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A monograph of the *Hydriastele wendlandiana* group (Arecaceae: *Hydriastele*)

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Summary. A taxonomic revision is presented of the *Hydriastele wendlandiana* group, a well-defined species grouping within the Indo-Pacific palm genus *Hydriastele* that occurs in New Guinea, the Bismarck Archipelago and northern Australia. We accept five species: *Hydriastele kasesa*, *H. rheophytica*, *H. variabilis*, *H. wendlandiana* and *H. apetiolata* sp. nov. and provide fundamental information about each of those taxa including a summary of the group's taxonomic history and phylogeny, a distribution map, a key to the species, species descriptions with scientific illustrations, and IUCN Red List assessments.

Key Words. Areceae, Arecoideae, *Hydriastele microspadix*, Indonesia, Papua New Guinea, Palmae, taxonomy.

Introduction

The palm genus *Hydriastele* H. Wendl. & Drude (Arecoideae: Areceae) currently contains 49 accepted species (Govaerts *et al.* 2017). Most of these occur in Papuasia, but the genus extends to Sulawesi, northern Australia, Fiji and Palau (Dransfield *et al.* 2008). The species are an important and conspicuous component of the palm floras in the areas in which they occur. Some of the species are used in horticulture (Riffle *et al.* 2012) whilst others are of great significance for subsistence and livelihoods (Essig 1982).

Members of *Hydriastele* display different growth habits ranging from small and clustered understorey palms to very robust, solitary canopy emergents. All species have reduplicately pinnate leaves, a well-defined crownshaft and leaflets that are irregularly jagged at the tip (praemorse). The floral arrangement, with flowers arranged in units of three (triads), is typical of the Arecoideae, and in *Hydriastele* the triads are moreover inserted throughout the length of the rachillae. These ultimate inflorescence axes are inserted closely together and are swept forward giving the inflorescence a horsetail-like appearance. The staminate flowers are larger than the pistillate flowers and have lanceolate, valvate petals that vary slightly in size (Dransfield *et al.* 2008).

The monophyly of *Hydriastele* is well supported, as is its placement in the major Indo-Pacific tribe Areceae, but current molecular evidence is insufficient to place the genus to subtribe (Loo *et al.* 2006; Dransfield *et al.* 2008; Baker *et al.* 2009; Baker *et al.* 2011; Baker & Dransfield 2016). The phylogenetic relationships among the species of *Hydriastele* have been explored (Loo *et al.* 2006). Here, we present a monograph of an infrageneric species grouping within *Hydriastele*, a monophyletic group identified by Loo *et al.* (2006) that we term *Hydriastele wendlandiana* group. It occurs in New Guinea, the Bismarck Archipelago, northern Australia, and immediately adjacent islands, and is distinguished from the rest of the genus by its slender to moderate growth habit combined with protogynous inflorescences in which the stigmas are congenitally exposed (i.e. not covered by perianth, even in bud; Essig 1973; Uhl & Dransfield 1987). We focus on this group because it is common throughout much of New Guinea, widely used by local people and is ecologically important. Moreover, the taxonomy of the group is very poorly understood and has not been the focus of a modern monographic revision. Prior to this treatment 10 species were accepted: *Hydriastele wendlandiana* (F. Muell.) H. Wendl. & Drude, *H. geelvinkiana* (Becc.) Burret, *H. variabilis* (Becc.) Burret, *H. microspadix* (Warb. ex K. Schum. & Lauterb.) Burret, *H. kasesa* (Lauterb.) Burret, *H. beccariana* Burret, *H. rostrata* Burret, *H. carrii* Burret, *H. lepidota* Burret and *H. rheophytica* Dowe & M. D. Ferrero (Baker & Loo 2004).

Material and methods

We examined 128 herbarium specimens from key international herbaria (A, BRI, CANB, FI, K, LAE, MEL; herbarium abbreviations following Thiers [2017]) including dried and spirit material, photographs, and field notes. A morphological species concept (Davis & Heywood 1963; McDade 1995) was used in which co-varying characters and disjunct character states were taken as evidence of support for the existence of different species.

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Spirit material was used as far as possible for floral and fruit descriptions. Before dissecting, dried material was rehydrated by boiling, but because this does not eliminate drying artefacts, e.g. the pericarp still appeared shrunken, we have indicated the use of dried material in appropriate places in the descriptions.

Coordinates used for the distribution map were harvested directly from specimens or derived from online and hard-copy gazetteers. We created the map using Quantum GIS computer software (Quantum GIS Development Team 2017), and in doing so we supplemented the new coordinates we had obtained for Australia, derived from the specimens we have cited in this monograph, with what was already known about the distribution of *Hydriastele wendlandiana* in Australia (Dowe 2010). GeoCAT (Bachman *et al.* 2011) was used to make preliminary IUCN conservation assessments following the International Union for the Conservation of Nature (IUCN) categories and criteria version 3.1 (IUCN 2001). Palm terminology used in the descriptions is based on the *Genera Palmarum* glossary (Dransfield *et al.* 2008) supplemented by *The Kew Plant Glossary* (Beentje 2016).

Taxonomic history and phylogeny

Mueller described the first species in the group in 1870 as *Kentia wendlandiana* F. Muell. from northern Australia. The same species was soon renamed *Hydriastele wendlandiana* when, in 1875, Wendland & Drude erected the genus *Hydriastele*. In 1877, *Nenga geelvinkiana* Becc. and *N. variabilis* Becc. were described by Beccari from northwest New Guinea and subsequently Schumann & Lauterbach described *Kentia microspadix* Warb. ex K. Schum & Lauterb. and *Ptychosperma kasesa* Lauterb. from Kaiser-Wilhelmsland (German New Guinea) and the Bismarck Archipelago in 1900 and 1911 respectively. All four species were subsequently transferred to *Adelonenga* (Becc.) Hook. f. by Beccari (1885 and 1914) and then eventually to *Hydriastele* by Burret (1937) who recognised that *Adelonenga* was congeneric with *Hydriastele*. Burret also described four species himself; *Hydriastele beccariana* (1928), *H. carrii* (1936), *H. rostrata* (1937) and *H. lepidota* (1939).

Burret's generic delimitation of *Hydriastele* was accepted in the first modern genus-level monograph of palms (Uhl & Dransfield 1987), and this circumscription corresponds with the *Hydriastele wendlandiana* group, which we treat in this monograph. A further species from the highlands of Papua, *Hydriastele rheophytica*, was added to this group by Dowe & Ferrero (2000). Subsequently, the molecular phylogenetic analysis of Loo *et al.* (2006) led to a substantial expansion of the generic limits of *Hydriastele*. Their study revealed that *Hydriastele sensu* Burret (1937) is monophyletic, but embedded within a larger paraphyletic group of three closely related genera, *Gronophyllum* Scheff., *Gulubia* Becc. (both polyphyletic) and *Siphokentia* Burret (paraphyletic). As a result, *Hydriastele* was expanded to include these three genera (Baker & Loo 2004) and this delimitation prevails today (Dransfield *et al.* 2008; Baker & Dransfield 2016).

Revised taxonomy and distribution

Following our revision, we accept five species in the *Hydriastele wendlandiana* group, in contrast with the ten species recognised prior to this publication. The accepted species are: *H. apetiolata* **sp. nov.**, *H. kasesa, H. rheophytica, H. variabilis* and *H. wendlandiana*. The known distribution of these species is presented in Map 1.

Key to the species of the *Hydriastele wendlandiana* group

1. Clustering palm; stem pliable and usually leaning; leaflets linear, thin and soft, terminal leaflets comprising c. 2 – 3 folds, basal leaflets obliquely praemorse apically; restricted to stream banks . . . . . **3. H. rheophytica**
   Clustering or solitary palm; stem rigid and usually erect; leaflets linear or cuneate, relatively stiff and papery, terminal leaflets comprising 3 – 16 folds (very rarely fewer folds), basal leaflets pointed, obliquely praemorse or truncately praemorse apically; may occur on stream banks, but not restricted to this habitat **2**
2. Clustering palm; leaflets regularly to subregularly arranged, basal leaflets pointed to obliquely praemorse apically or if truncately praemorse apically then in addition with apetiolate adult leaves **3**
   Clustering or solitary palm; leaflets usually irregularly arranged, with a group of closely spaced single- or bi-fold leaflets in the middle of the leaf rachis, or leaflets regularly arranged with the basal leaflets being truncately praemorse apically and inserted onto a rachis that extends into a well-defined petiole **4**
3. 4 – 7 leaves in crown; stem up to 4 cm in diam.; sheath 27 – 45 cm long, crownshaft 33 – 70 cm; petiole more than 9 cm long; leaflets 11 – 23 each side of rachis with the basal leaflets being pointed or obliquely praemorse apically; juvenile leaves pinnately compound; inflorescence 12 – 25 cm long with 1 or 2 orders of branching; primary branches bearing up to one rachilla each; fruit ellipsoid to ovoid; endosperm deeply ruminate . . . . . **4. H. variabilis**
   7 – 10 leaves in crown, stem more than 4.5 cm in diam.; sheath c. 60 cm long, crownshaft 120 – 150 cm; petiole absent; leaflets 23 – 25 each side of rachis with the basal leaflets being obliquely or truncately praemorse;

juvenile leaves entire bifid; inflorescence 25 – 35 cm long with 2 orders of branching; primary branches bearing up to 3 rachillae each; fruit subglobose; endosperm ruminate . . . . . **1. H. apetiolata**

4. Slender palm, stem up to 3.8 cm in diam.; sheath 15 – 30 cm long, crownshaft 30 – 35 cm; leaflets 6 – 13 each side of rachis; inflorescence branched to 1 or 2 orders, with 5 – 10 primary branches bearing up to 3 rachillae each; endosperm ruminate . . . . . **2. H. kasesa**

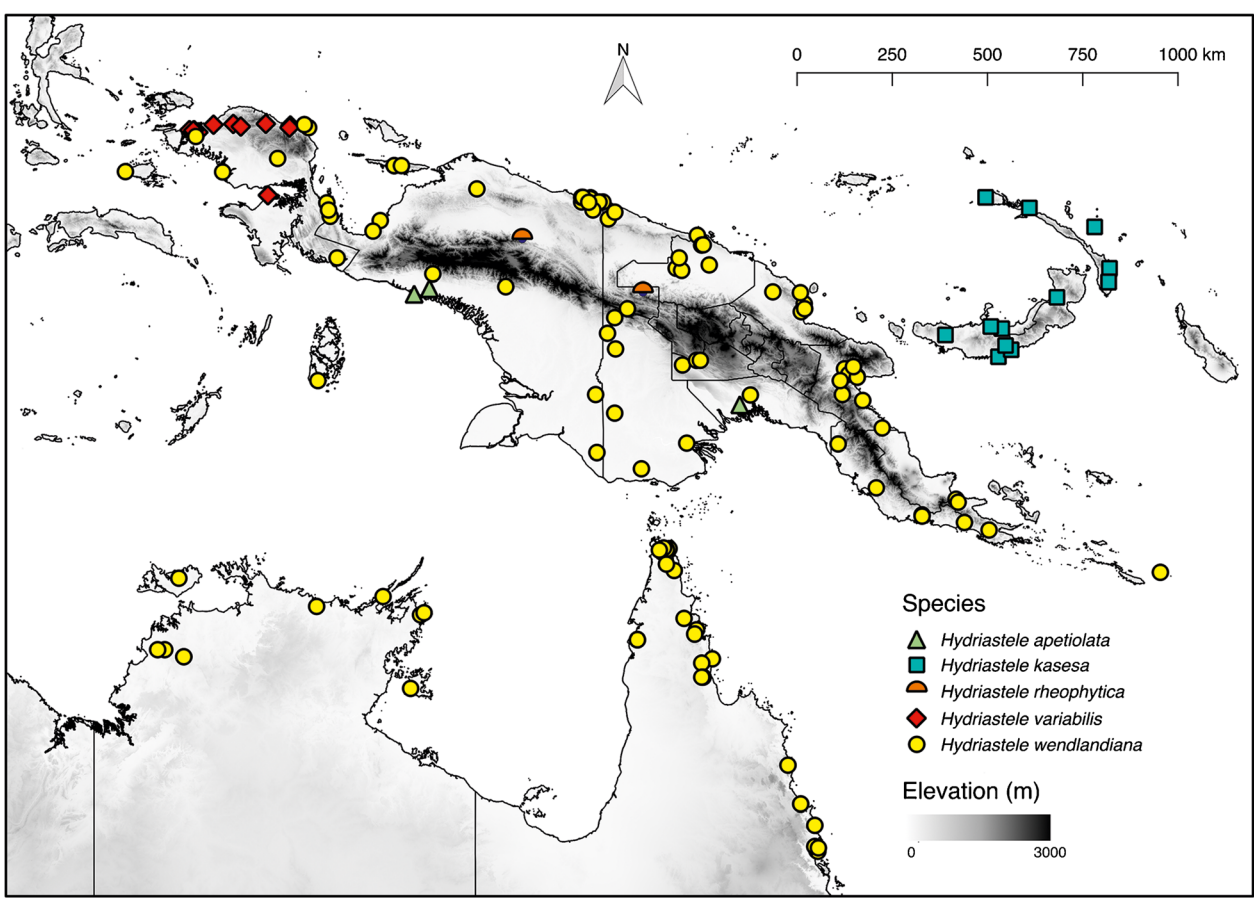
Slender to moderate palm, stem up to 10 cm in diam.; sheath 40 – 73 cm long, crownshaft 30 – 160 cm; leaflets 12 – 30 on each side of rachis (rarely 12 – 13 per side); inflorescence usually branched to 2 orders, with 8 – 15 primary branches bearing up to 5 rachillae each; endosperm homogeneous or ruminate . . . . . **5. H. wendlandiana**

Taxonomic treatment

1. Hydriastele apetiolata *Petoe & W. J. Baker* **sp. nov.** Type: Indonesia, Papua Province, Mimika Regency, Timika, Nursery: Kuala Kencana, [4°47'S, 136°33'E], c. 50 m elev., 27 Feb. 1998, *Baker et al.* 884 (holotype K!; isotypes BH, BO, L, MAN).

http://www.ipni.org/urn:lsid:ipni.org:names:60475907-2

Clustering, moderately slender palm to c. 6 m tall, bearing 7 – 10 leaves per crown. *Stem* 4.5 – 6 cm in diam., smooth and dark with lighter blotches; internodes 9 – 25 cm long. *Leaves* to 125 cm long; sheath c. 60 cm long, with lacerate-peltate, dark purple scales and ferrugineous filaments sometimes covered with scurfy scales, crownshaft 120 – 150 cm long; petiole lacking; rachis slightly arching, indumentum as sheath, if less dense; leaflets 23 – 26 each side of rachis, arranged regularly, borne c. 3.5 – 4.5 cm apart, ± horizontal, praemorse apically, transverse veinlets obscure, ramenta present; terminal leaflets c. 25 – 35 × 4 cm, comprising 4 – 6 folds, cuneate; longest leaflet in middle of rachis c. 70 – 90 × 2 – 3 cm, single-fold,



Map 1. Distribution map of the species of the *Hydriastele wendlandiana* group. Species and elevation legends are included within the figure.

linear; basal leaflets single-fold, ± grouped, linear, obliquely or truncately praemorse apically; juvenile leaves different from adult leaves, entire and bifid, with or without petiole, with lamina 100 – 130 cm long. *Inflorescences* 25 – 35 cm long including 3.5 – 5.5 cm peduncle, branched to 2 orders; prophyll not seen, caducous; peduncular bract attached 1 – 1.5 cm above the prophyll; primary branches 8, to 27.5 cm long, closely spaced and bearing up to 3 rachillae each; rachillae up to 27.5 cm long, 2 – 3 mm in diam.; triads 5 – 8 mm apart, opposite and decussate. *Staminate flower* 11 – 12 × 5 – 6 mm shortly before anthesis; calyx c. 1 × 3 mm, sessile, consisting of 3 slightly different triangular and basally connate sepals, petals unequal in size 11 – 12 × 3 – 6 mm, valvate; stamens 6 – 8; filaments c. 0.5 × 0.3 – 0.4 mm, variously epipetalous, conical; anthers 4 – 5 × 0.4 – 0.7 mm, pointed; pistillodes 3 – 5 minute lobes. *Pistillate flowers* 2 – 3 × 2.5 – 3 mm near anthesis, ± conical; sepals 1.5 – 2 × 1.2 – 2 mm, rounded, imbricate, interior surface striate; petals 1.8 – 2.5 × 2 – 4 mm, rounded with slightly acuminate tips, broadly imbricate; ovary 1.5 – 2 × 0.8 – 1.3 mm, ovoid; well-defined style lacking; stigma minute and congenitally exposed; staminodes 3 – 6, tooth-like, connected by a thin basal ring. *Fruits* 7.4 – 9.4 × 6.6 – 8.2 mm when ripe, subglobose, smooth, drying ridged; perianth appressed to the fruit; pericarp c. 0.8 mm thick, epicarp red. *Seeds* 5.1 – 7.2 × 5 – 6.8 mm, globose to subglobose; hilum lateral, elongate; endosperm ruminate (Fig. 1).

RECOGNITION. Distinguished from all other species in the group by its apetiolate adult leaves and entire bifid juvenile leaves.

DISTRIBUTION. Known from two localities on the southern coast of New Guinea (Map 1).

SPECIMENS EXAMINED. INDONESIA. PAPUA PROVINCE: Mimika Regency, Timika, Nursery, Kuala Kencana [4°47'S 136°33'E], c. 50 m elev., 27 Feb. 1998, *Baker et al.* 884 (BH, BO, K!, L, MAN); Mimika Regency, Timika, East Levee by drowned forest, 5 km S of Kpg Kali Kopi, Loc 11, [4°39'S 136°55'E], 20 m elev., 18 Feb. 1998, *Witono* 20 (BH, BO, K, L!, MAN); Mimika Regency, Timika, East Levee by drowned forest, 5 km S of Kpg Kali Kopi, Loc 11, [4°39'S 136°55'E], 20 m elev., 18 Feb. 1998, *Witono* 21 (BO, K!, MAN). **PAPUA NEW GUINEA. GULF PROVINCE**: Kikori Distr., Kopi-Kikori road, 3 km NW of Kikori, [7°24'S 144°13'E], 40 m elev., 21 Nov. 2000, *Baker et al.* 1103 (AAU, BRI, K!, L, LAE, NY).

HABITAT. This species is known from cleared lowland rainforest in Timika, Indonesia, and from hill forest with abundant *Hydriastele*, *Licuala* and *Orania* in Kikori, Papua New Guinea; 20 – 50 m elevation.

LOCAL NAMES AND USES. None recorded.

GLOBAL CONSERVATION STATUS. Data Deficient (DD). More data are needed about the distribution and abundance of this species.

NOTES. *Hydriastele apetiolata* is known from three collections, all of which were sequenced for two genes by Loo *et al.* (2006) along with other specimens belonging to the *Hydriastele wendlandiana* group. In the resulting phylogenetic trees, *H. apetiolata* is distinguished by consistently falling outside of a well-supported clade containing all other members of the group that were included in the study. This noticeable phylogenetic pattern is consistent with the morphological distinctness of the species. The species is highly distinctive on account of its apetiolate leaves and the bifid juvenile leaves.

The type was collected from a palm that had been dug up from the wild, not far from the nursery in Timika, to where it was subsequently transplanted.

2. Hydriastele kasesa (*Lauterb.*) *Burret* (1937: 484). *Ptychosperma kasesa* Lauterb. (Lauterbach 1911: 357). *Adelonenga kasesa* (Lauterb.) Becc. (Beccari 1914: 26). Type: Papua New Guinea, New Ireland Province, Namatanai, *Peekel* 109 (holotype B†, isotype FI!).

Solitary or clustering, slender palm with 5 – 15 stems per clump, 2 – 6 m tall, bearing 6 – 8 leaves per crown. *Stem* 1.5 – 3.8 cm in diam., smooth and dark with blotches; internodes c. 2 – 10 cm long. *Leaves* 70 – 150 cm long including petiole; sheath 15 – 30 cm long, covered with lacerate-peltate, dark purple scales sometimes attached to ferrugineous filaments and covered by ± aggregated scurfy scales, crownshaft 30 – 35 cm long; petiole 15 – 40 cm, indumentum as sheath; rachis c. 35 – 90 cm, indumentum as sheath; leaflets 6 – 13 each side of rachis, mostly single-fold, arranged irregularly and usually with a clear interruption right above a group of closely spaced single- or bi-fold leaflets in different planes in the middle of rachis, cuneate and praemorse apically, ramenta lacking (always absent?), adaxially dark green – bluish green and somewhat glossy, abaxially a little paler, transverse veinlets obscure, thick and papery; terminal leaflets 16 – 27 × 5 – 10 cm, comprising 5 – 8 folds; middle leaflet to 45 × 10 cm; basal leaflets truncately praemorse apically. *Inflorescences* 17 – 30 cm long including 2 – 4 cm peduncle, branched to 1 or 2 orders; prophyll 15 – 27 × 3 – 4 cm; peduncular bract attached 0.5 – 1 cm above the prophyll; primary branches 5 – 10, to 23.5 cm long, closely spaced and bearing up to 3 rachillae each; rachillae up to 23.5 cm long, 1 – 2 (– 3) mm in diam.; triads 4 – 7 mm apart, opposite and decussate. *Staminate flowers* 8 × 3 – 4 mm when dry, shortly before anthesis; calyx c. 1 × 2 mm, sessile, consisting of 3 slightly different triangular and basally connate sepals, petals unequal in size 7 × 2 – 4 mm, valvate, white – pink; stamens 6; filaments c. 0.5 × 0.2 mm, variously epipetalous, conical; anthers 3 – 3.5 × 0.5 – 1 mm, pointed; pistillodes forming minute clump.

Fig. 1. *Hydriastele apetiolata*. **A** leaf apex; **B** mid-leaf portion; **C** leaf base with sheath; **D** juvenile leaf; **E** infructescence; **F** portion of rachilla with triads; **G** staminate flower in longitudinal section; **H** pistillate flower whole and in longitudinal section; **J** portion of rachilla with fruits; **K** fruit in longitudinal section. Scale bar: **A – C, E** 6 cm; **D** 12 cm; **F** 7 mm; **G** 5 mm; **H** 3.3 mm; **J** 1.5 cm; **K** 1 cm. All from *Baker* 884. DRAWN BY LUCY T. SMITH.

Pistillate flowers c. 2.5 × 2.5 mm when dry, shortly after anthesis, ± conical; sepals 1.8 – 2 × 2 – 3 mm, rounded, imbricate, interior surface striate; petals c. 2.2 × 3 mm, rounded with short obtuse tips, broadly imbricate; ovary c. 2 × 1 – 1.5 mm, ovoid; well-defined style lacking; stigma minute and congenitally exposed; staminodes c. 2, tooth-like and minute. *Fruits* c. 12 × 9 mm when ripe, ovoid to subglobose, smooth and drying wrinkled or ridged; perianth appressed to the fruit; epicarp red or scarlet, shiny. *Seeds* c. 6.7 × 5.4 mm when dry, ovoid; hilum lateral, elongate; endosperm ruminate (Fig. 2).

DISTRIBUTION. This species occurs in West New Britain Province, East New Britain Province, and New Ireland Province in the Bismarck Archipelago (Map 1).

SPECIMENS EXAMINED. PAPUA NEW GUINEA. WEST NEW BRITAIN PROVINCE: Eiliak, [5°45'S 149°5'E], 15 m elev., 7 May 1958, *White* 10070 (BRI, CANB!, L!, LAE); Gasmata Sub-distr., Gasmata patrol post, [6°15'S 150°19'E], 40 m elev., 30 May 1987, *Kerenga* 62320 (LAE!); Gasmata Sub-distr., 6 miles E of Fullerborn Harbour [6°6'S 150°38'E], 300 m elev., 8 May 1973, *Isles* 34405 (A, BRI, K!, L!, LAE, CANB!); Talasea Sub-distr., Koimumu-Lavege Road, [5°36'S 150°25'E], 17 April 1959, *White* 10889 (A, BRI, K!, LAE); Talasea Sub-distr., Kimbe, [5°33'S 150°9'E], 0 m elev., 26 April 1972, *Essig* 55214 (LAE!); Mt Klangal, 25 miles NNE of Gasmata, [6°00'S 150°30'E], 800 m elev., 15 May 1973, *Croft* 15567 (BH, L!, LAE). **EAST NEW BRITAIN**: Rabaul Sub-distr., Matanakunei, [4°52'S 151°43'E], 0 m elev., 29 March 1968, *Ridsdale* 38004 (BH, BRI, CANB, L!). **NEW IRELAND PROVINCE**: Namatanai, *Peekel* 109 (B†, FI!); Namatanai Sub-distr., Hans Meyer Range, Danfu R. Valley about 8 km W and upstream of the Danfu bridge nr Manga, [4°11'S 152°57'E], 800 m elev., 14 Feb. 1970, *Sands* 866 (K!, L, LAE); inland from Lossuk to Bagaterra, [2°45'S 151°4'E], 0 m elev., 3 Feb. 1967, *Coode* 29729 (LAE!); near the junction of the Niagara and Weitin R., [4°30'S 152°56'E], 240 m elev., 19 Jan. 1994, *Takeuchi* 9902 (A!); near the junction of the Niagara and Weitin R., [4°30'S 152°56'E], 240 m elev., Jan. 1994, *Takeuchi* 9994 (A!); Sub-distr. Lamet, West New Hanover, 2 km E of Metemulai village, [2°30'S 150°2'E], 50 m elev., 7 Oct. 1974, *Croft* 65490 (BH, L!, LAE); Namatanai Sub-province, Lihir Island, Mt Tementa above Palie Mission, [3°12'S 152°36'E], 600 m elev., 7 Nov. 1984, *Gideon* 57205 (L!, LAE, USP).

HABITAT. *Hydriastele kasesa* occurs in the understorey of lowland tropical primary rainforest, occasionally in swampy areas or on stream banks, and on premontane mixed forest slopes and ridges, on clay-loam; 0 – 800 m elevation.

LOCAL NAMES AND USES. None recorded.

GLOBAL CONSERVATION STATUS. Least Concern (LC). *Hydriastele kasesa* is relatively widely distributed with an EOO of c. 113,000 km^2. The species' small AOO of 48 km^2 is most likely a low estimate due to under-collecting. It has been reported as common in some localities. The biggest future threat appears to be deforestation and land-use change (Shearman *et al.* 2008; Global Forest Watch 2017).

NOTES. This species is distinguished by its slender habit with sheaths of 15 – 30 cm in length, leaves with 6 – 13 pairs of irregularly arranged leaflets, the basal ones of which are truncately praemorse apically, and rather small inflorescences with 5 – 10 primary branches. *Hydriastele kasesa* can be confused with *H. wendlandiana*, which is the only other species in the group with a similar leaflet arrangement, but *H. wendlandiana* is normally not quite as slender, has longer sheaths (40 – 73 cm), nearly always more numerous leaflets (12 – 30 per side), and the inflorescences have 8 – 15 primary branches. The distribution of *H. kasesa* does not appear to overlap with that of any other member of the *H. wendlandiana* group.

3. Hydriastele rheophytica *Dowe & M. D. Ferrero* (2000: 195). Type: Indonesia, Papua Province, Idenburg R., Araucaria Creek [3°29'S 139°6'E], March 1939, *Brass* 13700 (holotype A!, isotype L!).

Clustering, slender palm with up to 30 stems per clump, 4 – 6 m tall, bearing 4 – 12 leaves per crown. *Stem* 2 – 2.5 cm in diam., pliable, cream with red patches turning green; internodes to 14 cm long. *Leaves* c. 95 – 120 cm long including petiole; sheath 40 – 45 cm long, dark green, coated with lacerate-peltate, dark purple scales sometimes covered by scurfy scales, petiole 20 – 30 cm long, pliable, indumentum as sheath; rachis c. 60 – 80 cm long, slightly arching, indumentum as sheath; leaflets 18 – 32 each side of rachis, arranged ± regularly at 2 – 5 cm intervals, linear and praemorse, adaxially dark green, abaxially slightly paler green, transverse veinlets obscure, ramenta present, thin and soft; terminal leaflets 22 – 27 × 0.7 – 2 cm, comprising 2 – 3 folds; sub-apical leaflets c. 30 × 0.7 – 2 cm, single-fold; basal leaflets c. 40 × 1.2 – 2 cm, single-fold, obliquely praemorse apically. *Inflorescences* 16 – 30 cm long including 2.5 – 7 cm peduncle, branched to 1 or 2 orders; prophyll to c. 20 cm long; first peduncular bract attached c. 0.8 cm above the prophyll; primary branches up to 10, to 20 cm long, closely spaced and bearing up to 2 rachillae each; rachillae 5 – 15 per inflorescence, 1 – 3 mm in diam.; triads c. 3 – 5 mm apart, opposite and decussate. *Staminate flowers* 6 – 8 × 3 – 4 mm when dry, pinkish cream; calyx 1 – 1.5 × 1.5 – 2 mm, sessile, with 3 slightly different triangular and basally connate sepals; petals unequal in size, 5.2 – 8 × 3 – 5 mm, valvate; stamens 6; filaments 0.5 – 1 × 0.5 – 0.8 mm, variously epipetalous, tubular – conical; anthers 3 – 4 × 1 mm, pointed; pistillodes absent. *Pistillate flowers* 2 – 2.5 × 2 mm when dry, close to anthesis, ± conical; sepals 1.5 – 2 × 2.5 –

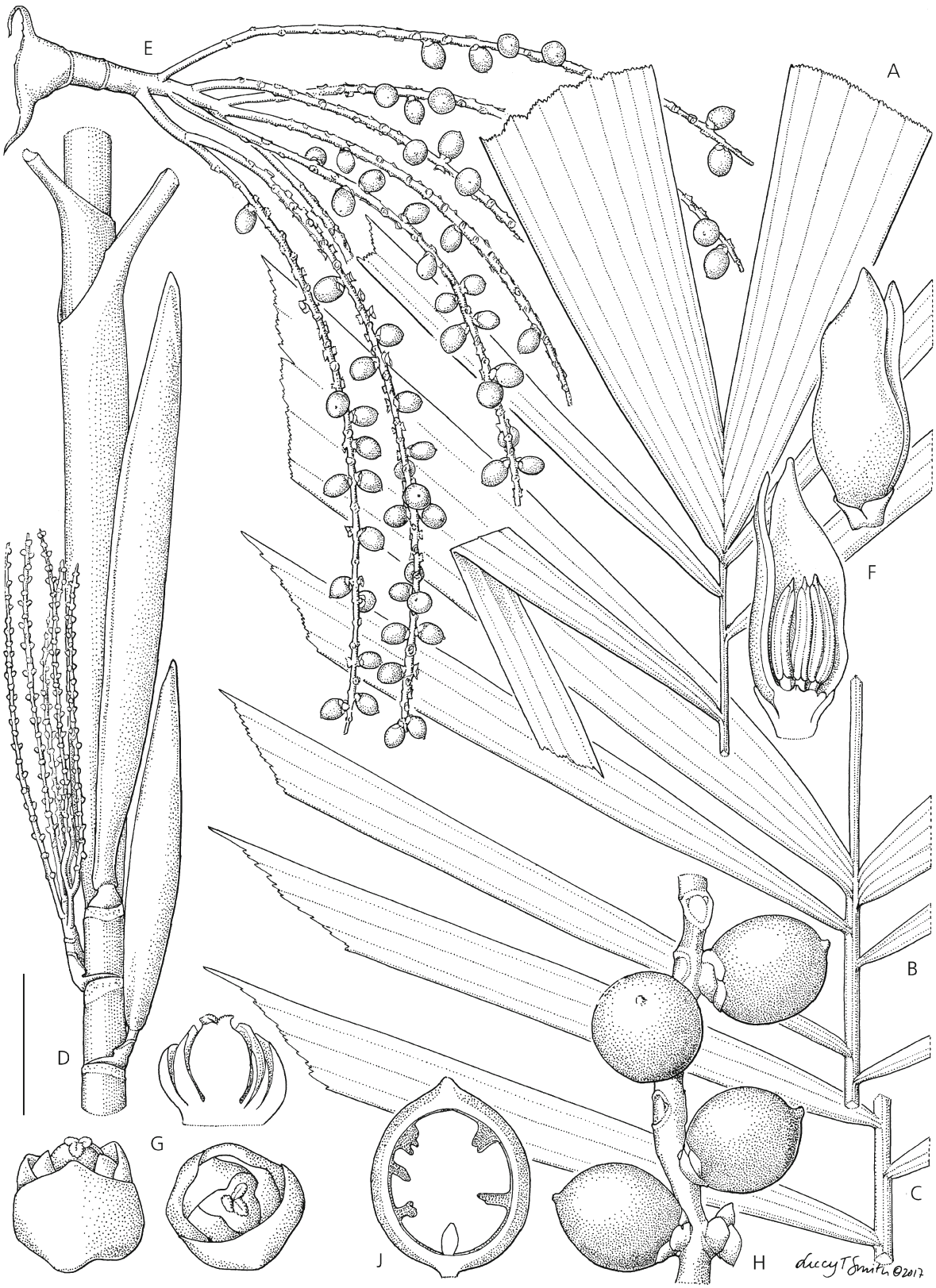


Fig. 2. *Hydriastele kasesa*. **A** leaf apex; **B** mid-leaf portion; **C** leaf base; **D** leaf sheaths above attached inflorescences with or without prophyll; **E** infructescence; **F** staminate flower whole and in longitudinal section; **G** pistillate flower whole, two views, and in longitudinal section; **H** portion of rachilla with fruits; **J** fruit in longitudinal section. Scale bar: **A** – **C** 8 cm; **D** 6 cm; **E** 4 cm; **F** 5 mm; **G** 2.2 mm; **H** 1 cm; **J** 7 mm. All from *Takeuchi* 9902. DRAWN BY LUCY T. SMITH.

3 mm, rounded, imbricate, internal surface striate; petals c. 1.5 × 2.5 mm, rounded, with short triangular apical lobe, broadly imbricate; ovary c. 1.5 × 1 mm, ellipsoid; well-defined style lacking; stigma minute and congenitally exposed; staminodes absent. *Fruits* c. 7 mm long, globose to broadly ellipsoid, smooth to shallowly ridged. *Seeds* globose, endosperm shallowly ruminate (Fig. 3).

DISTRIBUTION. *Hydriastele rheophytica* is known from the Idenburg River and its upper tributaries in Papua Province, Indonesia, and, according to Dowe & Ferrero (2000), from the Frieda River in Sandaun Province, Papua New Guinea (Map 1).

SPECIMENS EXAMINED. INDONESIA. PAPUA PROVINCE: Idenburg R., Araucaria Creek, 4 km SW of Bernhard camp, [3°29'S 139°6'E], March 1939, *Brass* 13700 (A!, L!); Same locality as preceding, [3°29'S 139°6'E], 850 m elev., March 1939, *Brass* 13608 (A!, L!).

HABITAT. Stream banks or river banks that are frequently subjected to inundation; c. 850 m elevation.

LOCAL NAMES AND USES. None recorded. Cultivated as an ornamental following introduction to Australia in the 1980s (Dowe & Ferrero 2000).

GLOBAL CONSERVATION STATUS. Data Deficient (DD). More information is needed about the distribution and abundance of this species.

NOTES. This apparently obligate rheophyte is distinguished by its pliable, mostly leaning stems, and soft, flexible leaves. These traits are often displayed by plants that grow in a rheophytic environment, on stream edges and riverbanks where frequent inundation occurs (van Steenis 1981). *Hydriastele rheophytica* may also be unique within the *H. wendlandiana* group in forming clumps with as many as 30 stems. The basal leaflets of *H. rheophytica* are linear and obliquely praemorse at the tip, prompting comparison with *H. variabilis* which has pointed to obliquely praemorse basal leaflets. However, the two species differ in the terminal leaflet morphology with the most distal pair comprising 4 – 11 folds in *H. variabilis* and only c. 2 – 3 folds in *H. rheophytica*. Furthermore, *H. variabilis* does not display rheophytic characters.

An original Brass photo which shows this elegant palm in its native habitat was reproduced in *Rheophytes of the World* (van Steenis 1981).

4. Hydriastele variabilis (*Becc.*) *Burret* (1937: 483). *Nenga variabilis* Becc. (Beccari 1877: 26). *Adelonenga variabilis* (Becc.) Becc. (Beccari 1885: 82). Type: Indonesia, Papua Barat Province, Ramoi, 1872, *Beccari* PP426 (holotype FI!, isotype K!).

Nenga variabilis var. *sphaerocarpa* Becc. (Beccari 1877: 27). *Hydriastele variabilis* var. *sphaerocarpa* (Becc.) Burret (1937: 483). Type: Indonesia, Papua Barat Province, Amberbakin, 1872, *Beccari* s.n. (holotype FI!, isotype K!).

Clustering, slender palm, 2 – 8 m tall, bearing 4 – 7 leaves per crown. *Stem* 2 – 4 cm in diam., greenish to dark brown to blackish, blotchy; internodes 5 – 14 cm long. *Leaves* 95 – 140 cm long including petiole; sheath 27 – 45 cm long, green, with lacerate-peltate, dark purple scales attached to ferrugineous filaments, sometimes additionally covered with scurfy scales and whitish bloom, crownshaft 33 – 70 cm long; petiole 9 – 30 cm long, indumentum as sheath; rachis 50 – 110 cm long, indumentum as sheath; leaflets 11 – 23 each side of rachis, arranged regularly to subregularly, borne 2.5 – 7 cm apart, ± horizontally held in a single plane with tips drooping slightly, linear, transverse veinlets obscure, with ramenta; terminal leaflets 20 – 44 × 2 – 10 cm, comprising 4 – 11 folds, praemorse apically; longest middle leaflet 40 – 80 × 1.2 – 3 cm, single-fold, praemorse apically; basal leaflets single-fold, pointed or obliquely praemorse apically. *Inflorescences* 10 – 25 cm long including 2 – 2.5 cm peduncle, branched to 1 or 2 orders; prophyll not seen, caducous; first peduncular bract attached 0.3 – 0.5 cm above the prophyll; primary branches 6 – 11, to 22 cm long, closely spaced and bearing up to 1 rachilla each; rachillae to 22 cm long, 1 – 2.5 mm in diam.; triads c. 3 – 5 mm apart, opposite and decussate. *Staminate flowers* not seen. *Pistillate flowers* 2 – 2.5 × 2 – 3 mm when dry, shortly after anthesis, ± conical; sepals c. 2 × 2 – 3 mm, connate at the base, rounded, imbricate, interior surface striate; petals 2 – 2.5 × 2.5 – 3 mm, rounded, broadly imbricate; ovary 2 – 2.5 × 1.2 – 1.5 mm, ovoid to ellipsoid; well-defined style lacking; stigma minute and congenitally exposed; staminodes c. 2, tooth-like and minute. *Fruits* 10 – 12 × 6.3 – 7.8 mm when ripe, ellipsoid to ovoid with ends tapering when dry, smooth, drying ridged; perianth appressed to the fruit; pericarp c. 0.8 mm thick, epicarp red. *Seeds* 7 – 8.2 × 5 – 6 mm, ovoid; hilum lateral, elongate; endosperm deeply ruminate (Fig. 4).

DISTRIBUTION. *Hydriastele variabilis* occurs in Papua Barat Province, Indonesia, with most records from the Bird's Head Peninsula (Map 1).

SPECIMENS EXAMINED. INDONESIA. PAPUA BARAT PROVINCE: Ramoi, 1872, *Beccari* PP426 (FI!, K!); Amberbakin, 1872, *Beccari* s.n. (FI!, K!); Manokwari Distr., Bintuni Sub-distr., beside trail between Saengga & Tanah Merah Villages, [2°27'S 133°7'E], 20 m elev., 13 Feb. 2002, *Maturbongs* 712 (BO, K!, LAE, MAN); Manokwari Distr., Bintuni Sub-distr., near Saengga Village, [2°27'S 133°6'E], 20 m elev., 13 Feb. 2002, *Sambas* 17 (BO, K!, LAE, MAN); Manokwari, around a construction main road of Manokwari-Sorong, between

Fig. 3. *Hydriastele rheophytica*. **A** habit; **B** leaf apex; **C** mid-leaf portion; **D** leaf base; **E** infructescence; **F** portion of rachilla with pistillate flowers; **G** staminate flower whole and in longitudinal section; **H** pistillate flower whole and in longitudinal section; **J** fruit whole and in longitudinal section. Scale bar: **A** 70 cm; **B – D** 6 cm; **E** 4 cm; **F – G** 5 mm; **H** 2.5 mm; **J** 5 mm. **A, J** from *Dowe* 536; **B – H** from *Brass* 13700. DRAWN BY LUCY T. SMITH.

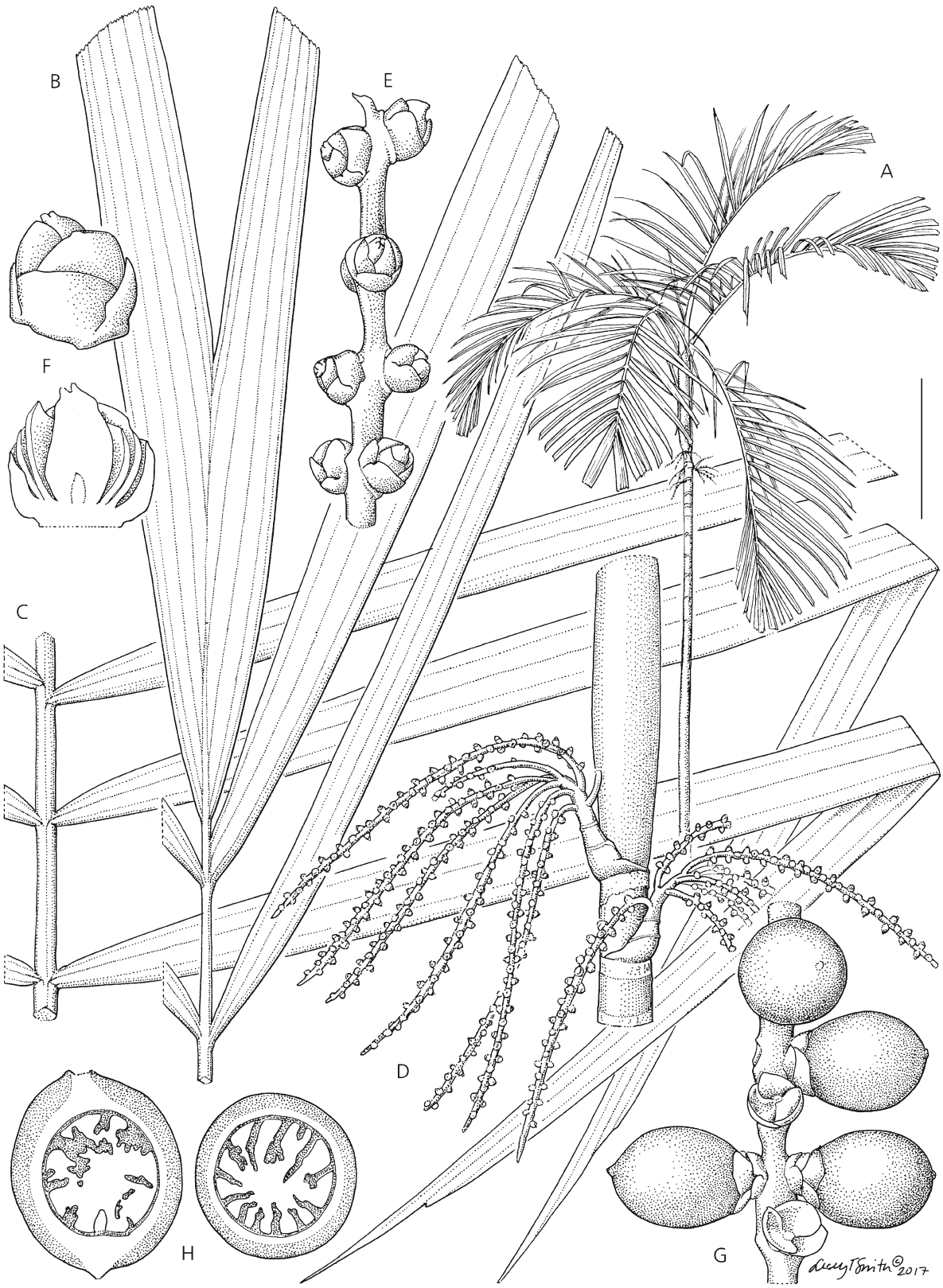


Fig. 4. *Hydriastele variabilis*. **A** habit; **B** leaf apex; **C** mid-leaf portion; **D** attached inflorescences with pistillate flowers; **E** portion of rachilla with pistillate flowers; **F** pistillate flower whole and in longitudinal section; **G** portion of rachilla with fruits; **H** fruit in longitudinal and transverse section. Scale bar: **A** 40 cm; **B – C** 4; **D** 6 cm; **E** 1 cm; **F** 3 mm; **G** 1.5 cm; **H** 7 mm. **A, D – F** from *Gardiner* 424; **B – C, G – H** from *Baker* 1369. DRAWN BY LUCY T. SMITH.

Wariori R. and Waramoi R., [0°48'S 133°38'E], 400 m elev., 26 April 1994, *Mogea* 6305 (AAU, BO, BRI, K!, L, MAN, NY); Manokwari, Kebar, Kebar Valley, trail from Andjai to G. Nettoti near base camp 'N' on ridge at 1000 m, [0°46'S 133°3'E], 1240 m elev., 3 May 1995, *Davis* 726 (BO, BRI, K!, MAN, NY); Sorong, Klasaman, Km 27, Intimpura Camp, [0°58'S 131°28'E], 120 m elev., 20 Sept. 1995, *Maturbongs* 292 (K!); Sorong, Klasaman, KM14, [0°55'S 131°22'E], 40 m elev., 15 Sept. 1995, *Wally* 464 (K!); Sorong, Roefei R. N of Sorong, c. 2 miles from the sea on northern bank, [0°51'S 131°15'E], 90 m elev., 24 March 1954, *van Royen* 3155 (CANB!, L!); Sorong Distr., Klasaman, Klabainem, [0°55'S 131°20'E], 10 m elev., 29 Feb. 2002, *Heatubun* 375 (K!, MAN); Tamrau Mts, Sorong-Manokwari road, beyond Bamus Buma, towards Fef and Manokwari, [0°45'S 132°17'E], 950 m elev., 28 Jan. 2013, *Gardiner* 424 (BO, K!, L, MAN); Tambrouw Regency, Fef Distr.; Pass above Fef, [0°49'S 132°27'E], 700 m elev., 24 Jan. 2013, *Baker et al.* 1369 (BO, K!, L, MAN); Sorong Regency, Klaso Distr.; Kalalin, near Megame, [0°46'S 131°49'E], 100 m elev., 31 Jan. 2013, *Baker et al.* 1390 (BO, K!, L, MAN); Locality info lacking, *Iwanggin* 134 (MAN, K!).

HABITAT. This species is occasional to locally abundant in pristine or degraded lowland tropical rainforest, sometimes growing near creeks or adjacent to savannah or swamp forest, and on slopes in premontane primary forest on soils with a varying composition of clay, sand, humus and fibrous roots; 0 – 1200 m elevation.

LOCAL NAMES AND USES. *sagarofa* (Sumuri), *pinang oetan* (Malay). No recorded uses.

GLOBAL CONSERVATION STATUS. Least Concern (LC). The EOO of *Hydriastele variabilis* is c. 26,000 km^2 and the AOO is 44 km^2 with the latter figure likely to be a low estimate resulting from under-collecting. It has been observed in some forested areas now known to have been replaced by oil palm plantations, the expansion of which may pose a future threat to this species compounded by its relatively narrow distribution.

NOTES. This species is distinguished by its slender habit, bearing 4 – 7 petiolate leaves per crown, and leaflets that are regularly arranged with the basal ones being linear and pointed to obliquely praemorse at the tip, and the terminal pair comprising 4 – 11 folds. Some resemblance to this basal leaflet morphology is seen in *Hydriastele apetiolata* and *H. rheophytica* but the apetiolate adult leaves and bifid juvenile leaves are highly distinctive in the former species, and the latter species has terminal leaflets comprising c. 2 – 3 folds and also displays rheophytic characters such as pliable stems. Confusion with *H. wendlandiana* is unlikely as this species usually has irregularly arranged leaflets, the basal ones of which are truncately praemorse apically.

In the protologue for *Hydriastele variabilis* the staminate flower morphology is described in detail by Beccari (1877) from the type specimen *Beccari* PP426.

5. Hydriastele wendlandiana (*F. Muell.*) *H. Wendl. & Drude* (Wendland & Drude 1875: 209). *Kentia wendlandiana* F. Muell. (Mueller 1870: 102). Type: Australia, Northern Territory, Liverpool R., 1867, *Gulliver* s.n. (holotype MEL!, isotype BRI, K!).

Hydriastele wendlandiana var. *microcarpa* H. Wendl. & Drude (Wendland & Drude 1875: 210). Type: Australia, Queensland, O'Connell R., *Nernst* s.n. (location of holotype unknown, not at MEL). *Nenga geelvinkiana* Becc. (Beccari 1877: 28). *Adelonenga geelvinkiana* (Becc.) Becc. (Beccari 1885: 82). *Hydriastele geelvinkiana* (Becc.) Burret (1937: 484). Type: Indonesia, Papua Province, Geelvinck Bay, April 1875, *Beccari* s.n. (holotype FI!, isotype K!). **synon. nov.**

Hydriastele douglasiana F. M. Bailey (1897: 232). Type: Australia, Queensland, Cape York Peninsula, Somerset, Polo Creek, June 1897, *Jardine* s.n. (holotype BRI!; cf. note in Baker & Loo [2004]).

Kentia microspadix Warb. ex K. Schum. & Lauterb. (Schumann & Lauterbach 1900: 206). *Adelonenga microspadix* (Warb. ex K. Schum. & Lauterb.) Becc. (Beccari 1914: 26). *Hydriastele microspadix* (Warb. ex K. Schum. & Lauterb.) Burret (1937: 484). Type: Papua New Guinea, Madang Province, Hatzfeldhafen, *Warburg* s.n. (lectotype FI!; selected by Baker & Loo [2004]). **synon. nov.**

Ptychosperma beccarianum Warb. ex K. Schum. & Lauterb. (Schumann & Lauterbach 1900: 208). **nom. nud.**

Hydriastele beccariana Burret (1928: 292). Type: Indonesia, Papua Province, Noord R [4°37'S 138°43'E], 25 Aug. 1907, *Versteeg* 1662 (holotype B†, isotypes BO, FI!, K!, L!). **synon. nov.**

Hydriastele carrii Burret (1936: 326). Type: Papua New Guinea, 1935, *Carr* s.n. (holotype B†). Neotype selected here: Papua New Guinea, Central Province, Koitaki, 22 Aug. 1935, *Carr* 12657 (neotype K!; isoneotypes A!, L!, NY!, SING!). **synon. nov.**

Hydriastele rostrata Burret (1937: 484). Type: Cultivated in Bogor Botanic Garden ex New Guinea, V1 4, April – May 1936, *Furtado SFN* 31139 (holotype B†, isotypes A!, K!, L!, SING). **synon. nov.**

Hydriastele lepidota Burret (1939: 204). Type: Papua New Guinea, Western Province, Tarara, Wassi Kussa R [8°55'S 141°55'E], Jan. 1937, *Brass* 8701A (holotype A!, isotypes BRI, L). **synon. nov.**

Solitary or clustering, slender to moderate palm with 3 – 10 stems per clump, 1 – 17 m tall, bearing 5 – 10 (– 12) leaves per crown. *Stem* 2 – 10 cm in diam., smooth,

with grey, brown and green blotches; internodes 2 – 25 cm long. *Leaves* 1 – 2.5 m long including petiole; sheath 40 – 73 cm long, yellowish to grey to green, with lacerate-peltate, dark purple scales sometimes attached to ferrugineous filaments and covered by ± aggregated, scurfy scales, occasionally with white bloom, crownshaft 30 – 160 (– 240) cm long; petiole (2 –) 10 – 80 cm long, indumentum as sheath; rachis 38 – 190 cm long, slightly arching, indumentum as petiole; leaflets 12 – 30 each side of rachis, mostly single-fold, arranged regularly or more frequently irregularly with varying distances between leaflets and a break just above a group of closely spaced single- or bi-fold leaflets in different planes in the middle of rachis, cuneate and praemorse apically, ramenta usually present, adaxially mid to dark green and somewhat glossy, abaxially paler green, transverse veinlets obscure, thick and papery to more thin and stiff; terminal leaflets 15 – 42 × (1.5 –) 3 – 20 cm, comprising (1 –) 3 – 16 folds; middle leaflets 35 – 71 × 2 – 8 cm; basal leaflets truncately praemorse apically. *Inflorescences* (16 –) 21 – 50 cm long including 2.5 – 7 cm peduncle, with (1 –) 2 (– 3) orders of branching; prophyll 27 – 50 × 4 – 7 cm, glabrous; first peduncular bract attached 0.5 – 2 cm above the prophyll; primary branches 8 – 15, to 46 cm long, closely spaced and bearing up to 5 rachillae each; rachillae to 43 cm long, 1 – 3 mm in diam.; triads 2.5 – 10 mm apart, opposite and decussate. *Staminate flowers* 8 – 10 × 3 – 5 mm shortly before anthesis, creamy white; calyx 1 – 2 × 2 – 3.5 mm, sessile, with 3 slightly different triangular and basally connate sepals; petals unequal in size 7 – 9.5 × 2.5 – 5 mm, valvate; stamens (5 –) 6 (– 8); filaments 0.3 – 1 × 0.1 – 0.5 mm, variously epipetalous, tubular to conical; anthers 3 – 5 × 0.3 – 1 mm, ± pointed; pistillodes 2 – 4 minute lobes. *Pistillate flowers* 1.8 – 3 × 1.8 – 2.5 mm at anthesis, greenish, ± conical; sepals 1.3 – 2 × 1.8 – 2.5 mm, rounded, imbricate, internal surface striate; petals 1.3 – 2.5 × 2.5 – 3 mm, rounded but occasionally with short apical lobe, broadly imbricate; ovary c. 1 – 1.8 × 1 mm, globose to ellipsoid to ovoid; well-defined style lacking; stigma minute and congenitally exposed; staminodes 1 – 3, tooth-like and minute. *Fruits* 7 – 9 (– 11) × 6 – 8 mm when ripe, globose to ovoid, smooth and drying wrinkled or ridged; perianth appressed to the fruit; pericarp c. 0.8 – 1.2 mm thick, epicarp orange, purple or various shades of red. *Seeds* 5 – 7 × 5 – 6.2 mm, globose to ovoid; hilum lateral, elongate; endosperm homogeneous or ± ruminate (Fig. 5).

DISTRIBUTION. *Hydriastele wendlandiana* is widespread in Queensland and Northern Territory (northern Australia), New Guinea and on islands in between (Map 1).

SPECIMENS EXAMINED. AUSTRALIA. NORTHERN TERRITORY: Liverpool R., 1867, *Gulliver* s.n. (BRI, K!, MEL!); Arnhem Land, Gulumarri, Elcho Island, [11°56'S 135°49'E], 18 July 1975, *Latz* 6269 (CANB, DNA, K!, NSW); Arnhem Land, Giddy R. Crossing, [12°22'S 136°42'E], 20 June 1972, *Maconochie* 1550 (DNA, K!); Arnhem Land, N side of Tomkinson R c. 13 km S of Maningrida, [12°10'S 134°15'E], 1974, *Rodd* 2912 (DNA, K!); Robins Falls, 105 km SSE of Darwin, [13°21'S 131°7'E], 1974, *Rodd* 2908 (K!, NSW); Robins Falls, 105 km SSE of Darwin, [13°21'S 131°7'E], 1974, *Rodd* 2909 (K!, NSW); **QUEENSLAND**: Coconut creek, 8 km upstream from Beagle North Camp c. 45 km NNE of Aurukun, [12°57'S 141°49'E], 50 m elev., 27 May 1982, *Clarkson* 4356 (BRI, K!); Cape Sidmouth, [13°24'S 143°35'E], 1876, *Candie* s.n. (K!); Cape York, 1875, *Hill* 5 (K!); Cape York Peninsula, Somerset, Polo Creek, June 1897, *Jardine* s.n. (BRI!); Cape York Peninsula, Bamaga Mission, 11.2 km SW of Cape York, E to mill and beyond, stony red hill, [10°53'S 142°24'E], 24 Oct. 1965, *Smith* 12413 (BRI, K!, L!); Cape York Peninsula, Newcastle Bay, 2.5 miles S of Somerset, [10°47'S 142°33'E], 20 m elev., 9 May 1948, *Brass* 18722 (A, K!, L!); Cape York Peninsula, Iron Range, [12°43'S 143°12'E], 150 m elev., 18 June 1948, *Brass* 19250 (A, K!, L!). **INDONESIA. MALUKU PROVINCE**: Aru Islands, Pulau Trangan, 6 km S of Sia, [6°50'S 134°17'E], 10 m elev., 22 Oct. 1994, *van Balgooy* 6588 (K!, L!); **PAPUA BARAT PROVINCE**: Rajah Ampat Regency, N Misool Island, about 20 km W of Waigama Village near Motlol Camp, [1°53'S 129°44'E], 10 m elev., 22 Jan. 2002, *Maturbongs* 701 (BO, FTG, K!, L, LAE, MAN); South Sorong Regency, Sayal village, Maampow forest, [1°28'S 131°53'E], 10 m elev., 21 Feb. 2003, *Heatubun* 416 (BO, K!, MAN); Sorong, Makbalim, Aimas (SP4), [1°4'S 131°24'E], 50 m elev., 1 July 1997, *Heatubun* 152 (K!); Manokwari Distr., mts S of Arfak Plains, steep ridges between the Arfak plains and Gunung Itsiwei, [0°51'S 133°37'E], 625 m elev., 26 April 1994, *Sands* 6354 (BO, K!, MAN); Manokwari Distr., Tatbei Ridge above Warmare, [0°47'S 133°58'E], 495 m elev., 24 Aug. 1995, *Zona* 688 (BO, FTG, K!, MAN); Manokwari Regency, Manokwari Distr., Warmare, Prafi R. Valley, [0°47'S 133°58'E], 375 m elev., 25 Aug. 1995, *Zona* 690 (BO, FTG, K!, MAN); Manokwari Regency, Manokwari, Cultivated, in the front of a mosque within the university area, Amban., [0°51'S 134°4'E], 120 m elev., 13 Aug. 1995, *Keim* 3 (K!); Teluk Wondama Regency, Wasior Distr., Wandammen Peninsula, near Dotir village, 11 km N of Wasior, near the confluence of the Mawoi R. and the Yois R., [2°37'S 134°29'E], 50 m elev., 20 Feb. 2000, *Baker et al.* 1043 (BO, K!, MAN); Teluk Wondama Regency, Wasior Distr., Vicinity of Wosimi R., Sikama R., 3 km SE of Senderawoi village, 26 km SSE of Wasior, [2°57'S 134°34'E], 150 m elev., 26 Feb. 2000, *Baker et al.* 1065 (BO, K!, L, MAN); Teluk Wondama Regency, Wasior Distr., Wandammen peninsula, near Wondiwoi Village, c. 9 km S of Wasior, [2°48'S 134°32'E], 23 Feb. 2000, *Rustiami* 36 (BO, K!,

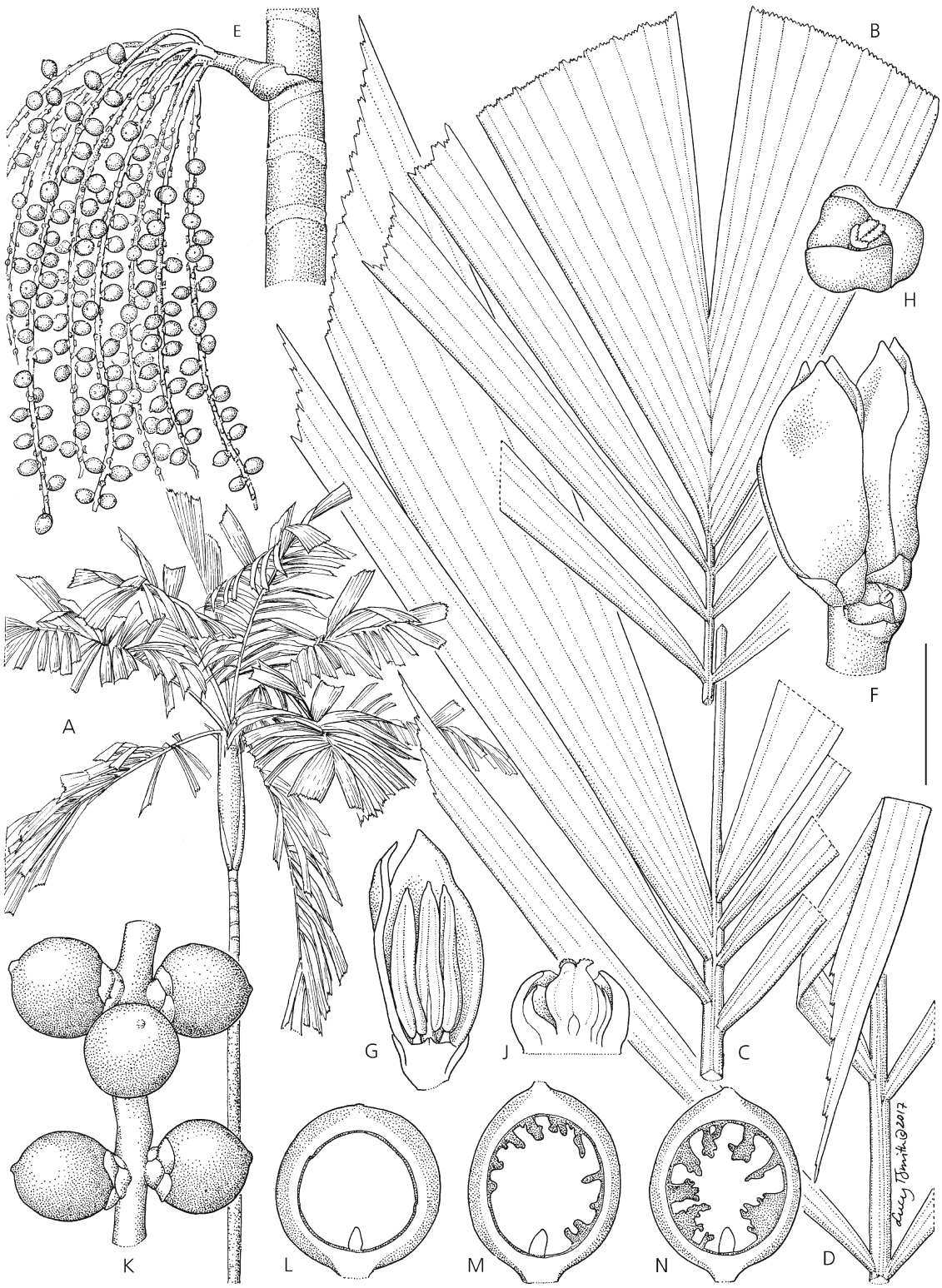


Fig. 5. *Hydriastele wendlandiana*. **A** habit; **B** leaf apex; **C** mid-leaf portion; **D** leaf base; **E** attached infructescence; **F** triad; **G** staminate flower in longitudinal section; **H** pistillate flower; **J** pistillate flower in longitudinal section; **K** portion of rachilla with fruits; **L** – **N** fruit in longitudinal section: **L** homogeneous endosperm; **M** shallowly ruminate endosperm; **N** ruminate endosperm. Scale bar: **A** 70 cm; **B** – **D** 8 cm; **E** 6 cm; **F** – **G** 5 mm; **H** – **J** 2.5 mm; **K** 1.5 cm; **L** – **N** 7 mm. **A, F** – **J** from *Baker* 1106; **B** – **E, N** from *Klappa* 151; **K** – **L** from *Baker* 1065; **M** from *Baker* 573. DRAWN BY LUCY T. SMITH.

L, MAN); Teluk Bintuni Regency, Merdey Sub-distr., [1°35'S 133°20'E], 600 m elev., 2 Aug. 1998, *Wally* 844 (BO, K!, MAN); **PAPUA PROVINCE**: Noord R [4°37'S 138°43'E], 25 Aug. 1907, *Versteeg* 1662 (B†, BO, FI!, K!, L!); Geelvinck Bay, April 1875, *Beccari* s.n. (FI!, K!); Keerom Regency, Arso Distr., Tami R., Yusfowor, [2°51'S 140°48'E], 100 m elev., 11 March 2002, *Gusbager* 1 (K!, LAE, MAN); Central Mamberamo Regency, Taritatu R., 6 km SW of Bernhard camp, [3°30'S 139°5'E], 1050 m elev., March 1939, *Brass* 13045 (A!, L!); Nabire Regency, Samabusa, [3°18'S 135°35'E], 10 m elev., 10 Feb. 2001, *Heatubun* 343 (AAU, K!, MAN); Nabire Regency, Km-45 road PT, Kaltim Hutama, [3°28'S 134°52'E], 100 m elev., 2 Feb. 2001, *Heatubun* 333 (AAU, K!, MAN); Nabire Regency, Napan, Makimi, Sungai Musairo, [3°3'S 135°45'E], 5 m elev., 3 May 1985, *Mogea* 5529 (BO, K!, L); Mamberamo Raya Regency, Albatross Biv., [2°18'S 138°2'E], 75 m elev., Nov. 1926, *van Leeuwen* 11201 (K!, L!); Mimika Regency, Timika, Km 64.5 on road to Tembagapura, [4°18'S 136°59'E], 380 m elev., 7 Feb. 1998, *Dransfield* 7654 (BH, BO, K!, L, MAN); Yapen Islands Regency, Yapen Island, Jalan trans Yapen, [1°45'S 136°15'E], 700 m elev., 26 Oct. 1998, *Maturbongs* 613 (BO, FTG, K!, L, MAN); Yapen Islands Regency, Yapen island, Konti-unai village, near trans-yapen main road, [1°45'S 136°5'E], 700 m elev., 21 Oct. 1998, *Maturbongs* 596 (BO, K!, L, MAN, NY); Yapen Islands Regency, Yapen island, Konti-unai village, [1°45'S 136°5'E], 600 m elev., 21 Oct. 1998, *Maturbongs* 591 (BO, FTG, K!, L, MAN); Yapen Islands Regency, Yapen Island, Konti-unai village, trans-Yapen main road, [1°45'S 136°5'E], 800 m elev., 21 Oct. 1998, *Maturbongs* 600 (BO, FTG, K!, MAN); Jayapura Regency, Tanjung Elmo, on the edge of Sentani lake, [2°37'S 140°30'E], 90 m elev., 19 Sept. 1998, *Maturbongs* 575 (BO, FTG, K!, MAN); Jayapura Regency, Angkasa, Cyclops Mts, Jayapura, [2°31'S 140°43'E], 385 m elev., 9 Aug. 1998, *Heatubun* 269 (BO, FTG, K!, MAN); Jayapura Regency, Cyclops Mts, Jayapura, [2°30'S 140°30'E], 190 m elev., 16 Aug. 1998, *Heatubun* 281 (BO, FTG, K!, L, MAN, NY); Jayapura, North Cyclops Mts, [2°30'S 140°32'E], 20 m elev., 31 Jan. 2001, *Desianto* 8 (AAU, K!, MAN); Jayapura, Dessa Tami-Monding, mouth of the R. Tami, [2°37'S 140°55'E], 15 m elev., 16 March 1956, *Kalkman* 3399 (CANB!, L); Jayapura and vicinity, [2°37'S 140°40'E], 7 July 1938, *Brass* 8963 (A!); Jayapura and vicinity, [2°32'S 140°42'E], 100 m elev., June 1938, *Brass* 8982 (A!, BRI, L!); Jayapura and vicinity [2°32'S 140°42'E], 60 m elev., June 1938, *Brass* 8891 (A!, BRI, L!); Merauke Regency, Kwell village, [7°10'S 140°50'E], 30 Sept. 2000, *Maturbongs* 652 (AAU, BO, K!, MAN); Merauke Regency, Yanggandur village, Wasur, [8°32'S 140°52'E], 2000, *Maturbongs* 658 (AAU, BO, K!, MAN); **UNKNOWN PROVINCE**: Locality info lacking, *Wally* 1040 (K!). **PAPUA NEW GUINEA. MADANG PROVINCE**: Hatzfeldhafen, *Warburg* s.n. (FI!); Madang, Baitabag Village; Baitabag village conservation area, near to Christensen Research Institute, [5°8'S 145°46'E], 30 m elev., 10 Jan. 1996, *Baker et al.* 566 (BH, BO, K!, KEP); North Ambenob, Baiteta Village, [5°1'S 145°45'E], 100 m elev., 11 Jan. 1996, *Baker et al.* 573 (BH, FTG, K!, L); Ohu Village Conservation Area, [5°12'S 145°41'E], 150 m elev., 9 Nov. 1996, *Barfod* 350 (AAU!, K!); Baitabag Village, [5°8'S 145°46'E], 2 Nov. 1999, *Cizek* 18 (K!); Josephstaal FMA area, along footpath towards Morasapa, W of expedition Camp 1 ('Kumamdeber') and to lower slopes N of the trail [9°38'S 149°20'E], 160 m elev., 29 July 1999, *Takeuchi* 13523 (A!, K!); near Merap Village, [4°45'S 145°40'E], 10 m elev., 9 Oct. 1958, *Pullen* 1193 (CANB!, LAE); Lower Ramu, half mile N of Josephstaal airstrip, [4°44'S 145°1'E], 75 m elev., 4 Oct. 1958, *Pullen* 1100 (L!, LAE, CANB!); **MOROBE PROVINCE**: Kanialia Wildlife Management Area, shoreline along Bulili ridge near Lababia, ultrabasics, [7°18'S 147°8'E], 0 m elev., 20 Feb. 2001, *Takeuchi* 15142 (A!); NW of Waria R., near Yai Village, [7°57'S 147°35'E], 200 m elev., 7 June 2001, *Takeuchi* 13213 (A, K!); below Red Hill, along Lae-Bulolo road 18 miles W of Lae, [6°50'S 146°36'E], 30 m elev., 3 Sept. 1964, *Hartley* 13082 (A, CANB!, L!, LAE); Busu R., [6°30'S 146°55'E], 15 Oct. 1957, *White* 9553 (K!, L!, LAE); Along Bulolo road, near Markham Bridge, [6°45'S 147°0'E], 15 m elev., 15 Sept. 1971, *Essig* 55001 (BH, CANB!, L, LAE); Oomsis, [6°41'S 146°48'E], 150 m elev., 18 April 1959, *Brass* 29249 (K!, L!, LAE); Anamapi Creek, Dengalu, Wau Sub-distr., [7°10'S 146°39'E], 1050 m elev., 18 Jan. 1964, *Millar* 23072 (A, BRI!, K!, L, LAE!); Lae, Wafok, near Nadzab, [6°33'S 146°42'E], 500 m elev., 30 Jan. 1996, *Baker et al.* 607 (FTG, K!, LAE); Oomsis, near Lae, [6°45'S 147°0'E], 100 m elev., 1 March 1959, *White* 10460 (BRI!, K, LAE!); Oomsis, near Lae, [6°45'S 147°0'E], 450 m elev., July 1958, *White* 10194 (A, K!, LAE); Lae, [6°44'S 147°0'E], 21 July 1939, *Clemens* 10465 (K!, MICH); **SANDAUN PROVINCE**: Vanimo Distr., Krisa Village, Kilimeri CD, [2°51'S 141°16'E], 21 May 1999, *Klappa* 151 (K!); Bewani, [3°1'S 141°8'E], 0 m elev., 19 March 2000, *Barfod* 501 (AAU, BRI, CANB, K!, LAE); Wutung Sub-Province, Oenake Range, foothills of Mt Bougainville, [2°37'S 141°0'E], 530 m elev., 7 Sept. 1982, *Kerenga* 56434 (CANB, K!, L!, LAE); Telefomin, Kak Valley, Gentry transect on slope above Nenem SE of Mianmin, [5°8'S 141°35'E], 940 m elev., 27 Oct. 1993, *Frodin* 3154 (K!); near Ambunti, [4°14'S 142°52'E], 90 m elev., 8 June 1966, *Hoogland*

10241 (BH, BRI, CANB, K!, L!, LAE); **EAST SEPIK PROVINCE**: Maprik Sub-distr., Wewak-Angoram Area, Prince Alexander range, SE side of Mt Turu above Ambakanja Village, [3°37'S 143°22'E], 600 m elev., 20 Aug. 1959, *Pullen* 1520 (CANB!); 31 km N of Ambunti, [3°56'S 142°48'E], 80 m elev., 12 Aug. 1966, *Heyligers* 1537 (CANB!); Maprik Sub-distr., Prince Alexander Range, S side of Mt Turu, [3°38'S 143°20'E], 700 m elev., 25 Aug. 1959, *Pullen* 1601 (CANB!, LAE); 5 miles N of Timbunke, [4°7'S 143°31'E], 30 m elev., 12 Sept. 1959, *Pullen* 1713 (CANB!, L!, LAE); old airstrip at But, [3°24'S 143°14'E], 75 m elev., 1 Aug. 1959, *Pullen* 1387 (CANB!, L!, LAE); Ambunti, Waskuk Hills, area around Langu and Garuka Villages, [4°11'S 142°44'E], 100 m elev., 28 June 1995, *Regalado* 1431 (A, K!, L); **WESTERN PROVINCE**: Tarara, Wassi Kussa R. [8°55'S 141°55'E], Jan. 1937, *Brass* 8701A (A!, BRI); 2 miles N of Kiunga, [6°5'S 141°18'E], 90 m elev., 11 Sept. 1967, *Pullen* 7302 (CANB!, L!, LAE); Oroville Camp, Fly R., 30 m above D'Albertis Junction, [5°43'S 141°7'E], Aug. 1936, *Brass* 7402 (A!, BRI); Gaima, Lower Fly R., [8°19'S 142°59'E], Nov. 1936, *Brass* 8333 (A!, BRI, L!); Lake Daviumbu, Middle Fly R., [7°36'S 141°17'E], Aug. 1936, *Brass* 7592 (A!, BRI, L!); Tarara, Wassi Kussa R., [8°55'S 141°55'E], Jan. 1937, *Brass* 8701 (A!, BRI, L!); North Fly Distr., Tabubil-Kiunga road, 11 km SE of Tabubil, [5°20'S 141°17'E], 360 m elev., 11 Dec. 2000, *Baker et al.* 1127 (AAU, K!, LAE, NY); **SOUTHERN HIGHLANDS PROVINCE**: Mubi R., Lake Kutubu divide near Tage, [6°21'S 143°18'E], 900 m elev., 27 Sept. 1961, *Schodde* 2284 (A, CANB!, L!, LAE); Mt Bosavi, near Bosavi Mission (also known as Dudessa or Ludessa Village), WWF Integrated Conservation and Development Project Area, [6°28'S 142°53'E], 750 m elev., 5 Feb. 1996, *Baker et al.* 632 (BH, K!, LAE); Lake Kutubu, Wanunuku, near Tugiri, WWF Integrated Conservation and Development Project Area, [6°21'S 143°13'E], 900 m elev., 13 Feb. 1996, *Baker et al.* 667 (BH, K!, LAE); **GULF PROVINCE**: Kikori Distr., TFI logging concession near Morere village, 38 km NE of Kikori, [7°10'S 144°29'E], 120 m elev., 22 Nov. 2000, *Baker et al.* 1106 (AAU, K!, LAE, NY); **CENTRAL PROVINCE**: Koitaki, 22 Aug. 1935, *Carr* 12657 (A!, K!, L!, NY!, SING!); Abau Distr., Waeana Swamp, 5 km E of More R. Bridge, [10°2'S 148°32'E], 30 m elev., 23 Feb. 2004, *Gideon* 20333 (K!, UPNG); 12 km N of Amazon Bay, [10°11'S 149°32'E], 60 m elev., 14 June 1969, *Pullen* 7588 (CANB!, L!, LAE); Mori R., Cape Rodney, [10°0'S 148°32'E], 15 m elev., 28 Aug. 1969, *Pullen* 8137 (CANB!, LAE); Kairuku Sub-distr., Maipa irstrip, [8°20'S 146°33'E], 50 m elev., 4 Sept. 1962, *Darbyshire* 880 (CANB!, LAE); **MILNE BAY PROVINCE**: Raba Raba Sub-distr., Kwagira R., Peria Creek, [9°42'S 149°23'E], 50 m elev., 30 Aug. 1953, *Brass* 24255 (A, CANB!, L!, LAE); Raba Raba Sub-distr., Kwagira R., Peria Creek, [9°38'S 149°20'E], 50 m elev., 5 July 1972, *Essig* 55219 (CANB!, LAE); end of logging road, [10°22'S 150°7'E], 0 m elev., 2 March 2000, *Barfod* 458 (AAU, BRI, CANB, K!, LAE); Rossel Island, Abaleti, [11°22'S 154°9'E], 100 m elev., 29 Sept. 1956, *Brass* 28256 (A!, K!, L!, LAE). **CULTIVATED. MALAYSIA**: Kuching Semenggoh Arboretum, 2 May 1981, *Dransfield* 5987 (K!). **NEW GUINEA**: Bogor Botanic Garden ex New Guinea, V1 4, April – May, 1936, *Furtado SFN* 31139 (A!, B†, K!, L!, SING). **SINGAPORE**: Singapore Botanic Gardens, Lawn Y 152B, 18 Sept. 1979, *Mohd Shah* s.n. (K!); Singapore Botanic Gardens, Palm Valley, Lawn W, Acc. no.: w/25/88/92, 27 April 2001, *Loo* 305 (K!); Singapore Botanic Gardens, Palm Valley, Lawn W, Acc. no.: Y152, 27 April 2001, *Loo* 306 (K!). **UNITED KINGDOM**: Royal Botanic Gardens, Kew, Acc. no.: 079-64.07901, *Womersley* (K!); Royal Botanic Gardens, Kew, Acc. no.: 486-66.48601 (K!); Royal Botanic Gardens, Kew, Acc. no.: 486-66.48601 (K!). **UNITED STATES OF AMERICA**: Fairchild Tropical Garden, Florida, Miami-Dade county, Coral Gables (Miami), Plot 112. 79-257A, 4 April 2001, *Zona* 890 (K!); Fairchild Tropical Garden, Florida, Miami-Dade county, Coral Gables (Miami), Plot 143. 81-608A, 4 April 2001, *Zona* 896 (K!).

HABITAT. *Hydriastele wendlandiana* is common in pristine or disturbed lowland rainforest, and sometimes grows along stream banks and ridge crests or in swampy areas and savannah-forest transition zones, on more or less sandy clay or ultrabasic soils. It is also frequent in premontane primary rainforest where it occasionally occurs on steep slopes and ridge tops or in swampy areas, on limestone and shales, limestone karst and volcanic soils; 0 – 1000 m elevation.

LOCAL NAMES AND USES. *kantrabel*, *inpsal* (Kanum), *honggomi*, *patani*, *sanggum* (Wondama), *sal* (Amele), *kitat* (Daga), *kenege* (Kutubu), *upo* (Meko), *lai* (Matbat), *sirata* (Sayal), *kelkal* (Aru Islands), *bil* (Mianmin), *koeyauw* (Yei), *befer* (Marap), *kava kava* (Patep, Buangs), *sapuh* (Maprik), *morr* (Gal), *salvaik* (Sempi), *fabu* (Ambakanja), *ndzip* (Timbunke), *kanyaweni* (Konti-unai), *kaikinei* (Woi).

Several uses are recorded from New Guinea: flooring (South Sorong, Morobe), roofing (Sandaun), bed construction material (Southern Highlands), arrows and/or spears (Sandaun, Southern Highlands, Merauke, Madang), harpoons (Wandammen Peninsula), chicken coops and consumption of young shoots (Merauke), ornamental (Manokwari).

GLOBAL CONSERVATION STATUS. Least Concern (LC). *Hydriastele wendlandiana* is very widely distributed resulting in an EOO of c. 3,287,000 km^2. In New Guinea it is most likely under-collected with its AOO of

800 km^2 likely to be a low estimate. The species' wide use amongst local people and the projected deforestation of large areas across New Guinea (Shearman *et al.* 2008; Global Forest Watch 2017) could pose a threat to sub-populations of this species in the future.

NOTES. This species is the most variable and widespread member of the *Hydriastele wendlandiana* group. It is distinguished by its petiolate leaves with 12 – 30 pairs of often irregularly arranged leaflets, the basal ones of which are truncately praemorse, and leaf sheaths of 40 – 73 cm in length. *H. kasesa* appears to be the most closely related species based on a similarity in leaflet arrangement, but it is distinguished from *H. wendlandiana* by having shorter leaf sheaths (15 – 30 cm long) and nearly always fewer leaflets (6 – 13 pinnae per side). *Hydriastele kasesa* also normally has more slender stems than *H. wendlandiana* and smaller inflorescences with fewer primary branches. In the relatively rare cases where leaflets of *H. wendlandiana* are regularly arranged it can be mistaken for *H. variabilis* and *H. rheophytica*, however the basal leaflets in the latter two species are obliquely praemorse or pointed at the tip, never truncately praemorse as in *H. wendlandiana*.

A wide continuum of morphological variation is found within this complex species meaning that two specimens representing opposite extremes of this spectrum can appear distinct when studied in isolation. This can help explain why several morphotypes, all of which we here include within *Hydriastele wendlandiana*, were thought to represent different species in the past when only a few specimens were available for study. We justify broadening the circumscription of this species by not having found disjunctions in the character states of any vegetative or floral characters nor any marked character covariance patterns supporting the recognition of more than one species within the complex.

For example, seed endosperm condition, which was historically given great weight in *Hydriastele* taxonomy (Burret 1937), is not found to be correlated with other morphological characters in this study and a transition form between the ruminate and the homogeneous endosperm condition is present in the form of a very shallowly ruminate endosperm (e.g. *Baker* 573; Fig. 5M), thus calling into question the taxonomic importance and the binary nature of this seed character for this group. Zona (2005) arrived at a similar conclusion for *Ptychococcus* Becc. and consequently synonymised species that had previously been defined by variation in endosperm condition. Even so, by no means are we claiming that endosperm condition cannot be a useful character for delimitation of other species, it just does not appear to be the case for *H. wendlandiana*.

Our data for *Hydriastele wendlandiana* give some indication that geography is correlated with endosperm condition in New Guinea east of Wandammen Peninsula where we found seeds to be ruminate north of the central New Guinea Highlands and homogeneous towards the south. However, it is quite possible that shallowly ruminate endosperm is present within individuals of *H. wendlandiana* in southern New Guinea but that this has not been captured by the material we have seen for this extensive area. For example, shallowly ruminate endosperm has been reported for *H. wendlandiana* in Australia (Dowe 2010) although the fertile Australian specimens cited here all had homogeneous endosperm.

One specimen (*Brass* 28256) from Rossel Island, Milne Bay, differs considerably from other collections and also represents the easternmost limit of *Hydriastele wendlandiana* (Map 1). With fruits of at least twice the volume of other fruits we have seen, and a thick and fleshy pericarp, it is tempting to describe a new species from Rossel Island, but we conclude that insufficient material is available to do so currently.

The holotype of *Hydriastele carrii* was likely lost in Berlin but we cannot be sure of this because the type collection number was not known by Burret and therefore not cited in the protologue (Burret 1936). *Carr* 12657, which we here designate as a neotype, is consistent with the protologue and, in any case, could very well be the original type collection because no other Carr specimens have been found that correspond morphologically or geographically.

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