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RESEARCH ARTICLE

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Bruguiera × *dungarra*, a new hybrid between mangrove species *B. exaristata* and *B. gymnorhiza* (*Rhizophoraceae*) recently discovered in north-east Australia

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Key words

Bruguiera × *dungarra*
hybrid
identification key
intermediate
mangrove
Rhizophoraceae
taxonomy

Abstract *Bruguiera* × *dungarra* (*Rhizophoraceae*), a previously undescribed hybrid species between *B. exaristata* and *B. gymnorhiza* is recorded from north-east Australia. Eight taxa are currently recognised in this Indo West Pacific genus, including three putative hybrids. The newly described hybrid is widely occurring, and it is described here with notes provided on typification, phenology, distribution and habitat. A revised identification key to all *Bruguiera* taxa is presented, along with a table of comparative diagnostic characters.

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INTRODUCTION

Bruguiera Lam. (*Rhizophoraceae*) is distributed from the Indian subcontinent through Malesia to tropical Australia and islands in the western Pacific (Ding Hou 1957, 1958). The family consists of 16 genera and about 120 species of trees and shrubs worldwide. Four genera, comprising *Rhizophora* L., *Ceriops* Arn., *Kandelia* (DC.) Wight & Arn. and *Bruguiera*, are all mangroves (Duke 2006, 2013, 2014, Tomlinson 2016), and are conspicuously viviparous.

Bruguiera is distinguished by calyces with 8–16 narrowly ovate lobes, 16–32 stamens, explosive pollen release, and with viviparous propagules emergent directly from swollen calyces, instead of from a visible fruiting body (Ding Hou 1957, 1958, Sheue et al. 2005, Duke 2013, 2014). The genus consists of two morphological groupings of taxa (Table 1):

1. three species and two hybrids with large, mostly solitary flowers (Duke & Ge 2011), namely *B. exaristata* Ding Hou, *B. gymnorhiza* (L.) Savigny ex Lam. & Poir., *B.* × *rhynchopetala* (W.C.Ko) N.C.Duke & X.J.Ge, *B. sexangula* (Lour.) Poir. and the new species *B.* × *dungarra*; and
2. two species and one hybrid with 2–5 small flowers in each inflorescence, namely *B. cylindrica* (L.) Blume, *B.* × *hainesii* C.G.Rogers and *B. parviflora* (Roxb.) Griff.

Recently, seven taxa of *Bruguiera* were recognised as occurring in Australia (Duke 2006, 2017, Cooper et al. 2016). The discovery of *B.* × *dungarra* means that eight taxa are now recognised in northern Australia.

Bruguiera has only recently been described as having hybrids, namely *B.* × *rhynchopetala* and *B.* × *hainesii* (Duke & Ge 2011, Cooper et al. 2016). *Bruguiera* × *rhynchopetala* is considered the natural hybrid of *B. gymnorhiza* and *B. sexangula,* known in mid-intertidal, intermediate-upstream estuarine positions (sensu Duke 2006). *Bruguiera* × *hainesii* is considered the intermediate of *B. gymnorhiza* and *B. cylindrica* (Cooper et al. 2016, Ono et al. 2016) occurring at a single Australian location in a higher intertidal, intermediate-upstream estuarine position. With the new taxon described here, three distinct hybrid species are now recognised for the genus. All three occur in northern Australia and possibly nearby in the Indo West Pacific within the overlapping ranges of sympatric parental occurrences.

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MATERIALS AND METHODS

Plant sampling

This study is based upon field observations, underpinned by reference to herbarium material at the Australian Tropical Herbarium (CNS) and the Queensland Herbarium (BRI). Plant material was collected mostly at locations selected according to a sampling program designed to investigate the occurrence and likely relationship between the sympatric taxa *Bruguiera exaristata* and *B. gymnorhiza,* and the new taxon *B.* × *dungarra*. Reference voucher collections of *B.* × *dungarra* were made for Machans Beach and Holloways Beach. The species and hybrids sampled (with numbers of samples for each shown in brackets; see Table 1), included: *B.* × *dungarra* (7), *B. exaristata* (10), *B. gymnorhiza* (9) and *B. parviflora* (3). The latter species was included as the outlier in the numerical analyses, and its occurrences were not necessarily sympatric with the other three. In all, 29 mature individual trees were assessed using a standardised set of morphological attributes, including numeric and discrete non-numeric multistate (descriptive) states. Measurements of foliage, floral parts and fruits are based on fresh material.

Further *Bruguiera* taxa were not considered in these particular analyses because this study focused on the specific relationships between populations of the taxa in sympatry (*B.* × *dungarra*, *B. exaristata* and *B. gymnorhiza*). Other species, like *B. sexangula* and *B.* × *rhynchopetala*, were mostly not locally present. Two key factors explain their absence:

1. the recorded southern latitudinal limit of *B. sexangula* and *B.* × *rhynchopetala* is the Herbert River (S18°31') on Australia's east coast – this study specifically included one sample location much further south in Shoalwater Bay (S22°21'); and

2. the almost exclusive restriction of *B. sexangula* and *B.* × *rhynchopetala* to areas of notable riverine influence and relatively high rainfall (Duke et al. 1998) – this study selectively sampled downstream estuarine sites, mostly away from riverine influence.

This does not imply that *B.* × *dungarra* was not found in wetter locations – the collection from the Johnstone River estuary validates its occurrence in such a riverine situation. But, for the purpose of this study, collections were mostly restricted to locations where other *Bruguiera* taxa were locally absent.

Study sites

From 2001 until 2018, *Bruguiera* plant material was collected and observations recorded at 10 locations in north-east Australia (Table 1). Site access was achieved using a combination of road vehicles, small boat transport and by foot. Aerial photographs, satellite imagery and detailed maps were used to navigate and validate site collection locations.

Morphological attributes

Attributes were observed and scored from fresh intact leafy shoots with mature flower buds, and mature propagules. Up to 56 numeric and multistate attributes were measured and recorded for each specimen (Table 2). The selection of measured attributes was earlier defined and established for *Bruguiera* by Duke & Ge (2011).

Numerical analyses

A comparative classificatory evaluation was undertaken to reveal patterns in foliage and floral morphology relationships among the samples included in this study. Collections of more advanced reproductive stages were limited to a smaller number of locations. Data from these stages were also found to be less reliable for discrimination of taxa. Therefore, for these analyses, attributes of the mature propagules were not used, leaving 41 multistate and numerical attributes of leaves and mature flower buds (see Table 2). Foliage and early reproductive stage attributes were complete (with no missing data) for the 29 specimens analysed. The data were analysed using two standard classificatory techniques, namely the non-parametric ordination Multi-Dimensional Scaling (MDS) and a Cluster Analysis. This combination of analytical methods was used because the attributes scored comprised both numeric and multistate data that were not always normally distributed. Tests followed standard methods and applied using PAST 3.x software (https://folk.uio.no/ohammer/past/). The MDS ordination was performed using a Gower similarity index with 2-D dimensionality. Cluster analyses were undertaken using a Gower Matrix of constrained data and the Paired group algorithm for the Unweighted Pair Group Method with Arithmetic mean (UPGMA).

Table 1 Collections of four specific *Bruguiera* species and hybrids including: *B.* × *dungarra* – BD (7), *B. gymnorhiza* – BG (9), *B. exaristata* – BE (10) and *B. parviflora* – BP (3) from north-east Australia, listing: location, collections per species, coordinates and collection dates. Field location sampling was made by the authors, unless noted otherwise. Herbarium voucher collections highlighted in **bold** text.

Region	Location record * Collection location	Collections/taxa	Latitude	Longitude	Collection date
Northern Australia, Queensland	Embly River estuary	BP (1)	S12°43'	E142°02'	24 Mar. 2001
	Boigu Island, Torres Strait	BP (1)	S9°14'	E142°13'	29 Apr. 2010
	Marrett River estuary, Princess Charlotte Bay	BG (1), BD (1), BE (1)	S14°31'	E144°12'	14 June 2018**
	Holloways Beach	**BD (1)**	S16°50'	E145°44'	31 Oct. 2016
	Machans Beach*	BG (1), **BD (1)**, BE (1)	S16°52'	E145°45'	18 May 2018
	Cairns, Esplanade	BE (4)	S16°54'	E145°46'	08 Mar. 2016
	Trinity Inlet, Chinamans Creek estuary	BG (2), BP (1)	S16°57'	E145°45'	03 Mar. 2016
	Johnstone River estuary	BG (2), BD (1)	S17°33'	E146°04'	28 Nov. 2001
	Hinchinbrook Channel, Waterfall Creek estuary	BG (2), BD (2), BE (2)	S18°28'	E146°10'	10 Feb. 2018*** 17 May 2018
	Shoalwater Bay, creek estuary	BG (1), BD (1), BE (2)	S22°21'	E150°10'	10 Aug. 2001

* location of type
** location record by Jock Mackenzie
*** location record by Andrew Mitchell

Table 2 Listing of 56 numeric and multistate characters of foliage, leaves, inflorescences, mature flower buds and mature hypocotyls used in descriptions and classificatory analyses of the genus *Bruguiera* (modified from Duke & Ge 2011).

Grouping (nos.)	Characters
Foliage (2)	number of leaves in rosette; apical shoot length.
Leaves (6)	leaf length (L), width (W), ratio of length to width (L/W), shape length (S = length from widest width to petiole juncture), ratio of length to shape length (L/S); petiole length.
Inflorescence (3)	leaf scar node position at attachment beneath apical shoot of mature flower bud, open flower, mature hypocotyl.
Mature flower bud (30)	peduncle length, width; calyx tube smooth or ribbed; calyx lobe number; calyx lobe margins retrorse (indented), or flat regular, or antrorse (raised); bud distil tip pointed or blunt; closed bud length, widest width, ratio of length to widest width, calyx tube width, calyx lobe length; corolla internal diameter; style length from ovary base, length from corolla rim, difference between style lengths (= depth of nectary), width at corolla, number of tip lobes; stamen length, width; anther length, width; petal length, closed width, open width, lobe length, lobe tip obtuse or acute; bristle number per lobe, length; spine length, ratio of spine to petal lobe length.
Mature calyx (with mature hypocotyl) (8)	calyx length, widest width, tube width, internal diameter; calyx lobe number, length; peduncle length, width.
Mature hypocotyl (7)	hypocotyl length (L), width at widest point, ratio of length to width, width at plumule end, shape length (S = length from widest width to distal end), ratio of length to shape length (L/S); plumule length.

Table 3 Morphological multistate and numeric attributes including ranges of 20 key characters (see Table 2), for all eight *Bruguiera* species and hybrids, including *B.* × *dungarra*. All measurements and observations refer to fresh material for location records listed in Table 1.

Component	Attribute*	*B. parviflora*	*B. cylindrica*	*B.* × *hainesii*	*B. exaristata*	*B.* × *dungarra*	*B. sexangula*	*B.* × *rhynchopetala*	*B. gymnorhiza*
Leaves	Leaf L	72–101	85–111	102–120	65–105	82–144	71–166	76–172	78–190
	Leaf W	29–34	41–50	45–57	23–47	39–62	28–66	36–68	32–78
	Leaf L/W	2.4–3	2–2.4	2.1–2.3	1.9–3	1.9–2.4	2.1–3.5	2.1–2.6	1.9–2.8
	Leaf L/S	1.9–2.3	1.8–2	1.8–2	1.7–2	1.8–2	1.8–2.1	1.9–2.1	1.9–2.4
Mature flower buds	Calyx tube D	Elongate, ribbed	Turbinate, smooth	Turbinate, smooth	Ribbed	Ribbed mostly	Ribbed	Ribbed, sometimes smooth	Smooth mostly
	Lobe margin D	Antrorse, raised	Antrorse to flat	Flat, regular mostly	Antrorse, raised mostly	Antrorse, raised	Antrorse mostly	Antrorse to retrorse	Retrorse to flat
Inflorescence	Bud N	3–7	2 or 3	3 mostly	1	1	1	1	1
	Bud tip D	Obtuse	Obtuse	Acute	Broadly acute	Acute	Acute	Acute	Acute
	Bud L	7–10	9–14	21–24	21–28	30–39	25–36	29–41	24–44
	Lobe N	8	8 or 9	9 or 10	8–10	9–11	10–12	9–12	9–15
	Lobe L	2–3	4–6	12–13	11–16	18–22	15–22	17–26	14–26
	Petal L	1–2	3–5	7–9	9–14	14–17	9–17	14–18	7–20
	Petal bristle N	3	3 or 4	3 or 4	0, rarely 1	2 or 3	0 or 1	~2	2–4
	Petal bristle L	0.2–0.5	0.5–1.5	2–3	0–0.2	0.5–2	2–3.5	0.5–2	1–4
	Petal spine L	1.3–1.9	1.7–2.4	3–5	0–0.7	2–4	2–4	3–5	4–7
	Petal spine D	Exceeds lobe	Exceeds lobe	Exceeds lobe	Absent, minute	Over half lobe L	Over half lobe L	Over half lobe L	Equal to lobe
	Petal tip D	Obtuse	Obtuse	Obtuse to Acute	Obtuse	Obtuse	Obtuse	Obtuse to acute	Acute
Mature propagule	Calyx lobes D	Adpressed	Reflexed	Reflexed	Reflexed	Reflexed	Reflexed tending to adpressed	Reflexed tending to adpressed	Reflexed tending to adpressed
	Hypocotyl L	142–192	81–226	75–197	53–114	52–161	24–113	95–222	31–303
	Hypocotyl W	4–7	5–8	9–11	9–10	13–15	7–18	13–19	6–22

* N = number; L = length in mm; W = width in mm; S = L from widest W to base; D = description.

RESULTS

A brief review of morphological attributes in the genus

Morphological multistate and numerical attributes were compiled for all *Bruguiera* taxa (see Fig. 1; Table 3) from the findings from this study along with those from earlier treatments (Duke 2006, 2013, 2014, Duke & Ge 2011). In Fig. 1, the multistate attributes of calyx lobe margins and calyx tube surfaces are described in specific detail because of their importance in the discrimination of morphotypes and taxa in this study. Overall discrimination of morphotypes is based on calyx tube ribbing, calyx lobe margins at junctions between lobes, bristle number and length and petal lobe length. These characters provide specific discrimination of *B.* × *dungarra* from the morphologically similar hybrid taxon, *B.* × *rhynchopetala*, by calyx lobes having antrorse or raised margins to form ribs at lobe junctions, petal spine around half lobe length instead of subequal to lobe (often 2/3 to 3/4 length of petal lobe), calyx lobe numbers mostly less than 10; smaller leaves mostly less than 110 mm long; slightly narrower leaves (leaf L/W around 2.2); calyx tube often pinkish orange instead of reddish blush; calyx tube mostly distinctly ribbed (Table 3).

These characters also show that *B.* × *dungarra* is intermediate between *B. gymnorhiza* and *B. exaristata*, with some characters shared between these taxa while others correspond to one or the other (Fig. 1; Table 3).

Differs from *B. exaristata* but similar to *B. gymnorhiza* in mature flower bud apices mostly acute, mature bud length mostly > 30 mm long, style length mostly > 12 mm long, petal length mostly > 13 mm long, and bristle numbers 2 or 3 instead of mostly absent.

Differs from *B. gymnorhiza* but similar to *B. exaristata* in surface of calyx often with distinct ribbing on tube corresponding to lobe junctures on closed mature buds, lobe margins antrorse or raised to form ribs at calyx lobe junctions, instead of retrorse or recurved to form grooves at calyx lobe junctions, number of calyx lobes mostly less than 10, and peduncle length mostly less than 12 mm.

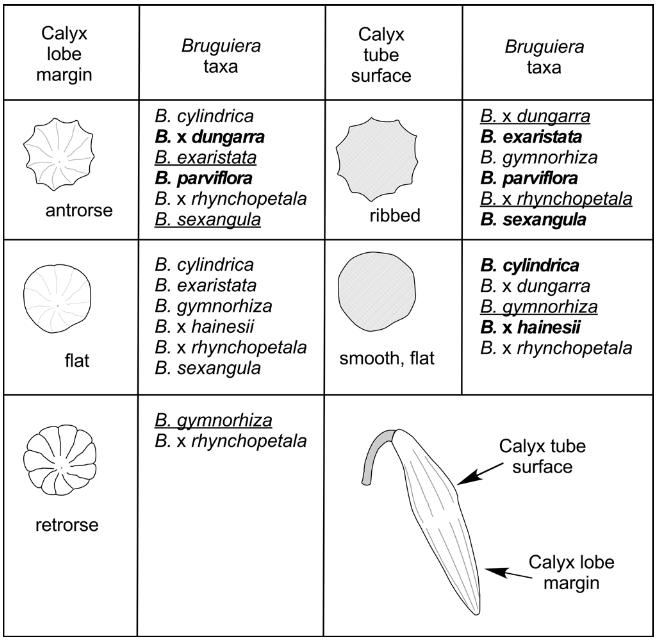

Fig. 1 Two morphological multistate attributes, calyx lobe margin (distil view) and calyx tube surface (cross section), for all *Bruguiera* taxa, including *B.* × *dungarra*. All observations refer to fresh material listed in Table 1 and from material described by Duke 2006, 2013, 2014, Duke & Ge 2011. Note: taxa names in **bold** refer to the predominant or exclusive state; names underlined refer to a majority state; and names in regular font refer to a shared or minor state.

Intermediate characters between *B. gymnorhiza* and *B. exaristata* include: leaf length around 105 mm; mature flower bud colour pink-orange instead of green or green with red blush; petal bristle length around 1.4 mm; petal spine between lobes notably around half of petal lobe length compared to either equal length in *B. gymnorhiza*, or absent in *B. exaristata*.

Numerical analyses

Analytical findings based on morphological characters affirm the determination and taxonomic status of *B.* × *dungarra* and its proposed paternity with putative parent species (see Fig. 2) growing in isolated sympatric populations. The MDS ordination plot (Fig. 2b) in particular shows the groupings of the three sympatric taxa, according to *a priori* classification, with no overlap between collections of *B. gymnorhiza, B. exaristata* and *B.* × *dungarra*. It is significant that the ordination accounted for 94.5 % of variation along the first coordinate axis. In this plot, the three species (*B. gymnorhiza*, *B. exaristata* and *B. parviflora*) are distributed in a triangular arrangement while the newly reported hybrid (*B.* × *dungarra*) collection locations are positioned between *B. gymnorhiza* and *B. exaristata*.

DISCUSSION

The intermediate position of *B.* × *dungarra* between *B. gymnorhiza* and *B. exaristata* is consistent with this taxon being the naturally occurring hybrid between these two taxa. The hybrid status of *B.* × *dungarra* is also supported by molecular studies currently in progress (Prof. Suhua Shi, pers. comm.), and by its distribution that is limited to locations of co-occurrence of the two putative parent taxa. All recorded occurrences of *B.* × *dungarra* to date occur within the overlapping ranges of the putative parent taxa (Fig. 3).

Compared with other mangrove genera with naturally occurring hybrids (Lo 2010, Duke 2017, Guo et al. 2018) like *Rhizophora* and *Sonneratia* L.f., the circumstances for this genus differ in that all three *Bruguiera* hybrid taxa appear to have fertile flowers and functional propagules. This aspect warrants further investigation.

The occurrence of this new hybrid confirms the Australian region as one of maximal diversity for the *Bruguiera* genus. The most recent complete taxonomic account of the genus in Australia enumerated five species and no hybrids (McClusker 1984).

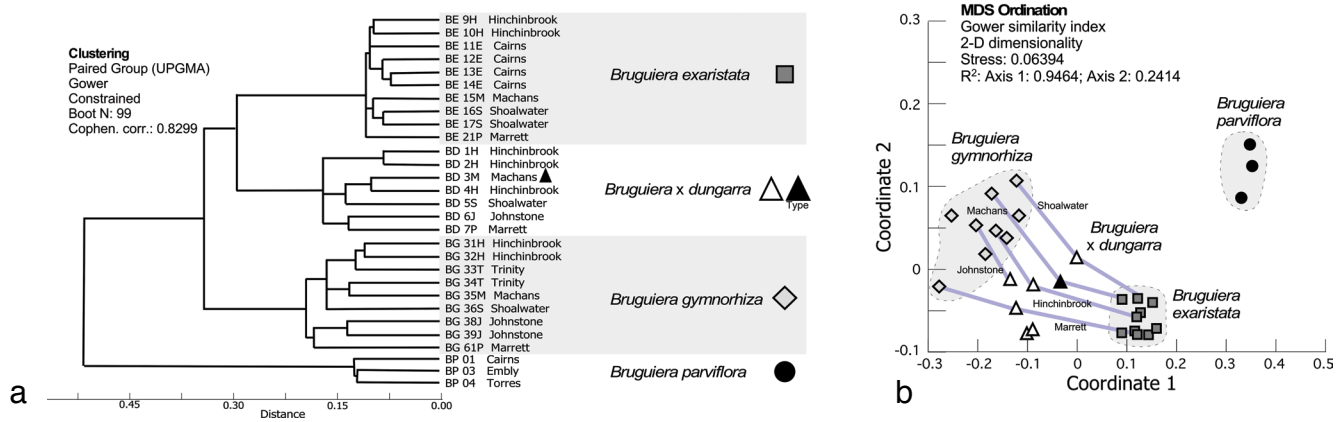

Fig. 2 Graphs of 'a' clustering and 'b' ordination analyses showing relationships between *Bruguiera* × *dungarra,* putative parent taxa, *B. exaristata* and *B. gymnorhiza* and outlier congeneric species, *B. parviflora*. Sympatric collections are shown in 'b' by blue lines linking data points between putative parents via the intermediate positioned hybrid at north-east Australian locations. The type location collection from Machans Beach (closed triangle symbol) is compared with other location records from Shoalwater Bay, Hinchinbrook Channel, Johnstone River estuary and Marrett River estuary in Princess Charlotte Bay (see Table 1). The clustering diagram and MDS multistate ordination plot were based on correlative relationships in 8 foliage and 33 mature floral characters (Table 2).

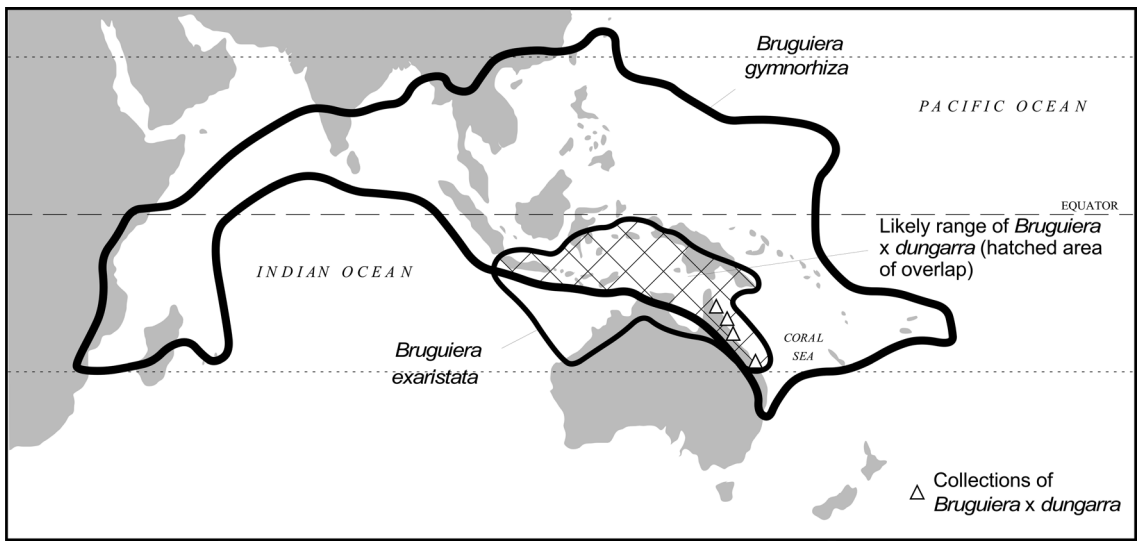

Fig. 3 Distributions of *Bruguiera* × *dungarra* (△ – collection locations) and putative parental species, *B. gymnorhiza* (heavier line outline) and *B. exaristata* (lighter line outline).

Accordingly, a revised key is presented to all currently known species and hybrids of the genus along with a full description of the new hybrid and its distribution.

TAXONOMIC TREATMENT

Key to Bruguiera species and hybrids (see Table 3)

1. Inflorescence consisting of a single flower (flowers solitary) 2
1. Inflorescence 1–5-flowered, rarely 1 6
2. Petals without a central spine, or spine minute, c. 0.2 mm long . . . . . *B. exaristata*
2. Petals with a central spine, greater than 2 mm long 3
3. Petals without apical bristles or bristles minute, c. 0.3 mm long . . . . . *B. sexangula*
3. Petals with apical bristles, > 1 mm long. 4
4. Petal lobes with 3 or 4 bristles; bristles > 2 mm long . . . . . *B. gymnorhiza*
4. Petal lobes with commonly 2 bristles; bristles < 2 mm long 5
5. Calyx tube of mature flower bud ribbed; < 10 lobes, edges of adjoining lobes antrorse or raised to form ridges at lobe junctions . . . . . *B.* × *dungarra*
5. Calyx tube of mature flower bud mostly smooth; ≥ 10 lobes, lobe margins flat or retrorse to form grooves at lobe junctions . . . . . *B.* × *rhynchopetala*
6. Mature flower buds 18–22 mm long, calyx lobes 9–11. . . . . *B.* × *hainesii*
6. Mature flower buds 10–15 mm long, calyx lobes 8 or 9 . 7
7. Calyx lobes stout, 2–3 mm long; fruit calyx lobes adpressed against hypocotyl . . . . . *B. parviflora*
7. Calyx lobes elongate, 4–6 mm long; fruit calyx lobes reflexed at right angles to the hypocotyl . . . . . *B. cylindrica*

Bruguiera × ***dungarra*** N.C.Duke & Hidetoshi Kudo, *hybrid nov*. — Fig. 1–4

Type: *Hidetoshi Kudo 190916A & Brian Venables* (holo CNS; iso BRI), Australia, Queensland, Cairns, Machans Beach, mangrove, high intertidal zone, S16°51.674' E145°44.844', sea level, 27 Oct. 2016.

Etymology. The location of the type of this new hybrid occurs on the ancestral lands of the Yirrganydji people. For these traditional custodians of the narrow coastal strip from Cairns to Port Douglas, the epithet *Dungarra* means, 'belonging to Machans Beach area'.

Tree or shrub to 22 m high, evergreen, columnar or multi-stemmed, branching mostly sympodial, stem base with sinuous, fin-like buttresses to 0.5 m high. Exposed breathing roots, pneumatophores knee-like, to 15 cm long. *Bark* dark grey to pale-brown, with horizontal and vertical fissures, with large corky lenticels of 1–2 cm diam, especially on buttresses. *Foliage* comprised of compact rosettes of paired leaves, clustered at 4–8 leaf scar nodes down from apical shoot, terminal, spicate, prominent, pink-green, 3–7 cm long. *Interpetiolar stipules* paired, narrowly ovate, green to yellowish, occasionally with pinkish tinge, enclose terminal bud to 7 cm long. *Leaves* opposite, simple, blade elliptic to elliptic-obovate, smooth, glossy green, 7–15 cm long, 3–6 cm wide, 4–8 cm shape length (see Table 2), length to width ratio 1.9–2.4, length to shape ratio 1.8–2 (see Table 2), base cuneate, margin entire, apex acute; petiole green, 2.1–3.8 cm long. *Inflorescence* axillary, 1-flowered (flowers solitary), buds generally nodding, maturing within leafy rosette; peduncle green, 8.4–16 mm long, 1.8–2.5 mm wide; mature buds present at 1 or 2 internodal segments below apical shoot; mature hypocotyls present at 3 or 4 internodal segments below apical shoot. *Mature flower buds* green with rosy blush to all green, 29.5–39.4 mm long, 4.9–7.4 mm wide around calyx tube, 7.8–11 mm wide at calyx lobes, distil tip acute; calyx tube turbinate, ribbed, with 9–11 lobes, slender pointed, longer than tube, 17.2–26 mm long, margins of lobes on closed mature buds antrorse to form ribs between adjoining lobes; petals 9–11, creamy white, turning orange-brown at anthesis, 14–18 mm long, 2.2–3 mm closed width, bilateral folded, 4.4–5.3 mm open width, bilobed; lobes 4.3–6.6 mm long, densely fringed with hairs along margin of outer side of petal lobe, apex of each lobe rounded with 2 or 3 bristles near apex, 0.5–1.8 mm long, sinus between lobes with hair-like spine, 2.4–3.9 mm long, about half lobe length, ratio of spine to petal lobe length 0.4–0.8; stamens 18–22, creamy white turning orange-brown at anthesis, 14.3–15.7 mm long, 0.2–0.6 mm wide, compressed pair within closed petal, dehiscing precociously when triggered, anthers linear, creamy pale yellow turning brown at anthesis, 5.5–8.5 mm long, 0.5–1 mm wide; style filiform, smooth, pale green, 17–23 mm long, 0.9–1.3 mm wide, stigma minutely 3-lobed, mounted centrally within calyx tube 3.2–4.6 mm wide, 3.9–4.9 mm long. *Mature fruit* cryptic within slightly enlarged calyx tube, turbinate, smooth to ribbed, 37–44 mm long, 13–16 mm wide, calyx lobes slightly reflexed, 17–20 mm long, 25–33 mm width; germination viviparous, hypocotyl emergent from calyx with maturation. *Mature hypocotyl* narrowly ovoid, straight, green, 5–16 cm long, 13–15 mm at widest point, 29–77 mm shape length (see Table 2), 4–7 mm width at plumule end, length to width ratio 3.9–11, length to shape ratio 0.9–4.1 (see Table 2), some longitudinal ribbing, distil end blunt, plumule 0.9–4.1 mm long, buoyant dispersal agent.

Distribution — Type location is Machans Beach (S16°52' E145°45'), near Cairns in Queensland, Australia. Other localities include Holloways Beach (S16°50' E145°44') also near Cairns in Queensland, Australia, south to around Hinchinbrook Channel (S18°29' E146°10') and Shoalwater Bay (S22°21' E150°10'), and further north to the Marrett River estuary (S14°31' E144°12') in Princess Charlotte Bay. Distribution elsewhere is likely, although possibly restricted to the zone of overlap of putative parents (Fig. 3). Putative parent species co-occur in eastern Indonesia, Timor Leste, southern New Guinea and northern Australia. In Australia, *B.* × *dungarra* is likely to occur from Darwin Harbour in the Northern Territory (S12°25' E130°48') to Port Curtis in Queensland (S23°49' E151°22').

Ecology & Local influences — Uncommon hybrid in the mid-high intertidal zone of intermediate estuarine position (sensu Duke 2006). Often in proximity of stands of higher intertidal *B. exaristata*, and mid-high intertidal *B. gymnorhiza*.

Phenology — In Australia, flowering reported for July to September, and maturation of propagules in October to May.

Additional herbarium specimens and vouchers. Australia, Queensland, Holloways Beach, mangrove, high intertidal, S16°49.825' E145°43.972', sea level, 27 Oct. 2016, *Hidetoshi Kudo 190916B & Brian Venables* (BRI, CNS); Queensland, Holloways Beach, mangrove near boat ramp, S16°49.826' E145°43.970', sea level, 6 Aug. 2018, *Hidetoshi Kudo 3* to *6* (BRI, CNS); Queensland, Holloways Beach, Willow Street, mangrove edge, S16°50.815' E145°44.501', sea level, 6 Aug. 2018, *Hidetoshi Kudo 7* to *10* (BRI, CNS); Queensland, Holloways Beach street near mangrove edge, S16°50.206' E145°44.176', sea level, 6 Aug. 2018, *Hidetoshi Kudo 11* to *14* (BRI, CNS); Queensland, Machans Beach boat ramp, high intertidal mangroves, S16°51.675' E145°44.845', sea level, 6 Aug. 2018, *Hidetoshi Kudo 15* to *18* (BRI, CNS); Queensland, Machans Beach, Dungarra Reserve, mangrove, S16°51.601' E145°45.217', sea level, 6 Aug. 2018, *Hidetoshi Kudo 19* to *22* (BRI, CNS).

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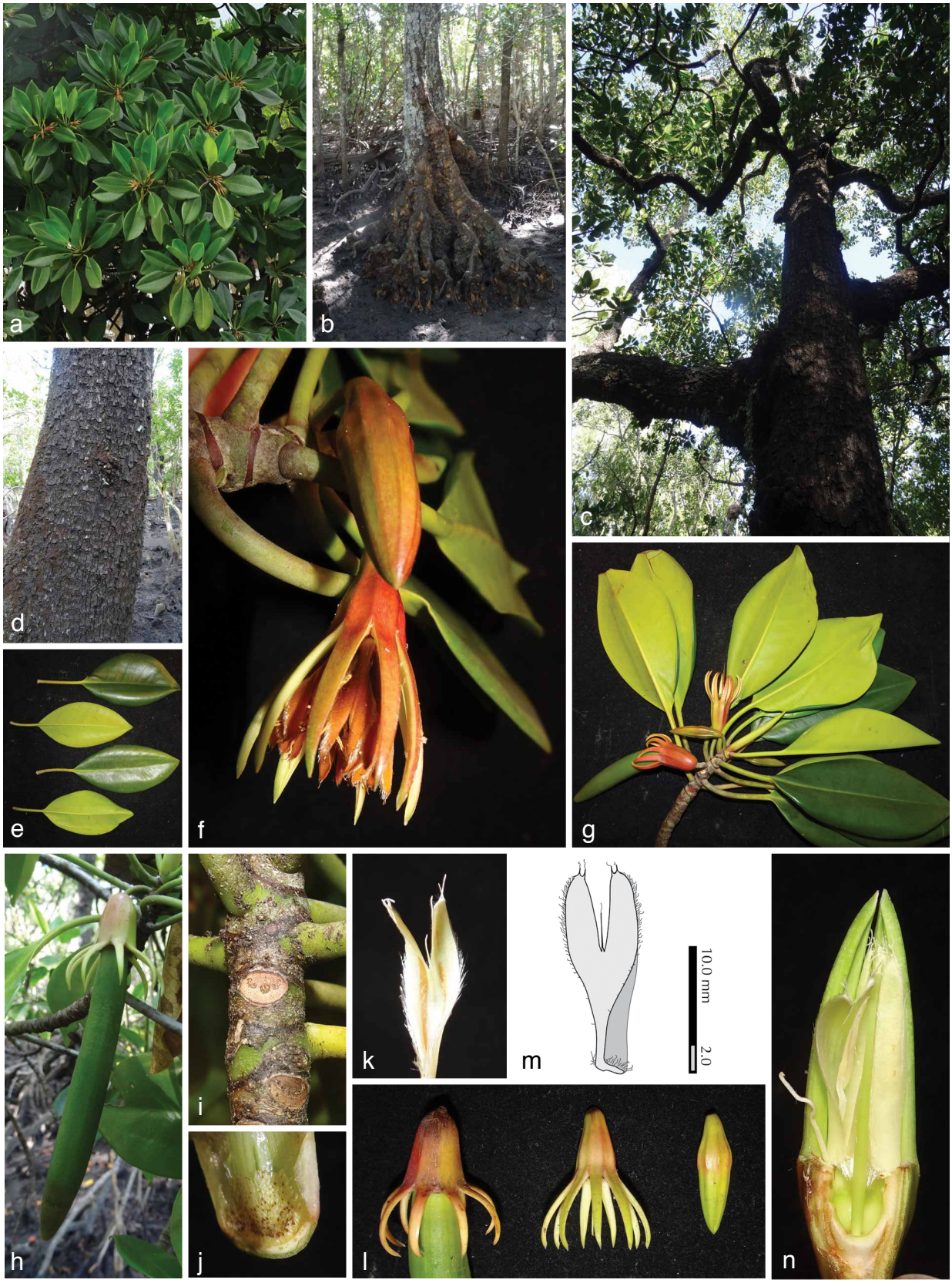

Fig. 4 *Bruguiera dungarra* N.C.Duke & Kudo, hybrid nov. a. Foliage with inflorescences; b. trunk and exposed roots; c. habit; d. bark; e. leaves upper and lower surfaces; f. open and closed flower buds; g. leafy rosette with flower buds and mature propagule; h. mature hypocotyl; l. leaf scar node; j. colleter at inner base of interpetiolar stipule; k. petal dehisced and open; l. calyces of mature propagule, expended flower and closed flower bud; m. diagram of open petal (bar length = 10 mm); n. sectioned flower bud showing petals and style. — Collection field reference images for Hidetoshi Kudo & Brian Venables, HK190916A, (CNS!), Cairns, Machans Beach.

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