pacific region (Kiribati, Federated states of Micronesia) and throughout Malesia. This ocean-dispersed species (GALLAHER et al., 2015) is frequently cultivated in the tropics and the leaves are used for basketry and roof thatching. The albumen of the ripe fruit is edible and used in Micronesia as a source of starch (LIM, 2012). It is easily recognizable by its habit (large tree with robust proproots at the base), its wide, coriaceous leaves (11-16 × 200 cm) with conspicuous long-aristate apices and its large pendulous subspherical syncarp (20-30 cm in diam.), composed of pale bluish-green drupes (Fig. 3D). *Pandanus tectorius*, another well-known, ocean dispersed and frequently cultivated species has a broad distribution from Malesia to the Southern Pacific islands (Fig. 2E). This species, which is known to have various medicinal, nutritive and construction properties (LIM, 2012), is taxonomically problematic and is currently regarded as a species complex in need of further study (GALLAHER et al., 2015). *Pandanus polycephalus* is also a strand plant on seashores, it reaches its western-most distribution in the Moluccas and is found through New Guinea and as far east as the Solomon Islands. The species forms a slender treelet to 10 m tall and can be easily recognized by its small multispicate infructescence with the drupes becoming red on ripening (Fig. 2H). A fourth species is confined to coastal areas, *P. kaernbachii* Warb. It is a robust solitary tree reaching up to 10 m high and can be easily identified in the field by its spicate infructescence consisting of 2 to 4 syncarps with incompletely fused phalanges (Fig. 3I). Unlike *P. tectorius*, *P. kaernbachii* is always solitary or in scattered populations (KEIM et al., 2009; Callmänder, pers. obs.). The presence of this species in the Moluccas was firstly reported by KEIM et al. (2008) from Seram Island, 200 km south of Halmahera.

Pandanus krauelianus K. Schum. seems to be a common inland species at low to mid elevation on Halmahera (Table 1). It is part of the morphologically homogenous *Pandanus* sect. *Maysops* H. St. John, in subgen. *Lophostigma* (Brongn.) H. St. John, characterised by a solitary, ovoid-ellipsoid syncarp hidden by persistent bracts, one-seeded drupes and a pileus generally topped apically with a small hardened turret bearing a lateral stigma (Fig. 2F, 2G) (see also STONE, 1974a). STONE (1992) published a review of the section for New Guinea, and accepted ca. 16 species and emphasised the need of further collections in this group in which species delimitation is difficult. In the latter revision, *Pandanus amboinensis* Warb., the first valid publication of *P. sylvestris* Rumph. from Ambon, is considered to be different from *P. krauelianus* from New Guinea (West Papua, Indonesia). JEBB (1992) and KEIM (2009) did consider these two species as synonyms and this broader species concept is followed here. *Pandanus krauelianus*, thus delimited, is distributed from the Moluccas to the Bismark archipelago through New Guinea. Another species with a similar distribution is

found in inland swamps at low elevation: *P. papuanus* Solms. It is a large tree species (to 20 m tall) with a large, impressive cone of proproots at the base and massive pendent syncarps (Fig. 3G, 3H). It is known from similar habitats at higher altitudes (ca. 900 m) in New Guinea (STONE, 1982). *Pandanus conoideus*, first mentioned by RUMPHIUS (1741-1755), has not yet been collected on Halmahera, but a photograph of it taken by one of us (PBP) during his first visit to the island in 2011 confirmed its presence on the island (Fig. 3J). *Pandanus conoideus* is widely cultivated in New Guinea for its edible fruits and may have originated from the Moluccas (STONE, 1982).

The 55 *Pandanus* collections currently known from Halmahera are summarized in Table 1.

Key to the *Pandanus* species on Halmahera

1. Carpels free in one-carpellate and one-seeded drupes (rarely bicarpellate in *P. dubius* Spreng.) 2
- 1a. Carpels connate into multicarpellate, several-seeded drupes 8
2. Stigma filiform or spinescent and linear 3
- 2a. Stigma oblique, flat or on an apical turret, but not filiform or linear 4
3. Infructescence lateral, born just below the base of leaves; drupes with a yellow pileus; stigma filiform, appressed towards the apex of the syncarp, 15-20 mm long (Fig. 2A-D) *P. benstoneiodes* Callm., Buerki & Phillipson
- 3a. Infructescence terminal, pendant; drupes with a red to purple shiny pileus; stigma spinescent, sharp, erect, 6-8 mm long (Fig. 3E, 3F) *P. halmaherensis* Callm. & A. P. Keim
4. Syncarps spicately arranged, small (4 cm long), ovoid; stigma reniform and flat (Fig. 2H) *P. polycephalus* Lam.
- 4a. Syncarp solitary, much larger (10-40 cm long), ellipsoid to oblong; stigma with various shapes but not reniform and flat 5
5. Leaves wide (11-16 cm); drupes large (> 10 cm) at maturity (Fig. 3D) *P. dubius* Spreng.
- 5a. Leaves narrow (< 8 cm); drupes smaller (< 8 cm) at maturity 6
6. Small monocaulous shrub (3 m tall) with few slender proproots at the base; leaves (<110 cm long); and syncarp small (< 15 cm); peduncle slender and short, c. 11 cm long (Fig. 2A-C) *P. beguinii* Callm. & A. P. Keim
- 6a. Tall ramified tree (8-15 m) with large cone of proproots at the base; leaves (>180 cm long); and syncarp large (> 25 cm); peduncle stout and long, > 30 cm long 7
7. Syncarp yellow at maturity; pileus topped apically with a small hardened turret bearing a lateral stigma (Fig. 2F, 2G) *P. krauelianus* K. Schum.

- 7a. Syncarp red at maturity; pileus with central vertical stigma (Fig. 3J) *P. conoideus* Lam.
8. Syncarps spicately arranged (Fig. 3I) *P. kaernbachii* Warb.
- 8a. Syncarp solitary 9
9. Large tree (to 20 m tall) with a large and impressive cone of proproots at the base; leaves large (200-600 cm × 10-15 cm); stigmas borne on the inner edge of the truncate carpel apices (Fig. 3G, 3H) *P. papuanus* Solms
- 9a. Medium-sized tree (< 15 m tall) with a narrow cone of proproots at the base; leaves smaller (mostly 60-150 × 3-6 cm); stigma borne on the top of each of the rounded carpel apices (Fig. 2E) *P. tectorius* Parkinson

Systematics

Pandanus beguinii Callm. & A. P. Keim, **spec. nova** (Fig. 3A-C, 4A, 5).

Typus: INDONESIA. Prov. North Maluku [Halmahera Isl.]: Central, Weda Bay, near Weda Bay, 00°28'38"N 127°59'38"E, 26 m, 30.I.2013, *Callmander, Haris, Lasut & Mahroji 1088* (holo-: G [G00341586]!; iso-: BO!, L!, MO-6465094!, MO-6465095!).

Haec species a congeneris habitu gracili, syncarpo parvo terminali erecto drupas truncatas in turriculam obscuram conicam lateraliter concavam stigma minutum laterale bicornutum gerentem desinente atque inflorescentia staminata ex spica solitaria constante distinguitur.

Shrub to 3 m tall, monocaulous; stem c. 3 cm in diam., with few proproots at the base. *Leaves* spirally arranged, linear, mostly (50-)70-110 cm long, (4-)5-8 cm wide in the middle, but gradually narrowing to 2-3 cm wide and more deeply folded in the lower third above the broader sheath, apex abruptly attenuate with a short acumen (3-10 mm), chartaceous; longitudinal veins visible and prominent on both surfaces; marginal prickles borne 3-4 cm above base to apex, antrorse, 0.4-1 mm long in the lower third, 0.5-1 mm apart, 0.7-1 mm long in the mid-third, 4-7 mm apart, to 0.5-1 mm long in the distal third, 0.5-1.5 mm apart, subappressed to appressed in the distal third; midrib unarmed, except the distal 7-13 cm with prickles > 1.5 mm long towards the apex, irregularly spaced but mostly 1-5 mm apart; sometimes sparsely armed on apical ventral pleats; sheath (2.5-)4-4.5 cm long, (2-)3-4 cm wide at apex, (3-)4-6 cm at base. *Infructescence* terminal, erect, green-orange when immature becoming red at maturity, the solitary syncarp ellipsoid, 10-15 cm long, 5-6 cm wide, peduncle short and slender, c. 11 cm long, c. 1 cm thick at apex, bearing multiple foliaceous bracts, crowded at peduncle apex, partly covering the syncarp, the proximal ones c. 45 cm long, the distal one 15 cm long. *Drupes* 400-500, 13-15 mm long, 5-7 mm wide, 4-5 mm thick, 1-celled, (4-)6-angled, ovoid, truncate, pileus



Fig. 2. – Field pictures of Halmahera *Pandanus* Parkinson species. **A, D.** *Pandanus benstoneoides* Callm., Buerki & Phillipson (pistillate plant); **B, C.** *Pandanus benstoneoides* Callm., Buerki & Phillipson (staminate plant); **E.** *Pandanus tectorius* Parkinson; **F, G.** *Pandanus krauelianus* K. Schum.; **H.** *Pandanus polycephalus* Lam.
 [Photos: **A:** E. Bidault; **D, F-G:** M. Callmänder; **B-C, E:** P. Phillipson; **H:** M. Merello]



Fig. 3. – Field pictures of Halmahera *Pandanus* Parkinson species. **A, C.** *Pandanus beguinii* Callm. & A. P. Keim (pistillate plant); **B.** *Pandanus beguinii* Callm. & A. P. Keim (staminate plant); **D.** *Pandanus dubius* Spreng.; **E, F.** *Pandanus halmaherensis* Callm. & A. P. Keim; **G, H.** *Pandanus papuanus* Solms; **I.** *Pandanus kaernbachii* Warb. [photo taken in Seram]; **J.** *Pandanus conoideus* Lam. [Photos: **A:** M. Merello; **B-G:** M. Callmänder; **H, J:** P. Phillipson; **I:** A. Keim]

Table 1. – The 55 *Pandanus* Parkinson collections currently known from Halmahera listed by species.

Species Name	Senior collector	N°	Locality	Alt. [m]	Date	Herbaria
<i>Pandanus beguinii</i>	Beguin	1819	Loleo Poeloe Rao		13 Oct. 1921	BO
	Beguin	1822	Loleo Poeloe Rao	30	14 Oct. 1921	BO
	Beguin	1825	Loleo Poeloe Rao	40	15 Oct. 1921	BO
	Beguin	2044	Soa Tobaroe	60	24 June 1922	BO
	Beguin	2067	Soa Tobaroe	60	28 June 1922	BO
	Beguin	2069	Soa Tobaroe	60	29 June 1922	BO, L
	Beguin	2071	Soa Tobaroe	60	29 June 1922	BO
	Beguin	2107	Sao Tobaroe	60	29 June 1922	BO, L
	Beguin	2167	Soa Tobaroe	60	6 Aug. 1922	BO
	Bidault	1089	Weda Bay, on the road to Bukit Limber	600	15 Apr. 2013	BO, G, L, MO
	Callmander	1086	Near Weda Bay	15	29 Jan. 2013	BO, G, L, MO
	Callmander	1088	Sagea Lagoon	26	30 Jan. 2013	BO, G, L, MO
	<i>Pandanus benstoneoides</i>	Callmander	1090	Pinto	340	01 Feb. 2013
Merello		3539A	Kao Rahai	366	09 Dec. 2012	BO, MO
<i>Pandanus dubius</i>	Bidault	1184	Bukit Limber	942	30 Apr. 2013	BO, G, L, MO
	Callmander	1077	Km 3 from Lelilef on the road to Doromesmesan	70	26 Jan. 2013	BO, G, L, MO, PH
	Callmander	1096	Pinto	340	1 Feb. 2013	BM, BO, G, L, MO
	Gushilman	646	Bukit Limber	1031	22 May 2013	BO, G, K, MO
	Gushilman	739	Tarsan Camp	495	2 June 2013	BO, G, L, MO
	Phillipson	6488	On road to Bukit Limber	712	12 Sept. 2013	BO, G, L, MO
	Phillipson	6489	On road to Bukit Limber	711	12 Sept. 2013	BO, G, K, L, MO
<i>Pandanus halmaherensis</i>	Beguin	1770	Galela	1	24 Sep. 1921	BO, L
	Beguin	1841	Galela	3	24 Oct. 1921	BO, L
	Beguin	1842	Galela	3	24 Oct. 1921	L
	Callmander	1081	Along road to Gemaf village	5	27 Jan. 2013	BO, G, L, MO
<i>Pandanus kaernbachii</i>	Bangun	843	Sake West	218	19 June 2013	BO, G, L, MO
	Callmander	1078	along the Road to Bukit Limber	600	27 Jan. 2013	BO, G, L, MO
	Callmander	1114	SE of Tofu Blewen camp	480	03 Feb. 2013	BO, G, K, L, MO
	Fabanyo	58	Kao Rahai	693	26 Feb. 2013	BO, G, L, MO
	Gushilman	560	Weda Bay	163	11 Apr. 2013	BO, MO
<i>Pandanus kaernbachii</i>	Beguin	1812	Loleo Poeloe Rao		1922 [?]	BO, L
	Beguin	1815	Loleo Poeloe Rao	60	12 Oct. 1921	L
	Beguin	1962	Tobelo	4	16 May 1922	BO, L
	Beguin	2214	Foeteo[?] ma Loleo		27 Sept. 1922	BO, L
	Beguin	2281	Tobelo	2	13 Dec. 1922	BO
	Beguin	2314	Berg Doekono, W Tobelo	800	28 Dec. 1922	BO, L

Species Name	Senior collector	N°	Locality	Alt. [m]	Date	Herbaria
	Beguin	2315	Berg Soekono, W Tobelo	800	28 Dec. 1922	BO
	Callmander	1076	Doromesmesan	70	26 Jan. 2013	BO, G, L, MO
	Callmander	1132	NE of Tofu Blewen camp	610	05 Feb. 2013	BO, G, L, MO
	Idjan	303	Gunung Sombilan		s.d.	BO, L
<i>Pandanus papuanus</i>	Beguin	1372	Tobelo	10	26 Jan. 1921	BO, L
	Beguin	1894	Galela	10	2 Dec. 1921	BO, L
	Beguin	2037	Sao Tobaroe	60	19 June 1922	BO, L, U
<i>Pandanus polycephalus</i>	Bangun	520	Tjetju, Weda Bay	17	15 Jan. 2013	BO
	Bangun	875	Lelilef, Weda Bay	107	14 Sept. 2013	BO, G, L, MO
	Beguin	1792	Galela	1	28 Sept. 1921	L
	Beguin	1966	Galela	20	19 May 1922	BO, L
	Beguin	s.n.	Galela, Sao Tobaroe		1920	BO
	Merello	3304	Weda Bay	33	10 Oct. 2012	BO, MO
	Merello	3312	Forest along Gomdi river	20	11 Oct. 2012	BO, G, L, MO
	Taylor	424	Jikolamo		6 June 1981	SAN
	Teijsmann	87	s.l.		s.d.	L
	Vriese	18	s.l.		s.d.	L
	Yoshida	2390	From Limau to Soa, Galela Dist.		12 Oct. 1976	L
<i>Pandanus tectorius</i>	Merello	3311	Gwomdi, Weda Bay	17	11 Oct. 2012	BO, G, K, L, MO

short, truncate, 2–3 mm long, with a flat to slightly concave dark coloured turret, bearing a lateral minute bicornate *stigma*, c. 0.5 mm wide. *Endocarp* bony, median, c. 5 mm long, circular, lateral walls > 0.5 mm thick; proximal mesocarp c. 2–3 mm long, fibrous, distal mesocarp c. 4–5 mm long, fibrous, chambered, seed locule c. 4 mm, spherical. *Staminate inflorescence* c. 30 cm long with a single terminal spike on a fleshy peduncle, c. 20 cm, covered with c. 9 caniculate foliaceous yellow bracts, distal ones c. 25 × 3.5 cm; proximal ones 8 × 1 cm; spike brown, short cylindric, mostly 11 cm long, 2 cm in diam., composed of crowded and congested flowers, formed by 4–12 briefly basally connate stamens; *stamens* c. 3 mm long; with a dilated basal column, c. 2 × 0.5 mm, the single anther born on a minute *filament*, c. 0.3 mm long; *anther* c. 1 × 0.3 mm, apiculate; apiculus c. 0.1 mm long.

Etymology. – This new species honours Victor E. Beguin (1886–1943) who collected this species nine times during his visits to Halmahera in 1921 and 1922 among the 50 collections of Pandanaeae gathered from the island.

Distribution and ecology. – *Pandanus beguinii* is mostly found at lower elevations (30–600 m) in primary and disturbed evergreen tropical forest. It grows on slopes and in open areas,

where individuals are scattered and discrete. The species is known from the northern, eastern and central regions of Halmahera (Fig. 4A).

Conservation status. – With an EOO of 1625 km², an AOO of 54 km², and 5 subpopulations, none of which are situated within the North Maluku protected area network, *P. beguinii* is assigned a preliminary status of “Endangered” [EN B1ab(iii)+2ab(iii)] based on the IUCN Red List Categories and Criteria (IUCN, 2012) (calculation following CALLMANDER et al., 2007). Four of the known subpopulations of *P. beguinii* have been recorded on or near WBN’s CoW, and we assume that some or all of them will be impacted by the proposed mining operations or associated environmental degradation. The current status of the subpopulation sampled by Beguin in northern Halmahera nearly a hundred years ago is unknown, but it occurs in an area that appears to be already somewhat degraded as judged by available satellite imagery. The conservation status is based on the currently available information on the geographical distribution of the species, and is justified because the extent of suitable habitat is expected to decrease in the coming years. Nevertheless, Halmahera is botanically poorly known and new subpopulations may occur in currently unexplored areas. If new

sub-populations are discovered, the estimated AOO and EOO for the species would increase, and reassessment of the conservation status of the species may result in a lower category of threat. Furthermore the establishment of conservation offset sites to mitigate mining and associated impacts that encompass natural subpopulations of the species would decrease the level of threat to the species.

Notes. – *Pandanus beguinii* can easily be distinguished by its small, slender habit, its small, terminal, erect syncarp of truncate drupes topped by a dark turret with a flat to concave apex, bearing a lateral minute bicornuate stigma, and its single-spiked staminate inflorescence (Fig. 3A-C, 5). The new species is a member of the morphologically well-defined *Pandanus* sect. *Maysops* H. St. John, that is characterized by “cephalia resembling an ear of maize, with flat-topped drupes” (JEBB, 1992: 116). This section, distributed throughout the Malesian region from the Moluccas to Papua New Guinea, is also present in the Bismarck Archipelago, the Solomon Islands and northern Queensland in Australian (STONE, 1992). Within this section, *P. beguinii* is similar to *P. kosteri* B. C. Stone in being miniature in all parts compared to all other species of the section, which develop into relatively robust trees. *Pandanus beguinii* can nevertheless be easily distinguished by its broader leaves, mostly 5–8 cm wide across the middle (vs. 2.5–3.7 cm in *P. kosteri*), its larger syncarp (10–15 × 5–6 cm vs. 6.5 × 3.5 cm), its simple staminate inflorescence with yellow bracts (vs. a compound inflorescence comprised of 6–7 spikes with red bracts) and its staminate flowers with their stamens shortly basally connate (vs. fused, i.e. forming a phalange) (see STONE, 1987: 436, Fig. 5).

Paratypes. – INDONESIA. Prov. North Maluku [Halmahera Isl.]: Loleo Poeloe [Loypoloy] Rao, 13.X.1921, *Beguin 1819* (BO); *ibid. loc.*, 30 m, 14.X.1921, *Beguin 1822* (BO); *ibid. loc.*, 40 m, 15.X.1921, *Beguin 1825* (BO); Soa Tobaroe, 60 m, 24.VI.1922, *Beguin 2044* (BO); *ibid. loc.*, 60 m, 28.VI.1922, *Beguin 2067* (BO); *ibid. loc.*, 29.VI.1922, *Beguin 2069* (BO, L [L1195381]); *ibid. loc.*, 29.VI.1922, *Beguin 2071* (BO); *ibid. loc.*, 60 m, 29.VI.1922, *Beguin 2071* (BO); *ibid. loc.*, 29.VI.1922, *Beguin 2107* (L [L1195381]); *ibid. loc.*, 6.VIII.1922, *Beguin 2167* (BO); Central Halmahera, Weda Bay, on the road to Bukit Limber, 00°31'01"N 127°59'41"E, 600 m, 15.IV.2013, *Bidault et al. 1089* (BO, G, L, MO); Weda Bay, Sagea Lagoon, 00°29'35"N 128°04'16"E, 29.I.2013, 15 m, *Callmander et al. 1086* (BO, G, L, MO-6465090); East Halmahera, Weda Bay, Pinto, 00°38'10"N 128°09'05"E, 340 m, 1.II.2013, *Callmander et al. 1090* (BO, G); East Halmahera, Weda Bay, Kao Rahai, 00°40'22"N 127°58'31"E, 366 m, 9.XII.2012, *Merello et al. 3539A* (BO, L, MO-6444045, MO-6444047).

Pandanus benstoneoides Callm., Buerki & Phillipson, *spec. nova* (Fig. 2A-D, 4B, 6, 7).

Typus: INDONESIA. Prov. North Maluku [Halmahera Isl.]: East Halmahera, Weda Bay, Pinto, 00°38'10"N 128°09'05"E, 340 m, 1.II.2013, *Callmander et al. 1096* (holo-: G [G00341588]!; iso-: BO!, BM!, L!, MO-6465097!, MO-6465098!).

Haec species a congeneris inflorescentiis lateralibus axillaribus, staminibus liberis atque drupis unilocularibus stigma filiforme adpressum rectum undulatumve syncarpi apicem versus dirigenis gerentibus distinguitur.

Treelet to 4–8(–15) m tall, stem c. 15 cm in diam., with a large cone of few propoots at base, up to 2 m high. *Leaves* linear-attenuate, mostly (110–)130–150(–160) cm long, 4.5–5.5 cm wide in the middle, apex gradually attenuate, ending with a flagellum (c. 7 cm long); sub-coriaceous, glaucous abaxially; longitudinal veins visible on both surfaces; marginal prickles borne 4–9 cm above base to apex, black near sheath, antrorse, erect, 0.8–1.5 mm long in the lower third, 0.5–2 mm apart, 0.5–1 mm long in the mid-third, 1–3 mm apart, to 0.2–0.5 mm long in the distal third, 0.2–1 mm apart, appressed in the distal third; midrib armed from 35–50 cm from base, prickles > 1 mm long towards the apex, irregularly spaced but mostly 2–4 mm apart in the middle and 1–2 mm towards the apex; prickles generally absent on apical ventral pleats, sometimes 5–10 minute prickles towards the apex; sheath straight, (4–)5–7(–8) cm long, 4.5–6 cm wide at apex, 5–8 cm at base. *Infructescence* lateral, comprising a solitary patent syncarp born in the axil of the leaves, several present in each fertile leaf rosette; each *syncarp* ovoid, obtuse at apex, 3-angled, 7–10 cm long, 5–7 cm wide, peduncle short, flattened dorso-ventrally, c. 7 cm long, 1–1.5 cm thick at apex, bearing multiple sub-coriaceous yellow bracts, broadly naviculate, the proximal ones c. 11 cm long, the distal one 7 cm long, crowded at peduncle apex, covering the syncarp. *Drupes* numerous, 500–800, 13–15 mm long, 3–4 mm wide, 4–5 mm thick, 1-celled, 5–6-angled, linear, pileus short, 1–2 mm high, with a flat to slightly concave apex with a rugose surface, bearing an appressed, straight to wavy, filiform *stigma* on its upper edge; stigma towards the syncarp apex, (10–)15–20(–30) mm long, 1 mm wide at base, 0.5 mm at apex; stigmatic groove ventral (adaxial), running along the proximal two thirds of the stigma. *Endocarp* bony, median, c. 4 mm long, obovate, lateral walls > 0.4 mm thick, extending laterally toward the apex of the drupe; proximal mesocarp c. 3 mm long, fibrous, distal mesocarp c. 3–5 mm long, chambered, seed locule c. 1.5 × 3 mm, obovate to ovate. *Staminate inflorescence* c. 18 cm long (immature); with a single terminal spike on a peduncle c. 7 cm long, covered with narrowly navicular yellow bracts, proximal ones c. 14 × 3 cm; distal ones 8 × 2 cm; spike yellow, c. 7 × 1.5 cm, linear, composed of crowded and congested flowers, composed of free stamens; *stamens* c. 5.5 mm long; *filament*, 4 × 0.5–0.7 mm, oblong, often larger at apex (c. 1 mm wide); *anther* c. 1.5 × 1 mm, sometimes apiculate with a long slender apiculus c. 1 mm long.

Etymology. – This new species is named after its resemblance to species of the genus *Benstonea*, a genus characterized

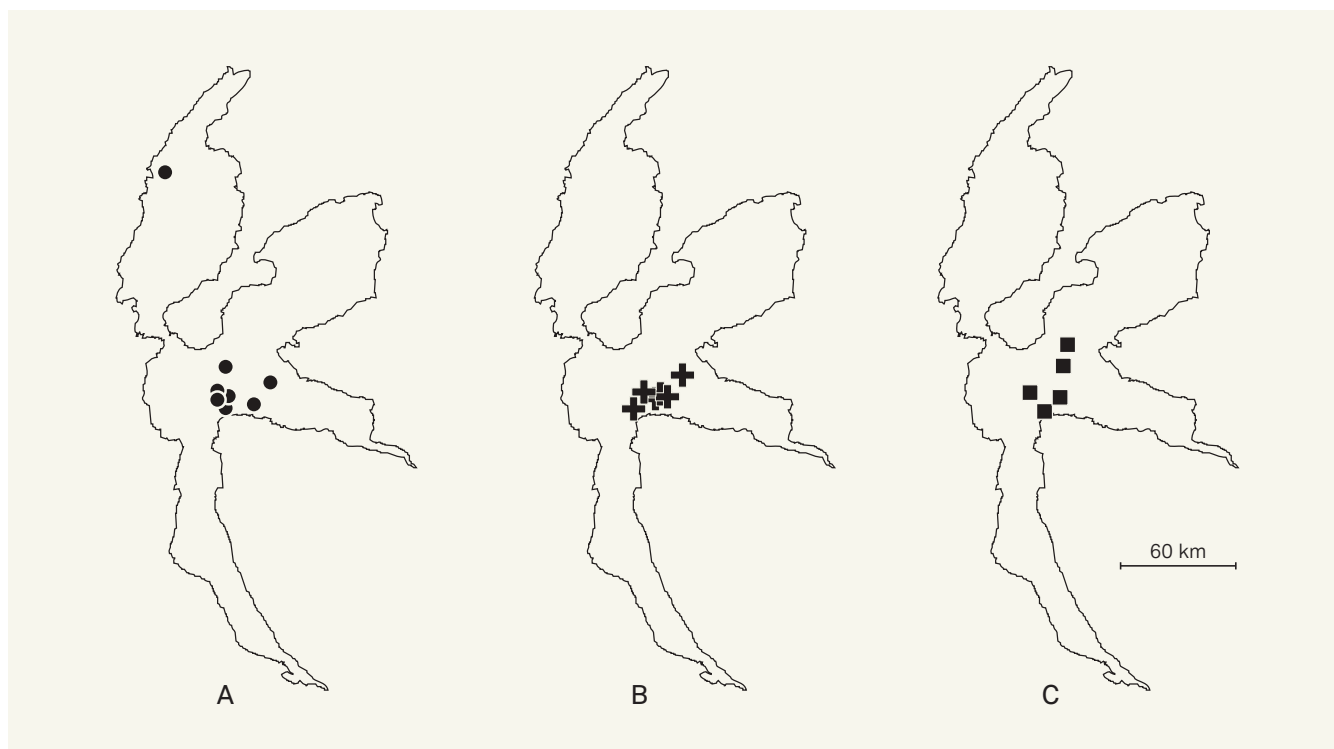


Fig. 4. – Distribution map of the three endemic new species of Halmahera. **A.** *Pandanus beguinii* Callm. & A. P. Keim; **B.** *Pandanus benstoneoides* Callm., Buerki & Phillipson; **C.** *Pandanus halmaherensis* Callm. & A. P. Keim.

by single celled drupes with a spiniform stigma, a dorsal (abaxial) stigmatic groove with respect to the long axis of the syncarp and staminate flowers sessile, composed of free stamens (CALLMANDER et al., 2012). When the first author collected it for the first time, he believed that he had discovered a new *Benstonea* species due to its typical single celled drupes with a spiniform stigma. Subsequently, more careful morphological study revealed that the stigmatic groove was ventral (adaxial) - unknown in *Benstonea*, and indicating the plant to be a remarkable new species of *Pandanus*. This conclusion has now been corroborated by molecular phylogenetic analysis. (Booth et al., unpubl. data) (see below).

Distribution and ecology. – *Pandanus benstoneoides* is found at lower to mid elevation (70–1030 m) in primary and disturbed evergreen tropical forest. The species is only known from our recent collections from the Eastern and Central Regencies of Halmahera (Fig. 4B).

Conservation status. – With an EOO of 66 km², an AOO of 45 km², and 4 subpopulations, none of which are situated within the protected area network, *P. benstoneoides* is assigned a preliminary status of “Endangered” [EN B1ab(iii)+2ab(iii)] based on the IUCN Red List Categories and Criteria (IUCN, 2012). See *P. beguinii* for further justification of the IUCN Category. The conservation status is based on the currently

available information on the geographical distribution of the species, and is justified because the extent of suitable habitat is expected to decrease in the coming years. However our remarks about the current inadequate knowledge of the flora of Halmahera and the possible establishment of conservation offset sites under *P. beguinii* above are applicable to *P. benstoneoides*.

Notes. – *Pandanus benstoneoides* is the only species of the genus known to have lateral inflorescences born in the axil of the leaves, with staminate flowers bearing free stamens and pistillate infructescence with drupes holding elongate appressed long filiform stigma. The longest stigma in the family is known from the New Guinean *Benstonea setistylus* (Warb.) Callm. & Buerki, where it can reach 10–15 mm (STONE, 1978). In the genus *Pandanus*, *P. princeps* B. C. Stone, a rare Malagasy endemic, is known to have long spiniform stigmas reaching 1 cm (STONE, 1972), but this magnificent tall monocaulous species has nothing else in common with our new species. *Pandanus benstoneoides* is morphologically isolated within the genus and cannot be placed in any of the infrageneric groups proposed by STONE (1974a). Further phylogenetic analyses will hopefully shed light into the evolution and systematics of this enigmatic and remarkable species.

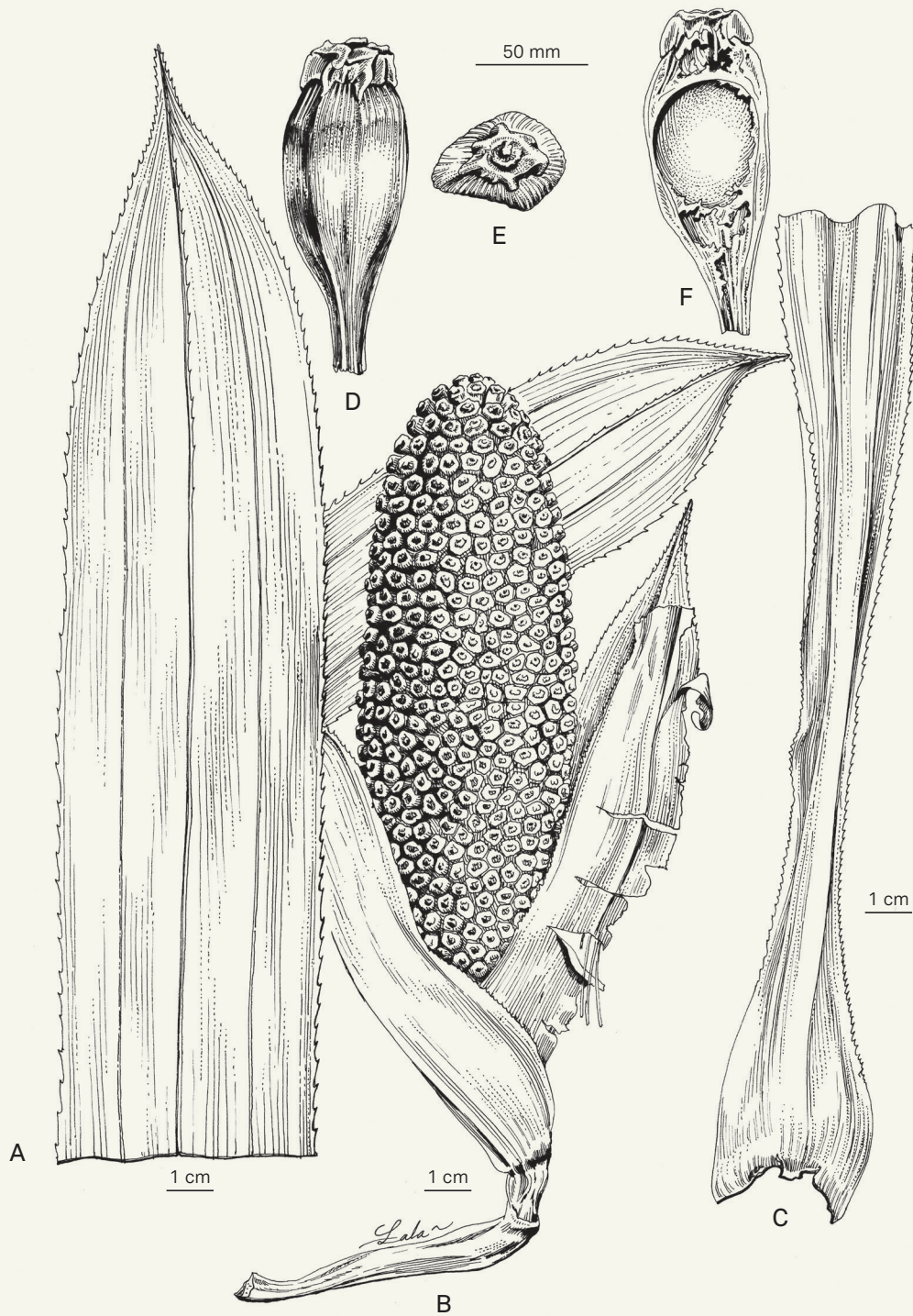


Fig. 5. – *Pandanus beguinii* Callm. & A. P. Keim. **A.** Tip of a leaf; **B.** Syncarp on peduncle; **C.** Basal section of a leaf; **D.** Side view of a drupe; **E.** Top view of the pileus; **F.** Cross section of a drupe. [A-G: Callmander, Haris, Lasut & Mahroji 1088, G] [Drawing: R. L. Andriamiarisoa]

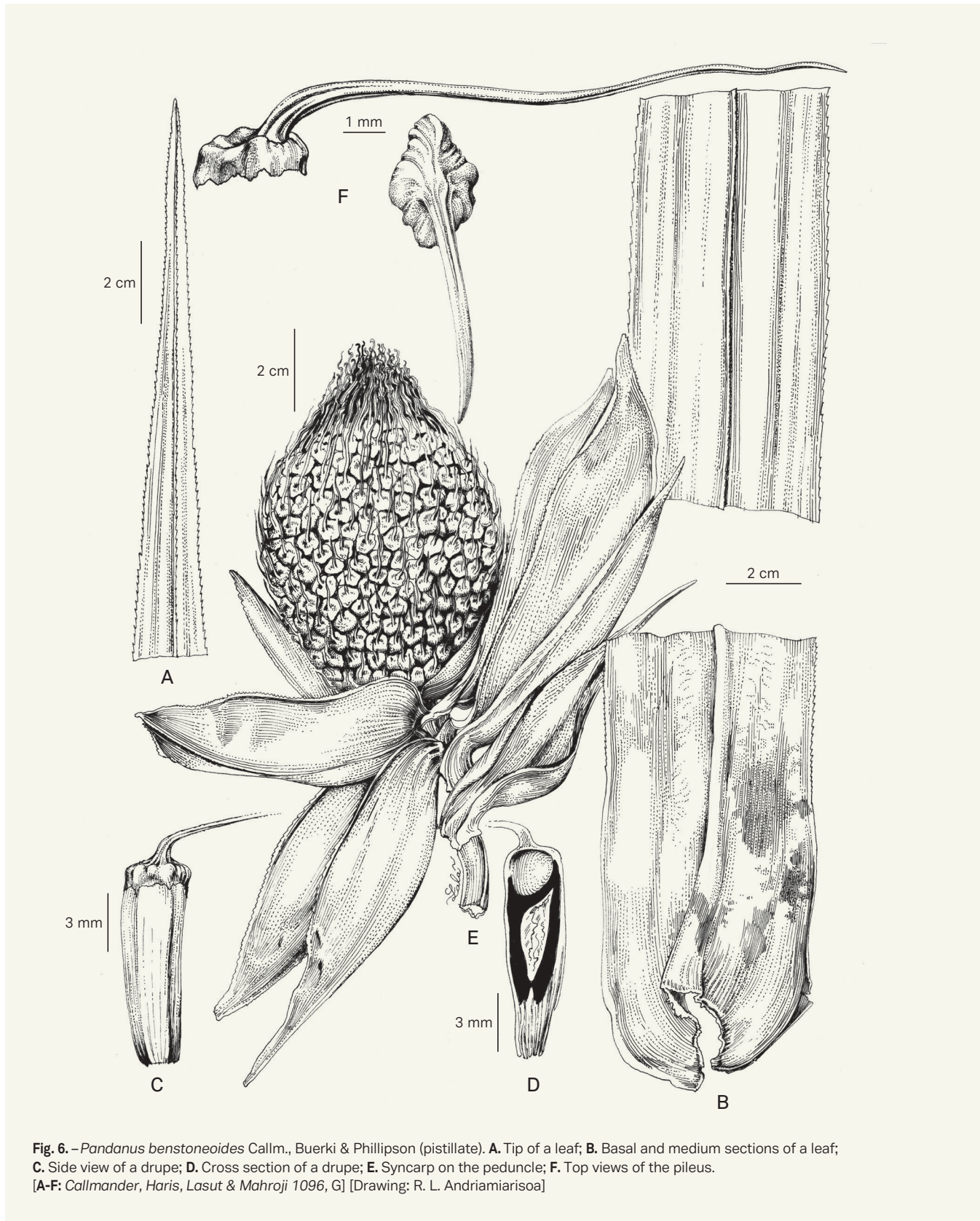


Fig. 6. – *Pandanus benstoneoides* Callm., Buerki & Phillipson (pistillate). **A.** Tip of a leaf; **B.** Basal and medium sections of a leaf; **C.** Side view of a drupe; **D.** Cross section of a drupe; **E.** Syncarp on the peduncle; **F.** Top views of the pileus. [A-F: Callmander, Haris, Lasut & Mahroji 1096, G] [Drawing: R. L. Andriamiarisoa]

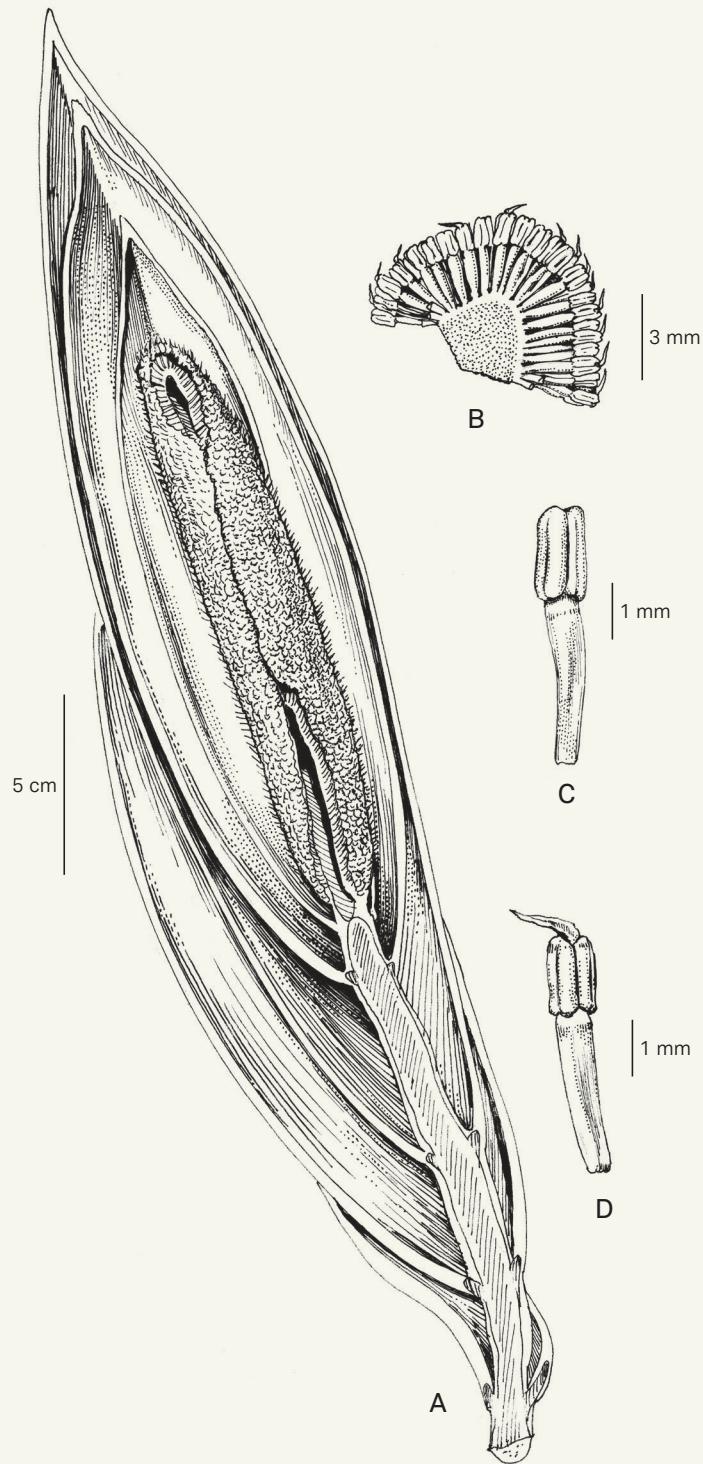


Fig. 7. – *Pandanus benstoneoides* Callm., Buerki & Phillipson (staminate). **A.** Staminate inflorescence; **B.** Section of tip of inflorescence showing arrangement of single stamens; **C, D.** Stamens. [A-G: Phillipson et al. 6488, G] [Drawing: R. L. Andriamiarisoa]

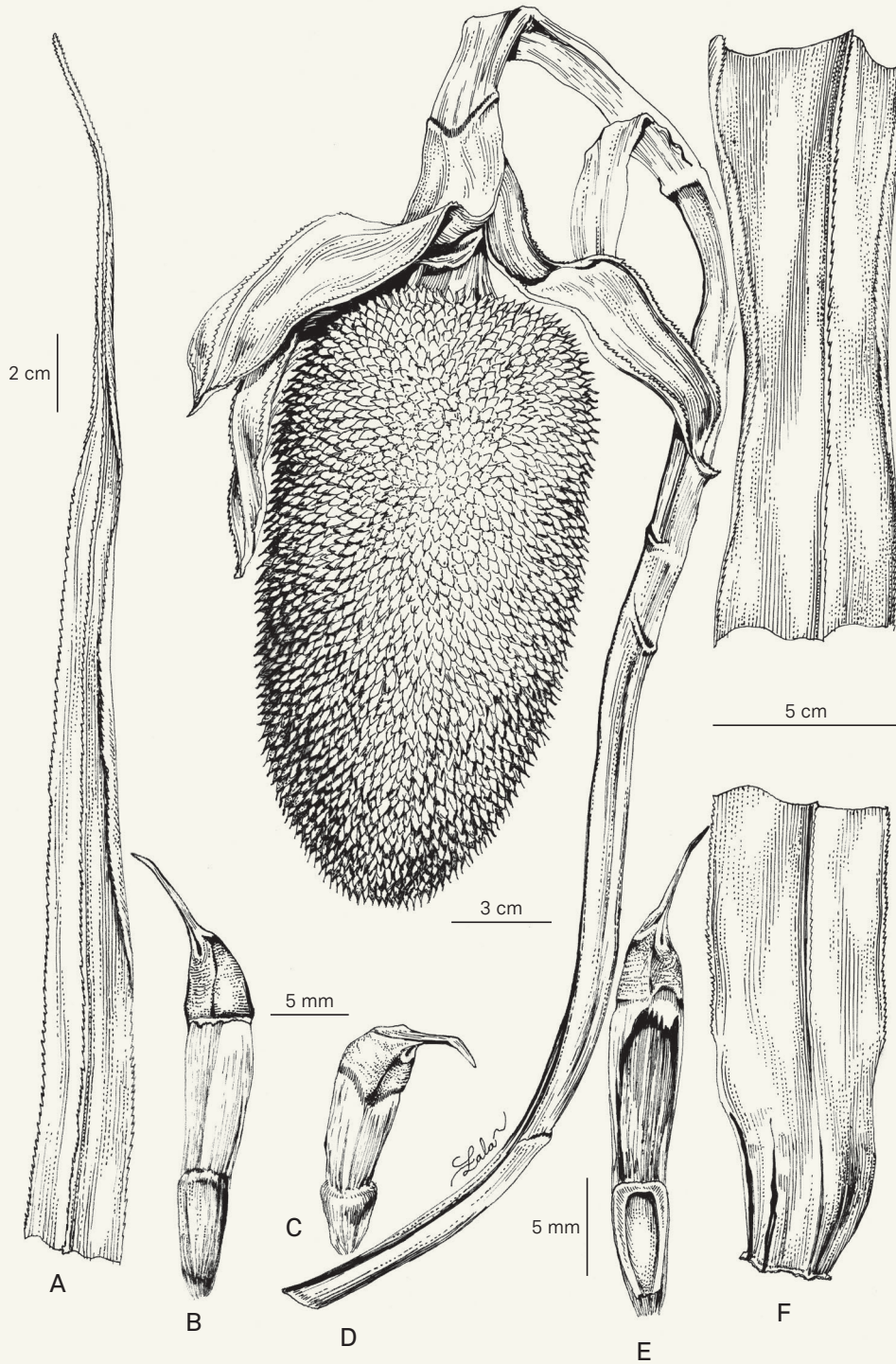


Fig. 8. – *Pandanus halmaherensis* Callm. & A. P. Keim. **A.** Tip of a leaf; **B, C.** Side view of a drupes; **D.** Syncarp on peduncle; **E.** Cross section of a drupe; **F.** Basal and medium sections of a leaf. [A-F: Callmander, Haris & Mahroji 1078, G] [Drawing: R. L. Andriamiarisoa]

Paratypes. – INDONESIA. Prov. North Maluku [Halmahera Isl.]: Central Halmahera, Weda Bay, Bukit Limber, 00°32'36"N 127°58'30"E, 942 m, 30.IV.2013, *Bidault et al. 1184* (BO, G, L, MO-6486429, MO-6398420 carpo); Weda Bay, Km 3 from Lelilef on the road to Doromesmesan, 00°28'50"N 127°55'17"E, 70 m, 26.I.2013, *Callmänder, Haris, Lasut & Gushilman 1077* (BO, G, L, MO-6451261, MO-6451262, PH); Weda bay, Bukit Limber, 00°33'14"N 127°59'17"E, 1031 m, 22.V.2013, *Gushilman, Lasut & Haris 646* (BO, G, K, MO-6489845); Weda Bay, Tarsan Camp, 00°31'41"N 127°56'18"E, 495 m, 2.VI.2013, *Gushilman et al. 739* (BO, G, L, MO-6486556, MO-6399935 carpo); On road to Bukit Limber, 00°31'39"N 128°00'19"E, 712 m, 12.IX.2013, *Phillipson et al. 6488* (G, MO); *ibid. loc.*, 00°31'44"N 128°00'21"E, 711 m, 12.IX.2013, *Phillipson et al. 6489* (BO, G, K, L, MO).

Pandanus halmaherensis Callm. & A. P. Keim, *spec. nova* (Fig. 2E-F, 4C, 8).

Typus: INDONESIA. Prov. North Maluku [Halmahera Isl.]: Central, Weda Bay, along the road to Bukit Limber, 00°31'13"N 127°59'56"E, 600 m, 27.I.2013, *Callmänder, Haris & Mahroji 1078* (holo-: G [G00341587]!; iso-: BO!, L!, MO-6465087!, MO-6465088!, MO-6465089!, MO-6124975 carpo!).

Haec species a congeneris infructescentia pendente solitaria ingente atque drupis pileo rubro prismatico-conico non profunde bullato in stigma spinescens desinente munitis distinguitur.

Tall tree to 10–20 m tall, trunk 15–25 cm in diam., with a large cone of proproots, 1–2(–5) m long, 6–7 cm in diam. Leaves linear-attenuate, mostly (180–)220–250 (–300) cm long, 5–8 cm wide, apex gradually attenuate; sub-coriaceous to coriaceous, paler green abaxially shiny axially (especially when dry); longitudinal veins visible on both surfaces; marginal prickles borne 7–11(–15) cm above base to apex, antrorse, 1.5–2.5 mm long in the lower third, (1–)3–10 mm apart, (0.5–)1–2 mm long in the mid-third, 2–5 mm apart, to 0.5–1 mm long in the distal third, 0.2–0.5 (–1) mm apart, subappressed to appressed in the distal third; midrib unarmed in the lower third, prickles < 0.5 mm long towards the apex, irregularly spaced but mostly 1–2 mm apart; prickles absent on apical ventral pleats; sheath (7–)11(–17) cm long, (7–)9–10 cm wide at apex, (8–)12–14(–19) cm at base. *Infructescence* terminal, pendant, red to purple, the solitary syncarp ovoid, (25–)30–35 cm long, 11–15 cm wide, peduncle (45–)50–80 cm long, c. 3 cm thick at apex, bearing foliaceous bracts, the proximal ones c. 60 cm long, the distal one 13 cm long, crowded at peduncle apex, spreading open at maturity. *Drupes* very numerous, crowded, (30–)35–40 mm long, 4–5 mm wide, 4–5 mm thick, 1-celled, 5–7-angled, linear, pileus prismatic-conic, 8–10 mm long, shiny, shallowly bullate. *Stigma* one, c. 6–8 mm long, spinose, deflected toward the syncarp apex: stigmatic groove ventral (adaxial), running along the whole length of the stigma and extending in a groove on distal part of the pileus. *Endocarp* bony, basal, c. 8 mm long, flat at apex, lateral walls

> 1 mm thick; proximal mesocarp 2–4 mm long, fibrous, distal mesocarp 15–25 mm long, sparsely fibrous, chambered, seed locule c. 5 × 3 mm, ellipsoid. *Staminate inflorescence* unknown.

Distribution and ecology. – *Pandanus halmaherensis* is found at low to mid elevations (160–700 m) in primary and disturbed evergreen tropical forests. It grows on slopes and in open areas. The species is only known from the eastern and central part of Halmahera (Fig. 4C).

Conservation status. – With an EOO of 178 km², an AOO of 45 km², and 4 subpopulations, none of which are situated within the protected area network, *Pandanus halmaherensis* is assigned a preliminary status of “Endangered” [EN B1ab(iii)+2ab(iii)] based on the IUCN Red List Categories and Criteria (IUCN, 2012). The conservation status is based on the currently available information on the geographical distribution of the species, and is justified because the extent of suitable habitat is expected to decrease in the coming years. However our remarks about the current inadequate knowledge of the flora of Halmahera and the possible establishment of conservation offset sites under *P. beguinii* above are applicable to *P. halmaherensis*.

Notes. – *Pandanus halmaherensis* is notable in having a large and massive pendant infructescence and drupes with a prismatic-conic shallowly bullate pileus with a spinose stigma, unlike any other known species of the genus. Our new species can, however, be compared to *P. sarasinorum* Warb., endemic to Sulawesi (see STONE [1974b] for a complete description of this species). The two species share a similar habit (tall trees with long aerial proproots) and syncarps (very numerous and crowded cylindrical drupes). *Pandanus halmaherensis* can nevertheless be easily distinguished by the larger dimensions of its leaves (mostly 220–250 × 5–8 cm vs. c. 150 × 4 cm in *P. sarasinorum*), much larger drupes (mostly 35–40 × 4–5 mm vs. 12–20 × 2–3 mm) and most notably by its larger (30–35 × 11–15 cm) solitary, ovoid syncarps (vs. an inflorescence with multiple, cylindrical syncarps, each 16–17 × 3–6 cm). This new species seems to be morphologically isolated within the genus and would only fit into *Pandanus* sect. *Rykiopsis* B. C. Stone (STONE, 1974a). However, the latter section was defined based on the multiple syncarps of its type species *P. sarasinorum*.

Paratypes. – INDONESIA. Prov. North Maluku [Halmahera Isl.]: Central Halmahera, Weda Bay, Sake West, 00°29'39"N 127°57'44"E, 218 m, 19.VI.2013, *Bangun, Mahroji & Fabanyo 843* (BO, G, L, MO-6486427, MO-3762979 carpo); East Halmahera, Weda Bay, SE of Tofu Blewen camp, 00°47'55"N 128°02'06"E, 480 m, 3.II.2013, *Callmänder, Fabanyo & Mahroji 1114* (BO, G, K, L, MO-6451256, MO-6451257, MO-6451258, MO-6149145 carpo); East Halmahera, Weda Bay, Kao Rahai, 00°41'54"N 128°01'02"E, 693 m, 26.II.2013, *Fabanyo et al. 58* (BO, G, L, MO-6199115, MO-6451255, MO-6451254 carpo); Central Halmahera, Weda Bay, 00°31'44"N 127°54'22"E, 163 m, 11.IV.2013, *Gushilman, Lasut & Fabanyo 560* (BO, G, L, MO-6472415, MO-6472416, MO-6398426 carpo).

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References

- BACKER, C. A. (1936). *Verklarend woordenboek der wetenschappelijke namen van de in Nederland en Nederlandsch-Indië in het wild groeiende en in tuinen en parken gekweekte varens en hoogere planten*. Noordhoff & Visser, Groningen & Batavia.
- BECCARI, O. (1924). *Nuova Guinea: Selesbes e Molucche: diarii di viaggio*. La Voce, Firenze.
- BUERKI, S., M. W. CALLMANDER, D. S. DEVEY, L. CHAPPELL, T. GALLAHER, J. MUNZINGER, T. HAEVERMANS & F. FOREST (2012). Straightening out the screw-pines: a first step in understanding phylogenetic relationships within Pandanaeae. *Taxon* 61: 1010-1020.
- CALLMANDER, M. W., S. BUERKI, A. P. KEIM & P. B. PHILLIPSON (2014). Notes on Benstonea (Pandanaeae) from the islands of Halmahera, New Guinea and Sulawesi. *Phytotaxa* 175: 161-165.
- CALLMANDER, M. W., P. P. LOWRY II, F. FOREST, D. S. DEVEY, H. BEENTJE & S. BUERKI (2012). Benstonea Callm. & Buerki (Pandanaeae): characterization, circumscription, and distribution of a new genus of screw-pines, with a synopsis of accepted species. *Candollea* 67: 323-345.
- CALLMANDER, M. W., G. E. SCHATZ, P. P. LOWRY II, M. O. LAIVAO, J. RAHARIMAMPIONONA, S. ANDRIAMBOLOLONERA, T. RAMINOSOA & T. CONSIGLIO (2007). Application of IUCN Red List criteria and assessment of Priority Areas for Plant Conservation in Madagascar: rare and threatened Pandanaeae indicate sites in need of protection. *Oryx* 41: 168-176.
- GALLAHER, T., M. W. CALLMANDER, S. BUERKI & S. C. KEELEY (2015). A long distance dispersal hypothesis for the Pandanaeae and the origins of the *Pandanus tectorius* complex. *Molec. Phylogen. Evol.* 83: 20-32
- HALL, R. (2001). Cenozoic reconstructions of SE Asia and the SW Pacific: changing patterns of land and sea. In: METCALFE, I., J. SMITH, M. MORWOOD & I. DAVIDSON (ed.), *Faunal and floral migrations and evolution in SE Asia-Australia*: 35-56. Swets and Zeitlinger Publishers.
- HALL, R., M. G. AUDLEY-CHARLES, F. T. BANNER, S. HIDAYAT & S. L. TOBING (1988). Late Palaeogene-Quaternary geology of Halmahera, Eastern Indonesia: initiation of a volcanic island arc. *J. Geol. Soc. London* 145: 577-590.
- IUCN (2012). *IUCN Red List Categories and Criteria: Version 3.1*. 2nd ed. IUCN Species Survival Commission, Gland & Cambridge.
- JEBB, M. (1992). *A field guide to Pandanus in New Guinea, the Bismarck Archipelago & the Solomon Islands*. Christensen Research Institute, Madang.
- KEIM, A. P. (2009). Pandanaeae of the island of Yapen, Papua (West New Guinea), Indonesia, with their nomenclature and notes on the rediscovery of *Sararanga sinuosa*, and several new species and records. *Blumea* 54: 255-266.

- KEIM, A. P., S. SUSIARTI & M. AMIR (2008). Taksonomi Pandanaceae Pulau Seram. In: UBAIDILLAH, R., E. B. WALUJO, A. J. ARIEF & H. JULISTIONO (ed.), *Laporan Teknik Pusat Penelitian Biologi-LIPI*: 1281-1326. LIPI, Bogor.
- LIM, T. K. (2012). *Edible medicinal and non-medicinal plants*. Vol. 4, Fruits. Springer.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. DA FONSECA & J. KENT (2000). Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- PURWANTO, Y., R. POLOSAKAN & M. F. ROYYANI (2009). Studi etnobiologi Pandanaceae di Pulau Halmahera. In: PURWANTO, Y. & E. B. WALUJO (ed.), *Prosiding Seminar Nasional Etnobotani IV*: 118-132.
- RICKLEFS, M. C. (2008). *A History of modern Indonesia since c. 1200*. Stanford University Press.
- RUMPHIUS, G. E. (1741-1755). *Herbarium amboinense*. Vol. 1-6. Franciscus Changuion, Amsterdam.
- SETIADI, M. I., A. HAMIDY, Z. ABIDIN, D. SUSANTO, R. M. BROWN, A. T. PETERSON, X. LI & B. J. EVANS (2010). Genetic structure of herpetofauna on Halmahera Island, Indonesia: implications for Aketajawe-Lolobata National Park. *Conservation Biol.* 24: 553-562.
- STONE, B. C. (1974a). Towards an improved infrageneric classification in *Pandanus* (Pandanaceae). *Bot. Jahrb. Syst.* 94: 459-540.
- STONE, B. C. (1974b). Studies in Malesian Pandanaceae XII. Taxonomic revision of *Pandanus* sections *Solmsia* and *Rykiopsis* and of section *Rykia* subsection *Gressettia*, all of subgenus *Rykia*. *Fed. Mus. J.* 17: 99-163.
- STONE, B. C. (1978). Revisio Pandanacearum, Part I. *Pandanus* subgenera *Coronata* and *Acrostigma*. *Flora Malesaina precursores*. *Fed. Mus. J.* 23: 1-74.
- STONE, B. C. (1982). New Guinea Pandanaceae: first approach to ecology and biogeography. In: GRESSIT, J. L. (ed.), *Biogeography and ecology of New Guinea* 1: 401-436. W. Junk Plush.
- STONE, B. C. (1987). New taxa of *Pandanus* (Pandanaceae) from Malesia and Papuaia. *Blumea* 32: 427-441.
- STONE, B. C. (1992). The New Guinea species of *Pandanus* section *Maysops* St. John (Pandanaceae). *Blumea* 37: 31-61
- TAYLOR, P. M. (1990) The Folk Biology of the Tobelo People: a Study in Folk Classification. *Smithsonian Contr. Anthropol.* 34.
- TEIJSMANN, J. E. (1861). Notes recueillies pendant un voyage dans les Moluques et l'île de Célèbes. *J. Bot. Néerl.* 1: 297-344.
- VAN STEENIS, C. G. G. J. (1950). *Fl. Malesiana* ser. I, 1. Noordhoff-Kolff, Jakarta.
- YOSHIDA, S. (1980). Folk Orientation in Halmahera with Special Reference to Insular Southeast Asia. In: NAOMICHI, I. (ed.), *The Galela of Halmahera*: 19-88. Senri Ethnological Studies 7, National Museum of Ethnology, Osaka.