



# Taxonomic revision of Australian *Erythrophleum* (Fabaceae: Caesalpinioideae) including description of two new species

Russell L. Barrett<sup>A,B,C,D,E,\*</sup>  and Matthew D. Barrett<sup>C,D,E,F</sup> 

For full list of author affiliations and declarations see end of paper

## \*Correspondence to:

Russell L. Barrett  
National Herbarium of New South Wales,  
Botanic Gardens of Sydney, Australian  
Botanic Garden, Locked Bag 6002, Mount  
Annan, NSW 2567, Australia  
Email:  
[russell.barrett@botanicgardens.nsw.gov.au](mailto:russell.barrett@botanicgardens.nsw.gov.au)

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## ABSTRACT

The genus *Erythrophleum* Afzel ex R.Br. is revised for Australia and three species are recognised, all previously included in *E. chlorostachys* (F.Muell.) Baill. *Erythrophleum arenarium* R.L.Barrett & M.D.Barrett is described as a new species to accommodate populations from desert sands of the Great Sandy Desert and Dampier Botanical Districts in north-western Australia, parapatric to the remaining species. *Erythrophleum pubescens* R.L.Barrett & M.D.Barrett is described as a new species spanning tropical Australia, and is sympatric with *E. chlorostachys sensu stricto* in the Northern Territory and adjacent areas of Western Australia and Queensland. Morphological examination has shown these three taxa to be consistently distinct across their respective ranges. Analyses of the nuclear ribosomal *ITS1* region recovered three well-supported clades corresponding to the three morphologically defined species, and *ITS1* has utility as a marker to separate sterile specimens. *Erythrophleum pubescens* is widespread in the Australian Monsoon Tropics, from the coast of Western Australia, near Derby, to Cape York Peninsula in northern Queensland. *Erythrophleum chlorostachys* is also widespread, from the eastern Kimberley Region, in Western Australia, to the Gulf of Carpentaria, in northern Queensland. A lectotype is chosen for *Labouchea chlorostachya* F.Muell. Full descriptions, illustrations of key features and identification keys are provided for the three Australian species. A summary of the significant utilisation of *Erythrophleum* species is presented.

**Keywords:** Australian monsoon tropics, *Dimorphandra*, *Dinizia*, Fabaceae, forestry timber, Indigenous utilisation, ironwood, new species, Ordeal tree, savanna, typification.

## Introduction

Ten species of *Erythrophleum* Afzel ex R.Br. are traditionally recognised, with six species being found in Africa (Ross 1977; Coates Palgrave and Drummond 2002; Lewis *et al.* 2005) and Madagascar (Du Puy *et al.* 2002), three species in Cambodia (Larsen *et al.* 1980), Thailand (Larsen *et al.* 1984), Vietnam and China (Chen *et al.* 2010), and a single species in northern Australia (Ross 1998). Interestingly, the genus is absent from Malesia (Ding Hou *et al.* 1996). Although this disjunct pattern of distribution may seem unusual, similar disjunctions are found in a number of other angiosperm clades, including *Causonis* Raf. (Parmar *et al.* 2021), Cyperaceae subtribe Tricostulariinae (Barrett *et al.* 2021), *Diplacrum* R.Br. (Wilson and Barrett 2023), *Schoenus* L. (Elliott *et al.* 2021), and *Terminalia* L. (Maurin *et al.* 2023), with dispersals between Africa and Australia–Asia having been inferred in both directions within these clades. There is no modern global revision of the genus and the last new species to be described was *Erythrophleum lasianthum* Corbishley (1922, in Anonymous 1922). A number of Asian species previously included in *Erythrophleum* are now placed in *Cynometra* L., *Gymnocladus* Lam. or *Sympetalandra* Stapf., including *E. angustifolium* Gagnep. (Gagnepain 1952). In Australia, *Erythrophleum* is widespread and locally common, but most other species in the genus are threatened to varying degrees by exploitation for medicinal or timber resources, or by development (Okeyo 2012; Missanjo *et al.* 2017; Maroyi 2019; Wang *et al.* 2019; Chauke and Kritzinger 2020; Delporte *et al.* 2021; De Meyer 2023).



## Phylogenetic relationships

The genus *Erythrophleum* is placed in subfamily Caesalpinioideae, where it is broadly related to *Bussea* Harms, *Campsiandra* Benth., *Dimorphandra* Schott, *Dinizia* Ducke, *Jacqueshuberia* Ducke, *Pachyelasma* Harms and *Parkinsonia* L. (Bruneau *et al.* 2001; Herendeen *et al.* 2003; Luckow *et al.* 2003; Duminil *et al.* 2013; Lewis *et al.* 2013; Azani *et al.* 2017; Koenen *et al.* 2020). Determining its closest allies is hampered by uneven sampling of both species and genetic markers. The phylogenetic reconstruction by Duminil *et al.* (2013) found a strong sister relationship with *Dinizia*; however, this relationship changes depending on the markers used (Manzanilla and Bruneau 2012). On the basis of nearly 1000 loci, Koenen (2019) and Ringelberg *et al.* (2022) recovered *Pachyelasma* as the sister clade to *Erythrophleum*, but with only moderate support. Analysis of transcriptome data by Zhao *et al.* (2021) demonstrated that *Erythrophleum* is sister to all of Mimoseae and Ingeae (although *Pachyelasma* was not included in their analyses), where it occupies an interesting position in the transition of nitrogen fixation syndromes (de Faria *et al.* 2022). On the basis of a sampling of five species utilising chloroplast non-coding sequences, *Erythrophleum chlorostachys sensu lato* was found to be sister to *E. fordii* Oliver from Asia, with an estimated mean divergence date of 12.2 (2.4–24.1) Ma between the two species (Duminil *et al.* 2013). However, later analyses based on more data by Duminil *et al.* (2015) reduced this mean divergence age estimate significantly, to 1.6 (0.5–2.8) Ma. Pollen studies have shown that *Erythrophleum* has tricolporate monads, common to several related genera in the *Dimorphandra* group (Banks and Lewis 2009; <https://apsa.anu.edu.au/>), but differing from the unique tricolporate tetrads of *Dinizia* (Banks *et al.* 2010).

## Taxonomic history in Australia

Ferdinand Mueller (1859) described the new genus *Laboucheria* F.Muell., which he considered to be related to *Adenanthera* L., for a single species (*L. chlorostachya* F.Muell.), from northern Australia. Mueller (1863) subsequently recognised that the species belonged in *Erythrophleum*, but used the illegitimate name *E. laboucheri*, which was followed by Benth (1864). Baillon (1870) recognised that Mueller's specific epithet from 1859 had priority and made the formal combination *Erythrophleum chlorostachys*. Regional treatments of *Erythrophleum* in Australia have been published by Symon (1981), Wheeler (1992), Dunlop *et al.* (1995) and Kenneally *et al.* (1996) (all as a single species, *E. chlorostachys*). Ross (1998) specifically documented a variant of *E. chlorostachys* (here recognised as *E. arenarium*), but did not suggest that it warranted taxonomic recognition. Fieldwork in northern Australia by the present authors suggested that further study was warranted and a taxonomic revision is presented here.

Morphological examination of herbarium specimens, supported by phylogenetic analyses of the nrDNA *ITS1* region,

has enabled the recognition of three species endemic to northern Australia, including two species that are newly described. *Erythrophleum pubescens* R.L.Barrett & M.D.Barrett is the most widespread species, from the western Kimberley Region of Western Australia to Cape York Peninsula, in northern Queensland, being sympatric with *E. chlorostachys* for much of its range. Where the two species have been observed in relative proximity, *E. chlorostachys* has occupied rockier substrates with relatively shallow soils than has *E. pubescens*. *Erythrophleum chlorostachys* has a more restricted distribution, from the eastern Kimberley, through the northern third of the Northern Territory (the Top End), into north-western Queensland. *Erythrophleum arenarium* R.L.Barrett & M.D.Barrett is restricted to the Dampier Botanical District and Great Sandy Desert in Western Australia. *Erythrophleum arenarium* joins a growing number of species recognised as endemic to the sand communities of the Pindan and Great Sandy Desert, and distinct from their savanna counterparts (Barrett and Barrett 2015; Barrett and Telford 2015; Barrett 2015, 2016, 2019; Barrett *et al.* 2015a, 2015b). The flora of northern Australia remains poorly studied and new species from the region, including shrubs and trees, are still being described on a regular basis (e.g. Harrington *et al.* 2012; Barrett 2006, 2007, 2013; Maslin *et al.* 2013; Jobson 2014; Barrett and Barrett 2015; Cowie and Guymer 2015; Barrett *et al.* 2015c; Craven *et al.* 2016; Jackes 2017; Nicolle and Barrett 2018; Dillon *et al.* 2020; Callmander *et al.* 2021; Ford and Wilson 2021; Ford *et al.* 2021; Cooper 2022; Cooper and Lamei 2023).

## Utilisation and cultural significance of *Erythrophleum*

The genus *Erythrophleum* has a significant place in the northern Australian tree flora (Addicott *et al.* 2018; Hunter *et al.* 2022), and specific notes on its importance are provided here. Because *Erythrophleum* was previously considered monotypic in Australia, no distinction among the three species recognised here has been made in the literature. In some cases, published records can be linked to one or other of the revised species' concepts, but in many cases the record is insufficient to discriminate between the sympatric species *E. chlorostachys* and *E. pubescens*. The disjunct distribution of *E. arenarium* allows the relevant literature records to be reliably attributed to that species. Specific utilisation of the three Australian species recognised here should be reviewed to determine whether usage may have been species-specific.

## Chemistry and toxicity

*Erythrophleum* as a genus includes the African ordeal trees (Maroyi 2019; Chauke and Kritzing 2020; De Meyer 2023), so it is not surprising that the Australian species



are highly toxic and are also utilised for medicinal purposes (Quattrocchi 2016). Australian *Erythrophleum* is well known as a stock poison (Hall 1964; Cribb and Cribb 1981; Harborne and Baxter 1996). The first detailed chemical investigations based on leaves and seeds provided by Walter Hill in Darwin were undertaken by James Petrie (1921a, 1921b), who confirmed the presence of erythrophleine and demonstrated its highly toxic effects. Griffin *et al.* (1971) recognised only a single species of *Erythrophleum* in Australia, but identified at least two chemical varieties differing markedly in their alkaloidal constituents. A voucher from Mareeba (W. Griffin in V.K. Moriarty HN 557; CANB 335549) is *E. pubescens*. Definite vouchers for the other samples cited by Griffin *et al.* (1971) from near Darwin and Cooktown could not be traced at CANB or BRI for lack of detailed information, but the Darwin samples may represent *E. chlorostachys sensu stricto*, whereas the Cooktown samples will belong to *E. pubescens*. This suggests regional variation in chemical constituency, something also noted for African species (Fernández-Marín *et al.* 2017; Delporte *et al.* 2021).

Erythrophleine has also been isolated from populations here included in *E. arenarium* (Gardner and Bennetts 1956). Loder *et al.* (1972) further documented the chemical structure of alkaloids in Australian *Erythrophleum*. Bisby *et al.* (1994) listed numerous terpenoids and alkaloids recorded from *E. chlorostachys (sensu lato)*. The complex chemistry associated with toxic compounds in Australian taxa has been further refined by Qu *et al.* (2006) and Sim (2023), with there being similar studies on African (Armah *et al.* 2015; Kablan *et al.* 2020; Imolede *et al.* 2022) and Asian (Yu *et al.* 2005; Huang *et al.* 2018) species. The diterpinoid alkaloids, particularly erythrophleine, which are found in wood dust, wood, bark and leaves, are highly toxic, and contact can cause nausea, headaches, asthma, blindness, skin irritations and dermatitis (McKenzie 2012). The extreme toxicity of erythrophleine, which can cause heart failure if ingested, has been responsible for large numbers of stock deaths following consumption of even small quantities of the foliage, particularly from root suckers, but also from fallen crown leaves (Bailey 1900; Everist 1974; Milson 2000; McKenzie 2012). Cattle, sheep, goats, horses, donkey and camels are all known to have been poisoned by this species, often fatally, whereas several native possums and parrots such as little corellas appear to be immune to the poison, at least within their native ranges where they co-occur (Cribb and Cribb 1981; McKenzie 2012; Carmelet-Rescan *et al.* 2022). Caterpillars of the large saturn moth, *Neodiphthera excavus* (Lane), a species that is unusual in that the caterpillars pupate underground, do feed on the leaves (Lane 1995); however, no butterfly larvae is known to feed on *Erythrophleum*.

## Utilisation

All plant parts of Australian *Erythrophleum* species have been extensively utilised by First Nations Australians or

post-colonial humans, including timber, gum, pigments, and various parts for ceremonial and medicinal purposes, making it one of the most utilised native taxa in tropical Australia (Si 2020; Thompson 2020). Early colonial records of wooden utensils include spears, spear-point and prongs, spear-throwers, digging-sticks, throwing sticks, mallets, clubs, and as a handle for a hafted elouera (scraper knife) (Palmer 1883, 1884; Blackman 1904; Roth 1909; Tindale 1925, 1926; Spencer 1928; Thomson 1936, 1939; Setzler and McCarthy 1950). In northern Queensland, bark was used to cover huts (Roth 1910). In some regions, trees were culturally modified, reflecting their traditional utilisation, especially cutting into the cambium to retrieve honey from native bees (Morrison *et al.* 2010; Cole 2022). Because utilisation of the genus is so significant in northern Australia, a review of each usage is provided here.

The commercial timber use of *E. chlorostachys (sensu lato)*, including *E. pubescens*, usually referred to by the common name of Cooktown Ironwood, has been documented by Boland *et al.* (1984), Bootle (2010) and Lake (2015). An English author commented on Australia that ‘You could laugh at the idea of wooden weapons until you saw the kind of wood that grew here’ (Pratchett 1998). *Erythrophleum chlorostachys sensu lato* has a density of 1220–1300 kg m<sup>-2</sup> (at 12% moisture), being one of the densest native timbers in Australia (Boland *et al.* 1984; Cause *et al.* 1989; Bootle 2010). In fact, it is one of the densest timbers in the world, with 7 of the 10 densest woods globally having density very similar to that of *E. chlorostachys sensu lato*, with only *Acacia cambagei* R.T.Baker, *Guaiacum officinale* L. and *Schinopsis* Engl. species having significantly higher density (Meier 2015). The strength of the timber is a key reason that many trees were uprooted, rather than having most branches broken off, from the intense winds of Cyclone Tracey, which devastated Darwin on 25 December 1974 (Stocker 1976). Missing branches are probably more commonly associated with lightning strikes, and large scars and hollows are also commonly attributable to past cultural modification. Australian *Erythrophleum* species are long-lived, and large trees may be over 500 years old (Taylor 2002).

A tightly interlocking grain, good termite resistance, and a smooth finish enable use for fencing, railway sleepers, boat building, firewood, charcoal, decorative turning and joinery, balls for lawn bowls and replacement of worn-out machine bearings, with potential for musical instrument manufacturing (Swain 1928; Boland *et al.* 1984; Bootle 2010; Lake 2015; Zich *et al.* 2020). The exceptional qualities of the timber mean that it was one of the earliest timber products exported from Australia, being utilised by Macassan fishermen since about the 17th century for both masts and anchors (MacKnight 1976; Clarke 2007, 2008), and some export of wild-harvested timber continues today. A private catalogue from 2019 listed the timber at A\$20 kg<sup>-1</sup> (~A\$25 000 m<sup>-3</sup>). It was also utilised as a favoured timber in the earliest construction of European settlements in the



Northern Territory (Woinarski *et al.* 2002). Commercial wild-harvesting continues today (Taylor 2002; Cook *et al.* 2005). It is noted that dried timber can be susceptible to lyctine beetles (Cookson *et al.* 2009). The tightly interlocking grain does make *Erythrophleum* species generally resistant to white-rot fungi (Nguyen *et al.* 2018), although some brown and white rot (particularly *Truncospora* Pilát) fungi have been observed on Australian *Erythrophleum* (M. D. Barrett, pers. obs.).

Australian *Erythrophleum* species have been extensively used by First Nations Australians for medicinal purposes, for manufacturing canoes, tools and ceremonial artefacts (Brock 1988; Aboriginal Communities of the Northern Territory 1993; Lazarides and Hince 1993; Dunlop *et al.* 1995; Kenneally *et al.* 1996; Clarke 2012). Some specific examples identifiable to species are listed here, with more extensive records presented in Table 1. *Erythrophleum pubescens* has been used to make boomerangs and ceremonial clap-sticks in the north Kimberley (Karadada *et al.* 2011) and also harpoon points and axe handles on the Cobourge Peninsula (Blake *et al.* 1998). It is interesting to note that the wood is of sufficient density that it was historically used to make flat fighting swords by the *Alawa* people, from south-east of Katherine in the Northern Territory (Wightman *et al.* 1991). Stems of young saplings have been utilised for spear shafts (Wightman *et al.* 1992). Many uses are recorded for *E. pubescens* on Groote Eylandt, the dense wood being used for woomera pegs, the heads of hooked spears, bamboo spears and harpoons, for roasting sticks and for grinding food (Levitt 1981).

In Australia, *Erythrophleum* bark produces a red dye, the extruded gum contains a tanning agent and can be eaten raw and a resin from the roots has been used to affix spearheads to shafts and pegs to spear throwers (Blake *et al.* 1998; Clarke 2007; Beasley 2009). A gum from the roots of young *E. pubescens* plants has also been used to affix spear and axe heads (Powell *et al.* 2013); a gum from saplings being used as a poison; and leaves being used in cleansing ceremonies on Groote Eylandt (Levitt 1981). The unique chemistry of these gums allows identification of *Erythrophleum* products associated with historical First Nations artefacts using spectroscopy, confirming their long-term use in First Nations Australians societies (Georgiou *et al.* 2022). Smoke from burning bark can cause female sterility, whereas burning leaves repel mosquitos and sand-flies (Beasley 2009). Smoke from burning leaves is also used in cleansing ceremonies (Blake *et al.* 1998; Clarke 2007). Crushed bark is effective as a fish poison and in African species; crushed seeds have been used to poison arrows (Lewis *et al.* 2005). In northern Queensland, medicinal properties from bark of *E. pubescens* are reported as effective for the treatment of sores, skin lesions, wounds, cuts, pain, and sprains (Turpin *et al.* 2022). Numerous traditional medicinal uses have been documented (e.g. Devanesen and Henshall 1982; Aboriginal Communities of the Northern Territory

1993), and bark material is known to be active against tumour cell cultures (Collins *et al.* 1990). African species have been reported to have medicinal and toxic properties similar to those of the Australian species (Dongmo *et al.* 2001; Coates Palgrave and Drummond 2002; Okeyo 2012; Son 2019; Teclair *et al.* 2019).

Although published records probably represent only a small portion of actual utilisation, identified uses are summarised in Table 1 to reflect the current state of recorded knowledge. Most of these records may apply to either *E. chlorostachys* or *E. pubescens*, but it is likely that most apply (at least primarily) to *E. pubescens* as the more common and widespread species, especially on plains. A few records can be categorically assigned to *E. pubescens* or *E. arenarium* on the basis of distribution.

## Ecology

All species are trees, usually growing in savanna or seasonally dry forests, but sometimes in tropical wet forests or rainforests. Members of *Erythrophleum* species are semi-deciduous, maintaining only a sparse canopy in spring, when new foliage is produced (Williams *et al.* 1997). Reproduction can occur from seeds, root suckers, or lignotubers (Lacey and Whelan 1976; Fensham and Bowman 1992). Germination is reasonably straightforward for *Erythrophleum* species because the seeds behave like most legumes (Missanjo *et al.* 2017). Stem survival following fire is low (often <10%), although survival of lignotubers is high (88%; Williams *et al.* 1999b) because greater resource allocation is made to root mass relative to co-occurring eucalypts (Paramjyothi *et al.* 2020). Interestingly, both smaller (DBH < 20 cm) and larger (DBH > 30 cm) trees are most likely to die following fire, with mid-aged trees being most resilient (Williams *et al.* 1999b). This is directly related to bark thickness (Lawes *et al.* 2011), so they may be useful indicators of recent fire history (Paramjyothi *et al.* 2020). Whitau *et al.* (2018) provided evidence for the fluctuation in abundance of *Erythrophleum* related to long-term fire regimes in the northern Kimberley on the basis of camp-fire deposits spanning a 45 000-year occupation sequence. In Australia, *Erythrophleum* species increase significantly in abundance when fire is excluded (Bowman *et al.* 1988; Fensham 1990; Bowman and Panton 1995).

*Erythrophleum* species provide important habitat hollows for animals, with a high density of hollows in the landscape compared with other northern savanna trees, although not uniformly across the landscape (Braithwaite *et al.* 1985; Taylor and Chisholm 2005). The flaky bark of *Erythrophleum arenarium* provides habitat for at least one species of pseudoscorpion (Harvey 1987). Although flowering can be infrequent (Williams *et al.* 1999a), *Erythrophleum* species also provide important nectar resources for birds and insects (Woinarski *et al.* 2000) and to some extent also for fruit bats (Mickleburgh *et al.* 1992; Fleming *et al.* 2009).



**Table 1.** First Nations peoples' utilisation of *Erythrophleum* species in Australia.

Language group or location (local names)	Use	References
Alawa ( <i>Marlbamba</i> ), Marra ( <i>Malbamba</i> ), Marra ( <i>Wirwirl</i> )	Timber used to make boomerangs, woomeras, flat fighting swords, clap-sticks, and for building; resin used to affix spear heads, axe heads; leaves used to make smoke for funeral ceremonies	Wightman <i>et al.</i> (1991), Roberts <i>et al.</i> (2018), Yugul Mangi Rangers (2023)
Bardi ( <i>Joonggoomarr</i> )	Timber used to make clap-sticks	Kenneally <i>et al.</i> (1996)
Batjamal ( <i>Melhe</i> ), Emi ( <i>Mawuny</i> )	Timber used to make clap-sticks and for building	Smith and Wightman (1989)
Belaa ( <i>Winjabarr minya</i> , <i>Winjabarr</i> )	Wood for long-lasting fires, timber for clap-sticks ( <i>limburr</i> ), fighting-sticks ( <i>waalu</i> ), leaves used in various cleansing smoking ceremonies	Cheinmora <i>et al.</i> (2017)
Ngarinyin ( <i>Unggarrun</i> )	Smoke ( <i>Bijagun</i> ) from leaves used for cleansing ceremonies	Wilinggin Aboriginal Corporation (2012)
Dalabon ( <i>Kirdidjirr</i> , <i>Mulyurrunj</i> , <i>Murutilla</i> )	Gum ( <i>Marnû</i> ) eaten or boiled to make a drink, or eaten for stomach upsets; inner bark used as antiseptic wash for skin sores; resin ( <i>Kabbay</i> , <i>Kalanjan</i> ) from roots used to affix spear heads and woomera hooks; smoke from green leaves used for cleansing ceremonies; timber used for clap-sticks, digging-sticks, woomeras, fighting-sticks, heads of shovel-spears	Smith (1991), Bordulk <i>et al.</i> (2012)
Djambarrpuynu ( <i>Maypiny</i> ), Kunwinjku ( <i>Mandubang</i> )	Leaves, inner bark boiled for antiseptic wash for skin lesions; muscle and bone pain; inner bark from roots used to make smoke to stop lactation; timber used for building	Smith (1991), Aboriginal Communities of the Northern Territory (1993)
Gija ( <i>Berawooroony</i> )	Timber used to make fighting-sticks and digging-sticks	Purdie <i>et al.</i> (2018)
Iwaidja ( <i>Gardungun/Kartungkun</i> )	Bark used to treat skin sores and boils; timber used for fighting sticks ( <i>Murrigan</i> ), harpoon point, clap-sticks ( <i>Arrilil</i> ); axe handles; resin from roots used to fasten spear heads; sticks used to pierce nasal septum; green leaves used in smoking ceremonies for cleansing	Aboriginal Communities of the Northern Territory (1993), Blake <i>et al.</i> (1998)
Jamindjung ( <i>Jirrili</i> ), Jawoyn ( <i>Marukkal</i> ), Kunwok ( <i>Mandubang</i> )	Leaves heated and applied to body to relieve pain; timber used for spear-tips	Thompson (2020)
Jingulu, Mudburra ( <i>Mandarngarra</i> )	Bark of roots used to treat skin sores; leaves used to make smoke to cleanse houses during funeral ceremonies; timber used to make clap-sticks, nulla-nullas, boomerangs	Raymond <i>et al.</i> (2018)
Kriol ( <i>Ainud tri</i> ); Ritharrngu/Wägilak ( <i>Maypiny</i> ); Wubuy ( <i>Yirrbara</i> ); Rembarrnga ( <i>Mirniyarrah</i> )	Timber used for many purposes because of strength and density; leaves used to make smoke for cleansing ceremonies; bark boiled and applied to skin sores	Yugul Mangi Rangers (2023)
Kuku Thaypan ( <i>Ku Morteall</i> )	Leaves used to make smoke for ceremonial purposes and cleansing ceremonies; an important tree for sugarbag nests	Standley (2019)
Mangarrayi ( <i>Yangarr</i> ); Yangman ( <i>Yarramala</i> )	Timber used for spear shafts, spear heads, clap-sticks ( <i>Gundarl</i> ), fighting-sticks ( <i>Barrgu</i> ), boomerangs ( <i>Barlgan</i> ); sin from roots ( <i>Gabay</i> ) used to affix spear heads; boiled bark produces red dye and treats skin ailments; leaves used to make smoke for cleansing ceremonies; gum eaten	Roberts <i>et al.</i> (2011)
Marri Ngarr, Magati Ke ( <i>Nandji Tjiwi</i> )	Timber used for clap-sticks, boomerangs, shields, heads of double-sides hooked spears, large war swords, making hammers ( <i>Nanji Pamuri</i> ) for crushing cycad seeds, firewood, carved fish-hooks; saplings used for digging sticks; smoke from leaves used in cleansing ceremonies; resin from roots used to affix spear heads and woomera shafts; leaves warmed on fire and held to head for headache relief	Nambatu <i>et al.</i> (2009)
Mudburra ( <i>Mandarngarra</i> )	Bark of roots used to treat skin sores; leaves used to make smoke to cleanse houses during funeral ceremonies; timber used to make clap-sticks, nulla-nullas, boomerangs	Wightman <i>et al.</i> (1992)

(Continued on next page)



Table 1. (Continued)

Language group or location (local names)	Use	References
Ngalkbun ( <i>Murutilla</i> )	Leaves, inner bark and root bark used for skin lesions; muscle and bone pain; to end lactation	Aboriginal Communities of the Northern Territory (1993)
Ngandi ( <i>Ma-mirniyarrah</i> ); Ngalakgan ( <i>Malbah</i> )	Timber used to make clap sticks, fighting swords	Daniels <i>et al.</i> (2019)
Ngan'gikurunggurr ( <i>Mawuny</i> ); Ngan'giwumirri ( <i>Kinimannnggini</i> )	Leaves used as a skin wash; stems heated to pierce nasal cavity; timber used to make boomerangs, fighting sticks, clap-sticks, digging sticks, firewood (but not when cooking); roots for spear heads; sap eaten; resin from roots used to affix spear heads, woomera pegs, plugging holes in dugout canoes; leaves used to make smoke for cleansing ceremonies	Aboriginal Communities of the Northern Territory (1993), Marrfurra <i>et al.</i> (1995)
Ngarunyman ( <i>Dilwirli</i> )	Timber used to make nulla-nullas, clap-sticks, woomeras	Smith <i>et al.</i> (1993)
Rirratjinu ( <i>Buwatji</i> , <i>Maypiny</i> )	Timber used to make clap-sticks ( <i>Bilma</i> ), boomerangs ( <i>Galiwali</i> ); roots used to make woomera hooks and spear points and as a source of resin; leaves used during funeral ceremonies	Yunupingu <i>et al.</i> (1994)
Tiwi ( <i>Kartukunu</i> , <i>Pijitinga</i> , <i>Tumpurama</i> )	Timber used for clap-sticks, fighting-sticks, axe handles; dry logs used to carve <i>Pukamani</i> poles and ornamental carvings; sharpened sticks used pierce nasal septum and as needles for sewing; smoke from leaves used in cleansing ceremonies; inner bark used for skin sores; young babies waved in smoke to make them strong	Puruntatameri <i>et al.</i> (2001), Thompson (2020)
Uunguu ( <i>Winjabarr</i> )	Timber used to make fighting sticks, clap-sticks, digging-sticks and spear-heads; root-stem joints used to make number-7 boomerangs	Karadada <i>et al.</i> (2011)
Yawuru ( <i>Jun'ju</i> and <i>Bilamana</i> )	Timber used to make clap-sticks	Kenneally <i>et al.</i> (1996)
Darwin region (–)	Medicinal purposes; ceremony; utilitarian artefacts including shovel-nosed spear heads; bark gum eaten; red dye from bark	Clark and Traynor (1987), Dunlop <i>et al.</i> (1995)
Kakadu (–)	Leaves steamed at childbirth and death; tannin-rich bark infused in water and used for skin sores; smoke used to deter mosquitoes	Low (1990)

Extrafloral nectaries found on the leaf rachis are likely to provide an important food resource to ants (Pascal *et al.* 2000; Marazzi *et al.* 2019). *Erythrophleum chlorostachys sensu lato* has been reported to form vesicular-arbuscular mycorrhizae, although the specific fungal species involved was not identified (Brundrett *et al.* 1995; Wang and Qiu 2006). A number of different *Bradyrhizobium* species are associated with *Erythrophleum* across the range of the genus, often being unique to distinct species (and multiple *Bradyrhizobium* Jordan species are commonly present; Yao *et al.* 2015).

## Materials and methods

### Specimens

Herbarium specimens have been examined at AD, BRI, CANB, DNA, MEL, NSW and PERTH by using light microscopy. Images of specimens at E (<http://elmer.rbge.org.uk/bgbase/vherb/bgbasevherb.php>), K (<http://apps.kew.org/herbcat/>) and P (<https://science.mnhn.fr/institution/mnhn/collection/p/item/search>) were examined in March 2018. Field

photographs were taken with a 60-mm Sigma Macro lens (Sigma Corporation of America, New York). All three species have been examined in the field by the authors.

### DNA extraction and polymerase chain reaction (PCR)

All taxa newly sampled for DNA sequencing are represented by voucher specimens in Australian herbaria. Voucher specimens sampled for this paper are detailed in Table 2. All Sanger-derived sequences deposited to GenBank contain *ITS1* and partial *5.8S* only, except for *Dauncey H666*, PERTH 08422060 (indicated with an asterisk), for which a full-length internal transcribed spacer (*ITS*) sequence (including *ITS1*, *5.8S* and *ITS2*) was obtained. Gene complements assembled from short-read archives are described under each sample in Table 2.

DNA extraction, PCR and sequence alignment followed the protocol for sequencing the *ITS* region of ribosomal DNA (rDNA) described in Anderson *et al.* (2016), with the exception of primers used. Initially, amplification of the full *ITS*



**Table 2.** Taxa analysed, vouchers, and GenBank and ENA reference numbers.

Species	Voucher	GenBank and ENA accession numbers
<i>Erythrophleum arenarium</i> R.L.Barrett & M.D.Barrett	Western Australia (WA), Barrett 9080 (NSW, PERTH)	MT581272
	WA, Bean 25079 (BRI)	MT581273
	WA, Byrne 1271 (PERTH 07148453)	MT581270
	WA, Forbes 2465 (PERTH 01958534)	MT581269
	WA, Sweedman 8997 (PERTH 08786607)	MT581271
<i>Erythrophleum chlorostachys</i> (F.Muell.) Baill.	WA, Byrne 3693 (PERTH 08793034)	MT581275
	Northern Territory (NT), Lazarides 8845 (CANB 295340)	MT581276
	WA, Weston 12284 (PERTH 02211750)	MT581274
	NT, Larcombe 2 (DNA D0057605)	MT581277
	NT, Wightman 5205 (DNA D0051920)	MT581278
<i>Erythrophleum fordii</i> Oliv.	China, no voucher	<i>ITS1</i> only, consensus assembly from SRR8191117 (Wang <i>et al.</i> 2019) <sup>A</sup>
	China, no voucher	Contiguous nearly complete (with gaps) <i>18S-ITS1-5.8S-ITS2-28S</i> sequence, consensus assembly from SRR8191118 (Wang <i>et al.</i> 2019)
<i>Erythrophleum ivorense</i> A.Chev.	Gabon, Wieringa 5487 (WAG)	OQ572325; contiguous complete <i>18S-ITS1-5.8S-ITS2-28S</i> sequence, consensus assembly from ERR4363217 (Koenen <i>et al.</i> 2020)
<i>Erythrophleum pubescens</i> R.L.Barrett & M.D.Barrett	WA, Barrett MDB5902 (plant 1) (PERTH)	MT581285
	WA, Barrett MDB5902 (plant 2) (PERTH)	MT581286
	WA, Byrne 3721 (PERTH 08760632)	MT581282
	WA, Coate 224 (PERTH 02888580)	MT581279
	WA, Dauncey H666 (PERTH 08422060) <sup>B</sup>	MT581297
	WA, Foulkes 340 (PERTH 02523922)	MT581280
	NT, Brennan 4583 (DNA D0146433)	MT581290
	NT, Clark 1670 (DNA D0034313)	MT581291
	NT, Cowie 5303 (DNA D0121980)	MT581292
	NT, Dunlop 7145 (NSW 451601)	MT581293
	NT, Egan 2873 (DNA D0077644)	MT581294
	NT, Evans 3270 (NSW 451600) <sup>C</sup>	MT581289
	NT, Smith 101 (DNA D0044224)	MT581295
	NT, Smith 128 (DNA D0029224)	MT581296
	NT, Whaite 3979 & Whaite (NSW 415299)	MT581283
	Queensland (Qld), Blake 23184 (PERTH 02211556)	MT581281
	Qld, Leitch QDA003815 (BRI AQ854110)	MT581288
	Qld, McDonald KRM9767 (BRI AQ846978)	MT581287
	Qld, Wannan 213 & Lynch (NSW 396373)	MT581284
	Qld, McDonald KRM17554 (MEL 2416964A)	OQ471964 (dominant copy, contiguous complete <i>18S-ITS1-5.8S-ITS2-28S</i> sequence) and

(Continued on next page)



**Table 2.** (Continued)

Species	Voucher	GenBank and ENA accession numbers
		OQ396764 (minor copy, <i>ITS1</i> – <i>5.8S</i> – <i>ITS2</i> only), consensus assembly from ERR7599610
<i>Pachyelasma tessmannii</i> (Harms) Harms	Gabon, Wieringa 5229 (WAG)	OQ572326; contiguous complete <i>18S</i> – <i>ITS1</i> – <i>5.8S</i> – <i>ITS2</i> – <i>28S</i> sequence, consensus assembly from ERR4363236 (Koenen et al. 2020)

<sup>A</sup>Sample was assembled from short-read archives, but could not be uploaded to GenBank because third-party assemblies require wet-lab experiments to meet requirements. Sequences are provided in the ribosomal alignment (see File S1.nex in the Supplementary material).

<sup>B</sup>The only full-length *ITS* sequence obtained from Sanger sequencing.

<sup>C</sup>The sample *Evans 3270* was excluded from further analyses. Although the sample was resolved with *E. pubescens* (77% BS in RAxML tree, data not shown) as expected from its morphology, the sequence chromatograms were messy, resulting in ambiguous base calls, and the edited sequence still somewhat divergent from other *E. pubescens*. Because it was not possible to distinguish among hybridisation, paralogy or contamination as the cause of different base calls to other *Erythrophleum* haplotypes, the sequence was excluded from analyses. A second sample (*Egan 2873*) from the same locality (Cutta Cutta Caves, NT) produced a haplotype belonging to the *E. pubescens* clade, as expected from its morphological features, and it is likely that *Evans 3270*, likewise, represents *E. pubescens*; however a hybrid origin for this specimen with *E. chlorostachys* cannot be confidently excluded.

region was attempted by using a range of primers and PCR reaction conditions, but only a single sample (*Dauncey H666*) could be amplified, by using the primers *ITS* S3 (5'-AACCTGCGGAAGGATCATG-3') and *ITS*4 (5'-TCCTCCGCTTATTGATATGC-3'). Subsequently, *ITS* amplification was attempted for two smaller fragments (*ITS1* and *ITS2* respectively); however, only the *ITS1* region could be reliably amplified from herbarium samples, using the primers S3 and *ITS2*-R (5'-GCTGCGTCTTCATCGATGC-3'), despite a wide range of conditions and nested primers being applied. Attempts to perform PCR for chloroplast *matK* and *trnF*–*trnL* regions by using a range of primers also failed for *Erythrophleum*. Consequently, only the *ITS1* dataset was used for phylogenetic analyses. The high failure rate using standard primers could be due to the concentration of tannins, terpenoids and alkaloids in the leaves (Bisby et al. 1994; Blake et al. 1998), which are known inhibitors of PCR amplification (Katterman and Shattuck 1983).

### Ribosomal assembly from short-read archives

Four *Erythrophleum* short-read archives (Table 2) generated for other studies were downloaded from European Nucleotide Archive (ENA) and mined for ribosomal sequences. The mined archives were generated by hybrid-capture (*Erythrophleum pubescens* and *Pachyelasma tessmannii* (Harms) Harms) or RADseq (two *E. fordii* Oliv. accessions), but all proved to have sufficient bycatch of nuclear ribosomal DNA for confident assembly (>20× coverage) of the full ribosomal region, including *18S*, *ITS1*, *5.8S*, *ITS2* and *28S* in all samples except for the *E. fordii* samples, for which there were some short gaps in the full ribosomal assembly of SRR8191118, and only *ITS1* could be recovered from SRR8191118. Sanger-derived *ITS* sequences were used as a reference to map reads in Geneious Prime (ver. 2023.0.1), using the default Map to Reference module, setting 5% maximum mismatches per read, three iterations of fine tuning, maximum gaps per read = 15%, word length = 14, maximum gap size = 50,

index word length = 12, and maximum ambiguity = 4. The mapped reads were then *de-novo* assembled using the De Novo Assemble module in Geneious, using the Geneious Assembler set to medium sensitivity, and merging homopolymer variants, saving the consensus sequence of assembled reads calling heterozygous positions when variants present at greater than 35% (threshold 65%). Assembled contigs were then re-mapped to the original reference, and contigs covering the *ITS* region at depth greater than five times the coverage were treated as independent ribosomal copies. Only a single ribosomal contig was assembled for the *E. ivorensis* A.Chev. sample, whereas two very similar contigs were assembled for the *E. pubescens* sample. For the dominant copy in each case, the contigs were extended to include the *18S* and *26S* genes by mapping to reference with 1% similarity and 20–30 iterations in Geneious, saving the consensus sequence and calling heterozygous positions when variants present at greater than 35% (threshold 65%).

All recovered Australian *ITS* haplotypes were verified as genuine *ITS* homologs by their ability to form plausibly folding *ITS1* (and a single *ITS2*) RNA molecules with free energy  $\Delta G$  comparable to that of other *Erythrophleum* species, using the web server for m-fold (Zuker 2003; <http://unafold.rna.albany.edu/?q=mfold>), and that *5.8S* and ends of *18S* and *28S* genes present in the transcripts could be aligned to related Fabaceae, and contained no indels.

### Outgroups

Two other non-Australian *Erythrophleum* samples of *ITS* are available on GenBank (*E. fordii* MH844617 and *E. suaveolens* KY306573). Unfortunately, both of the samples on GenBank were highly divergent in *ITS* from all *Erythrophleum* samples used here (including newly assembled *ITS* of *E. fordii*), with few regions that could be readily aligned, and almost no parsimony-informative sites relevant to resolving relationships between the Australian species. Consequently, these GenBank sequences of *E. fordii* and *E. suaveolens* were



excluded from further analyses. We were unable to amplify *ITS* from a recent collection of *Erythrophleum africanum* Harms located in an Australian herbarium. The final alignment, therefore, included ribosomal assemblies only from *E. fordii* and *E. ivorensense* as the only non-Australian *Erythrophleum* representative. A ribosomal assembly of *Pachyelasma tessmannii* (Harms) Harms, one of the closest relatives to *Erythrophleum* in previous analyses, was used to root the tree.

## Alignment and phylogenetic analyses

The four full-length ribosomal sequences, and 30 *ITS* sequences were assembled using the MAFFT (ver. 7.490, see <https://mafft.cbrc.jp/alignment/server/index.html>) module in Geneious Prime, using default settings (Katoh and Standley 2013).

Partitions were grouped using the program PartitionFinder2 (ver. 2.1.1, see <https://www.robertlanfear.com/partitionfinder/>; Lanfear *et al.* 2016), using the corrected Akaike information criterion (AICc), greedy search (Lanfear *et al.* 2012) with PhyML (ver. 3.0, see <http://www.atgc-montpellier.fr/phyml/>; Guindon *et al.* 2010), and the models limited to those accommodated by MrBayes (ver. 3.2.6, see <https://nbisweden.github.io/MrBayes/>; Huelsenbeck and Ronquist 2001). The best partition scheme found three partitions (18S, 5.8S) (*ITS1*, *ITS2*) (26S), with the best substitution models being GTR, GTR and GTR + G respectively.

Two methods of generating phylogenetic trees were used, namely, maximum likelihood (ML) by using RAxML (ver. 8.2.11, see <https://github.com/stamatak/standard-RAxML>; Stamatakis 2014), and Bayesian inference (BI) in MrBayes (ver. 3.2.6; Huelsenbeck and Ronquist 2001), both being implemented in Geneious Prime (ver. 2023.0.1, see <http://www.geneious.com/>; Kearse *et al.* 2012). RAxML was run using partition and substitution models described above, by using 10 searches for the best maximum-likelihood tree, and support values were calculated from 100 bootstrap replicates. MrBayes was run using four heated chains over 1 100 000 generations with a burn-in length of 100 000 generations, under partition and substitution models described above. MrBayes analyses were evaluated by confirming that all runs converged on similar log-likelihood scores, traces had reached stationarity, and all run parameters had effective sample sizes greater than 500. Trees were visualised and edited using FigTree (ver. 1.4.4, see <http://tree.bio.ed.ac.uk/software/figtree/>).

## Results

The ribosomal alignment consisted of four full-length ribosomal sequences, covering all three non-Australian outgroups, plus one representative of the Australian clade (*E. pubescens*). In total, 30 *ITS* sequences (all but two consisting of *ITS1*

only), represented all three Australian morphological species, plus an additional sample of the Asian *E. fordii*.

The alignment consisted of 5840 and 1479 total aligned residues and variable residues respectively, with 1809 aligned bases in 18S, 276 in *ITS1*, 159 in 5.8S, 207 in *ITS2* and 3389 in 26S. The *ITS1* dataset, when restricted to the Australian samples only, had 11 parsimony-informative sites. Four indels were not coded, but were diagnostic for (1) *E. arenarium* ( $n = 1$ , 1-bp insertion, A at Position 1818), (2) *E. chlorostachys* ( $n = 1$ , C insertion at Position 1900), (3) *E. pubescens* ( $n = 1$ , 8-bp deletion relative to *E. arenarium* and *E. chlorostachys* at Positions 2026–2033), and (4) *E. arenarium* + *E. chlorostachys* ( $n = 1$ , GAA insertion at Positions 2076–2078); indels are labelled as per Fig. 1, whereas alignment positions refer to aligned residues in the full ribosomal alignment (see File S1.nex in the Supplementary material).

Sampling within Australia covered all three morphological species, and all broad geographic regions were represented for each species (although no Queensland representatives of *E. chlorostachys sensu stricto* were included). The RAxML tree is shown in Fig. 1, and bootstrap (BS) and posterior probability (PP) support values from the RAxML and MrBayes analyses respectively are indicated on relevant nodes. The tree rooted with *Pachyelasma tessmannii* recovered the African species, *E. ivorensense*, sister to the remaining sampled *Erythrophleum* (96% BS, 1.00 PP), and the Asian *E. fordii* sister to a monophyletic Australian clade (98% BS, 1.00 PP). Within the Australian clade, all samples clustered into one of three strongly supported clades (94–97% BS, 1.00 PP), corresponding to the three morphologically defined species, namely, *E. arenarium*, *E. chlorostachys* or *E. pubescens*. *E. arenarium* and *E. chlorostachys* were weakly supported (74% BS, 0.55 PP) as sister species, with *E. pubescens* being the most divergent lineage within the Australian clade.

One short-read archive (*E. pubescens* McDonald 17554) allowed assembly of two similar *ITS* haplotypes (OQ471964 and OQ396764), both of which fell within the clade interpreted here as *E. pubescens* (Fig. 1).

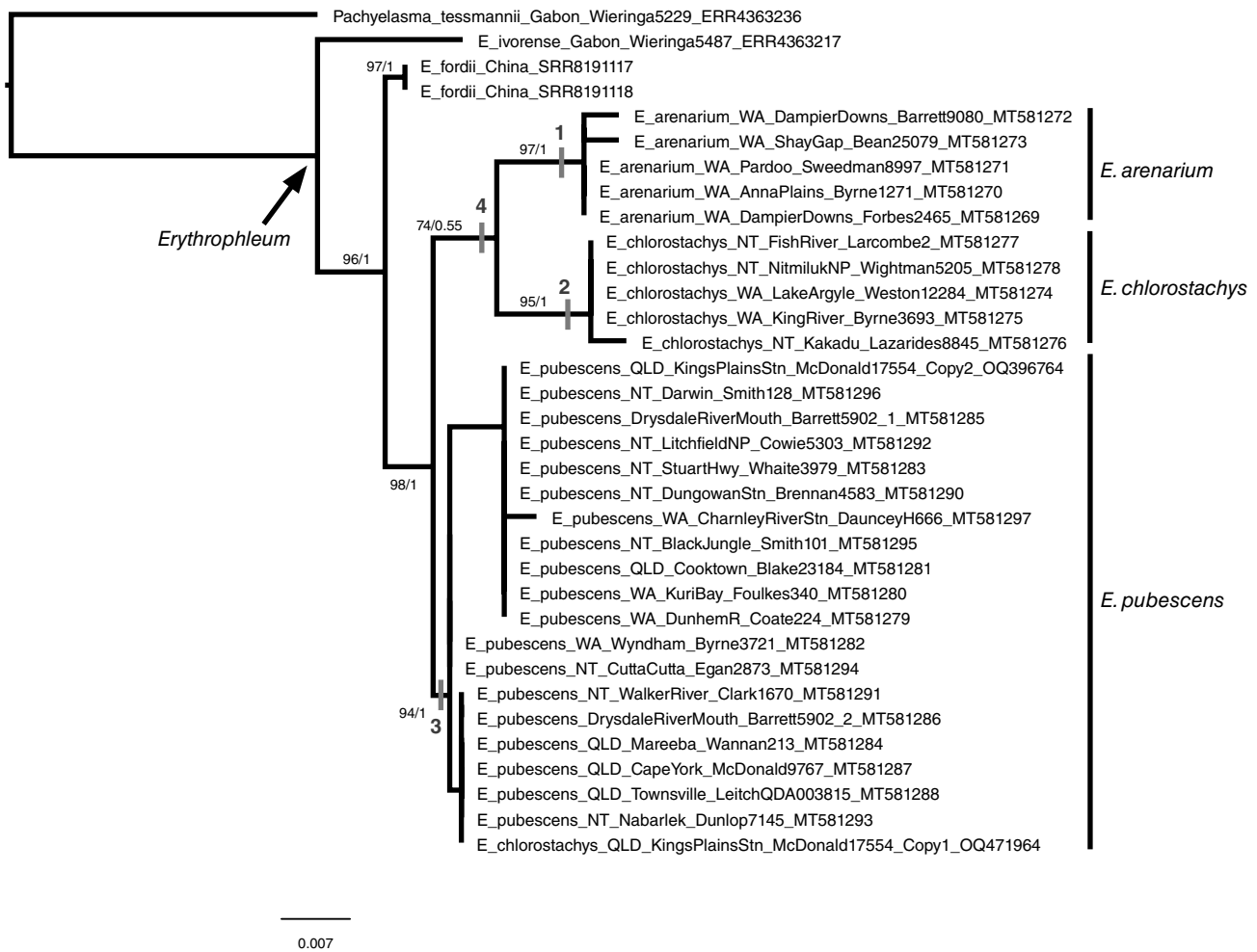
## Discussion

### Phylogeny of *Erythrophleum*

Although only two non-Australian *Erythrophleum* species were represented in the ribosomal tree, the Australian clade was strongly supported as sister to the Asian species *E. fordii*, as recovered in chloroplast phylogenies (Duminil *et al.* 2013, 2015). Denser sampling of African *Erythrophleum* is required to further elucidate relationships and biogeography of the genus.

Although most samples used for this study were represented by *ITS1* only, careful phylogenetic selection of full-length ribosomal sequences enabled robust phylogenetic





**Fig. 1.** Maximum-likelihood tree of aligned ribosomal sequences of *Erythrophleum*, rooted with *Pachyelasma tessmannii*. Nodal support values are bootstrap support values (RAxML) followed by posterior probabilities (MrBayes). Indel positions in *ITS1* are indicated by grey bars, and numbered as in the text (see Results). Three clades (*E. arenarium*, *E. chlorostachys* and *E. pubescens*) match species designations from morphology, as described in the taxonomy section. Within the sampled *Erythrophleum* taxa, the three Australian species form a clade, and there is weak support for a sister relationship between *E. arenarium* and *E. chlorostachys*. The intraspecific variation within *E. pubescens* lacks support, and is not considered taxonomically informative. Sample names indicate species, state, location, collector and number, and GenBank or ENA accession number.

reconstruction. Because all Australian samples were recovered as a well-supported monophyletic Australian clade (Fig. 1), the sampled taxon–locus combination enabled the full-length ribosomal sequences to resolve relationships of the Australian clade to the outgroups, for which *ITS1* alone proved too variable to resolve with high support (data not shown), whereas the *ITS1* region alone was sufficient to resolve relationships within the more densely sampled Australian clade, with high support values.

The division of Australian *Erythrophleum* into three species was supported by the moderately to well-supported clustering of *ITS1* sequences into three discrete clades, matching morphological designations. The greatest intraspecific variation in *ITS1* sequences was found within the most widely distributed species, *E. pubescens*; however,

clades within this species were not supported by maximum-likelihood bootstrap or Bayesian analyses, and there is no geographical trend to the clades. Indeed, two plants from the same population (Drysedale River Mouth, Barrett MDB 5902) were placed divergently, one each in the two most numerous clades. Similarly, two *ITS* assemblages representing each clade were reconstructed from the single available *E. pubescens* short-read archive, indicating that these copies can both be present within individuals; it is possible that this is a fixed polymorphism in *E. pubescens*, through duplication of the ribosomal locus. Consequently, we interpret both variants as intraspecific variation within a single species, *E. pubescens*.

Within the three Australian species, *E. arenarium* and *E. chlorostachys* were recovered as sister taxa in the RAxML



tree (74% BS), but not in the MrBayes tree (0.55 PP). This node was supported by a diagnostic 3-bp (GAA) insertion in the *ITS1* alignment (Indel 4, Fig. 1), as described under results, providing additional evidence for this sister relationship in the ribosomal phylogeny. The sister relationship of these two species is a plausible result, with the two species sharing (relative to *E. pubescens*) non-corky branchlets, fewer leaflets per pinna, not or slightly asymmetric leaflets, glabrous raceme axis and pedicels, and longer calyx, anthers and pod stipe, and generally shorter aril, which are possible apomorphies for the clade. However further multi-locus data are required to conclusively demonstrate this relationship.

### Species concepts in *Erythrophleum*

Taxonomy of the genus *Erythrophleum* has not been revised as a whole, but several regional treatments with adequate descriptions for all species are available (Larsen *et al.* 1980, 1984; Ross 1977, 1998; Coates Palgrave and Drummond 2002; Du Puy *et al.* 2002; Lewis *et al.* 2005; Chen *et al.* 2010); however, consistently distinguishing among some of the African species across their respective ranges is not without its challenges (Gorel 2019). The Australian species are probably most closely related to *E. fordii*, which is morphologically most similar to *E. pubescens* (see Chen *et al.* 2010). *Erythrophleum fordii* differs most obviously from *E. pubescens* in having rough (but not corky) bark, larger (5–8 cm long *v.* 2–6 cm long), acute (*v.* obtuse) leaflets, longer inflorescences (15–25 cm *v.* 7–16 cm) and shortly pedicellate flowers.

The Australian species have probably been historically maintained as a single taxon, largely owing to the variability of leaf morphology within each species (and even a single plant), confusing the boundaries between them. Plants can demonstrate three different leaf types at various growth stages, as seedling leaves, resprouting leaves, or an adult crown, similar to the ontogenetic stages seen in *Corymbia* (Hill and Johnson 1995; Myrtaceae). Careful field observations of each taxon by the authors have shown that three distinct leaf forms are present on each taxon at these stages (and two leaf forms can be present on any individual, depending on life stage or regeneration phase), and comparison of leaves at the same stage makes identification quite simple, whereas comparing alternate stages between species can lead to occasional confusion (such as herbarium specimens consisting entirely of juvenile leaves). Leaves of *Erythrophleum* species are bipinnate, with two to five pairs of opposite pinnae in the Australian species, but sometimes one or two pinnae abort, so they can appear alternate, and the leaflets are alternate. Seedling and adult crown leaves tend to be small, whereas resprouting leaves (both from lignotubers and trunks) can be much larger. Resprouting leaves (following disturbance such as fire) are often more symmetrical than are juvenile or adult crown leaves, so resprout leaves of *E. pubescens* can look similar to adult

crown leaves of *E. chlorostachys* in some cases, making occasional sterile collections difficult to place in either species where their distributions overlap. When present, cork on the upper branchlets is diagnostic for *E. pubescens*, but younger branchlets sometimes cannot reliably be distinguished from *E. chlorostachys* if leaflet shape is also ambiguous. There is also regional variation in the size of crown leaves within *E. pubescens* in particular, largely correlating with a rainfall gradient, with very small (~1 cm long) leaflets in the northern Kimberley, and very large (up to 6 cm long) leaflets on Cape York. Misinterpretation of leaf-stage variation has led to similar taxonomic confusion in *Corymbia* (see Nicolle 2014).

Once leaf-stage variation was understood, correlating significant differences in floral morphology could be identified in each of the three taxa recognised here, and the combined differences are considered sufficient to justify recognition at species rank. Past confusion has generally led to this variation being described under a single entity. On the basis of *ITS1* data and comprehensive geographic sampling, three monophyletic phylogenetic lineages were recovered, perfectly matching morphological distinctions, and consistent with the phylogenetic species concept. Two of the species overlap broadly, through the Top End of the Northern Territory and adjacent parts of Western Australia and Queensland, while maintaining morphological and genetic distinction, consistent with reproductive isolation. Consequently, three taxa are recognised at species rank, with two species being newly described.

### Taxonomy

*Erythrophleum* Afzel. ex R.Br. in D.Denham,  
H.Clapperton & W.Oudney, *Narr. Travels Africa*  
235 (1826)

Type: *Erythrophleum suaveolens* (Guill. & Perr.) Brenan.

*Fillaea* Guill. & Perr. in Guillemin, Perrottet & A.Richard, *Fl. Seneg. Tent.* t. 55 (1832). Type: *F. suaveolens* Guill. & Perr.

*Mavia* Bertol.f., *Mem. Accad. Bologna* 2: 570, t. 39 (1850). Type: *M. judicialis* Bertol.f.

*Laboucheria* F.Muell., *J. Proc. Linn. Soc., Bot.* 3: 158 (1859). Type: *L. chlorostachya* F.Muell.

### Notes

Brenan (1960) nominated *Fillaea* Guill. & Perr. for rejection on the basis of a later publication date for *Erythrophleum* Afzel. ex G.Don. (1832); however, Brown (1826) is considered to have validated the name *Erythrophleum*, so rejection was deemed unnecessary by the nomenclature committee.

A genus of 12 species in the tropical regions of Africa, Madagascar, Asia, and Australia; three species endemic to northern Australia.



***Erythrophleum arenarium* R.L.Barrett & M.D.Barrett, sp. nov.**

*Type:* Frome Rocks Road, 18 miles [~29 km] south-east of Mangel Creek Station Homestead, SW Kimberley, Western Australia, 21 October 1984, *D.Fell* 297 (holo: PERTH 02211947; iso: BRI AQ444796).

*Tree* up to 6(–8) m tall, sometimes a shrub, few-branched with a compact crown, resprouting after fire; *bark* dark grey to blackish, roughly tessellated; *branchlets* usually glabrous, sometimes a little corky, sometimes slightly glaucous at the nodes. *Leaves* with petiole 42–55 mm long; rachis 14–40 mm long; *pinnae* usually 2(3) pairs, sometimes 1 or 2 pinna aborted so appearing alternate; secondary rachises 40–110 mm long; *leaflets* alternate, mostly 2–5(–7) per pinna, orbicular to somewhat deltoid, mostly 29–74 mm long, 27–83 mm wide, slightly larger on resprout growth (up to 87 mm long, up to 97 mm wide), obtuse to cordate,  $\pm$  symmetric or slightly asymmetric, rounded, obtuse or emarginate apically, glabrous or slightly glaucous; petiolules 4–9(–11) mm long; venation conspicuous. *Racemes* mostly 80–140 mm long; axis 1.0–2.1 mm thick below the flowers, glabrous. *Flowers* 72–88; distinctly pedicellate, pedicels 3.0–5.5 mm long at anthesis; cream to greenish-yellow. *Floral bracts* 1.5–2.5 mm long, margins fimbriate, lamina glabrous. *Calyx* 3.6–5.0 mm long; lobes shorter than the tube, 1.1–2.1 mm long, pubescent only on margins. *Petals* 4.2–6.4 mm long, with pubescent margins and scattered hairs on the adaxial surface. *Stamens* alternately long and short, filaments 4.6–9.7 mm long, glabrous. *Anthers* 1.0–1.3 mm long. *Ovary* densely pubescent, 3.6–5.3 mm long. *Style* 1.0–2.2 mm long. *Pod* often slightly curved, dehiscing along both sutures, (1–)3–6-seeded, (85–)145–175 mm long, 30–38 mm wide, apex acute to apiculate; dark reddish-brown, glabrous; stipe of pod often asymmetric, 11–33 mm long. *Seeds* brown, suborbicular, 12–14 mm long, 10–13 mm wide, 4.0–5.0 mm thick; aril 3–6 mm long. (Fig. 2)

## Illustrations

D. E. Symon in J. P. Jessop (Ed.), *Fl. Centr. Australia* 104, fig. 127 (1981); K. F. Kenneally *et al.*, *Broome & Beyond. Pl. & People Dampier Peninsula* 76, [lower pl. only] (1996); B. Kane, *Broome's Natural Environment* (2023); <http://wkfl.asn.au/nature/ironwood.html> (accessed 9 August 2023), (all as *E. chlorostachys*).

## Distribution

Endemic in northern Australia, from the northern edge of the Pilbara, north to the Dampier District in the southern Kimberley and east through most of the Great Sandy Desert.

## Habitat

Usually found in open pindan woodland or savanna on sand, often on old, subdued sand dunes.

## Phenology

Flowering recorded for August–November and fruiting recorded for April, May, August, October and November.

## Etymology

The epithet is derived from the Latin *arenarius* (pertaining to sand), in reference to the specific habitat of this species on sands associated with the Great Sandy Desert (see McKenzie *et al.* 1983).

## Notes

The following combination of characters is diagnostic: tree up to 6(–8) m tall, few-branched with a compact crown, branchlets usually glabrous, sometimes glaucous. Leaves with pinnae usually in 2(3) pairs; leaflets mostly 2–5(–7) per pinna, orbicular to somewhat deltoid, not or slightly asymmetric; glabrous or slightly glaucous; petiolules 4–9(–11) mm long; raceme axis glabrous. Calyx 3.6–5.0 mm long; lobes 1.1–2.1 mm long, pubescent only on margins; pedicels 3.0–5.5 mm long at anthesis; stipe of pod 11–33 mm long.

Ross (1998) noted that plants from the south-western Kimberley differed from the majority of the species' range in their almost glabrous, pedicellate flowers that are also larger. Field observations have found these characteristics to be consistent, with plants readily identifiable as either *E. arenarium* or *E. pubescens* in a narrow zone of overlapping distribution in adjacent habitats between Willare Bridge and Blina, in Western Australia.

Known as camel poison. The common name of desert ironwood is suggested here as a more definitive name. First Nations names include *joonggoomarr* (Bardi), *jun'ju*, and *bilamana* (Yawuru) (Kenneally *et al.* 1996).

Although reasonably widespread and not currently threatened, it is noted that some populations may be affected by mining for mineral sands on the Dampier Peninsula (<https://www.epa.wa.gov.au/1080-thunderbird-mineral-sands-project>).

## Representative specimens

**WESTERN AUSTRALIA.** 1 km NW of Dampier Downs Station northern gate, 1 Nov. 2014, *R.L.Barrett & M.Gresser* RLB 9080 (CANB, DNA, NSW, PERTH); 23.3 km along pipeline track, ESE of Shay Gap, and NE of Marble Bar, 23 Apr. 2006, *A.R.Bean* 25079 (BRI); Great Sandy Desert, 25 Apr. 1964, *J.S.Beard* 3249 (PERTH); Anna Plains Road, 3 km from Great Northern Highway, 28 Sep. 2004, *G.Byrne* 1271 (PERTH); between De Grey River and La Grange Bay, *Carey s.n.* (MEL); near Racecourse, Broome, 31 Aug. 1991, *B.J.Carter* 484 (DNA, *n.v.*, PERTH); 55 km SW of Derby, 12 Oct. 1985, *H.Demarz* 10906 (PERTH); 25 km E of Port Hedland Road on Dampier Downs Road, 26 June 1984, *S.J.Forbes* 2465 (HO *n.v.*, MEL, PERTH); Millijiddee Homestead, St George Ranges, 5 May 1960, *C.A.Gardner* 12389 (PERTH); McLarty Hills, Great Sandy Desert, 5 Aug. 1977, *A.S.George* 14639 (PERTH); 94 km ESE of Telegraph Line, Anketell Ridge Road, Great Sandy Desert, 13 Aug. 1977, *A.S.George* 14819 (PERTH); [near] Beagle Bay, 1879, *A.Forrest & Carey* (MEL); 58 km SSW of No. 1 McHugh Bore on Dampier Downs Station, 26 Sep. 1980,





**Fig. 2.** *Erythrophleum arenarium*: (a) habitat and habit; (b) bark; (c) fruiting branchlet; (d) slightly glaucous leaf; (e) seedling; (f) portion of inflorescence; (g) inside view of legume with attached seeds; (h) young sapling with main stems killed by fire and multiple stems resprouting. Vouchers: north of Pardoo Roadhouse, WA, not vouchered (a, b, d); north of Dampier Downs Station, WA, R.L.Barrett & M.Gresser RLB 9080, PERTH (c, e, g, h); Anna Plains, WA, G.Byrne 1271, PERTH (f). Images by R. L. Barrett (a–e, g, h), and G. Byrne (f).



*S.D.Hopper 1733* (PERTH); near Roebuck Bay, Nov. 1967, *F.Lullfitz s.n.* (PERTH); Dampier's Land near Broome, July 1911, *E.M.Mjöberg s.n.* (NSW); ~32 km E of Yeeda Homestead on the Great Northern Highway, 27 May 1967, *E.A.Shaw 810* (AD); 12 km N of Pardoo Roadhouse on North West Coastal Highway, 23 Oct. 2015, *L.S.J.Sweedman 8997* (PERTH).

***Erythrophleum chlorostachys* (F.Muell.) Baill.,  
Hist. Pl. 2: 150 (1870)**

*Laboucheria chlorostachya* F.Muell., *J. Proc. Linn. Soc., Bot.* 3: 159 (1859). *Erythrophleum laboucheri* F.Muell., *Ann. Rep. Gov. Bot. & Dir. Bot. Gard.* 1862–1863: 12 (1863), *nom. illeg.*, *nom. superfl.*, as '*E. laboucherii*'. *Erythrophleum laboucheri* F.Muell. ex Benth., *Fl. Austral.* 2: 297 (1864), *nom. nov.*, isonym, as '*E. laboucherii*'. *Erythrophleum chlorostachys* (F.Muell.) Hennings ex Taub., *Nat. Pflanzenfam.* [Engler & Prantl] 3(3): 127 (1892), isonym.

*Type citation*: 'A plagis boreali-occidentalibus Australiae usque ad flumen Burdekin tractus orientalis, tam in solo fertilior quam steriliore planitiebus montiumque satis frequenter obvia.'

*Type*: Victoria River, [Northern Territory], September 1855, *F.Mueller s.n.* (lecto, here designated: MEL 1524198; isolecto: MEL 1524197).

*Residual syntypes* (all representing *E. chlorostachys*): Northern Territory: Arnhem Land, *F.Mueller s.n.* (K 000756965, K 000756966 (photos at MEL)); Victoria River, June 1856, *F.Mueller s.n.* (K 000756961, K 000756963, K 000756967); Gulf of Carpentaria, *F.Mueller s.n.* (MEL 1524187); seen at the Burdekin River, Queensland, and Port Essington, Northern Territory, 1849, *F.W.L.Leichhardt s.n.* (NSW 415300, P 02939477).

*Possible syntypes*: Australia: location, collector and date unknown (K 000756964); northern coast of Arnhem Land, *J.M.Kinlay s.n.* (MEL 1524178); scrub towards the Gulf of Carpentaria, lat. 17°S, *J.M.Stuart* (MEL 1524189).

*Excluded syntype* (representing *E. pubescens*): Strangways River, n.d., *F.Mueller* (AD 97813219, MEL 1524186).

*Tree* up to (4–)6–9 m tall, many-branched with a spreading crown, resprouting after fire; *bark* dark grey to blackish, roughly tessellated and irregularly, shallowly furrowed; *branchlets* smooth, rarely with any cork, usually glabrous, not glaucous. *Leaves* with petiole 23–72 mm long; rachis 24–115 mm long; *pinnae* usually (1)2(3) pairs, sometimes 1 or 2 pinna aborted so appearing alternate; secondary rachises 50–170 mm long; *leaflets* alternate, mostly 3–6(–7) per pinna, orbicular to somewhat deltoid, mostly 31–87 mm long, 31–80 mm wide, slightly larger on resprout growth (up to 90 mm wide), obtuse to cordate, slightly asymmetric, rounded, obtuse or emarginate apically, glabrous or rarely very finely pubescent when very young, soon glabrescent; petiolules 2.5–7 mm long; venation conspicuous. *Racemes* usually simple, rarely once-branched, mostly 60–105 mm long; axis 0.9–1.6 mm thick below the flowers, glabrous. *Flowers* 55–100; distinctly pedicellate, pedicels 0.5–1.2 mm long at anthesis (occasionally sessile in bud); cream to greenish-yellow. *Floral bracts* 0.7–0.9 mm long, margins ciliate, lamina glabrous. *Calyx* 2.3–3.8 mm long; lobes shorter than the tube, 0.9–1.2 mm long, ciliate only on margins. *Petals* 2.8–3.8 mm long, exerted by 0.8–2.3 mm, with ciliate

margins and glabrous adaxial surface. *Stamens* alternately long and short, filaments 3.2–6.4 mm long, glabrous. *Anthers* 0.7–1.0 mm long. *Ovary* densely pubescent, 1.8–2.7 mm long. *Style* 1.9–2.8 mm long. *Pod* often slightly curved, dehiscing along both sutures, (2–)3–8-seeded, (90–)120–210 mm long, 23–32 mm wide, apex acute to apiculate; dark reddish-brown, glabrous; stipe of pod often asymmetric, 12–20 mm long. *Seeds* brown, suborbicular, 10–11 mm long, 9–10 mm wide, 2.5–5.1 mm thick; aril 2–4.8(–7) mm long. (Fig. 3)

## Illustrations

K. Brennan, *Wildfl. Kakadu* 52, pl. 83 (1986); M. Clark & S. Traynor, *Pl. Trop. Woodl.* 50, fig. (1987); J. Brock, *Top End Native Pl.* 150, pl. (1988); J. H. Ross in A. E. Orchard (Ed.), *Fl. Australia* 12: 70, fig. 28 (1998); P. Moore, *Guide Pl. Inland Australia* 392–3, pl. (2005).

## Distribution

Endemic in northern Australia, from Wyndham and along the Ord River, through central Northern Territory to the Gulf of Carpentaria, Queensland.

## Habitat

Usually found in open woodland or savanna on sand or clay-loam soils.

## Phenology

Flowering recorded for August–December and fruiting recorded for February–September.

## Etymology

The epithet is derived from the Greek *chloro-* (green) and *-stachys* (spike), in reference to the greenish flower spikes.

## Notes

The following combination of characters is diagnostic: tree (4–)6–9 m tall, many-branched with a spreading crown, branchlets glabrous, not glaucous; leaves with pinnae usually in (1)2(3) pairs; leaflets mostly 3–6(–7) per pinna, orbicular to somewhat deltoid, slightly asymmetric; glabrous or rarely very finely pubescent when very young, soon glabrescent; petiolules 2.5–7 mm long; raceme axis glabrous; pedicels 0.5–1.2 mm long; calyx 2.3–3.8 mm long; lobes 0.9–1.2 mm long, ciliate only on margins; stipe of pod 12–20 mm long.

Close examination of specimens at MEL and images of the remaining syntypes of *Laboucheria chlorostachys* showed that most of the specimens are referable to the taxon defined here as *E. chlorostachys*. Of the six possible syntypes identified above, three possible syntypes were likely to be available to Mueller at the time of description, but cannot be verified as original material. One syntype is referable to a different taxon than the majority, namely *E. pubescens*. Of





**Fig. 3.** *Erythrophleum chlorostachys*: (a, b) habit and habitat; (c) bark; (d) inflorescence with very young buds; (e) flower buds; (f) flowering inflorescence (g) portion of flowering inflorescence showing shortly pedicellate flowers, glabrous axis and glabrous calyx; (h) glabrous new adult growth; (i) pod; (j) seed. Vouchers: King River, Kununurra, WA, G.Byrne 3693, PERTH (a, c–g); Ragged Range, WA, not vouchered (b); Katherine, NT, L.G.Adams 1653, NSW (h); ‘Katherine National Park’, NT, M.D.Tindale 6040 & C.R.Dunlop, NSW (i, j). Images by G. Byrne (a, c–g), and R. L. Barrett (b, h–j).



the remaining two specimens, the more complete specimen was selected as lectotype.

The lectotype bears a label with the name '*Laboucheria chlorostachys* Ferd. Mueller.' This collection is in fruit, so the distinguishing floral characteristics cannot be determined on this specimen, but the leaf characters and location clearly distinguish it from *E. arenarium* and *E. pubescens*.

Ferdinand Mueller (1859) described *Laboucheria chlorostachya* on the basis of material that mostly belonged to the entity here typified; however, material later illustrated for the *Iconography of Australian Species of Acacia and Cognate Genera* (Mueller 1888) actually represents *E. pubescens*. The excellent lithograph from that work is reproduced here to illustrate the new species. In the treatment by Ross (1998), fig. 28 represents *E. chlorostachys*, whereas fig. 31 and 43 represent *E. pubescens*.

Known as Top End ironwood.

## Representative specimens

**WESTERN AUSTRALIA.** Cambridge Gulf, 1886, *H.S.Banford & E.W.Nyulasy s.n.* (MEL); Buttons Gap, Ord River, 17 Apr. 1956, *N.T.Burbridge 5196* (CANB, MEL); E bank of the King River, Kununurra, 12 Dec. 2009, *G.Byrne 3693* (MEL, PERTH); Wyndham, 24 May 1944, *C.A.Gardner 7257* (PERTH, 2 sheets); W of Cambridge Gulf, 1887, *A.J.Keiller s.n.* (MEL); Five Rivers Lookout, Wyndham, 20 Aug. 2001, *R.C.H.Shepherd 76* (MEL); ~1 km uphill from Camp Nicholas, Smoke Creek, SW of Lake Argyle, 5 May 1980, *A.S.Weston 12284* (PERTH). **NORTHERN TERRITORY.** Stuart Hwy, 6 miles [~9.6 km] NW of Katherine, *L.G.Adams 811* (BRI, CANB); 4-mile farm, CSIRO Research Station, Katherine, 7 Dec. 1966, *L.G.Adams 1653* (BRI, CANB, E, MEL, NSW); 3 km N of Dunmurra, Stuart Highway, 2 July 1974, *A.C.Beaglehole 46481 & G.W.Carr 2702* (BRI *n.v.*, MEL); U.D.P. Falls, ±80 km NE of Pine Creek, 12 Aug. 1978, *A.C.Beaglehole 58566 & E.G.Errery* (MEL); Weimoor Springs, 9 Aug. 1962, *M.Cole 132 & D.Provan* (BRI); Fitzmaurice River basin, 13 May 1994, *C.R.Dunlop 9979 & P.K.Latz* (DNA *n.v.*, MEL); Maningrida, 1961, *L.Gressitt 2668* (BRI); Fish River, 11 Feb. 1991, *D.Larcombe 2* (DNA); Kakadu National Park, 22 km SSW of Cooina on Pine Creek Road, 19 May 1980, *M.Lazarides 8845* (CANB, DNA); Pine Creek, 6 June 1973, *M.Parker 113* (BRI, DNA, NT); Tortilla Flats, 4 Nov. 1974, *M.Parker 528* (CANB, DNA, *n.v.*, NE, *n.v.*); No. 7 Stock Route Bore (S of Dunmarra), undated, *A.L.Rose s.n.* (BRI); 40 miles [~64.4 km] S of Katherine, 7 Sep. 1961, *N.H.Speck 1643* (AD, BRI, CANB, MEL, NSW, PERTH, 2 sheets); 17 mi. W of Katherine on road to Willaroo, 17 July 1967, *D.E.Symon 5188* (AD, CANB, K, NT); Katherine National Park, 8 July 1979, *M.D.Tindale 6040 & C.R.Dunlop* (CANB, DNA *n.v.*, NSW); Ranger HQ, Nitmiluk National Park, 13 Dec. 1990, *G.Wightman 5205* (DNA); Mary River Camp, June 1955, *M.White M.R. 18* (CANB). **QUEENSLAND.** Etheridge River, *Armit 679* (MEL, 2 sheets); 14 miles [~22.6 km] SE of Carpentaria Downs Station, 12 July 1954, *N.H.Speck 4702* (AD, CANB, NSW, PERTH).

## *Erythrophleum pubescens* R.L.Barrett & M.D.Barrett, sp. nov.

Type: Carson Escarpment, N of Coucal Gorge, Drysdale River National Park, Western Australia, 17 August 1975, *A.S.George 13961* (holo: PERTH 2211939; iso: CANB 267799, K, *n.v.*).

Tree 8–20(–30) m tall, many-branched with a spreading canopy, resprouting after fire, rarely flowering as a shrub

when frequently burnt; bark dark grey to blackish, tessellated; branchlets usually prominently fissured, corky, pubescent when young, newest growth with rusty hairs, eventually becoming glabrous. Leaves with petiole 18–51 mm long; rachis 35–138 mm long; pinnae usually 2 or 3 pairs; secondary rachises 35–155 mm long; leaflets alternate, mostly 5–11 per pinna, obliquely elliptic, ovate or obovate, mostly 19–62 mm long, 9–45 mm wide, resprout growth often markedly larger; attenuate, distinctly asymmetric, rounded, obtuse or emarginate apically, discolourous, with scattered hairs basally and on the petiolules, eventually becoming glabrous; petiolules 1.5–4 mm long; venation conspicuous. Racemes simple to 5-branched, (45–)70–160 mm long; axis 1.0–1.7 mm thick below the flowers, moderately to densely pubescent, hairs white or rusty. Flowers 62–125; sessile; cream to greenish-yellow. Floral bracts 0.5–0.7 mm long, margins ciliate and lamina pubescent. Calyx 1.9–2.5 mm long; lobes shorter than the tube, 0.5–0.9 mm long, pubescent on surface and margins. Petals 2.3–2.9 mm long, pubescent at the margins, otherwise glabrous. Stamens alternately long and short, filaments 3.4–8.9 mm long, glabrous. Anthers 0.6–0.7 mm long. Ovary densely pubescent, 2.1–3.4 mm long. Style 0.7–1.7 mm long. Pod often slightly curved, dehiscing, at least initially, along one suture only, (1–)2–7-seeded, 97–120 mm long, 26–46 mm wide, apex acute to apiculate; dark reddish-brown, pubescent when young, glabrescent; stipe of pod often lateral, 8–10 mm long. Seeds dark brown, suborbicular, 12–15 mm long, 9–12 mm wide, 4.5–6.0 mm thick; aril 5–8 mm long. (Fig. 4, 5.)

## Illustrations

F. Mueller, *Iconogr. Austral. Acacia* 13: t. 9 (1888). C. A. Gardner & H. W. Bennetts, *Poison. Pl. West. Australia*, pl. 3 (1956); D. Levitt, *Pl. People* pl. 8 (1981); J. R. Wheeler in J. R. Wheeler (Ed.), *Fl. Kimberley Region* 347, fig. 104a (1992); C. R. Dunlop *et al.*, *Fl. Darwin Region* 2: 32, fig. 13 (1995); K. F. Kenneally *et al.*, *Broome & Beyond. Pl. & People Dampier Peninsula* 76, [upper pl. only] (1996); J. H. Ross in A. E. Orchard (Ed.), *Fl. Australia* 12: 70, fig. 31, 43 (1998); J. Milson, *Trees Shrubs NW Queensl.* 18–19, pl. (2000); W. Cooper, *Fruits Austral. Trop. Rainfor.* 102, fig. (2004); J. Beasley, *Pl. Trop. N. Queensl.* 156, pls (2006); J. Beasley, *Pl. Cape York* 43, pls (2012), (all as *E. chlorostachys*).

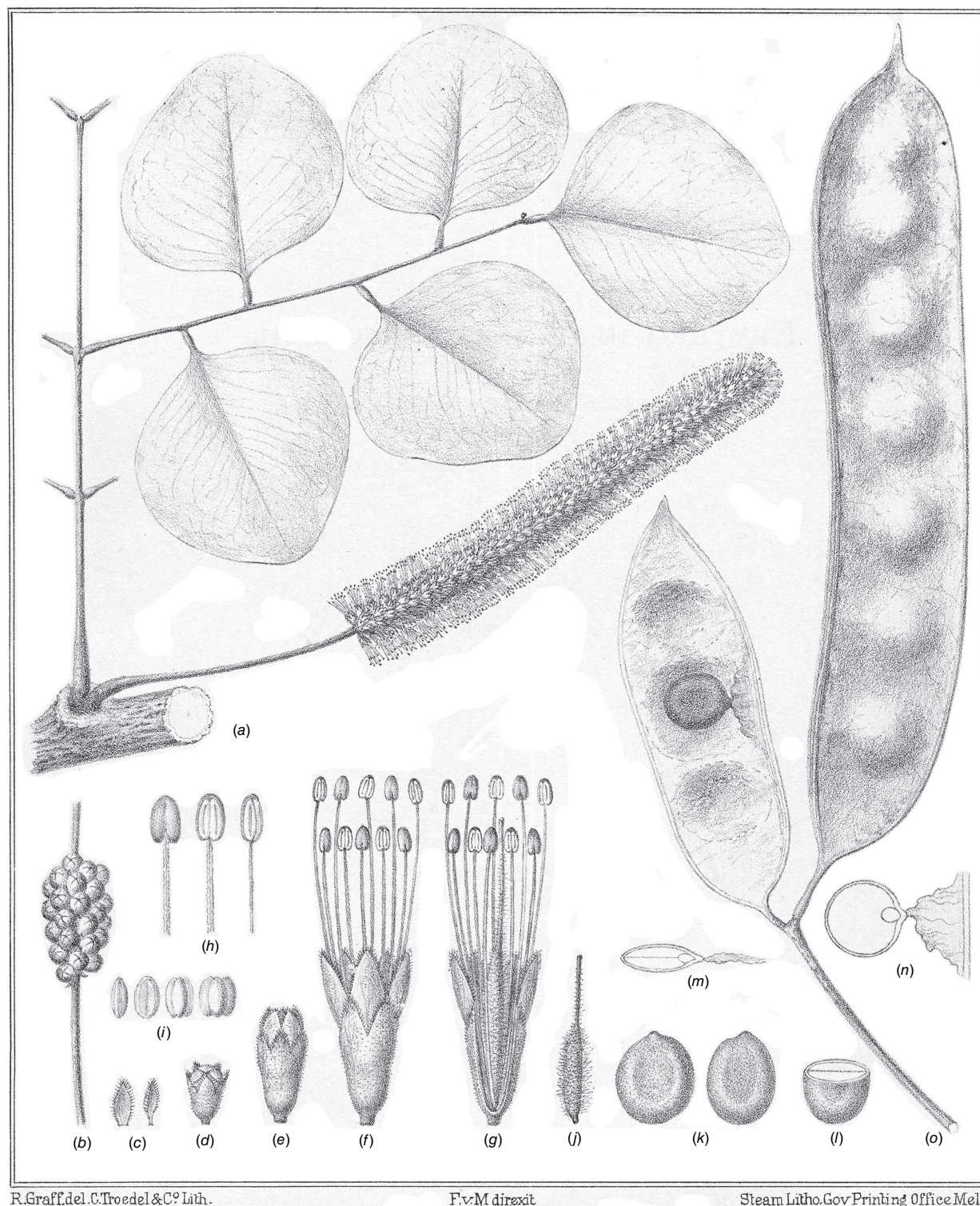
## Distribution

Endemic in northern Australia, from near Derby in the western Kimberley, WA, through NT and islands of the Gulf of Carpentaria to north-eastern Qld, Cape York and some Torres Strait islands.

## Habitat

Usually found in open *Eucalyptus* or mixed forest, woodland or savanna on sandstone- or basalt-derived soils.





R.Graff del. C.Troedel & C<sup>o</sup> Lith.

F.v.M. direxit

Steam Litho. Gov. Printing Office. Melb.

# *Erythrophlaeum Labouchei* F.v.M.

Fig. 4. (Caption on next page)



**Fig. 4.** *Erythrophleum pubescens* (published as '*Erythrophlaeum Laboucherii*'). (a) Flowering branchlet and portion of a bipinnate leaf (probably resprout leaf growth, or possibly leaflets representing *E. chlorostachys*); (b) flower buds on inflorescence; (c) floral bracts; (d) flower bud; (e) flower just prior to anthesis; (f) staminate flower at anthesis; (g) partially dissected bisexual flower; (h) back, front and lateral view of a stamen; (i) pollen grains; (j) ovary and style; (k) two seeds; (l) transverse section of a seed; (a, b) longitudinal sections of seeds; (o) pods, left hand pod opened to show seed and aril (voucher: not specified). Original lithograph by R. Graff under supervision of F. von Mueller. Originally published in Mueller (1888, t. 9).

## Phenology

Flowering mostly July–November, but also recorded for March and May. Fruiting mostly recorded for April–August.

## Etymology

The epithet is from the Latin *pubescens* (with short, soft hairs), in reference to the presence of hairs on most parts at least when young, diagnostically always present on the raceme axis and outer surfaces of the calyx.

## Notes

The following combination of characters is diagnostic: tree 8–20 m tall, many-branched with a spreading canopy, branchlets pubescent when young; leaves with pinnae usually in 2 or 3 pairs; leaflets mostly 5–11 per pinna, attenuate, distinctly asymmetric, with scattered hairs basally and on the petiolules; petiolules 1.5–4 mm long; raceme axis moderately to densely pubescent; calyx 1.9–2.5 mm long; lobes 0.5–0.9 mm long, pubescent on surface and margins; flowers sessile; stipe of pod 8–10 mm long.

Although the majority of the syntypes represent the taxon here recognised as *E. chlorostachys sensu stricto*, the most-used concept in the literature, and apparently the main source for Mueller's original description and his illustration in *Iconogr. Austral. Acacia* 13: t. 9 (1888) is the taxon described here as *E. pubescens*.

Resprout foliage of *E. pubescens* is large, similar in size to that of *E. arenarium*, but it can be separated by the presence of scattered to dense hairs on the branchlets, petioles and petiolules. Juvenile pinnae also remain distinctly asymmetric in most cases, although not always as distinctly as the adult pinnae.

Widely known as Cooktown ironwood under the name *E. chlorostachys*, a species that is not known to occur near Cooktown; so, this common name must logically be transferred to *E. pubescens*, or its use discontinued. There are many First Nations names, which may also include *E. chlorostachys*, as detailed in Table 1.

The most useful characters for distinguishing the three species are presented in Table 3.

## Representative specimens

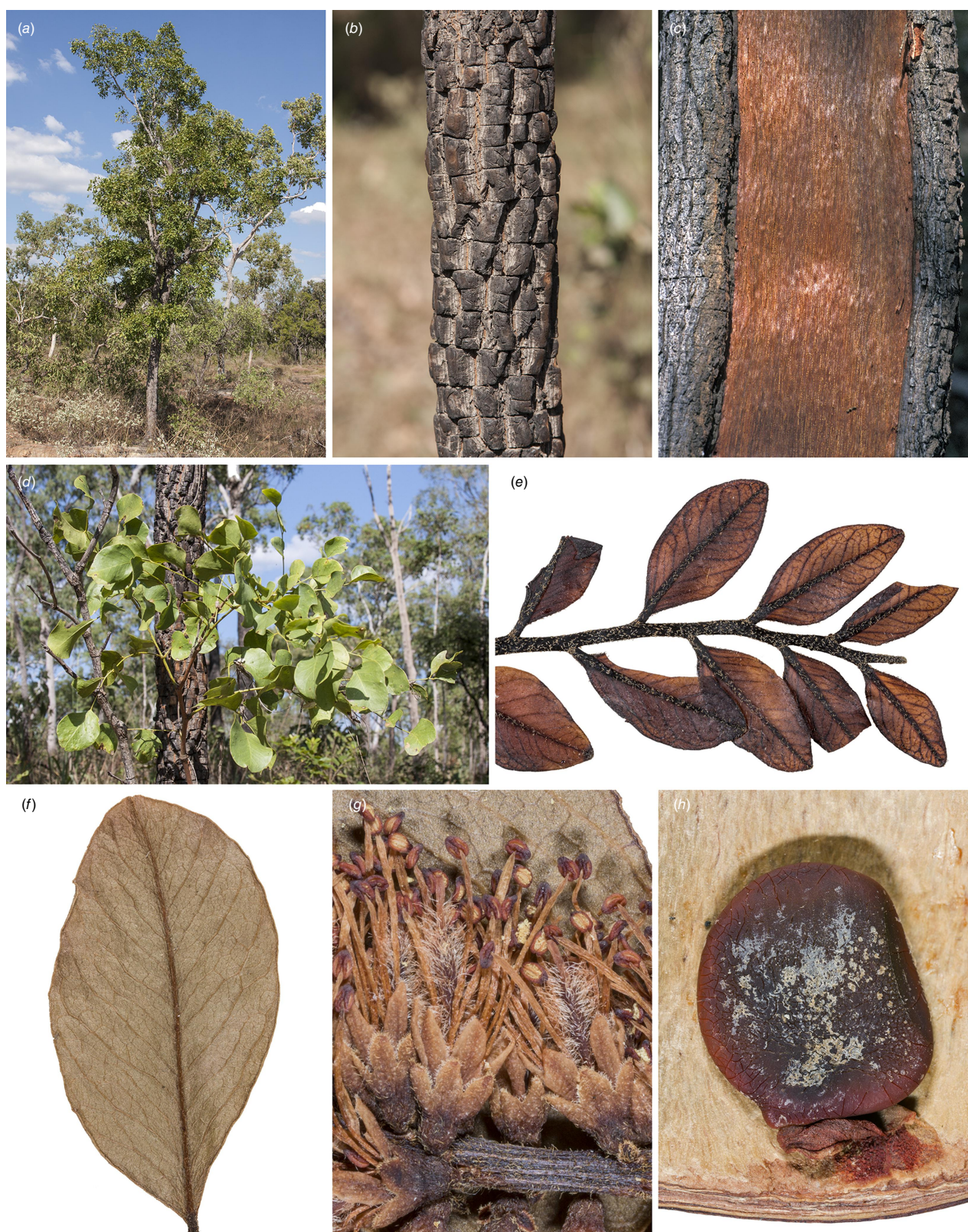
**WESTERN AUSTRALIA.** Drysdale River, S of river mouth on Carson River Station, 24 June 2018, *M.D.Barrett MDB5902* (PERTH); 'Prince Regent' [Roe] River, 1891, *Bradshaw & Allen s.n.* (MEL, NSW); Five Rivers Lookout, 7 Feb. 2010, *G.Byrne 3721* (PERTH); Gorge in Saw

Ranges, NW of Dunham River, 6 Nov. 1992, *K.Coate 224* (PERTH); Careening Bay, 1820, *A.Cunningham 227* (BM, n.v., K, NSW); Charnley River [Station], 1 km N of Potts Camp, 26 June 2012, *H.Dauncey H 666* (PERTH); Cone Mountain, on peninsula between Vansittart Bay and Napier Broome Bay, ±25 km WNW of Kalumburu, 22 May 1984, *S.J.Forbes 2085a* (MEL); Kuri Bay, Bonaparte Archipelago, 2 Sep. 1985, *P.R.Foulkes 340* (PERTH); Lawley River, 30 July 1921, *C.A.Gardner 997* (PERTH); Bushfire Hill, Prince Regent [Nature] Reserve, 15 Aug. 1974, *A.S.George 12300* (PERTH); Kununurra, 15 Sep. 1982, *C.Glover 112* (MEL, PERTH); Boiga Falls, Drysdale River National Park, 4 Aug. 1975, *K.F.Kenneally 3046* (CANB, PERTH); Loc. 4.0, SE of Beverley Springs Homestead, 19–26 May 1979, *B.G.Muir et al. 734* (PERTH); Jameson Arch, Bachsten Camp track, Mount Elizabeth Station, 15 Sep. 2003, *G. & N.Sankowsky 2249* (PERTH); Adcock Gorge, 13 Apr. 1980, *D.E.Symon 12095* (AD, K, PERTH). **NORTHERN TERRITORY.** Darwin, Nov. 1929, *F.A.K.Bleeser 503* (MEL); Sturt Plateau, Dungowan Station, 12 Oct. 2000, *K.Brennan 4583* (DNA); Black Point, 29 Sep. 1968, *N.Byrnes 1043* (AD, NT, PERTH); 77.3 miles [~124.4 km] S of Katherine, 9 Sep. 1957, *G.Chippendale NT 3732* (AD, NSW, NT, PERTH); Arnhem land 8.6 km S of Walker River airstrip, 11 Oct. 1987, *M.Clark 1607* (DNA); Kapalgua Ref. 1211, 15 Dec. 1976, *R.Collins BC172* (CANB, DNA, n.v., MEL, NSW); Litchfield NP, Walker Creek area, 15 Mar. 1995, *I.Cowie 5303* (DNA); Narbalek, 25 Oct. 1987, *C.R.Dunlop 7145* (DNA, n.v., MEL, NSW); Cutta Cutta, 13 July 1990, *M.Evans 3270* (CANB, DNA, MEL, NSW); Cutta Cutta Reserve, 23 Nov. 1993, *J.Egan 2873* (DNA); Newcastle Waters, 17 July 1911, *G.F.Hill 473* (MEL); Port Darwin, 1883, *Holtze* (MEL); Black Jungle area, 17 Sep. 1986, *N.M.Smith 101* (DNA); Lameroo Beach, Darwin, 8 Oct. 1986, *N.Smith 128* (DNA); on Stuart Highway 42 km N of Carpentaria Highway junction, 5 Sep. 1981, *T.Whaite 3979 & J.Whaite* (CANB, DNA, n.v., K, n.v., MO, n.v., NSW). **QUEENSLAND.** Georgetown, n.d., *Armit 717* (MEL); Cooktown, 13 May 1970, *S.T.Blake 23184* (BRI, CNS, n.v., MEL, NSW, PERTH); Laura sandstone area N of Laura River near Early Man site, 16 May 1975, *N.B.Byrnes 3365* (BRI, MEL, QRS, n.v.); Croydon, 24 Aug. 1913, *R.H.Cabbage 3920* (NSW, 2 sheets); Dutton River Station, ~46 km NW of homestead and 110 km E of Richmond, 15 June 2012, *E.Leitch QDA003815* (BRI); Emu Creek Station, NE of Petford, 12 Nov. 2005, *K.R.McDonald KRM4610*, *L.J.Roberts & J.A.Covacevich* (BRI, MEL); creek flowing into Emu Lagoon, Errk Oygangand National Park, 1 Sep. 2010, *K.R.McDonald KRM9767* (BRI); 42.9 km by road W of Georgetown, near Blancourt Station turnoff, 19 Sep. 2010, *K.R.McDonald KRM9840* (BRI, MEL); Kings Plain Station, near Lily Dam, 5 Nov. 2015, *K.R.McDonald KRM17554* (BRI, MEL); Weipa North township, State School oval, Jan. 1981, *A.Morton 1183* (AD, MEL, 2 sheets); Endeavour River, 1882, *W.A.Persieh 719* (MEL); Granite Creek, 12 km SW of Mareeba, 16 Nov. 1995, *B.S.Wannan 213 & L.Lynch* (NSW); Mareeba, road from Kennedy Highway to Springmount, 27 June 2001, *J.J.Wieringa 4178*, *L.J.G. van der Maesen, A.Bruneau & P.Herendeen* (NSW, WAG, n.v.); Gamboola, Mitchell River, 22 Sep. 1882, *Wools s.n.* (MEL).

## Key to Australian *Erythrophleum* species

1. Branchlets commonly with fissured, corky bark; petiolules, leaf bases and inflorescence axis pubescent, at least when young; pinnae





**Fig. 5.** *Erythrophleum pubescens*: (a) habit and habitat; (b) bark; (c) natural blaze on trunk showing red heartwood prized for woodworking; (d) juvenile, asymmetric pinnae; (e) pubescence on new adult growth; (f) asymmetric pinna with sparse hairs; (g) portion of inflorescence showing sessile flowers, pubescent axis and pubescent calyx; (h) seed. Vouchers: King Edward River, WA, not vouchered (a, b, d); Mount Fyfe, Drysdale River Station, WA; not vouchered (c); Prince Regent Nature Reserve, WA, A.S.George 12300, PERTH (e, h); Drysdale River National Park, WA, A.S.George 13961, PERTH (f, g). Images by R. L. Barrett.



**Table 3.** Morphological characters for distinguishing Australian *Erythrophleum* species.

Item	<i>E. arenarium</i>	<i>E. chlorostachys</i>	<i>E. pubescens</i>
Habit	(2–)4–6(–8) m tall, few-branched with a compact crown	(4–)6–9 m tall, many-branched with a spreading crown	8–20(–30) m tall, many-branched with a spreading crown
Branchlet bark	Smooth, sometimes a little corky	Smooth, rarely any cork	Prominently fissured-corky
Branchlets & leaves	Usually glabrous, sometimes glaucous	Glabrous, not glaucous	Pubescent when young, not glaucous
Pinnae	2(3) pairs	(1)2(3) pairs	2 or 3 pairs
Leaflets	29–74 mm long, 27–83 mm wide, 2–5(–7) per pinna, orbicular to somewhat deltoid, not or slightly asymmetric; glabrous or slightly glaucous	31–87 mm long, 31–80 mm wide, 3–6(–7) per pinna, orbicular to somewhat deltoid, slightly asymmetric; glabrous	19–62 mm long, 9–48 mm wide, 5–11 per pinna, attenuate, distinctly asymmetric with scattered hairs on and near the petiole
Petiolules	4–9(–11) mm long	2.5–7 mm long	1.5–4 mm long
Inflorescence	Simple	Simple or once branched	Simple or once branched
Raceme axis	Glabrous	Glabrous	Pubescent
Floral bracts	1.5–2.5 mm long, margins fimbriate, lamina glabrous	0.7–0.9 mm long, margins ciliate, lamina glabrous	0.5–0.7 mm long, margins ciliate and lamina pubescent
Pedicel	3.0–5.5 mm long	0.5–1.2 mm long	Absent
Calyx	3.6–5.0 mm long, glabrous	2.3–3.8 mm long, glabrous	1.9–2.5 mm long, pubescent
Calyx lobes	1.1–2.1 mm long	0.9–1.2 mm long	0.5–0.9 mm long
Petals	4.2–6.4 mm long (exserted by 2.3–4.5 mm)	2.8–3.8 mm long (exserted by 0.8–2.3 mm)	3.1–3.3 mm long (exserted by 1.6–1.9 mm)
Anthers	1.0–1.3 mm long	0.7–1.0 mm long	0.60–0.7 mm long
Stipe of pod	11–33 mm long	12–20 mm long	8–10 mm long
Aril	3–6 mm long	2–4.8(–7) mm long	5–8 mm long
Distribution	Great Sandy Desert, Dampier Peninsula	Wyndham to Cape York	Derby to Cape York

regularly in 2 or 3 pairs (i.e. both mixed on branchlets); leaflets 5–11 per pinnae, distinctly asymmetric; calyx 1.9–2.5 mm long; stipe of pod 8–10 mm long; flowers sessile.....*E. pubescens*  
 Branchlets smooth, rarely with corky bark, and then poorly developed; petiolules, leaf bases and inflorescence axis usually glabrous, sometimes glaucous; pinnae mostly in 2 pairs; leaflets 2–6(–7) per pinnae, usually  $\pm$  symmetric or only slightly asymmetric; calyx 2.3–5.0 mm long; stipe of pod 11–33 mm long; flowers pedicellate (pedicels < 0.5 mm long).....2  
 2. Leaflets usually  $\pm$  symmetric; floral bracts 1.5–2.5 mm long, margins fimbriate; pedicels 3.0–5.5 mm long; petals 4.2–6.4 mm long; anthers 1.0–1.3 mm long.....*E. arenarium*  
 Leaflets usually slightly asymmetric; floral bracts 0.7–0.9 mm long, margins pubescent; pedicels 0.5–1.2 mm long; petals 2.8–3.8 mm long; anthers 0.75–0.95 mm long.....*E. chlorostachys*

## Supplementary material

Nexus alignment file of the ribosomal sequence data.  
 Supplementary material is available [online](#).

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**Data availability.** All newly generated sequence data are available on GenBank.

**Conflicts of interest.** Dr Russell Barrett is an editor for *Australian Systematic Botany* but did not at any stage have editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this journal. *Australian Systematic Botany* encourages its editors to publish in the journal and they are kept totally separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

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**Author contributions.** Both authors conceived the study, conducted fieldwork, sampled and analysed the genetic data, interpreted results, prepared taxon treatments, and wrote and revised the paper.

#### Author affiliations

<sup>A</sup>National Herbarium of New South Wales, Botanic Gardens of Sydney, Australian Botanic Garden, Locked Bag 6002, Mount Annan, NSW 2567, Australia.

<sup>B</sup>Australian National Herbarium, Centre for Australian National Biodiversity Research, National Research Collections Australia, CSIRO, GPO Box 1600, Canberra, ACT 2601, Australia.

<sup>C</sup>Department of Biodiversity, Conservation and Attractions, Kings Park and Botanic Garden, West Perth, WA 6005, Australia.

<sup>D</sup>School of Plant Biology, Faculty of Science, The University of Western Australia, Crawley, WA 6009, Australia.

<sup>E</sup>Western Australian Herbarium, Department of Biodiversity, Conservation and Attractions, Locked Bag 104, Bentley Delivery Centre, WA 6983, Australia.

<sup>F</sup>Australian Tropical Herbarium, Sir Robert Norman Building, James Cook University Cairns Campus, McGregor Road, Smithfield, Qld 4878, Australia.