ROYAL
BOTANIC GARDENS
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# Muelleria

Plant, Algal and Fungal Taxonomy and Systematics

Vol 35, 2016-2017

*Pimelea lanata*

**Pimelea sericea R.Br. [as Pimelea lanata Hemsley]**
**Source: Maund, B. and Henslow, J.S., *The Botanist*, vol. 2: t. 61 (1838)**
**Illustration: Miss Hall**

The generic name *Pimelea* arises from the Greek pimele (fatty), referring to oily seeds and cotyledons, or glossy leaves. The first use of the name was in a handwritten, unpublished manuscript by
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Instructions to authors: Please consult the instructions to authors at the website below. A concise version is printed inside the back cover of each issue.
www.rbg.vic.gov.au/science/publications/muelleria

Publication frequency: One issue per year

Subscription rates: The following rates include postage and GST. All payments must be in $AUD. Cheques should be made payable to the Royal Botanic Gardens Victoria. Contact the Subscription Manager for additional payment options.

| | Australia | International |
|---|---|---|
| Individuals | $40 | $62 |
| Organisations | $50 | $77 |

Layout: SUBStitution Pty Ltd

Printer: tmp

Printed on recycled paper

Where a paper in this issue was first published online, the publishing date is specified on the title page.

ISSN 0077-1813

***Muelleria* volume 34 was distributed on 29 April 2016.**

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# Three new species and one new combination in *Hibiscus* (Malvaceae)

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## Introduction

Ongoing studies of Australian *Hibiscus* L. have revealed the presence of three undescribed species. One of these, *Hibiscus kirstyae* Craven, from the Kimberley Region of Western Australia, appears to be unique within the Australian *Hibiscus* species belonging in sect *Furcaria* DC. This section is defined by a prominently thickened midrib and thickened marginal ribs on the calyx lobes. The glaucous, waxy foliage, sparse aculei and lack of other indumentum set *H. kirstyae* apart from the other species of *H.* sect. *Furcaria* in Australia, as well as all species known from Asia, Africa (Borssum Walkes 1966; Wilson 1999) and southern India (Sivarajan & Pradeep 1996).

The opportunity arose for me [LC] to cultivate many accessions of *Hibiscus* from north-eastern Australia in a common greenhouse environment in Canberra, and it became evident that three quite distinct species had been erroneously brought together as *H. forsteri* F.D.Wilson. The two newly segregated species, *H. sankowskyorum* Craven and *H. townsvillensis* Craven, occur in north-eastern Australia; *H. sankowskyorum* occurs in the region along the Iron Range road, on the Lockhart River road, and north-west of Cooktown along the McIvor River road; and *H. townsvillensis* occurs in the Mt Spec–Townsville region.

## Abstract

*Hibiscus kirstyae* Craven, *H. sankowskyorum* Craven and *H. townsvillensis* Craven are newly described. These three species all belong in *Hibiscus* sect. *Furcaria* DC. *Hibiscus kirstyae* has no obvious close relationship with the other Australian members of sect. *Furcaria*, whereas *H. sankowskyorum* and *H. townsvillensis* are closely related to *H. forsteri* F.D.Wilson. A new description is provided for *H. forsteri*. *Talipariti bowersiae* Fryxell is transferred to *Hibiscus* L., as *H. bowersiae* (Fryxell) Craven, since *Talipariti* Fryxell has been well demonstrated to be an integral component of *Hibiscus*. Modified keys are presented to include the new species.

**Key words:** *Hibiscus* sect. *Furcaria*, *Talipariti*, new species, new combination

ISSN: 0077-1813 (print) · ISSN: 2204-2032 (online)

The morphological terminology used here follows Craven et al. (2003). As specified there, indumentum is an especially important source of diagnostic information. The stout, unbranched hairs that commonly occur on the branchlets, epicalyx and calyx of Australian *Hibiscus* sect. *Furcaria* species are termed aculei (sometimes called prickles in other treatments). The aculei are sometimes inserted on tubercles (see Fig. 1g); the aculei themselves sometimes also carry stellate trichomes (see Fig. 1a). The term peduncle is also used in a specific manner following Craven et al. (2003), as some *Hibiscus* species have both a pedicel and peduncle, with a distinct articulation between the two and the indumentum can differ on each of the two parts.

The main portion of this manuscript was in an advanced stage of preparation at the time of Lyn Craven's death in July 2014. Subsequently, the manuscript was revised by Russell Barrett and Matt Barrett. This revision included the addition of keys to complement those published by Wilson and Craven (1995) and Craven et al. (2003), diagnostic characters for each new species, updated information on *H. kirstyae* and a revised description of *H. forsteri*. Additional populations ascribed to *H. forsteri*, but outside the ranges described for the three taxa recognised here, are known with vouchers at 8RI that are not represented at CANB and these are yet to be assessed. It is likely that the known ranges of these taxa will increase once the identities of these specimens are determined.

## Taxonomy

### *Hibiscus kirstyae* Craven, **sp. nov.**

***Type*: WESTERN AUSTRALIA.** Kimberley Region, Morgan River near Theda Station homestead, 17.ii.2005, *M.D. Barrett 15B9* (holotype: PERTH 7213425, 7213433; isotypes: CAN8 527708.1, 527708.2, K).

*Hibiscus* sp. Theda (M.D. Barrett & R.L. Barrett MDB 2144), Western Australian Herbarium, in *FloraBase*, http://florabase.dpaw.wa.gov.au/ [accessed 22 March 2016].

Single-stemmed *shrub* to 3 m tall. *Branchlets* glabrous (stem of seedlings with very sparse tubercle-based aculei c. 1–1.25 mm long). *Stipules* at length deciduous, glabrous, subulate, unlobed, 8–12 mm long. *Petioles* 70–115 mm long; *climax leaves* with the petiole glabrous, petiole of seedling leaves with tubercle-based aculei. *Leaves* palmately-veined. *Lamina* very broadly ovate, transversely broadly elliptic or broadly elliptic, unlobed, 80–110 mm long, 70–170 mm wide, the margin weakly serrate, base cordate, or truncate, apex rounded, concolorous, with yellowish-pink hairs, the indumentum generally similar on each surface. Abaxial surface with midrib and primary vein indumentum similar to that of the interveinal regions, with sparse aculei, c. 1–1.25 mm long. *Foliar nectary* present at base of the lamina, 5–6 mm long. *Distal leaves* on flowering shoots reduced in shape and size, elliptic, or broadly elliptic (sometimes trilobed), distinctly petiolate on reproductive shoots. *Flowers* solitary in leaf axils, pedunculate, chasmogamous. *Peduncles* well developed, glabrous, 25–80 mm long. *Pedicels* glabrous, 12–15 mm long. *Epicalyx* present, persistent, glabrous, 9–10-lobed, 8–12 mm long, segments free at the base, 0.3 times the length of the calyx at anthesis, incurved, subulate, at the apex entire. *Calyx* at anthesis 5-lobed or -partite but not splitting per se, not adnate to the corolla and not falling with it after anthesis, glabrous between the ribs, lobes with prominent marginal ribs, these glabrous or occasionally pubescent, with sparse aculei, apex very narrowly acute, 25–27 mm long at anthesis, nectary absent. *Petals* yellow with a red nectary at the base, 80–85 mm long. *Staminal* column straight, 5-toothed at the apex, 30 mm long. *Stamens* scattered along distal c. 30 mm of the column (more or less along the entire length). *Anthers* dark purple-red. *Pollen* dark purple-red. *Style* one, 5-branched, with branches c. 1.5 mm long, exserted c. 4 mm beyond apex of staminal

**The key to species of *Hibiscus* sect. *Furcaria* in the Northern Territory and Western Australia by Craven et al. (2003) can be modified to include *H. kirstyae* as follows:**

**3.** Flowers pedunculate; capsule glabrous or at the apex with a few hairs .................... **3A**
**3A:** Leaves entire; epicalyx 0.3 times the length of the calyx; petals yellow .................... ***H. kirstyae***
**3A:** Leaves deeply 2–3-lobed; epicalyx 0.5–0.8 times the length of the calyx; petals white .................... ***H. meraukensis***
**3:** Flowers not pedunculate; capsule densely hairy .................... **4**

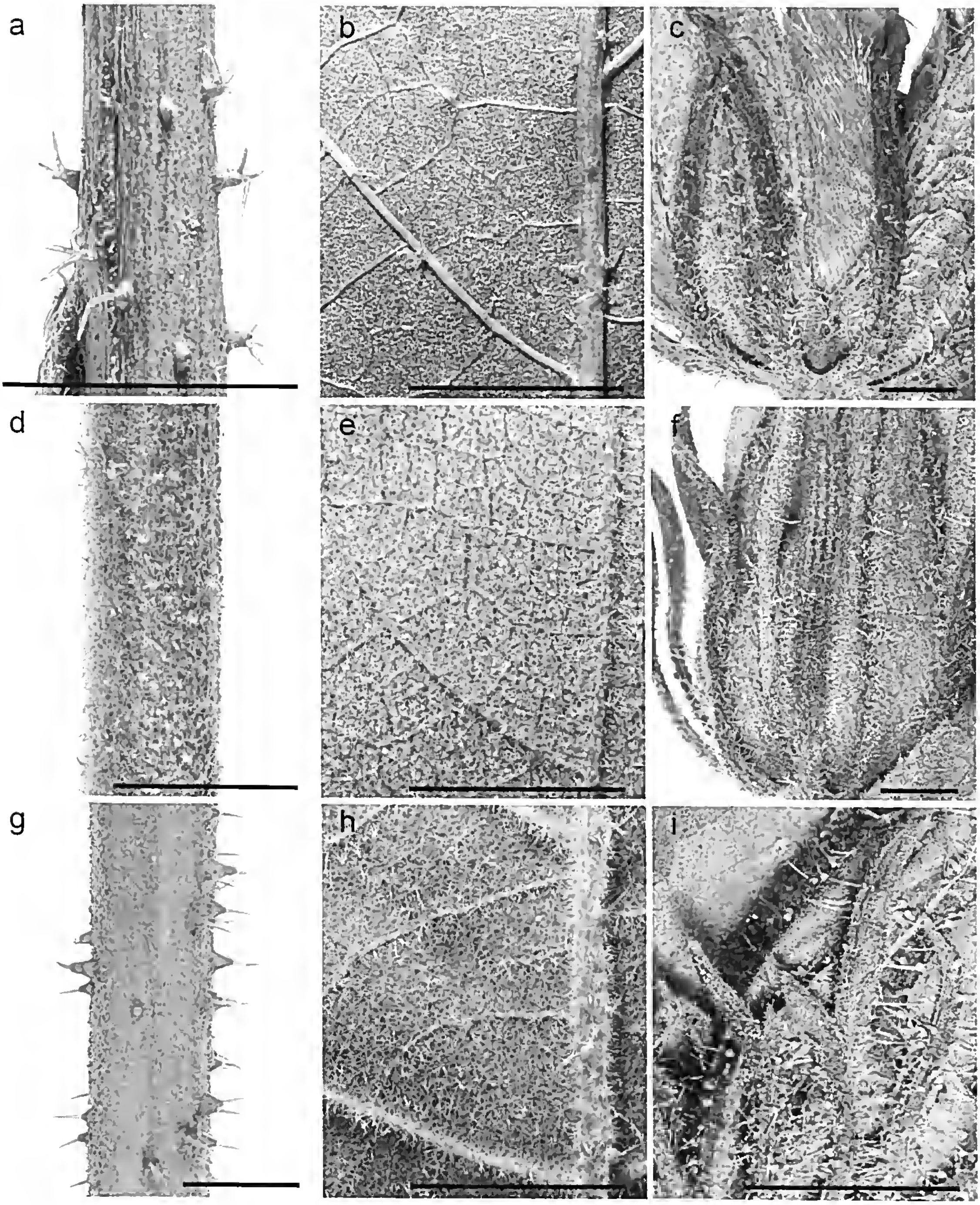


**Figure 1.** Indumentum on type specimens in the *Hibiscus forsteri* complex. *Hibiscus forsteri* (*Clarkson 8866*, CANB 576920.1): **a.** branchlet indumentum (sparse, fine stellate indumentum and prominent aculei with apical stellate hairs); **b.** leaf abaxial indumentum; **c.** epicalyx and calyx indumentum. *Hibiscus sankowskyorum* (*Clarkson 7341*, CANB 572995): **d.** branchlet indumentum (dense, fine stellate hairs with sparse, obscure aculei); **e.** leaf abaxial indumentum; **f.** epicalyx and calyx indumentum. *Hibiscus townsvillensis* (*Craven 10469*, CANB 875440): **g.** branchlet indumentum (dense, fine stellate hairs with prominent aculei on tubercles); **h.** leaf abaxial indumentum; **i.** epicalyx and calyx indumentum (note epicalyx apices are distinctly flattened and spathulate). Scale bars = 5 mm. (Photos by Russell Barrett)

column. *Stigmas* entire, capitate. *Ovary* glabrous. *Calyx* in fruit not distinctly inflated or accrescent. *Fruits* dry, dehiscent capsule. *Capsules* 15–18 mm long, glabrous, capsule beak present. *Seeds* glabrous, striate and minutely pectinate-pubescent, angular, subreniform, c. 4 mm long. (Fig. 2)

***Diagnostic characters:*** This species is distinguished from all species of Australian sect. *Furcaria* by its glaucous leaves, glabrous branchlets and capsule, 9–10 short epicalyx lobes, and yellow corolla.

***Additional specimens examined:*** **WESTERN AUSTRALIA.** Morgan River, 15.ii.2005, *M.D. Barrett 1589* (PERTH); Cultivated in a CSIRO greenhouse, Canberra, ex: Morgan River, Kimberley, (coll. *R.L. & M.D. Barrett*), iii.2005, *L.A. Craven 15049* (CANB 875441); Morgan River, 28.iv.2008, *M.D.* Barrett *& R.L. Barrett MDB 2144* (PERTH 08103062); Morgan River, 17.v.2011, *M.D. Barrett 3730* (PERTH).

***Distribution and habitat:*** Occurs on two large sandstone pavements 15 km apart near the Morgan River on Theda Station. Each pavement is 0.9–1.2 km long and c. 300 m wide, however, the *Hibiscus kirstyae* populations occupy only a portion of each pavement. *Hibiscus kirstyae* is restricted to ridges away from the pavement margins, presumably to afford them some degree of protection from fire. The type population consists of around 200 individuals that are estimated to live for 3–6 years between fire periods.

***Notes:*** Considerable effort has been undertaken to locate additional populations in the region over a period of 12 years, including extensive observations by helicopter, but no further populations have been located to date.

The glabrous capsule is unusual amongst Australian indigenous species, shared only with *Hibiscus meraukensis* Hochr. *H. meraukensis* is distinguished from *H. kirstyae* by having deeply 2–3-lobed leaves, longer epicalyx lobes more than half as long as the calyx lobes, and white petals.

Flowering observed between January and April.

Plants are obligate seeders, being killed by fire.

From a distance the glaucous leaves, yellow flowers and tall shrub habit have the appearance of a *Calotropis* R.Br. with yellow deciduous leaves, which are noxious weeds elsewhere in the Kimberley.

***Conservation status:*** *Hibiscus kirstyae* is rare. Listed as Priority One under Department of Parks and Wildlife Conservation Codes for Western Australian Flora as *Hibiscus* sp. Theda (M.D. Barrett & R.L. Barrett MDB 2144) (Jones 2015), and the IUCN category Vulnerable (VU D1+2) is considered appropriate (IUCN 2012).

***Etymology:*** This species is named in honour of Christine (Kirsty) L. Craven, wife of Lyn Craven, in recognition of her many years of support and patience during many family 'holidays' undertaken to collect plants.

## *Hibiscus forsteri* species complex

Wilson and Craven (1995: 442) noted that Paul Forster (pers. comm. 1994) recognised that at least two forms were included under their concept of *Hibiscus forsteri*, but, at that time, the available material was insufficient to define additional taxon boundaries. The specimens noted by Forster to differ from typical *H. forsteri* are herein described as *H. sankowskyorum*. Growing a range of specimens under common conditions allowed for critical comparison and recognition of three species. *Hibiscus forsteri* and *H. sankowskyorum* occur in relatively close proximity to each other, but have not been noted to co-occur, growing on different substrates. A revised key to all Queensland and New South Wales species of *Hibiscus* sect. *Furcaria* is presented to distinguish the two new species from *H. forsteri* and includes *H. zonatus* F.Muell., which has been recorded from NW Queensland (since Craven et al. 2003).

## *Hibiscus sankowskyorum* Craven, sp. nov.

***Type:*** **QUEENSLAND.** Cook District: Brown Creek crossing on the road to Iron Range, on levee of the stream in *Eucalyptus tetrodonta–E. nesophila* woodland, 9.viii.1987, *J.R. Clarkson 7341* (holotype: CANB 572995.1, 572995.2 (mounted on two sheets); isotypes: BRI, L, QRS, all *n.v.*).

*Hibiscus forsteri auct. non* F.D.Wilson: F.D.Wilson & Craven, *Austrobaileya* 4(3): 439–442 (1995), *p.p.*, as to *S.T. Blake 23449*; *J. Brass 19181*; *J.R. Clarkson 7341*; *J.R. Clarkson 9078 & V.J. Neldner*; *R. Coveny & P. Hind 7100*; *Cummings 100*; *P.I. Forster 4249*; *P.I. Forster 9040*; *J. Wrigley & I. Telford NQ1386*.

*Shrub*, or *tree*, apparently evergreen, often multistemmed from ground level, perhaps as a response to fire, 2–3(–10) m tall, dbh up to 20 cm. *Branchlets* hairy, with stellate

### Revised key to species of *Hibiscus* sect. *Furcaria* in Queensland and New South Wales based on Wilson and Craven (1995)

| | | |
|---|---|---|
| 1 | Nectary present on calyx midrib | ***H. diversifolius*** |
| 1: | Nectary absent | **2** |
| 2 | Capsule glabrous or at the summit sparsely pubescent; pedicel glabrous or aculeate | ***H. meraukensis*** |
| 2: | Capsule sparsely or densely pubescent throughout; pedicel stellate-pubescent and with or without aculei | **3** |
| 3 | Flowers pedicellate and pedunculate | **4** |
| 3: | Flowers pedicellate, peduncle absent | **5** |
| 4 | Branchlets with very dense, velvety, simple to stellate fine hairs and simple to branched aculei to 2 mm long; capsule densely pubescent | ***H. splendens*** |
| 4: | Branchlets with 1–4-fid soft and flexible hairs to 3 mm long; capsule sparsely pubescent | ***H. saponarius*** |
| 5 | Epicalyx segments distinctly flattened and slightly to markedly widened towards the apex | **6** |
| 5: | Epicalyx segments not flattened or if somewhat flattened, not widened towards the apex | **8** |
| 6 | Branchlets with scattered aculei that are often obscured by stellate indumentum; stellate indumentum dense (sometimes sparse with age); evergreen shrub or tree; habitat on granite substrates | ***H. sankowskyorum*** |
| 6: | Branchlets with prominent aculei; indumentum generally sparse to moderately dense; evergreen or deciduous; habitat on granite or sandstone substrates | **7** |
| 7 | Aculei tipped with stellate hairs; indumentum very sparse, stellate; deciduous shrub; habitat on sandstone substrates | ***H. forsteri*** |
| 7: | Aculei tipped with a single hair; indumentum moderately dense, simple and stellate; evergreen tree; habitat on granite substrates | ***H. townsvillensis*** |
| 8 | Calyx sparsely stellate-pubescent and/or aculeate, the indumentum not distinctly coloured | ***H. divaricatus*** |
| 8: | Calyx densely stellate-pubescent and without aculei, the indumentum often distinctly coloured (straw- to rust-coloured when dry) | **9** |
| 9 | Leaves often deeply 3-lobed, lobes acute | ***H. heterophyllus*** |
| 9: | Leaves usually entire, or if shallowly 3-lobed, lobes obtuse | ***H. zonatus*** |

indumentum of two hair size classes: numerous dense fine short stellate hairs 0.2–0.4 mm long, and scattered tubercle-based coarse stellate hairs 0.4–0.8 mm long; tubercle-based aculei rarely occur (may be 1-rayed coarse stellate hairs). *Stipules* at length deciduous, hairy, subulate, unlobed, 6–13 mm long with stellate hairs. *Petioles* 40–95 mm long; *climax leaves* with the petiole indumentum similar to that of branchlets (lacking aculei). *Leaves* palmately-veined when trilobed, or pinnately-veined when unlobed. *Lamina* narrowly ovate, or ovate, or broadly ovate, unlobed, or rarely shallowly 1- or 3-lobed with the lobes shorter than wide, 120–190 mm long, 90–180 mm wide, the margin serrate (rarely crenate), base cuneate, or truncate, the apex acute, or obtuse, concolorous, with whitish hairs, indumentum more dense on abaxial surface. Abaxial surface with the midrib and primary vein indumentum similar to that of the interveinal regions, with moderately to very dense, mainly fine stellate hairs. *Foliar nectary* present at base of the lamina, 4–7 mm long. *Distal leaves* on flowering shoots reduced in shape, narrowly elliptic, or elliptic, or narrowly ovate, distinctly petiolate on reproductive shoots. *Flowers* solitary in leaf axils, not pedunculate, chasmogamous. *Pedicels* hairy, 15–38 mm long, with stellate hairs. *Epicalyx* present, persistent, with fine stellate hairs and tubercle-based coarse stellate hairs, 9–11-lobed, 17–27 mm long, segments flattened, free at the base, shorter than the calyx, or equally as long as the calyx, 0.6–1 times the length of the calyx at anthesis, straight, or incurved, narrowly but distinctly spathulate, or subulate, with apex entire. *Calyx* at anthesis not splitting (5-lobed or -partite but not splitting per se), not adnate to the corolla and not falling with it after anthesis, whitish, with fine and coarse moderately dense or very dense stellate hairs, evenly distributed on the abaxial surface, lobes narrowly triangular with prominent marginal ribs, apex acute, 25–35 mm long at anthesis, nectary absent. *Petals* white, red petal spot present, 60–95 mm long. *Staminal column* straight, 5-toothed at the apex, c. 45 mm long. *Stamens* scattered

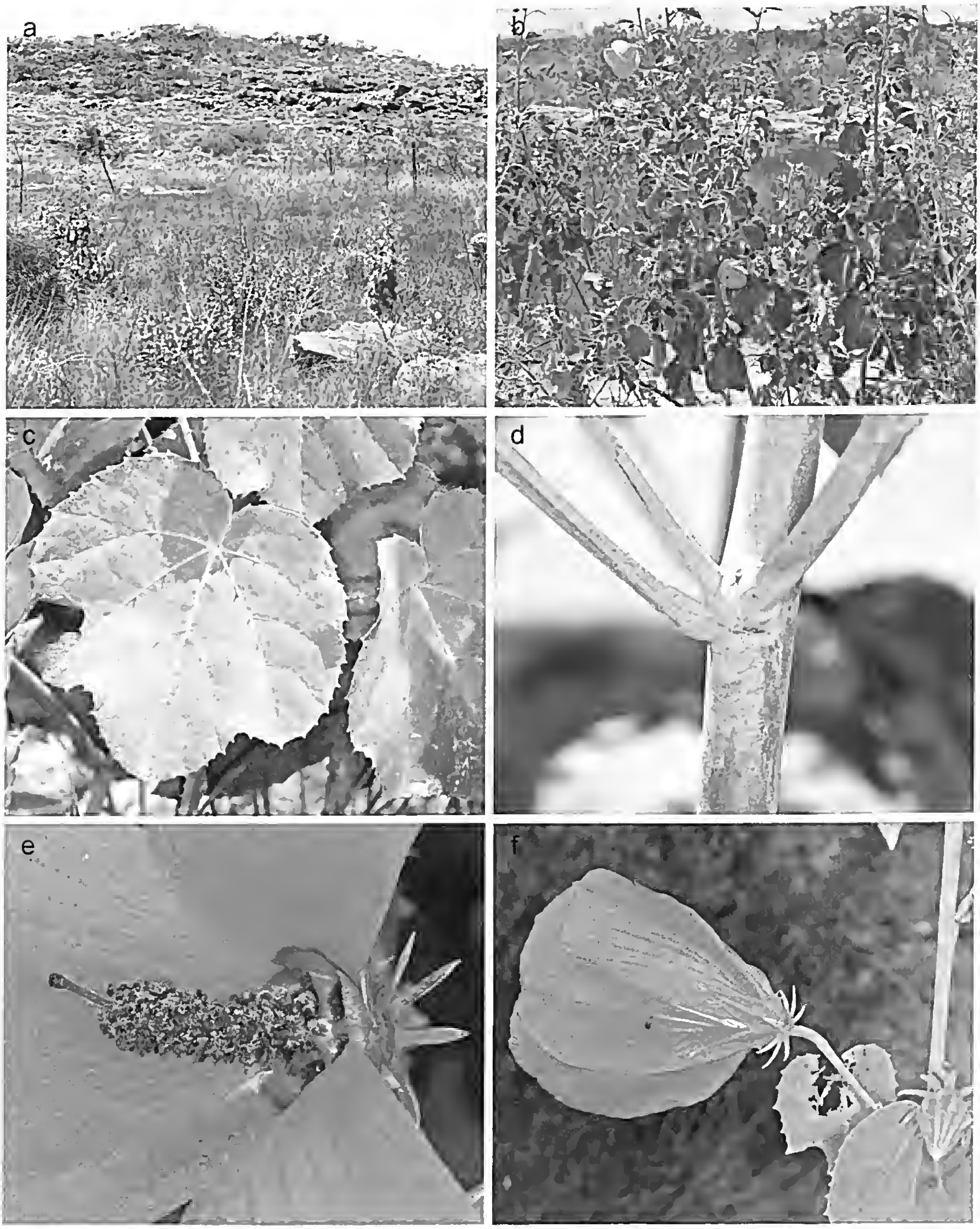


**Figure 2.** *Hibiscus kirstyae* **a.** habitat on shallow sand over sandstone pavement, type location, Theda Station (*Barrett & Barrett MDB 2144*); **b.** habit on sandstone pavement; **c.** leaves with dentate margins and glaucous appearance; **d.** glaucous stems; **e.** centre of flower with one petal removed to show red nectary and epicalyx; **f.** flower, calyx and epicalyx. (Photos by Russell Barrett)

along distal c. 25 mm of the column, inserted singly. *Anthers* dark red. *Pollen* dark red. *Style* one, 5-branched, branches c. 4 mm long, exserted c. 14 mm beyond apex of staminal column. *Stigmas* entire, capitate. *Ovary* hairy. Calyx in fruit not distinctly inflated or accrescent. *Fruits* dry, dehiscent, a capsule. *Capsules* ovoid, c. 20 mm long with ascending dense hairs, capsule beak present. *Seeds* glabrous. (Figs 1d–f, 3)

***Diagnostic characters:*** Distinguished from Australian members of *Hibiscus* section *Furcaria* by the following combination of characters: evergreen large shrub or small tree; flattened, often spathulate epicalyx segments; sparse, small aculei tipped by short stellate hairs and otherwise short, very dense indumentum on the branchlets and leaves.

***Specimens examined:*** **QUEENSLAND.** Cook District: 53 km from Cooktown on Old McIver Road, 6 km from Hope Vale Turn Off, 21.v.1970, *S.T. Blake 23449* (BRI, *n.v.*, CANB 310413); Brown's [Brown] Creek, Pascoe River, Cape York Peninsula, 13.vi.1948, *L.J. 8rass 19181* (CANB 192489); 9.2 km north of the Lockhart River Road on the track to Wattle Hill, B.viii.1991, *J.R. Clarkson 9078 & V.J. Neldner* (BRI, *n.v.*, CANB 572996, QRS, n.v.); 49.6 km (by road) N of Cooktown, on the Cooktown McIvor River Road, 5.3 km N of southern turnoff to Hopevale Mission, 31.v.1992, *8J. Conn 3595, E.A. 8rown & A.N.L. Doust* (NSW, 256566, *n.v.*, QR5 114277); CSIRO glasshouse, Canberra, ex: 27 miles from Cooktown on McIvor River road, 9.vi.19B3 *L.A. Craven s.n.* (CANB 332429); From cuttings, G. 5ankowsky's garden, Tolga, Atherton Tableland, ex: Browns Creek, Iron Range road, (coll. *G. Sankowsky*) 25.x.1997, *L.A. Craven, G. Sankowsky, J.A. Matarczyk 10012* (CANB 49B126); CSIRO glasshouse, Canberra, ex: 9.2 km north of the Lockhart River, (coll. *Clarkson 9078*) 2001, *L.A. Craven 10466* (CANB B75439); C5IRO glasshouse, Canberra, ex: 9.2 km north of the Lockhart River, (coll. *Clarkson 9078*), i.1998, *L.A. Craven 15051* (CANB 875443); CSIRO glasshouse, Canberra, ex 27 miles NW of Cooktown along McIvor road, (coll. *Wrigley & Telford NQ1386*), i.199B, *L.A. Craven 15052* (CANB B75444); Canberra Botanic Gardens, ex: McIvor River road, as cuttings 722449 (Coll. *I.R. Telford & J. W. Wrigley NQ 1386*), 17.ii.1977, *DJ. Cummings 100* (CBG 67595); Yuruga, Atherton Tablelands, Walkamin ex Heathlands, [?actually from Brown's Creek] 6.viii.1996, *S. Donaldson 955, I.R. Telford & L.W. Cayzer* (CBG 9612927); Garraway Hill, southern slopes, 17.vii.1991, *P.I. Forster 9040* (BRI, n.v., CANB 573001); 33 miles [53 km] from Wenlock on the Iron Range road [Portland Roads road], vii.196B, *C.H. Gittins 1796* (CANB 743794); Claudie River, 26.vi.1972, *A.K. Irvine 213* (CANB 690231, QRS, *n.v.*); Iron Range Road, E of crossing over Pascoe River, 15.v.2003, *D.L. Jones 18865 & B. Gray* (CANB 59825B, QR5, *n.v.*); Brown's Creek, ii.2003, *Sankowsky s.n.* (CANB B75445); Canberra Botanic Gardens, ex: 27 miles NW of Cooktown along McIvor River road, i.1974, *I.R. Telford s.n.* (CBG 67473); 27 miles [43km] NW of Cooktown along McIvor River road, 1B.vi.1972, *J. Wrigley NQ1386 & I. Telford* (CBG 4B220).

***Distribution and habitat:*** Occurs in far north Queensland, in the Cooktown and Lockhart River areas, where it has been recorded growing on granite substrates.

***Conservation status:*** Restricted in distribution but population sizes are not well documented so the IUCN category Data Deficient (DD) is considered appropriate (IUCN 2012).

***Etymology:*** The epithet honours Garry and Nada Sankowsky for their many collections and efforts in cultivating Malvaceae, including this species, provided to LC for study over a period of many years.

***Notes:*** The epicalyx in *Clarkson & Neldner 9078* in part is quite short and it may be that a population of this species may occasionally contain plants with a reduced epicalyx as occurs, for example in *Hibiscus zonatus*.

The holotype is mounted on two sheets marked as sheets 1 and 2. As plants are quite large, a single sheet is not sufficient to incorporate all the relevant morphological features and variation present.

### ***Hibiscus townsvillensis*** Craven, **sp. nov.**

***Type:*** **CULTIVATED.** CSIRO glasshouse, Black Mountain, Australian Capital Territory, xii.2003, *L.A. Craven 10469* (holotype: CANB 875440.1, 875440.2, 875440.3, 875440.4, 875440.5, 975440.6 (mounted on 6 sheets); isotypes: A, ASU, B, BISH, BRI, CNS, G, K, L, MEL, NY, P, US).

*Hibiscus forsteri auct. non* F.D.Wilson: F.D.Wilson & Craven, *Austrobaileya* 4(3): 439–442 (1995), *p.p.*, as to *B. Hyland 5916*.

*Tree* up to 10 m tall, apparently evergreen. *Branchlets* hairy, with scattered tubercle-based aculei c. 2 mm long and scattered to moderately dense tubercle-based stellate indumentum of two hair size classes: fine short hairs, 0.2–0.3 mm long and coarse tubercle-based hairs, 0.5–0.7 mm long. *Stipules* caducous, hairy, filiform, or subulate, unlobed, 6 mm long, with stellate hairs. *Petioles* 65–90 mm long; *climax leaves* with the petiole indumentum dissimilar to that of branchlet (often lacking aculei and coarse stellate hairs). *Leaves* pinnately-veined (approaching palmate in trilobed leaves). *Lamina*

**Figure 3.** Part of Holotype specimen of *Hibiscus sankowskyorum* (*Clarkson 7341*, CANB 572995)

ovate, unlobed or shallowly 1- to 3-lobed, hairy, 170–260 mm long, 90–150 mm wide, the margin crenate, or serrate, the apex obtuse, or acute, concolorous, with whitish hairs, the indumentum generally similar on each surface. Abaxial surface of lamina moderately dense, fine and coarse stellate hairs, the midrib and primary vein indumentum dissimilar to that of the interveinal regions. *Foliar nectary* present at base of the lamina, 4–8 mm long. *Distal leaves* on flowering shoots not reduced in shape but reduced in size, ovate, or narrowly elliptic, distinctly petiolate on reproductive shoots. *Flowers* solitary in leaf axils, not pedunculate, chasmogamous. *Pedicels* hairy, 45–60 mm long, with stellate hairs and aculei. *Epicalyx* present, persistent, hairy with aculei and stellate hairs (stellate hairs mostly fine, but occasional coarse tubercle-based stellate hairs occur), 9–13-lobed, 20–27 mm long, segments flattened, free at the base, shorter than or equally as long as the calyx, 0.6–1 times the length of the calyx at anthesis, straight, narrowly but distinctly spathulate, or subulate, with apex entire (lobes sometimes bifurcate in the proximal half). *Calyx* at anthesis not splitting (5-lobed or -partite but not splitting per se), not adnate to the corolla and not falling with it after anthesis, whitish, fine stellate (occasionally coarse) hairs and aculei, moderately dense, evenly distributed on the abaxial surface, lobes narrowly ovate, or narrowly triangular, with prominent marginal ribs, apex acute, 25–35 mm long at anthesis, nectary absent. *Petals* white, some reddish markings towards the base, petal spot small, c. 75–80 mm long. *Staminal column* straight, 5-toothed at the apex, c. 30 mm long. *Stamens* scattered along distal c. 25 mm of the column, inserted singly. *Anthers* dark red. *Pollen* dark red. *Style* one, 5-branched, branches c. 1.5 mm long, exserted c. 4 mm beyond apex of staminal column. *Stigmas* entire, capitate. *Ovary* hairy. *Fruits* dry, dehiscent, a capsule. *Capsules* ovoid, 16–19 mm long with ascending dense hairs, capsule beak present. *Seeds* glabrous, brown with darker spots, c. 4.6 mm long. (Figs 1g–i, 4)

***Diagnostic characters:*** Distinguished from Australian members of *Hibiscus* section *Furcaria* by the following combination of characters: evergreen small tree; flattened, often spathulate epicalyx segments; large aculei tipped by a single hair and otherwise short, moderately dense indumentum on the branchlets and leaves.

***Specimens examined:*** **QUEENSLAND.** C5IRO glasshouse, Canberra, ex near Mt Elliot, Townsville area, (coll. *Sankowsky s.n.*), ii.2000, *L.A. Craven 10342* (CANB 875437.1, B75437.2, 875437.3); Mt 5torth, 5E of Townsville, 1.ix.1995, *R.J. Cummings 13705* (CANB 507214); Atherton Tablelands, Tolga, ex near Mt Elliot, Townsville area, (coll. *Sankowsky s.n.*), 22.ii–6.iv.2009, *G. Harvey s.n.* (CANB 798177.1); Ollera Creek Holding near N.P.R. 477, Mt Spec, 17.ii.1972, *B. Hyland 5916* (QR5 21252); Mt Elliot, Townsville, ii.2003, *G. Sankowsky s.n.* (CANB 875446.1, B75446.2).

***Distribution and habitat:*** Occurs in north Queensland in open eucalypt forest on granite substrates in the Mt Spec–Townsville district.

***Conservation status:*** Restricted in distribution but population sizes are not well documented so the IUCN category Data Deficient (DD) is considered appropriate (IUCN 2012).

***Etymology:*** The specific epithet is derived from the type locality, Townsville.

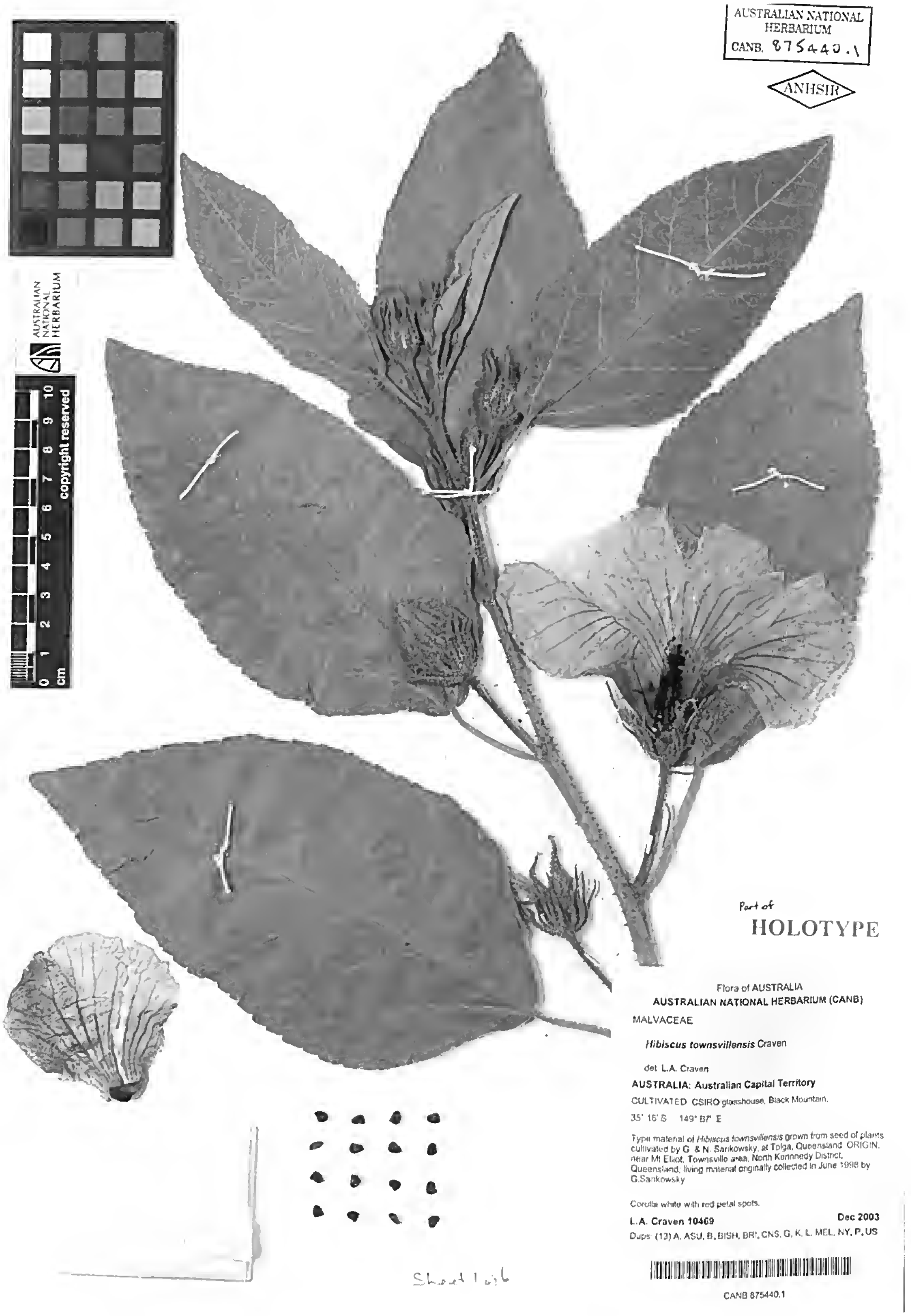
***Notes:*** Type material of *Hibiscus townsvillensis* was grown from seed of plants cultivated by G. & N. Sankowsky, at Tolga, Queensland, from living material originally collected from near Mt Elliot, in the Townsville area, Queensland, in June 1998 by G. Sankowsky.

The holotype is mounted on six sheets marked as sheets 1 through 6. As plants are quite large, a single sheet is not sufficient to incorporate all the relevant morphological features and variation present.

### ***Hibiscus forsteri*** F.D.Wilson in F.D.Wilson & Craven, *Austrobaileya* 4(3): 439–442 (1995), *p.p.*, excluding specimens included under *H. sankowskyorum* & *H. townsvillensis* above.

***Type:*** **QUEENSLAND.** Cook District: 6.8 km from Bromley on the track to Carron Valley, 16 July 1990, *Eucalyptus tetrodonta–E. nesophila* woodland on grey, sandy soil, 16.vii.1990, *J.R. Clarkson 8866 & V.J. Neldner* (holotype: CAN8 576920.1, 576920.2 (mounted on 2 sheets); isotypes: 8RI AQ0517379, DNA D0064525, K, L, CNS (M8A 758.1), NY, *n.v.*, TEX 00208139).

*Shrub* 1–2 m tall, apparently deciduous. *Branchlets* with fine stellate hairs scattered on the internode; with coarse stellate hairs sparse and sometimes inserted upon tubercles; with aculei 0.5–0.9 mm long, tipped by hairs 0.7–1.2 mm long; with minute sessile glands; the aculei and glands more or less evenly distributed. *Stipules* at length deciduous, unlobed, linear to subulate,



Part of
HOLOTYPE

Flora of AUSTRALIA
AUSTRALIAN NATIONAL HERBARIUM (CANB)
MALVACEAE

*Hibiscus townsvillensis* Craven

det L.A. Craven

AUSTRALIA: Australian Capital Territory
CULTIVATED CSIRO glasshouse, Black Mountain.
35° 16' S 149° 07' E

Type material of *Hibiscus townsvillensis* grown from seed of plants cultivated by G. & N. Sankowsky, at Tolga, Queensland. ORIGIN: near Mt Elliot, Townsville area, North Kennedy District, Queensland; living material originally collected in June 1998 by G.Sankowsky

Corolla white with red petal spots.

L.A. Craven 10469 Dec 2003
Dups: (13) A, ASU, B, BISH, BRI, CNS, G, K, L, MEL, NY, P, US

CANB 875440.1

**Figure 4.** Part of Holotype specimen of *Hibiscus townsvillensis* (*Craven 10469*, CANB 875440)

with stellate and glandular hairs, 0.6–1.4 cm long. *Petioles* 5–68(–130) mm long; *climax leaves* with the petiole indumentum dissimilar to that of the branchlet, scattered aculei always absent, the fine stellate hairs present only as a longitudinal adaxial band, 1.0–18.0 cm long. Lamina usually weakly discolorous, in general outline elliptic, ovate, narrowly ovate, broadly ovate or orbicular, unlobed to shallowly 3-lobed, 9.0–14(–22.0) cm long, 5.0–10.0(–18.0) cm wide, the base cuneate to truncate, the margin serrate to serrulate (to subcrenulate, with minute teeth in the sinuses), the lobes as long as wide to shorter than wide, the apex acute to rounded (to rarely retuse), the indumentum similar on both surfaces. Abaxial surface with midrib and primary vein indumentum of very sparse stellate hairs and sessile glands, interveinal regions with sessile glands only. *Foliar nectary* present at base of the lamina, 3–9 mm long. *Distal leaves* reduced in shape and size or only in size, narrowly elliptic, elliptic, or ovate. *Flowers* solitary in leaf axils and in short sympodia, not pedunculate, chasmogamous. *Pedicel* with sparse to dense fine stellate hairs, sometimes with sparse aculei, or with scattered to moderately dense coarser stellate hairs inserted upon small tubercules, 13–38 mm long. *Epicalyx* present, persistent, with sparse fine stellate hairs, sometimes with moderately dense coarser stellate hairs inserted upon tubercles (these mostly on the segment margins), 12–20 mm long at anthesis, elongating and 22–31 mm long in fruit, 10–12-segmented, the segments free, 0.65–0.95 times the length of the calyx, incurved, linear, 3-nerved, rounded or flattened in cross-section proximally, variously flattened and widened distally. *Calyx* at anthesis not splitting (5-lobed or -partite but not splitting per se), with whitish to yellowish, adaxial indumentum very sparse to sparse fine stellate hairs, sometimes with moderately dense aculei on ribs, or scattered coarser tubercle-based stellate hairs (these mostly on the ribs), 27–40 mm long; abaxial indumentum short, densely pubescent, nectary absent. *Petals* white with a pink flush on one margin, reddish at base, 65–85 mm long. *Staminal column* straight, 20–30 mm long. *Stamens* distributed throughout the length of the column, the filaments 1–2 mm long. *Anthers* dark red. *Pollen* dark red. *Style* one, 5-branched, with branches 4–7 mm long, exserted 10–16 mm beyond apex of staminal column. *Stigmas* entire, capitate, the hairs 0.2 mm long. *Ovary* hairy. Calyx in fruit not distinctly inflated or accrescent. *Fruits* dry, dehiscent capsule. *Capsules* 19–31 mm long, densely appressed-pubescent, ovoid and beaked, the beak glabrous, conspicuous or inconspicuous, 1–3 mm long. *Seeds* striate and minutely pectinate-pubescent, angular-reniform, c. 4 mm long. (Fig. 1a–c)

***Diagnostic characters:*** Distinguished from Australian members of *Hibiscus* section *Furcaria* by the following combination of characters: deciduous shrub; flattened, often spathulate epicalyx segments; large aculei tipped by stellate hairs and otherwise sparse indumentum on the branchlets and leaves.

***Specimens examined:*** **QUEENSLAND.** Cultivated in CSIRO glasshouse, Canberra, ACT, (ex *Gray 6896*), 4.xi.1997, *L.A. Craven 10024* (CANB 00497688); Maloneys Springs, 40 km E by road of Moreton Telegraph Station, vi.1989, *P.I. Forster 5234* (ASU, BRI, CANB, MEL, DNA, QRS, *n.v.*); Near Glennie Mt, Bolt Head Road, off Maloneys Springs Road, vi.1989, *P.I. Forster 5518* (ASU, BRI); Maloneys Springs, Bromley Station, vii.1991, *P.I. Forster 8792* (BRI, CANB 572828); Old Lockhart-Nundah Road, x.1973, *B. Hyland 6947* (CANB 689760, QRS); near Carron Valley turnoff, 15.ix.1983, *D.L. Jones 1231, B.E. Mentiplay & K. Black* (CANB 665144.1, 665144.2, 665144.3).

***Distribution and habitat:*** Apparently restricted to a small area between Bromley Station and Nundah, south of Lockhart River on Cape York Peninsula, where it grows on sandstone substrates.

***Conservation status:*** Restricted in distribution but population sizes are not well documented so the IUCN category Data Deficient (DD) is considered appropriate (IUCN 2012).

***Notes:*** As the original description of *Hibiscus forsteri* included the taxa named here as *H. sankowskyorum* and *H. townsvillenensis*, a new description was required. The description was revised based on the specimens listed above (including the holotype but excluding the isotypes which were not re-examined).

The holotype is mounted on two sheets marked as sheets 1 and 2. As plants are quite large, a single sheet is not sufficient to incorporate all the relevant morphological features and variation present.

## New combination in *Hibiscus*

The species recognised by Fryxell (2001) as the genus *Talipariti* were characterised by six main morphological characteristics: 1. Large, often ±oblong stipules that are deciduous, leaving annular scars; 2. Calyx lobes with nectaries at the midribs; 3. Capsules 5-valved, with false dissepiments (appearing 10-loculed); 4. Some species with a cupuliform involucel; 5. Arborescent habit; 6. Broadly ovate or elliptic leaves. Most of these characters are shared with other members of *Hibiscus* s.l. Fryxell (2001: 237) segregated *Talipariti* from *Hibiscus*, claiming that "*its phylogenetic affinities are perhaps to be sought elsewhere*" – a claim not supported by molecular data (Pfeil et al. 2002; Pfeil et al. 2004). Consequently *Talipariti* was placed in synonymy with *Hibiscus* (Pfeil & Crisp 2005), and accordingly, *H. bowersiae* is here moved to *Hibiscus*.

***Hibiscus bowersiae*** (Fryxell) Craven, **comb. nov.**

***Basionym:*** *Talipariti bowersiae* Fryxell, *Contr. Univ. Michigan Herb.* 23: 237–238, Fig. 3 (2001).

***Type:*** **PAPUA NEW GUINEA.** Western Highlands: Hagen Subdistrict, Kurupili, Kepaka, Upper Kaugal, 7450 ft, 5.ii.1969, *N. Bowers 635* (holotype: US; isotypes: A, BISH, BO, BRI, CANB 203877, K, L, PNH, SING, SYD, UH, US).

## Acknowledgements

Thanks are due to Paul Forster and Garry and Nada Sankowsky for specimens of *Hibiscus sankowskyorum and H. townsvillensis*. Elizabeth Minchin, Classics, ANU, as ever is thanked for her comments on the suggested epithets. Jo Palmer, Kirsten Cowley and Brendan Lepschi, CANB, kindly assisted with some editing and facilitated the editorial process. Paul Forster and two referees are thanked for comments that significantly improved the manuscript.

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ROYAL
BOTANIC GARDENS
VICTORIA

# *Pimelea leiophylla* (Thymelaeaceae): a new endemic species from Tasmania's east coast

Alan M. Gray and Matthew L. Baker

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## Abstract

*Pimelea leiophylla* A.M.Gray & M.Baker sp. nov., a new species restricted to Freycinet Peninsula and Schouten Island, Tasmania is described and illustrated, and its distribution and habitat are discussed. The new species is most similar to *Pimelea sericea* R.Br. but differs chiefly by its leaves being hairy on the adaxial surface and by its opposite-decussate phyllotaxy. The species is uncommon and localised throughout its distribution range.

***Key words:*** granite, new species, taxonomy, diagnostic features, morphology, Australia

## Introduction

The genus *Pimelea* Banks & Sol. ex Gaertn. consists of approximately 125 species (Rye 1990, 1999; Copeland & Telford 2006; Burrows 2011). Of these species, 90 are endemic to Australia (Rye 1990, 1999; Copeland & Telford 2006) and a further 35 species occur in New Zealand (Burrows 2011). In Tasmania, the genus is represented by 18 species, seven of which are endemic to the state, including the novel species described here (de Salas & Baker 2015).

Rye's (1990) treatment of Australian *Pimelea* divided the genus into seven infrageneric sections. Rye (1999) later suggested that the boundaries of the proposed sections are unresolved and require work, particularly with addressing the placement of the New Zealand species. Burrows (2008, 2011) agreed, noting that some New Zealand species of *Pimelea* do not fit well with Rye's infrageneric classification, and as such it was not adopted for the species occurring in New Zealand. Instead, the New Zealand taxa were informally divided into two groups: those with leaf hair and those without (Burrows 2008). He later suggested that the genus originated in Australia and migrated to New Zealand where, unlike in Australia, it is rife with hybridisation between many species, complicating the taxonomy and species boundaries (Burrows 2011).

Characteristics of the group that are useful as diagnostic features include phyllotaxy (opposite or alternate), indumentum of the leaf

ISSN: 0077-1813 (print) · ISSN: 2204-2032 (online)

surfaces (e.g. presence and/or absence of hairs), hypanthium dehiscence (e.g. above or below the ovary) and indumentum, and characters of the fruit (e.g. naked or enclosed in the ovary section of the hypanthium and/or the fruit being dry or fleshy).

In 1989, A.M. Buchanan collected several samples of an unknown species of *Pimelea* from The Hazards mountain range, Freycinet National Park, and determined each as '*Pimelea* sp.'. Soon after, in 1991, J. Pannell collected a specimen from Callitris Creek on the southern Freycinet Peninsula, which he determined as *P. nivea* Labill., an endemic montane to lowland species that is widely distributed throughout the state especially in the central and eastern regions. One of us (A.M. Gray) examined this specimen in 2003 noting that 'the [leaf] indumentum in no way matched that of *P. nivea* but, rather, it was more typical of that of *P. sericea*!'. *Pimelea sericea* R.Br. is an endemic Tasmanian species of montane habitats on dolerite mountains of the Central Plateau, southern ranges and north-eastern highlands. For it to be growing at the Freycinet Peninsula was considered odd due to its being far removed from its known distribution, and growing on Devonian granite substrates, the dominant geological formation of the Freycinet Peninsula. This sheet, and some others, including one determined as '*Pimelea*' by Buchanan in 2001, were later examined and annotated by Gray as *Pimelea* sp. nov. In 2000, its range was extended by collections from the granite hills of Schouten Island, located off the southern tip of the Freycinet Peninsula and part of the Freycinet National Park. During the course of our study, a specimen collected by Canning and Telford from The Hazards in 1969, and identified as *P. sericea*, was examined and is regarded as the first collection of this putative new species.

Although not common throughout its range, it is somewhat surprising that this rather showy-flowered novelty should have remained unnamed for so long. We here recognise this taxon as a new species closely related to *P. sericea*, differing chiefly by the indumentum of the adaxial leaf surface and its phyllotaxy, and formally describe it as *Pimelea leiophylla* A.M.Gray & M.Baker.

## Materials and methods

The study is based on wild-collected material by the authors and on collections held in the Tasmanian Herbarium (HO). Two specimens held at the Australian National Herbarium (CANB) and the National Herbarium of Victoria (MEL) were also included. Due to the scarcity of fruiting material on herbarium specimens, measurements and characteristics of fruits and seeds were made from specimens of plants in cultivation at the Royal Tasmanian Botanical Gardens in Hobart.

## Taxonomy

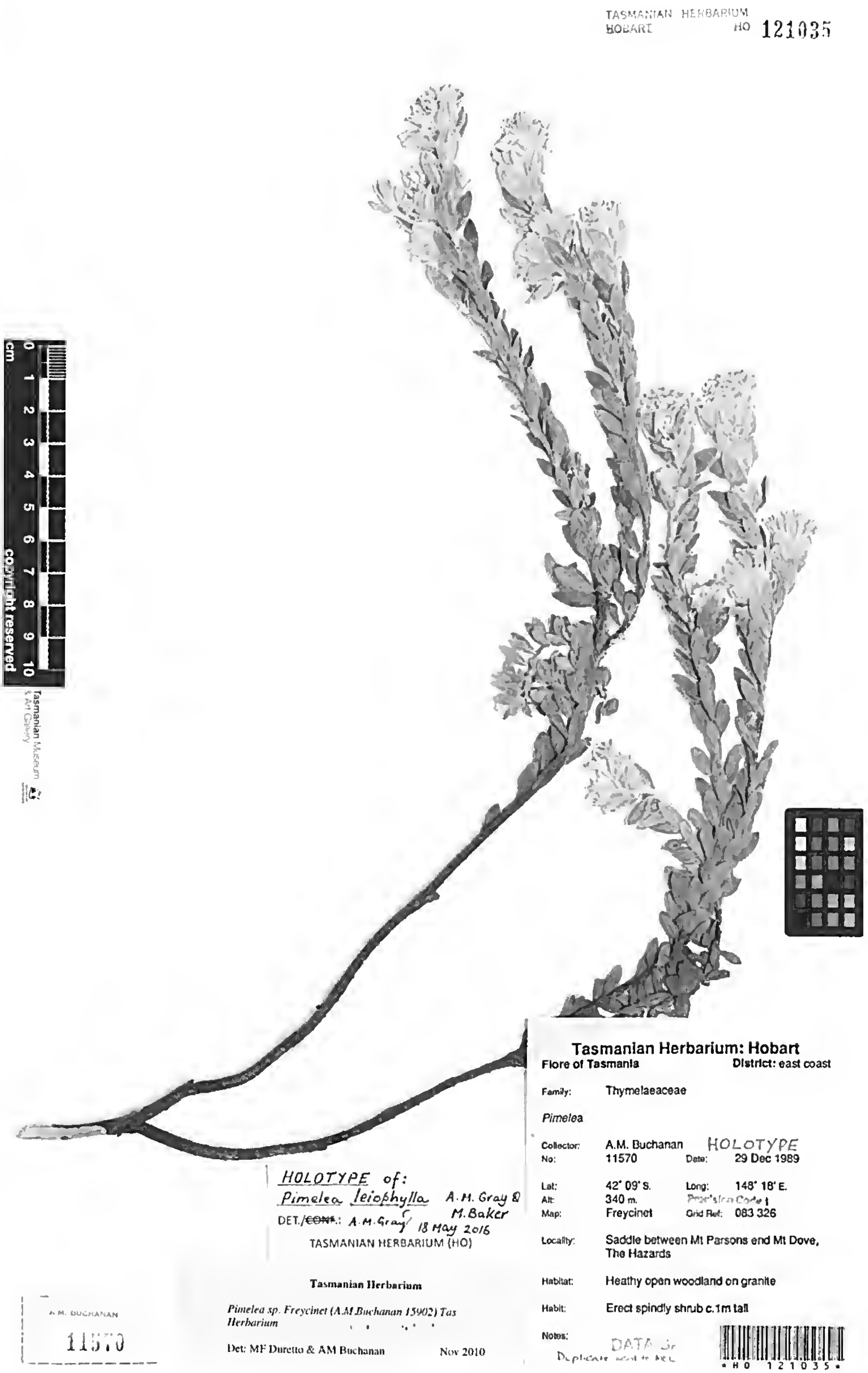
***Pimelea leiophylla*** A.M.Gray & M.Baker, **sp. nov.**

***Type*: TASMANIA.** The Hazards, saddle between Mt Parsons and Mt Dove, 29.xii.1989, *A.M.Buchanan 11570* (holotype: HO 121035 (Fig. 1); isotype: MEL 2383961A).

*Pimelea* sp. Freycinet (A.M. Buchanan 15902) Tas. Herbarium sensu Baker & Duretto (2011).

Similar to Pimelea sericea but differing in its sparsely branched open habit, its opposite-decussate leaves and the presence of sparse, silky-villous hairs on the adaxial leaf surfaces.

*Small shrubs*, 0.3–1.5 m high. *Branches* sparse, slender, erect to spreading, ± arranged dichotomously, initiating immediately below the previous season's floral receptacle, appressed silky-hairy, glabrescent; leaf scars prominent; bark tough, stringy. *Leaves* 5–15 mm long, 3–10 mm wide, pale to mid-green, opposite, decussate, spreading to loosely appressed, often crowded on younger branches; petiole c. 1 mm long; lamina broadly ovate to elliptic, flat; adaxial surface sparsely appressed silky-hairy, glabrescent with age; abaxial surface densely appressed villous to silky-hairy, soft, with the hairs extending beyond the margin; margin fimbriate; apex acute or minutely apiculate. *Inflorescence* an erect, compact terminal head of (10–)15–25+ flowers; receptacle densely hairy, ± convex; involucral bracts 4 or 8, a little broader but otherwise scarcely differentiated from subtending leaves. *Flowers* female or hermaphrodite, protandrous; pedicels very short, obscured by long, dense hairs. *Hypanthium* bright white, occasionally pink, drying pale creamy-yellow, fusiform-tubular; style portion 8–15 mm long, circumcissile immediately above the ovary; ovary portion 4–6 mm long, persisting briefly post-anthesis; adaxial surface glabrous; abaxial surface densely appressed-hairy. *Sepals* 4, 3–5 mm long, spreading or slightly recurved, two sepals somewhat larger, often ± cucullate, with a central, raised ridge; apices of lobes with a distinctive



**Tasmanian Herbarium: Hobart**

**Flora of Tasmania** **District:** east coast

| | | | |
|---|---|---|---|
| Family: | Thymelaeaceae | | |
| *Pimelea* | | | |
| Collector: | A.M. Buchanan | HOLOTYPE | |
| No: | 11570 | Date: | 29 Dec 1989 |
| Lat: | 42° 09' S. | Long: | 148° 18' E. |
| Alt: | 340 m. | Precision Code | |
| Map: | Freycinet | Grid Ref: | 083 326 |
| Locality: | Saddle between Mt Parsons and Mt Dove, The Hazards | | |
| Habitat: | Heathy open woodland on granite | | |
| Habit: | Erect spindly shrub c.1m tall | | |
| Notes: | DATA | | |

Duplicate sent to MEL

HOLOTYPE of:
*Pimelea leiophylla* A.M. Gray & M.Baker
DET./~~CONF.~~: A.M.Gray 18 May 2016
TASMANIAN HERBARIUM (HO)

**Tasmanian Herbarium**

*Pimelea sp. Freycinet (A.M.Buchanan 15902) Tas Herbarium*

Det: MF Duretto & AM Buchanan Nov 2010

A.M. BUCHANAN
11570

**Figure 1.** Holotype of *Pimelea leiophylla* (HO 121035)

tuft of hairs. *Stamens* 2, inserted at the base of the larger sepals; filaments equal to or a little shorter than the sepal lobes, erect at first, then curving outwards during and following anther dehiscence; anthers 1–2.5 mm long, dehiscence latrorse. *Style* slender, filiform, enclosed, or exserted and often contorted, a little longer than the stamens; stigma minutely papillose. *Fruit* dry, sparsely hairy at the apex, enclosed within the persistent base of the hypanthium. *Seed* greyish-black, ovoid, 3.5–5 mm long, enclosed within a thin, green exocarp. Flowering Oct.–Feb. (Fig. 2).

***Distribution and habitat:*** *Pimelea leiophylla,* as far as is known, is confined to the granite areas of the Freycinet Peninsula and Schouten Island (Fig. 3). It is uncommon throughout its range and rarely forms extensive or conspicuous populations. It usually occurs as isolated individuals or small, widely separated groups of few individuals, mostly in the shelter of large granite boulders in shaded areas with shallow soils and minimal moisture. The species appears to be more common on Schouten Island with at least 18 sites recorded (N.Tapson pers. comm.), whereas on the Freycinet Peninsula, it has been recorded from only three general locations. All known populations of this species are protected within the Freycinet National Park. Furthur investigation into the conservation status of this species may see it qualify for listing as 'rare' under the *Threatened Species Protection Act 1995* (Tas).

The associated vegetation consists of sparse, dry woodland, either of impoverished *Eucalyptus amygdalina* Labill. or, less commonly, *E. tenuiramis* Miq., with *Hakea* spp., *Kunzea ambigua* (Sm.) Druce and *Leptospermum* spp. all common components of the scrubby understory. Extensive areas of *Gleichenia microphylla* R.Br. form a low, tangled undergrowth in the damper and sheltered areas.

The Freycinet Peninsula, on Tasmania's East Coast, consists of a range of low mountains of rounded relief, composed mostly of pink Devonian granites. Schouten Island, a small island lying immediately to the south, is of added interest in that only the eastern section is granitic, whereas the majority of the western section is of Jurassic dolerite and conforms with the geology of the mainland Tasmanian coast immediately to the west.

The general topography is characterised by extensive, often very steep, slabs and shelves of granite. Craggy outcrops and small to massive boulders are strewn throughout. Small gullies and clefts between the boulders accumulate soils that are generally skeletal and infertile and consist chiefly of leached humic peats combined with a high proportion of weathered granitic sands and gravels.

Fire frequency and scant, erratic rainfall with rapid run-off determine the development and composition of the vegetation. Despite environmental limitations, a diverse range of plant communities is present, including a suite of endemic or otherwise uncommon species, for example: *Philotheca freyciana* Rozefelds, *Conospermum hookeri* (Meisn.) E.M.Benn., *Epacris barbata* Melville and *Boronia rozefeldsii* Duretto.

***Remarks:*** The distinguishing morphological characteristics of *Pimelea leiophylla* include the nature of the sexual system, hairy leaves and stems, lack of any distinctive sessile involucral bracts, circumscissile hypanthium, and fruits that are hairy at the apex. The features place it in *Pimelea* sect. *Eppalage* (Endl.) Benth. *sensu* Rye (1988, 1990). In Australia, this section is comprised of 18 species and has a widespread distribution. It includes the following Tasmanian species: *P. sericea*, *P. nivea*, *P. micrantha* F.Muell. ex Meisn. and *P. curviflora* R.Br. Of these, *P. leiophylla* is most similar to the endemic *P. sericea* but differs in the presence of sparse hairs on the adaxial leaf surfaces. In contrast, the adaxial leaf surfaces of *P. sericea* are always glabrous. The two species also differ in their phyllotaxy, the leaves of *P. leiophylla* being opposite-decussate. We examined numerous herbarium sheets of *P. sericea* as well as fresh material from Mt Wellington and can confirm that the phyllotaxy of *P. sericea* is alternately arranged leaves forming spirals and not arranged in opposite ranks, as described by Rye (1990).

There are also floral differences between these two taxa. The length of the hypanthium is longer in *P. leiophylla* (8–15 mm) compared to that of *P. sericea* (5.5–7.5 mm). The inflorescences of *P. leiophylla* are usually more floriferous and are composed of up to 25 flowers whereas those of *P. sericea* rarely have more than 15 flowers per inflorescence. The indumentum of the hypanthium is longer and more densely packed in *P. leiophylla* and almost obscures the surfaces of the flowers. In contrast *P. sericea* has shorter hairs that scarcely obscure the flowers.

These species also differ in their habit and habitat. *Pimelea leiophylla* is an open, sparsely branched shrub, uncommon and restricted to lowland (< c. 450 m asl), skeletal granitic soils on the Freycinet Peninsula and Schouten Island on Tasmania's east coast, whereas *P. sericea* is a densely compact shrub, common at high altitudes (> c. 900 m asl) on chiefly dolerite mountains of the Central Plateau, southern ranges and the north-eastern highlands. These differences are summarised in Table 1.

**Figure 2.** *Pimelea leiophylla* flowering branch, showing the adaxial leaf indumentum and the opposite and decussate leaf phyllotaxis that distinguish this species from *P. sericea* (photo courtesy of Tim Rudman)

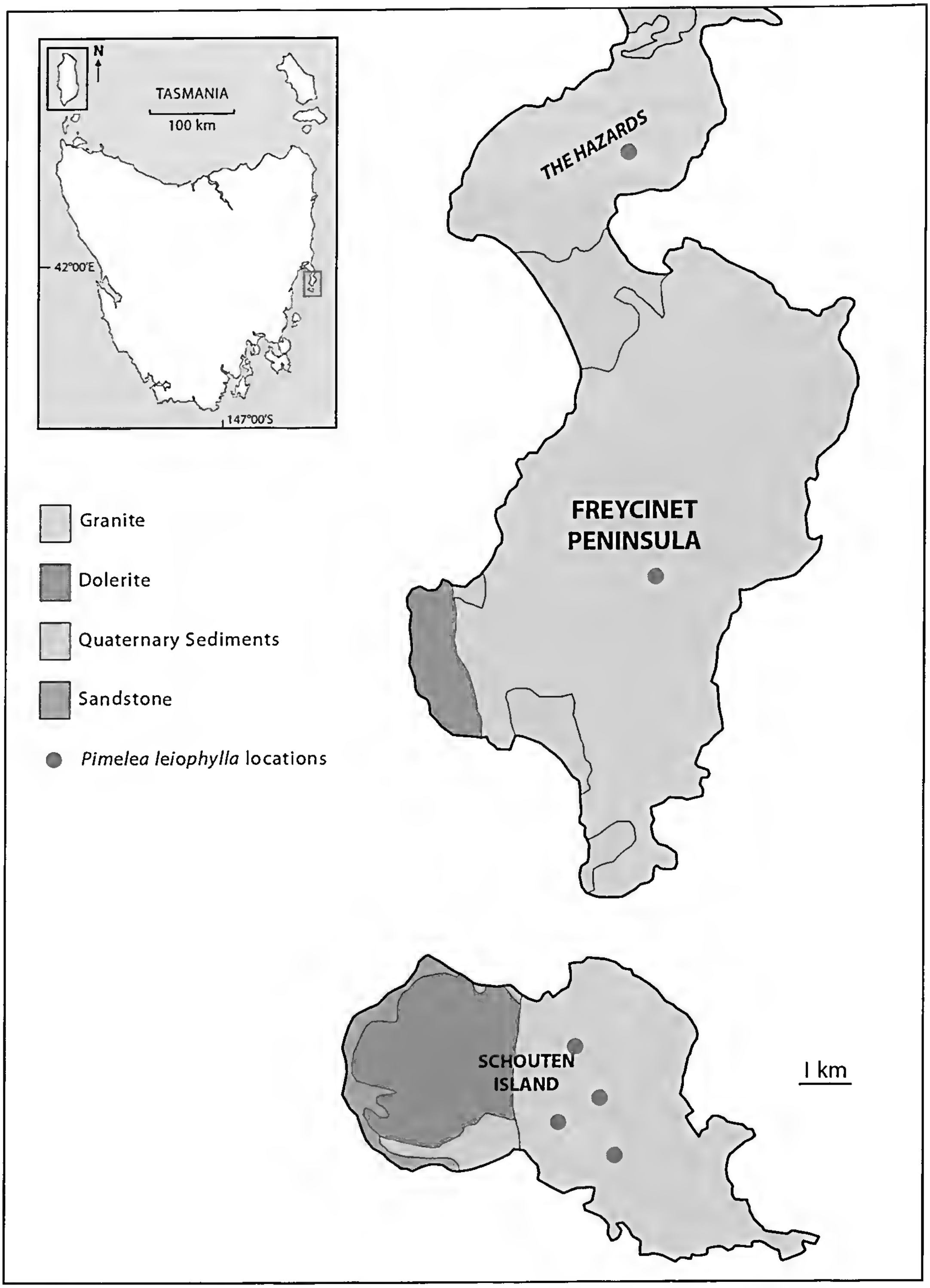


**Figure 3.** Distribution of *Pimelea leiophylla*

**Table 1.** Summary of key morphological and distribution features of *Pimelea leiophylla* and *P. sericea*

| | ***Pimelea leiophylla*** | ***Pimelea sericea*** |
|---|---|---|
| Habit | sparsely branched, 'open' shrubs | densely branched, compact shrubs |
| Adaxial leaf surface | sparsely silky-villous, with the hairs antrorse, and glabrescent | glabrous |
| Leaf arrangement | opposite-decussate | alternate, spiral |
| Hypanthium length | 8–15 mm long | 5.5–7.5 mm long |
| Flowers per inflorescence | (10–)15–25+ | 10–15(–20) |
| Distribution | lowland habitats on granite substrates of Freycinet Peninsula and Schouten Island on the Tasmanian east coast | montane habitats on dolerite mountains of the Central Plateau, southern ranges and NE highlands |

*Pimelea nivea*, an endemic species of montane to lowland habitats, is widely distributed throughout the state, particularly in the central and eastern regions. It differs from *P. leiophylla* by having elliptic to almost orbicular leaves and glabrous adaxial leaf surfaces.

*Pimelea curviflora*, a common species of dry, open forests, shrubberies and grasslands in the Derwent Valley, Bass Strait Islands and north and north-eastern parts of the state, differs from *P. leiophylla* by having a much shorter and slightly curved hypanthium tube. In addition, the leaves of *P. curviflora* are thinner in texture when compared to *P. leiophylla*. Some uncertainty exists regarding the presence of *P. micrantha* in Tasmania and specimens identified as such from the state are doubtfully distinct from *P. curviflora*. Further investigation into the taxomony of these two species is warranted.

Whilst many of the mainland Australian species in this section bear at least some indumentum on the adaxial leaf surfaces, the combination of morphological characteristics, habitats, and locations where they grow do not concur with those of *P. leiophylla*. *Pimelea venosa* Threlfall, a rare species of granite boulder fields in north-eastern New South Wales, differs from *P. leiophylla* by having inflorescences with fewer flowers, and has leaves with a relatively sparse covering of long patent hairs on both leaf surfaces.

Several New Zealand *Pimelea* species have hairs on both leaf surfaces, but these species differ from *P. leiophylla*, in having fleshy fruits and/or less flowers per inflorescence.

*Pimelea leiophylla* flowers with pink coloration on the proximal portion of the hypanthium have been noted in plants grown at the Royal Tasmanian Botanical Gardens for conservation purposes. This coloration is also shared with *P. sericea* and *P. nivea* and is occasionally seen in New Zealand species (Burrows 2008).

***Etymology:*** From the Greek *leio* - smooth and *phylla* - leaves. The epithet refers to the very soft, smooth foliage of this taxon.

***Selected specimens examined:*** **TASMANIA.** Mt Graham, Freycinet Peninsula, 10.ii.1969, *E.M. Canning and I.R. Telford 2576* (CANB, AD *n.v.*); The Hazards, gulch between Mt Parsons and Mt Dove, 29.xii.1989, *A.M. Buchanan 11569* (HO); Callitris Creek, Freycinet National Park, 29.ix.1991, *J. Pannell s.n.* (HO 142618); Milligans Hill, Schouten Island, 14.xi.2000, *A.C. Rozefelds 1905* (HO); Milligans Hill, Schouten Island, 14.xi.2000, *A.C. Rozefelds 1906* (HO); Schouten Island, 14.xi.2001, *A.M. Buchanan 15902* (HO); Western side of Mount Dove near saddle between Mount Dove & Mount Amos, Hazards, Freycinet Peninsula, 17.ii.2002, *A.C. Rozefelds and N. Papworth 2282* (HO); SW side of Schouten Island, 25.ii.2002, *A.C. Rozefelds 2294* (HO).

## Acknowledgements

We would like to extend our gratitude to James Wood, Natalie Tapson, Lorraine Perrins and Chris Lang, horticultural staff of the Royal Tasmanian Botanical Gardens, for their willing and enthusiastic assistance in providing habitat information and samples of cultivated material for our study. We also thank Fiona Everts, Rob Connell and Richard Dakin of the Freycinet National Park, Tasmanian Parks and Wildlife Service, for providing logistics and access to the Park (including Schouten Island). The directors of CANB and MEL are thanked for the loan of specimens for our study. We also thank Alex Buchanan for bringing this taxon to our attention, Tim Rudman, for the use of his photograph, Maria MacDermott for photographing the type specimen, Miguel de Salas for helping us to locate the species on The Hazards and the Forwood family for accommodating us. For providing advice and constructive criticism on the manuscript, our sincere gratitude is due to Dr Gintaras Kantvilas. Two anonymous referees are thanked for their pertinent and constructive comments.

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Muelleria

35: 23–33

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# Noteworthy desmids (Desmidiales, Conjugatophyceae) from water supply reservoirs in south-east Queensland, Australia

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## Abstract

Eight desmid taxa are presented herein, of which five are new records for Australia. One new species is proposed, *Euastrum planctonicum* A.Kenins, and the zygospore of a planktic *Staurastrum* Meyen ex Ralfs that defies certain identification is described. The taxa reported suggest south-east Queensland has elements of an Indo-Malaysian/North Australian desmid flora.

***Key words***: algae, plankton, Australia, Zygnematophyceae, new records

## Introduction

Knowledge of freshwater algae in the state of Queensland is considered 'generally poor' (Bostock & Holland 2010). While desmids have gained more attention than other groups of algae, most published records concerning this group date back to the late 19th to early 20th centuries. Early literature includes: Möbius (1882, 1884), Bailey (1893, 1895, 1898), Borge (1896, 1911) and Schmidle (1896), with subsequent significant works by Mcleod (1975), Grimes (1988), Ling and Tyler (2000) and Dingley (2001a). The majority of the desmids catalogued in these works were sampled from south-east Queensland. Much of the state, such as the far north and central regions, remains scarcely surveyed (Coesel & Dingley 2005).

Constructed water storages for potable supplies are the most common, permanent lentic habitats in south-east Queensland (McGregor 2013), and their protected catchments provide ideal habitats for desmids (Entwisle et al. 1997). Previous studies from this type of environ from other regions within Australia have resulted in newly described species and varieties (e.g. West 1909; Playfair 1912). This paper documents eight

ISSN: 0077-1813 (print) · ISSN: 2204-2032 (online)

desmids from south-east Queensland, including five new records and one new species.

## Materials and methods

***Site description:*** Sites in this survey were Baroon Pocket Dam (26°42′23.8″S, 152°52′14.1″E), Ewen Maddock Dam (26°46′53.8″S, 152°59′34.0″E), Hinze Dam (28°03′28.5″S, 153°16′55.8″E), Leslie Harrison Dam (27°32′10.3″S, 153°10′20.3″E), Lake Manchester Dam (27°28′57.1″S, 152°45′54.3″E) and Cooloolabin Dam (26°32′48.5″S, 152°52′51.2″E). These reservoirs lie within 200 km of the east coast of south-east Queensland and represent a subset of the many disconnected groups of small to medium sized catchments enclosed to the west by the Great Dividing Range. This south-east region only forms a small part of the state, but due to population pressures, much of the area has been developed for urban and agriculture enterprises resulting in numerous constructed water storages that regularly experience seasonal, cyanobacterial blooms during the Austral summer (McGregor 2013).

***Analysis of material:*** The samples examined are part of an algal monitoring program from 2012 to 2015. Surface plankton grabs or, more often, five metre depth-integrated (three metres if the depth of the waterbody was too low) samples were taken throughout the study catchments for analysis. These samples were preserved on site with lugols iodine solution. Material was examined by brightfield and phase contrast microscopy with an Olympus BX51 compound microscope. Photomicrographs were taken of the preserved material using an Olympus SC30 Digital microscope camera at 400x magnification. Measurements of cellular dimensions (which are explained in Table 1) were taken from the digital images using Olympus cellSens software standard version 1.6. Means are provided when a sufficient number of measurements were taken. Presented focal-stacked images were created using FIJI (*Schindelin et al. 2012*).

***Taxonomic determinations and treatment:*** Whole-group treatments that encompassed the Australian desmid biogeographic regions as circumscribed by Coesel (1996) and Vyverman (1996) were primarily consulted for identification (i.e. Scott & Prescott 1961; Croasdale & Flint 1986, 1988; Vyverman 1991; Croasdale et al. 1994; Ling & Tyler 2000). Some additional monographs, floras and other publications were also consulted and are referenced herein. While the available dichotomous keys were utilised, 'comparative iconography' where examined specimens are compared to illustrations from the available literature and cross-checked with the descriptions, was largely employed. Identifications were then cross-checked again with the original descriptions when accessible.

## Taxonomy

### Mesotaeniaceae Oltmanns

### 1. ***Netrium oblongum*** var. ***cylindricum*** W.West & G.S.West

West & West (1903), *J. Bot. (London)* 41: 40, pl. 446: 10.

Brook & Williamson (2010) *A Monograph on some British Desmids* 57, pl: 22: 1–18 & 23: 1–8.

***Dimensions:*** L. 36.9–63.2 µm, Br. 14.2–15.8 µm, L.:Br. 2.5–4.1. (Fig. 1A)

***Description:*** *Chloroplast* composed of dissected ridges; notches observed in cells undergoing division.

**Table 1.** Explanation of symbols and abbreviations

| | |
|---|---|
| µm = micrometres | Br. = Breadth |
| L. = Length | Br. cpr. = Breadth with processes |
| L. cpr. = Length with processes | Br. spr. = Breadth without processes |
| L. spr. = Length without processes | Br. csp. = Breadth with spines |
| L. csp. = Length with spines | Br. ssp. = Breadth without spines |
| L. ssp. = Length without spines | Ap. = Breadth of apices |
| Isth. = Isthmus | L.:Br. = Ratio of length to breadth |
| Th. = Thickness of cell | (*X*; *n*=x) = Mean (*X*), followed by "*n*" which is the number of specimens measured (x) |

*Pyrenoid* number unable to be determined due to lugols fixative darkening the central axis of said chloroplast.

***Remarks:*** This taxon is regarded as tychoplanktic in lakes (Brook & Williamson 2010) and was found forming a considerable component of the plankton.

***Location:*** Cooloolabin Dam.

***Distribution:*** A new record for Queensland. This taxon has previously been observed by Dingley (1995) in a wheel rut subject to drying from New South Wales; the Australian freshwater algae census (Entwisle & Nairn 2016) is yet to cite this record.

## Desmidiaceae Ralfs

### 2. *Cosmarium mikron* Skuja

Skuja (1949), *Nova Acta R. Soc. Sci. Upsal.*, ser. 4, 14(5): 129, pl. 27: 14.

***Dimensions:*** L. 7.8–8.6 µm, Br. 10–11.5 µm, Isth. 2.7–3.1 µm, Th. 5.4–5.8 µm. (Fig. 1D)

***Description:*** *Cells* small, broadly ellipsoid in outline; considerably constricted. *Apex* of semicell raised with a slight depression on both sides. *Sinus* narrowly open. *Lateral lobes* slightly swollen, terminating with mucros. *Semicell* depressed between the central axis and lateral lobes in apical view.

***Remarks:*** The cells match the original description by Skuja *l.c.* but are ever so slightly larger in dimensions. Williamson (2006) proposed a variety *asymmetricum* on the basis of asymmetrical torsion of the lateral lobes, based on his specimens from Sri Lanka as well as figures provided by Vyverman (1991). Such torsion was not seen in the several cells observed in end-view in this survey. A feature not mentioned in Skuja's *l.c.* original description or shown in his figures was the presence of mucros or tiny spines at the end of the lateral lobes. Neither Vyverman (1991) nor Williamson (2006) mention this feature; but Williamson's *l.c.* central depiction in figure 5 seems to show somewhat pointed lateral lobes.

***Location:*** Leslie Harrison Dam.

***Distribution:*** A new record for Australia. A species presumably confined within the Indo-Malayasian/North Australian desmid biogeographic region. Originally described from Burma by Skuja (1949) with a separate variety *asymmetricum* subsequently recorded from Papua New Guinea by Vyverman (1991) and Sri Lanka by Williamson (2006).

### 3. *Euastrum planctonicum* A.Kenins, **sp. nov.**

*Euastrum cuspidatum* var. *goyazense sensu* Dingley (2003)

Dingley (2003), *The Victorian Naturalist* 120: 116 & 117, pl 1: I (as *Euastrum cuspidatum* var. *goyazense*).

***Dimensions:*** L. 20.7–26.3 µm (*23.6 µm*; *n*=40), Br. 23.5–30.4 µm (*26.6 µm*; *n*=60), Isth. 4.1–5.9 µm (*5 µm*; *n*=45), Ap. 9.8–13.5 µm (*12 µm*; *n*=50). (Figs 1C, 2C)

***Diagnosis:*** *Cells* generally broader than long. *Basal lobes* wing-like, comma-shaped, tapering and arising slightly divergently, with a hemispherical protuberance bearing tubercules in its centre. *Sinus* open, rhomboid in outline. *Semicell* in apical view depressed between the basal lobes and the central axis; protuberances bearing tubercules are positioned on the inflated portions of the cell outline.

***Type:*** Figure I, Plate 1, p. 118 in Dingley (2003) Desmids (Chlorophyta) from two freshwater sites in Victoria with an emphasis on new records. *The Victorian Naturalist* 120, 116–120, under the misapplied name *Euastrum cuspidatum* var. *goyazense* (K.Förster & Eckert) K.Förster.

Due to insufficient material for adequate preservation and lodgement in a herbarium, Dingley's figure *l.c.* has been designated as the holotype as the examined cells were illustrated at much greater magnification, detailing the finer aspects of cell wall ornamentation. The species epithet was chosen due to this species being present in the plankton, where cells were frequently observed in mid-division.

***Description:*** A relatively small species of *Euastrum* Ehrenberg ex Ralfs that is usually slightly broader than long. *Semicells* consist of morphologically elaborate, wing-like basal lobes that extend horizontally with a single, prominent spine terminating at the very end. *Apical margin* of the polar lobe flat with an open notch. *Polar lobe* short, with sub-parallel margins, the angles furnished with a slightly diverging spine on each corner with a single subapical granule positioned nearby. Additional *granules* are found on the upper and lower margins of the basal lobes; the remainder of the cell wall apparently smooth. *Sinus* very widely open, acutely angled from the isthmus then narrowing and opening again. Three hemispherical *facial protuberances* bearing tubercules can be seen in faceview; one directly above the isthmus with the other two positioned on each of the basal lobes beside the aforementioned central one.

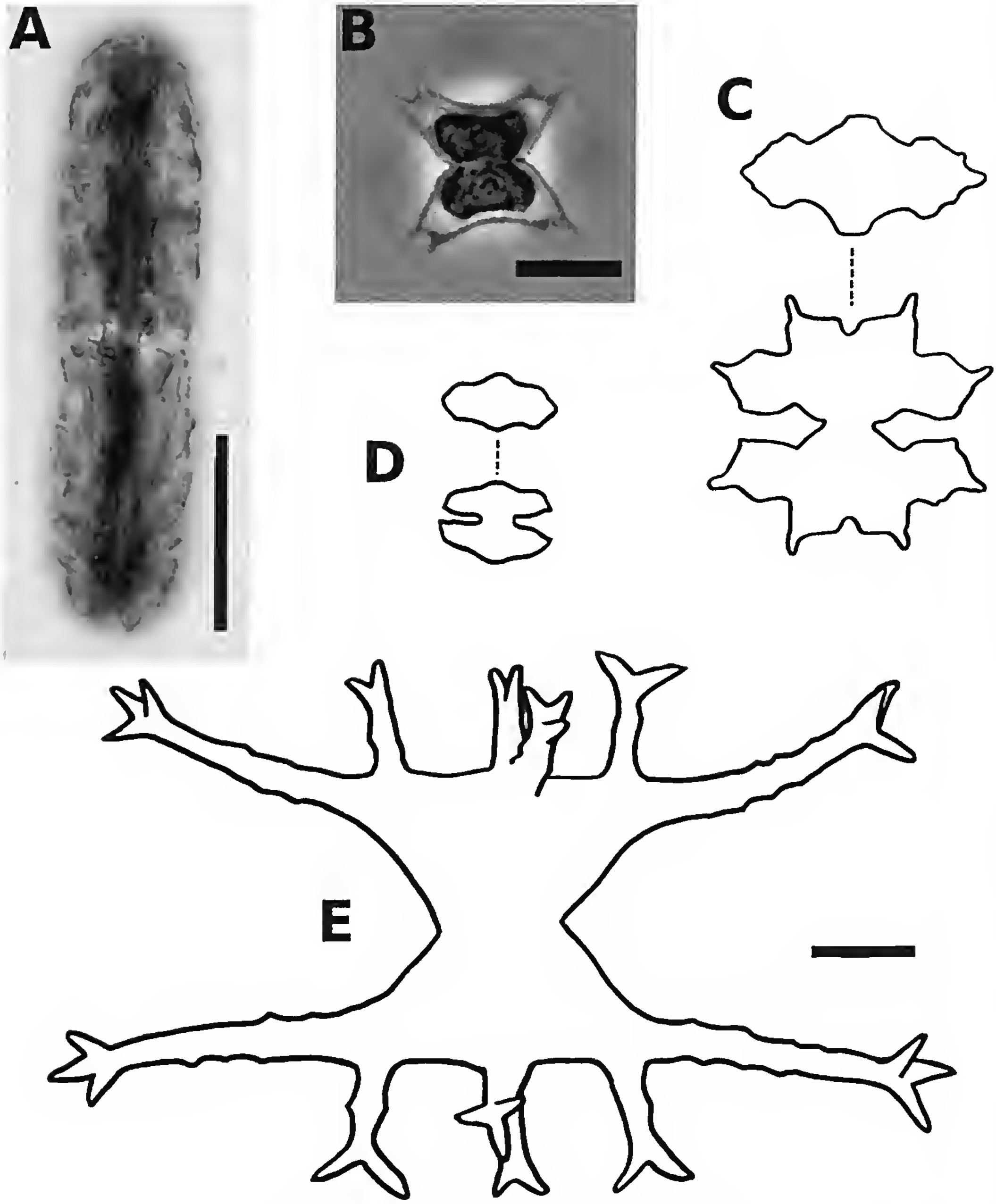

**Figure 1. A.** *Netrium oblongum* var. *cylindricum*, 400× mag. Focus-stacked, Brightfield. Scale Bar = 20 µm; **B.** *Xanthidium bifidum*, 400× mag. Brightfield. Scale Bar = 10 µm; **C.** *Euastrum planctonicum*, line drawing of apical and faceview; **D.** *Cosmarium mikron*, apical and faceview; **E.** *Staurastrum biwaense*. Scale bar for illustratraions = 10 µm.

*Chloroplast* axile with a centrally placed pyrenoid in each semicell. *Zygospore* unknown.

**Remarks:** On the basis of similarity of sinus shape and comparable dimensions, Viyakornvilas (1974) recorded the present form from Australia under the name *Euastrum cuspidatum* var. *goyazense* (Förster & Eckert) Förster & Eckert (synonym *Euastrum subtile* var. *goyazense* Förster & Eckert), originally described from South America. However, Viyakornvilas (1974) noted differences such as three pyrenoids (there may be confusion here where Viyakornvilas may have meant the term tubercule) per semicell instead of one and the polar lobes bearing a lesser number of spines. Dingley (2003) remarks that the specimens encountered are in agreement with Viyakornvilas (1974) and observed a single long spine with a sub-apical granule adjacent to it on each angle of the polar lobes. The cells in this survey agree with the previous authors' plants from Australia. Aside from the previously noted differences, *E. planctonicum* A.Kenins also differs from *E. cuspidatum* var. *goyazense* by having a more elaborate, arced, wing-like basal lobe instead of a cylindrical one and each lobe is beset with a tubercule; *E. cuspidatum* var. *goyazense* is not described nor figured to have any on its lobes (see Förster 1964 & 1969). The differences between the two taxa are even more apparent when compared in endview, where *E. planctonicum* is much more angular and pointed with respect to the cell margins as well as being depressed between the central axis of the cell and basal lobes. The aforementioned protuberances bearing tubercules are also prominent from this view. *Euastrum planctonicum* and *E. cuspidatum* var. *goyazense* are quite unique species in that they differ from other Euastra with horizontally extending basal lobes by having a sinus that is considerably open rather than tending to be closed. *Euastrum planctonicum* is a very morphologically distinct species which has considerable differences from *E. cuspidatum* var. *goyazense* and other Euastra and warrants recognition at species rank.

**Location:** Leslie Harrison Dam.

**Distribution:** *Euastrum planctonicum* is newly recorded from Queensland. Australian reports were previously misidentified as *E. cuspidatum* var. *goyazense*, as by Viyakornvilas (1974), who included records from Lakes Hume and Mulwala (Victoria); Dingley (2003), who subsequently recorded it in Victoria from a shallow stream flowing into Lake Nillahcootie; and Viyakornvilas (1974) and Brook (1981), based on personal communication by P.A. Tyler, who recorded it in Lakes Sorell and Crescent (Tasmania).

### 4. *Haplotaenium minutum* var. *elongatum* (W.West) Bando

Croasdale & Flint (1986), *Flora of New Zealand. Freshwater Algae, Chlorophyta, Desmids*, vol. I 73, pl. 14:2–4.

**Synonym:** *Pleurotaenium minutum* var. *elongatum* (W.West), Cedergren (1932), *Ark. f. Bot.* 25A(4): 13.

**Dimensions:** L. 233.69–317.72 µm (*266.7 µm; n*=34), Br. 9.73–11.36 µm (*10.5 µm; n*=34), Isth. 8.66–10.4 µm (*9.6 µm; n*=34), L.:Br. 21.2–30.3. (Fig. 2A)

**Description:** *Cells* elongate, cylindrical; *basal swelling* very slight. *Apex* smooth, varying from truncated to very slightly indented; *vacuoles* absent. *Chloroplast* axile, ribbon-like with 12 to 22 pyrenoids; its centre often contorted to accommodate for the nucleus.

**Location:** Ewen Maddock Dam.

**Distribution:** A new record for Australia. Considered widespread, found on most continents.

### 5. *Sphaerozosma aubertianum* var. *indicum* (W.B.Turner) Coesel & Ngearnpat

Coesel, Ngearnpat & Peerapornisal (2009), *Algol. Stud.* 131: 17, fig. 4.

**Basionym:** *Sphaerozosma vertebratum* var. *indicum* W.B.Turner (1893), *Kongl. Svenska Vet.-Akad. Handl.* 25(5): 140, fig. 18.

**Dimensions:** L. spr. 13.6–15.4 µm, Br. 16.3–20.6 µm, Isth. 4.5–5.9 µm. (Fig. 2B)

**Description:** *Semicells* elliptic; *sinus* open, cuneate; *isthmus* slightly elongate. A pair of *pores* giving a granule-like appearance were visible on the lateral sides of the cell wall.

**Remarks:** The open sinus and elliptic semicells differentiate *Sphaerozosma aubertianum* West from *S. vertebratum* Brébisson ex Ralfs (Coesel & Van Westen 2013). The variety *indicum* differs from the nominate in that the sinus is more open and cuneate, making the isthmus more elongate and distinct. The pores of the nominate variety of this species have been observed to cross each other in an 'x' fashion (Coesel & Van Westen 2013). Unfortunately, due to the lack of empty semicells in the material available, this feature was not discernible.

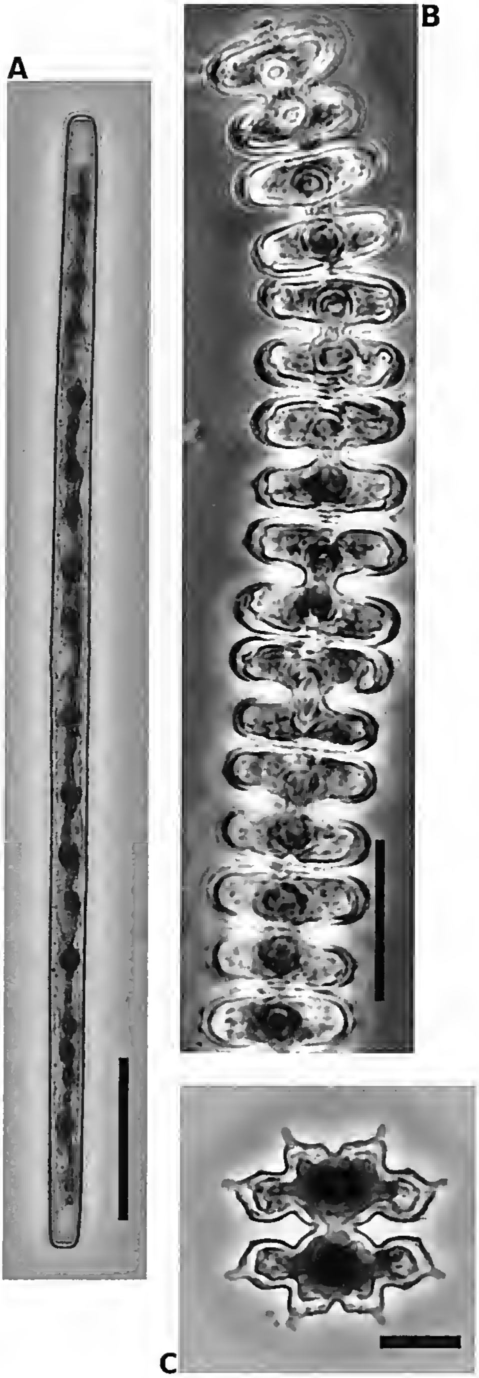

**Figure 2. A.** *Haplotaenium minutum* var. *elangatum*, 200× mag. Brightfield. Scale Bar = 40 µm; **B.** *Sphaerozosma aubertianum* var. *indicum*, 400× mag. Phase contrast. Scale Bar = 20 µm; **C.** *Euastrum planctonicum*, faceview, 400× mag. Brightfield. Scale Bar = 10 µm.

***Location:*** Ewen Maddock Dam.

***Distribution:*** New record for Australia; previously reported from India and Thailand. The nominate variety has been previously recorded from Victoria.

## 6. *Staurastrum biwaense* Hirano

Yamaguchi & Hirano (1953), *Acta Phytotax. et. Geobot.* 15: 56, figs. 7–9.

Hirano (1959), *Flora Desmidiarum Japonicum* VI 373, pl. 49:12–14.

***Dimensions:*** L. cpr. 45.4–64.3 µm, L. spr. 28.5–32.1 µm, Br. cpr. 75–94.8 µm, Br. spr. 24.6–28.2 µm, Isth. 9.5–10.8 µm. (Fig. 1E)

***Description:*** *Cells* triradiate, very rarely biradiate. *Cell body* slightly longer than broad, deeply constricted. *Semicell body* in face view triangular and cup-shaped, lacking any ornamentation or granulation. *Processes* dentate, extend horizontally then arise divergently, terminating with 3 robust, sharply-pointed spines. *Secondary vertical process* occasionally found above the base of each of the aforementioned processes which in comparison are much shorter, and terminate with 2 spines. The cells in endview are triangular with slightly concave sides, with the main, basal processes appearing to be slightly curved in an anticlockwise direction. *Chloroplast* furcoid, extending about two-thirds of the way into both the primary and secondary processes.

***Remarks:*** The dimensions and description match well with Hirano (1959) except for the short apical process being described as *'trispinatus'* rather than bispinate. However, figure 13 provided by Hirano (1959) clearly shows them as bispinate like the cells observed in this survey. This desmid has morphological affinities with *Staurastrum rosei* Playfair and the *S. sexangulare* complex.

***Location:*** Baroon Pocket Dam and Hinze Dam.

***Distribution:*** New record for Australia, originally described from Japan.

## 7. *Staurastrum* sp. 'SE Queensland'

***Dimensions:*** L. cpr. 40.5–88.6 µm (*71.3 µm*; *n*=26), L. spr. 35.9–51.3 µm (*41.8 µm*; *n*=29), Br. cpr. 68.6–112.8 µm (*88.8 µm*; *n*=26), Br. spr. 17.7–30.8 µm (*23.3 µm*; *n*=30), Isth. 8.6–13.3 µm (*10.4 µm*; *n*=32). (Figs 3 A–D; 4 A–C)

***Description:*** *Cells* triradiate, the occasional biradiate/triradiate janus forms are very rarely encountered. *Cell* *body* cup-shaped with a slightly swollen base above the isthmus which can on occasions be reduced and not apparent. *Processes* arising divergently, corrugated and ending with 4 robust spines. Below each process is a group of granules on the basal swelling. *Cell margin* in endview triangular in outline with several apical verrucae of the same size, arranged in an intramarginal arc, with the first and last verrucae projecting beyond said margins. *Annulus*, in endview, spherical with the aforementioned basal granules visible in line with each of the three processes. *Chloroplast* furcoid with a single, centrally placed pyrenoid in each semicell. *Zygospore*, L. cpr: 65.4–75.4 µm and L. spr: 31.3–37.1 µm, angularly globose to isohedral, sides flat with angles producing into processes that fork dichotomously three times.

***Remarks:*** The species described has clear morphological affinities with the *Staurastrum pingue/planktonicum* complex and matches what Thosmasson and Tyler (1971) designated as *S. pingue* Teiling from the plankton of Tasmanian lakes. However, there are marked differences which separate it from this complex in the strict sense, such as the ornamentation of the body and apex and the presence of four distinct spines that terminate the end of the processes rather than three as discussed by Kusber and Scharf (2009). These characters share similarities with *S. manfeldtii* var. *fluminense* (Deplonte) Schumacher, but the semicell body of the Australian populations is granulate rather than spinulate when compared to the original illustration by Schumacher and Whitford (1961). Furthermore, the supraisthmal granules, referred to as "teeth" in Schumacher and Whitford (1961) had combinations of three + four or two + three whereas the cells observed in this survey were much more variable and reduced

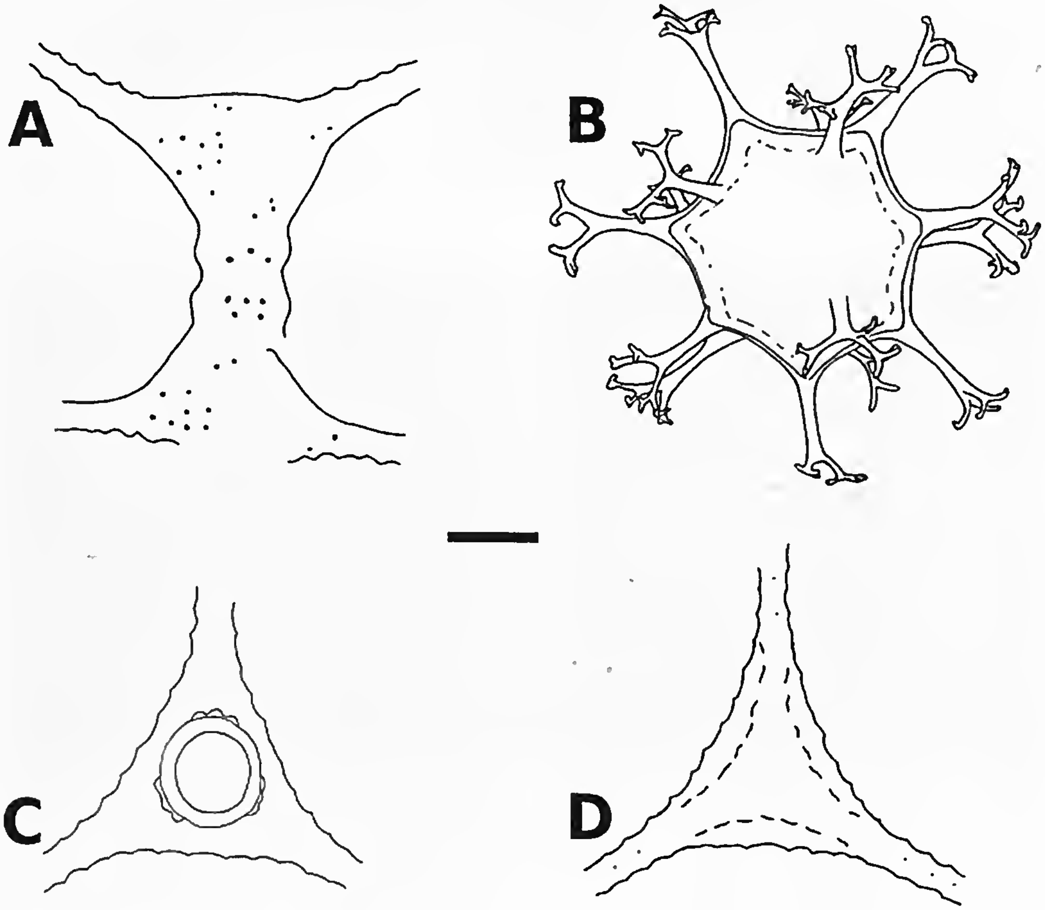

**Figure 3.** Line drawings of *Staurastrum* sp. from Baroon Pocket Dam. **A.** Ornamentation of basal inflation; **B.** Zygospore; **C.** Annulus, showing shape and ornamentation; **D.** Apex, showing intramarginal verrucae. Scale Bar = 10 µm.

in number, having at most the aforementioned two + three combination. Both Viyakornvilas (1974) and Ling and Tyler (2000) also reported a very similar looking *Staurastrum* from Australia under *S. pseudosebaldi* var. *planctonicum* Teiling and *S. pseudosebaldi* Wille respectively. *Staurastrum pseudsebaldi* is considered an artificial species due to taxonomically ill-defined morphological characters, so much so that Coesel and Meesters (2013) transferred it as a mere variety of *S. manfeldtii* and therefore many records under this name are likely to be other, unrelated Staurastra. Viyakornvilas (1974) considered *S. manfeldtii* var. *fluminense* (Deplonte) Schumacher but was not able to observe the ornamentation of the cell body, which was obscured by the chloroplast. Ling and Tyler's (2000) *l.c.* depictions of many of the *S. pseudosebaldii* forms have the characteristic supraisthmal granulation, especially on Pl. 143 figs 3–5. Whether the other depictions under the same name form a series of morphological continuity for a single species requires further investigation. The material from Queensland is also similar to *S. multispiniceps* A.M.Scott & G.W.Prescott from Indonesia but that species has an apparently smooth body with a convex apex bearing several small conical spines.

This study observed what could be best described as a mass-spawning event that occurred throughout the Baroon Pocket Dam catchment where seven different sample sites (some of which were kilometres apart) had 'blooms' of this *Staurastrum*. In these blooms cells were observed paired up, positioned perpendicular to one another within a common mucilaginous envelope. There were empty cells adjacent to the resultant zygospores.

***Location:*** Baroon Pocket Dam, Leslie Harrison Dam and Hinze Dam.

### 8. *Xanthidium bifidum* (Brébisson) Deflandre

Deflandre (1929), *Bull. Soc. Bot. France* 76: 137.

Croasdale & Flint (1988), *Flora of New Zealand. Freshwater Algae, Chlorophyta, Desmids*, vol. II 120, pl. 58: 5 & 6.

***Basionym:*** *Arthrodesmus bifidus* Brébisson (1856), *Mém. Soc. Imp. Sc. Nat. Cherbourg* 4: 135, pl. 1: 19.

***Synonym:*** *Octacanthium bifidum* (Brébisson) Compère (1996), *Nova Hedwigia* 112: 503, fig. 3.

***Dimensions:*** L. csp. 16.7–19.2 µm, Br. csp. 16.3–18.2 µm, Isth. 5.8–6.5 µm. (Fig. 1B)

***Description:*** *Semicells* semi-lunate with the emerging lateral angles bifurcate. *Sinus* open, slightly notched.

***Remarks:*** The plants most closely resemble those depicted by Scott and Prescott (1961) under the synonym *Arthrodesmus bifidus*.

***Location:*** Lake Manchester.

***Distribution:*** New record for Australia. This species is putatively cosmopolitan.

## Conclusion and discussion

Despite the low number of taxa reported here, their geographic distributions are of interest. *Cosmarium mikron* Skuja and *Sphaerozosma auberitianum* var. *indicum* (W.B.Turner) Coesel & Ngearnpat have thus far been recorded solely from what is known as the Indo-Malaysian/North Australian region (IMNAR) (Coesel 1996; Vyverman 1996). The presence of these taxa suggest that south-eastern Queensland has elements of an IMNAR desmid flora and supports the assumption that the yet to be catalogued parts of northern Queensland encompass this biogeographic region (Vyverman 1996; Coesel & Dingley 2005). Conversely, *Euastrum planctonicum* A.Kenins has thus far only been reported from south-eastern Australia which coincides with similar distributions of desmids known solely from southern Australia and/or New Zealand (Coesel 1996). The assemblage of taxa from the two bioregions found in this study correlates with a previous survey of freshwater algae from north-eastern New South Wales by Skinner (1979) who notes the desmid flora as having both elements of the IMNAR and temperate Australia-New Zealand flora, and suggests northern New South Wales may be part of the interface between the two floras. Such an interface would match patterns detected for higher plants. Far south-east Queensland and far north-eastern New South Wales comprise a floristic zone in higher plants known as the Mcpherson-Macleay overlap (Burbidge 1960); and much the same region is included in the eastern Queensland phytogeographical region developed by González-Orozco et al. (2014). As noted by previous Australian studies on desmids, such as Tyler (1970) and Dingley (2001b), records are scant and patchy, and further studies are required in order to synthesise a better understanding of distribution patterns for this group of algae, comparable to the knowledge of higher plant patterns.

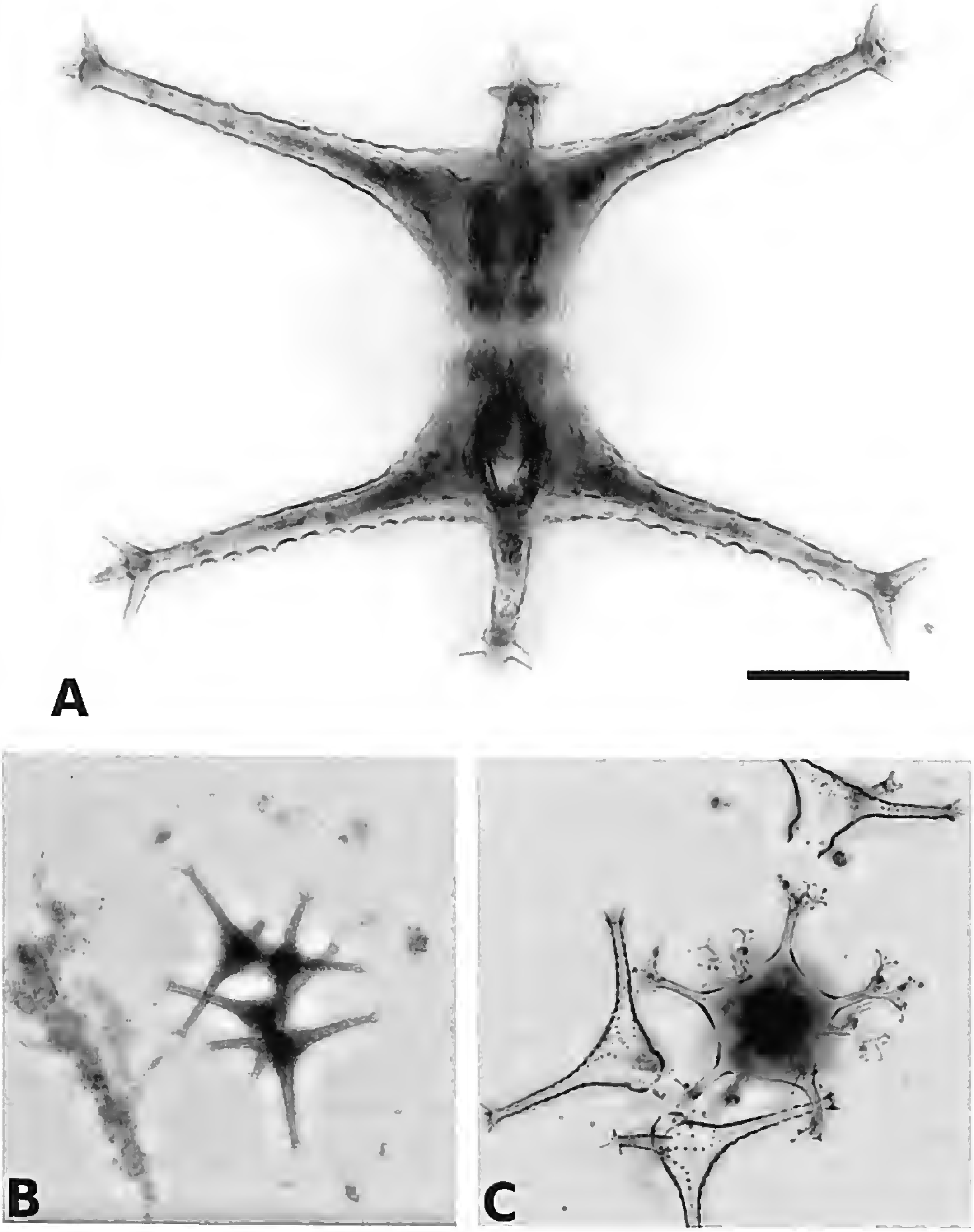

**Figure 4.** *Staurastrum* sp. from Leslie Harrison Dam. **A.** Faceview, 400× mag. Focus-stacked, Brightfield. Scale Bar = 20 µm; **B.** Pair initiating conjugation within common mucilaginous envelope, 200× mag. Focus-stacked, Brightfield; **C.** Empty semicells adjacent to resultant zygospore post conjugation, 400× mag. Focus-stacked, Brightfield.

## Acknowledgements

The corresponding author wishes to acknowledge the following people and organisations: Seqwater for permission to study and in some cases sample the study area for analysis; Australian Laboratory Services (Brisbane) for use of the laboratory equipment, obtaining samples from the study area and support from management, staff and colleagues; and, last but not least, my supervisor, Associate Professor Darren Ryder from University of New England.

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Muelleria

35: 35–42

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# Disjunct populations of *Monocarpus sphaerocarpus* (Monocarpaceae, Marchantiopsida) within Australia show no sequence variation

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## Introduction

*Monocarpus sphaerocarpus* D.J.Carr is a relatively rare and intriguing Southern Hemisphere liverwort. With extant plants known only from a few locations in Victoria, South Australia and Western Australia (Fig. 1), it is typically found growing on subsaline soils around saline lakes or near coastlines (Figs 2a, b). When initially described by Carr in 1956, its placement within the liverworts was not entirely clear (Carr 1956). Carr considered it closely related to *Sphaerocarpos* Boehm. and raised a new suborder Monocarpineae to accommodate the new species but argued that *Monocarpus* D.J.Carr, *Sphaerocarpos* and allied genera should be placed within the order Marchantiales. Subsequent authors have debated its position (see summary in Forrest et al. 2015). It was not until molecular data became available that this species was finally confirmed to be sister to members of the Sphaerocarpaceae, supporting its place within the Order Sphaerocarpales (Forrest et al. 2015).

## Abstract

Populations of the complex thalloid liverwort *Monocorpus sphaerocarpus* D.J.Carr (Monocarpaceae) found in a disjunct distribution across southern Australia were sequenced to investigate whether plants found in eastern Australia were a different species from those found on the west coast of Australia, in line with potential differences in spore morphology. Sequences from five plastid gene regions were generated from specimens collected from several populations found in the states of Victoria, South Australia and Western Australia and spore morphology was reviewed using light and scanning electron microscopy. All individuals belonged to a single haplotype on the basis of the five plastid markers *psb*A-trnH, *trn*L-F, *rbc*L, *rpo*C1, and *rps*4-trnAS. Moreover, observed morphological differences were not consistent with geographical provenance and more likely indicative of infraspecific variation or difference in spore maturity when collected. These results support the recognition of only a single species in Australia.

**Key words:** liverworts, plastid markers, invariant loci, spore

ISSN: 0077-1813 (print) · ISSN: 2204-2032 (online)

In this same study, Forrest et al. (2015) compared spores from Australian populations with spores from the single known South African collection of the species (Perold 1999), finding distinct differences between the South African and Australian plants. Forrest et al. (2015) also suggested that plants from populations in Western Australia may not be conspecific with those in Victoria, based on spore differences: the cingulum is more pronounced in the Victorian populations than that of the Western Australian population (Figs 2d, e). Moreover, the disjunct distribution was cited as possible evidence for the recognition of two different species (Forrest et al. 2015). In our study, several Australian populations were sampled in the eastern, southern and western parts of the country, and five molecular markers were sequenced from these samples in order to investigate the delimitation of the taxa.

## Materials and methods

### Molecular data: DNA extraction, amplification and sequencing

Samples of *Monocarpus sphaerocarpus* were obtained from a number of recent collections from previously known localities in Western Australia and Victoria, as well as from two new localities in South Australia (see Table 1). In total, 12 new samples were collected (five from Western Australia, five from Victoria and two from South Australia) and compared to a previously studied specimen from Western Australia (Forrest et al. 2015). DNA extractions were performed using a Qiagen DNeasy Plant Mini kit following the manufacturer's instructions (Qiagen, Melbourne, Victoria, Australia). Five plastid gene regions were amplified: *rbc*L, *rpo*C1,

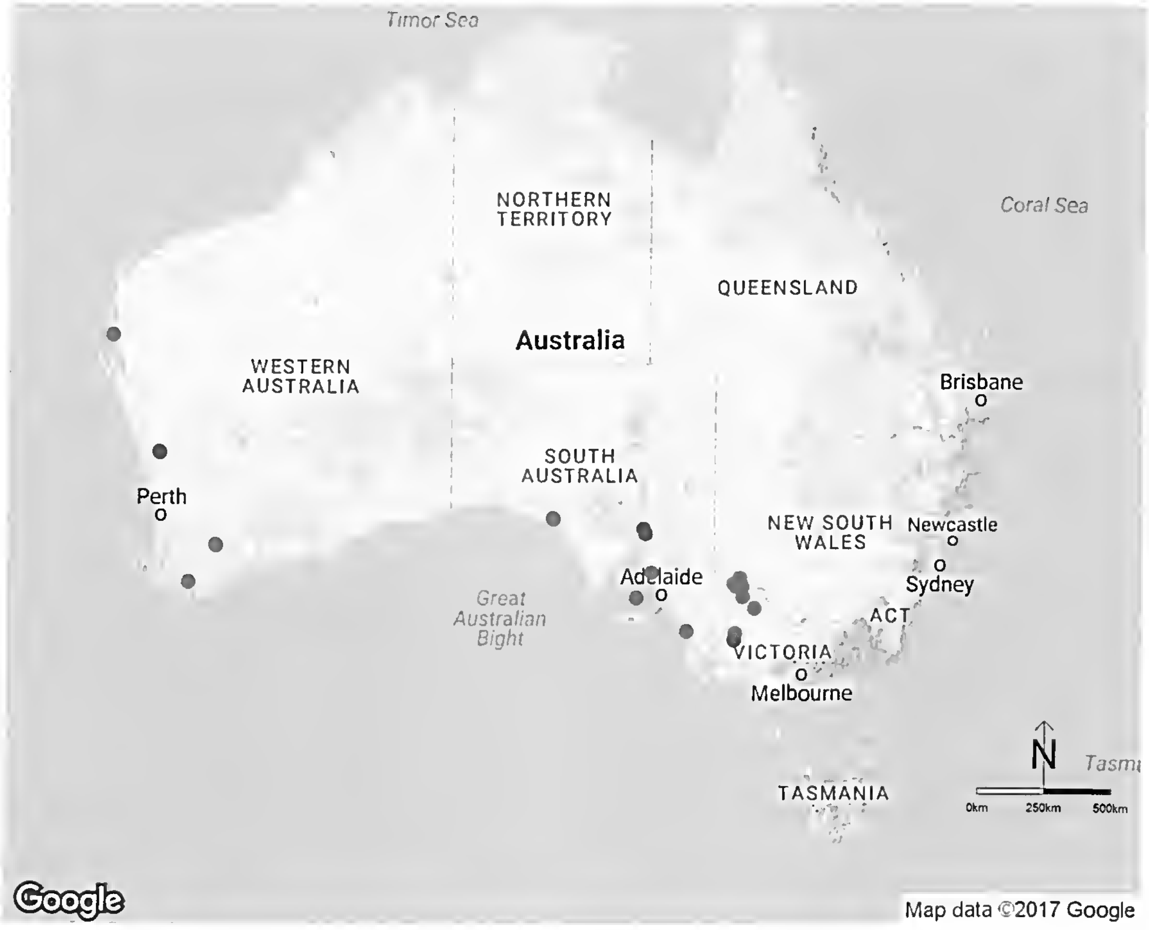

**Figure 1.** Map of known locations of *Monocarpus sphaerocarpus* in Australia, indicated by red filled circles, including locations of populations sampled for this study as blue filled circles

**Table 1.** Taxon and gene sampling for this study. GenBank numbers are listed for each marker and missing data are represented by a dash. GenBank numbers shown in bold were newly produced as part of this study.

| Species | Coll. number (herbarium) | DNA voucher | Locality details | *rbc*L | *rpo*C1 | *trn*L-F | *psb*A-trnH | *rps*4-trnAS |
|---|---|---|---|---|---|---|---|---|
| *Monocarpus sphaerocarpus* | HMJ171-1 (CANB) | HMJ171-1 | Australia, WA, at the edge of Yarra Yarra Lakes | **KY707128** | **KY707149** | **KY707155** | **KY707164** | **KY707139** |
| *Monocarpus sphaerocarpus* | HMJ171-2 (CANB) | HMJ171-2 | Australia, WA, at the edge of Yarra Yarra Lakes | **KY707129** | **KY707150** | **KY707156** | **KY707165** | **KY707140** |
| *Monocarpus sphaerocarpus* | HMJ172 (MEL) | HMJ172 | Australia, WA, at the edge of Yarra Yarra Lakes | **KY707130** | – | **KY707157** | **KY707166** | **KY707141** |
| *Monocarpus sphaerocarpus* | HMJ173 (MEL) | HMJ173 | Australia, WA, at the edge of Yarra Yarra Lakes | **KY707131** | – | – | **KY707167** | – |
| *Monocarpus sphaerocarpus* | HMJ174 (MEL) | HMJ174 | Australia, WA, at the edge of Yarra Yarra Lakes | **KY707132** | – | **KY707160** | – | **KY707142** |
| *Monocarpus sphaerocarpus* | Jalley & Milne 171 (E) | – | Australia, WA, at the edge of Yarra Yarra Lakes | KT356975 | KT357003 | – | KT356965 | KT356985 |
| *Monocarpus sphaerocarpus* | JM606 (MEL) | JM606 | Australia, VIC, red ochre pit, Raak Plain | **KY707133** | – | – | **KY707168** | **KY707145** |
| *Monocarpus sphaerocarpus* | JM607 (MEL) | JM607 | Australia, VIC, old gypsum mine, opposite red ochre pit, Raak Plain | **KY707134** | **KY707151** | **KY707161** | **KY707169** | – |
| *Monocarpus sphaerocarpus* | JM611 (MEL) | JM611 | Australia, VIC, Lake Duchembegarra Flora and Fauna Reserve | **KY707135** | **KY707152** | – | **KY707170** | **KY707146** |
| *Monocarpus sphaerocarpus* | JM605 (CANB) | JM605 | Australia, VIC, Nowingi Line Track, near Raak Plain | – | – | **KY707159** | **KY707171** | **KY707144** |
| *Monocarpus sphaerocarpus* | JM605-2 (CANB) | JM605-2 | Australia, VIC, Nowingi Line Track, near Raak Plain | **KY707136** | – | **KY707158** | **KY707172** | **KY707143** |
| *Monocarpus sphaerocarpus* | DCC13535A (CANB) | DCC1353SA | Australia, SA, Winninowie Conservation Park | **KY707137** | **KY707153** | **KY707162** | – | **KY707147** |
| *Monocarpus sphaerocarpus* | DCC13555A (CANB) | DCC13555A | Australia, SA, Port Augusta, on mud flats | **KY707138** | **KY707154** | **KY707163** | **KY707173** | **KY707148** |
| *Sphaerocarpos drewei* | Dayle 7193 (E) | 07-02394 | USA, California | **KY823573** | **KY823561** | – | **KY823485** | – |
| *Sphaerocarpos drewei* | Schill 142 (no. 233) (E) | 08-01271 | USA, California | **KY823573** | **KY823561** | – | **KY823486** | – |
| *Sphaerocarpos michelii* | Thauvenat *s.n.* (H918) | 06-06279 | France | **KY823573** | **KY823561** | – | **KY823487** | – |
| *Sphaerocarpos michelii* | Long 36568 (E) | 08-00257 | Portugal | **KY823573** | **KY823561** | – | **KY823488** | – |
| *Sphaerocarpos michelii* | Halyoak 03-417 (E) | 08-00485 | Great-Britain, Cornwall | **KY823573** | **KY823561** | – | **KY823489** | – |
| *Sphaerocarpos michelii* | Lang 36581-a (E) | 08-00495 | Portugal | **KY823573** | **KY823561** | – | **KY823490** | – |
| *Sphaerocarpos stipitatus* | Heddersan 16432 (E) | 07-01921 | South-Africa, Cape | **KY823573** | **KY823561** | – | **KY823491** | – |
| *Sphaerocarpos stipitatus* | Long 20843 (E) | 07-02112 | Nepal | **KY823573** | **KY823561** | – | **KY823492** | – |
| *Sphaerocarpos texanus* | Thauvenat *s.n.* (H917) (E) | 06-06278 | France | **KY823573** | **KY823561** | – | **KY823493** | – |
| *Sphaerocarpos texanus* | Lang 36573 (E) | 07-01671 | Portugal, Beira Litoral | **KY823573** | **KY823561** | – | **KY823494** | – |
| *Sphaerocarpos texanus* | Ghullam TG1868439155 (E) | 08-01275 | Great-Britain, Norfolk | **KY823573** | **KY823561** | – | **KY823495** | – |
| *Sphaerocarpos texanus* | Etdaej *s.n.* (E) | 08-01287 | Turkey | **KY823573** | **KY823561** | – | **KY823496** | – |

*trn*L-F, *psb*A-trnH and *rps*4-trnAS. Some DNA sequence data was also generated for accessions from four species of *Sphaerocarpos*, for the restricted set of plastid regions, *rpo*C1, *rbc*L and *psb*A-trnH (Table 1). Primer sequences and amplification parameters are shown in Table 2. For the amplification reactions, 1 μl of genomic DNA was added to the following PCR mix: 2.5 μl 10 × $NH_4$ PCR buffer, (Bioline, London, UK); 1.25 μl of $MgCl_2$ (50 mM); 2.5 μl dNTP (2 mM); 1 μl of each primer (10 μM); 0.3 μl DNA polymerase Bioline BioTaq (5 U/μl$^{-1}$), and water to a total volume of 25 μl. The PCRs were performed using a Mastercycler pro S (Eppendorf, Hamburg, Germany). The PCR products were sent to Macrogene (Seoul, South Korea) for cleaning and sequencing. Sequences were assembled and edited using Sequencher v. 5.4.1 (Gene Codes Corporation, Ann Arbor, Michigan, USA) and aligned manually with Mesquite v. 3.04 (Maddison & Maddison 2016) and inspected visually. GenBank numbers are available in Table 1.

### Morphology: scanning electron and light microscope images of spores

Mature or near mature spores were taken from fertile plants and placed in water on glass slides for light microscopy. Photos of the habitat and plants *in situ* were taken with a Canon Powershot G12 digital camera and light micrographs were taken with a Nikon Coolpix 500 digital camera. For scanning electron microscopy (SEM), spores were placed on double-sided sticky tape on aluminium stubs, coated with gold and viewed using a Zeiss EVO LS 15 Environmental SEM.

## Results

### Molecular data

Newly obtained sequences and sequences already available In GenBank were aligned manually and compared visually. Eleven new sequences were obtained for *rbc*L (Table 1). They were aligned together with the *rbc*L sequence of *Monocarpus sphaerocarpus* available from GenBank (KT356975), but show no variation among the 593 overlapping nucleotide sites. Similarly, the six new *Monocarpus* sequences of *rpo*C1 (797 nucleotide sites) were identical, and identical to the *rpo*C1 sequence available in GenBank for *M. sphaerocarpus* (KT357003). All nine new *Monocarpus* sequences of *trn*L-F (456 nucleotide sites) were the same. No variation was seen between ten new sequences of

**Table 2.** List of PCR primers used to amplify the five markers *psb*A-trnH, *rbc*L, *rpo*C1, *rps*4-trnAS and *trn*L-F. PCR conditions are described as follows: initial denaturation, number of cycles × (denaturation, annealing, extension), final extension.

| Gene region | Direction | Primer name | Primer sequence | Authors | PCR conditions |
|---|---|---|---|---|---|
| *psb*A-trnH | forward | psbA-501F | TTTCTCAGACGGTATGCC | C. Cox, Duke, NC, pers. comm. | 94°C (1 min), 35x [93°C (1 min), 50°C (1 min), 72°C (3 min)], 72°C (7 min) |
| | reverse | trnHR | GAACGACGGGAATTGAAC | C. Cox, Duke, NC, pers. comm. | |
| *rbc*L | forward | rbcL-aaf | ATGTCACCACAAACAGAGACTAAAGC | Kress & Erickson 2007 | 94°C (1 min), 35x [93°C (1 min), 50°C (1 min), 72°C (3 min)], 72°C (7 min) |
| | reverse | rbcL-aar | CTTCTGCTACAAATAAGAATCGATCTC | Kress & Erickson 2007 | |
| | reverse | rbcL-634R | GAAACGGTCTCTCCAACGCAT | Fazekas et al. 2008 | |
| *rpo*C1 | forward | rpoC1-LP1 | TATGAAACCAGAATGGATGG | Kew website as cited by Wynns & Asmussen-Lange 2014 | 94°C (1 min), 40x [94°C (30 sec), 48°C (40 sec), 72°C (40 sec)], 72°C (5 min) |
| | reverse | rpoC1-LP5 | CAAGAAGCATATCTTGASTYGG | Kew website as cited by Wynns & Asmussen-Lange 2014 | |
| *rps*4-trnAS | forward | rps5 | ATGTCCCGTTATCGAGGACCT | Nadot et al. 1994 | 94°C (1 min), 35x [93°C (1 min), 50°C (1 min), 72°C (3 min)], 72°C (7 min) |
| | reverse | trnAS | TACCGAGGGTTCGAATC | Baker pers. comm. in Cox et al. 2000 | |
| *trn*L-F | forward | trnLF-c | CGAAATCGGTAGACGCTACG | Taberlet et al. 1991 | 94°C (1 min), 35x [93°C (1 min), 50°C (1 min), 72°C (3 min)], 72°C (7 min) |
| | reverse | trnLF-f | ATTTGAACTGGTGACACGAG | Taberlet et al. 1991 | |

*rps*4-trnAS (1034 nucleotide sites), or between those and the *rps*4-trnAS sequence available in GenBank for *M. sphaerocarpus* (KT356985). Finally, no variation was found between ten new *Monocarpus* sequences of *psb*A-trnH (645 nucleotide sites), or between those and the *psb*A-trnH sequence available in GenBank for *M. sphaerocarpus* (KT356965). Obtained *psb*A-trnH sequences were short as the reaction for the reverse primer failed to sequence for nine out of ten samples. Our *psb*A-trnH sequences are, therefore, based on the single strand of the forward primer. A repeat at the 3′ end of *psb*A-trnH might have cause the sequencing problem. Although data were missing for all five markers (one sequence for *rbc*L, six for *rpo*C1, four for *trn*L-F, two for *psb*A-trnH and two for *rps*4-trnAS), sequences obtained came from specimens collected in all three sites: Western Australia, Victoria and South Australia. Based on our taxon sampling, none of these markers shows any variation across the Australian distribution range of the species (from Western Australia to Victoria).

## Spore morphology

The spores of *Monocarpus sphaerocarpus* are more or less hemispherical in equatorial view, between 42–60 μm in diameter and 40–50 μm in height. The distal face is distinctly spinose to tuberculate (Figs 2c, e, g). The proximal face is without a triradiate mark, may be flat or concave in equatorial view, and with a structure not unlike a short cylinder projecting from the proximal face (Fig. 2f). On the proximal surface runs a cingulum which is almost doughnut-shaped; within the 'hole', or central area of the cingulum, are a series of hole-like depressions (Figs 2d, e). The spores from all populations were re-examined and ornamentation patterns found to be more or less the same for the convex distal face, which in all cases consists of numerous spine-like or peg-like protuberances (Figs 2c, e). The variation between Victorian and Western Australian populations, as also noted by Forrest et al. (2015), related to the prominence of the proximal cingulum which surrounds the central portion of the proximal face. In equatorial view, this part of the proximal face projects as a short solid cylinder surrounding the flattened to slightly concave central part of the face (Fig. 2f). In proximal view, this central area is ornamented with irregular vermiform ridges and tubercles that form small, irregular holes or areolae. Spores from the Victorian populations have prominent cingula which are more or less smooth (Fig. 2d), whereas the cingula of Western Australian populations are variable with some spores in the same capsule with smooth cingula similar to those seen in the Victorian populations (Fig. 2g). In some spores, the cingulum is not as prominent or smooth but instead has raised uneven protuberances, making it more textured in appearance (Fig. 2e). However, spores have also been found within the Western Australian populations that possess the more prominent smooth cingulum, approaching those seen in the Victorian spores. The South Australian spores are more similar to the Western Australian spores, with a less prominent cingulum, but this too can vary. Measurements and observations were made on two collections from Victoria (*Carr s.n.* Nangiloc, Vic & *Carr s.n.* Salt Lake nr Nowingi, Vic, both at CANB), which had open mature capsules, and one from Western Australia (*HMJ 171* at CANB), which had capsules that are shrunken and intact and therefore immature. The diameter range of the mature Victorian spores is 52.5–65 μm while those from the Western Australian collections range from 37.5–55 um, considerably smaller. Cingula are well developed and prominent in equatorial views of the Victorian spores, while the cingula of the Western Australian spores have not developed at all. This observed variation amongst populations can be due to natural variation within a capsule, or amongst individuals within a population. Given that capsules of different ages were compared, the observed differences are explicable by different stages of maturity of the spores, whereby the cingulum did not fully develop until maturity.

# Discussion

All individuals belong to a single haplotype on the basis of five plastid markers. This was expected for the gene regions *rbcL* and *rpoC1*, but less so for the usually more variable spacer regions *trn*L-F, *psb*A-trnH and *rps4*-trnAS. No or little variation in markers commonly used for species-level phylogeny of bryophytes has previously been reported, e.g., for species in the moss genera *Bryum* Hedw. (Holyoak & Hedenäs 2006) and *Drepanocladus* (Müll.Hall) G.Roth (Hedenäs 2008). A lack of variation in common phylogenetic markers does not mean that there is only one species. For example,

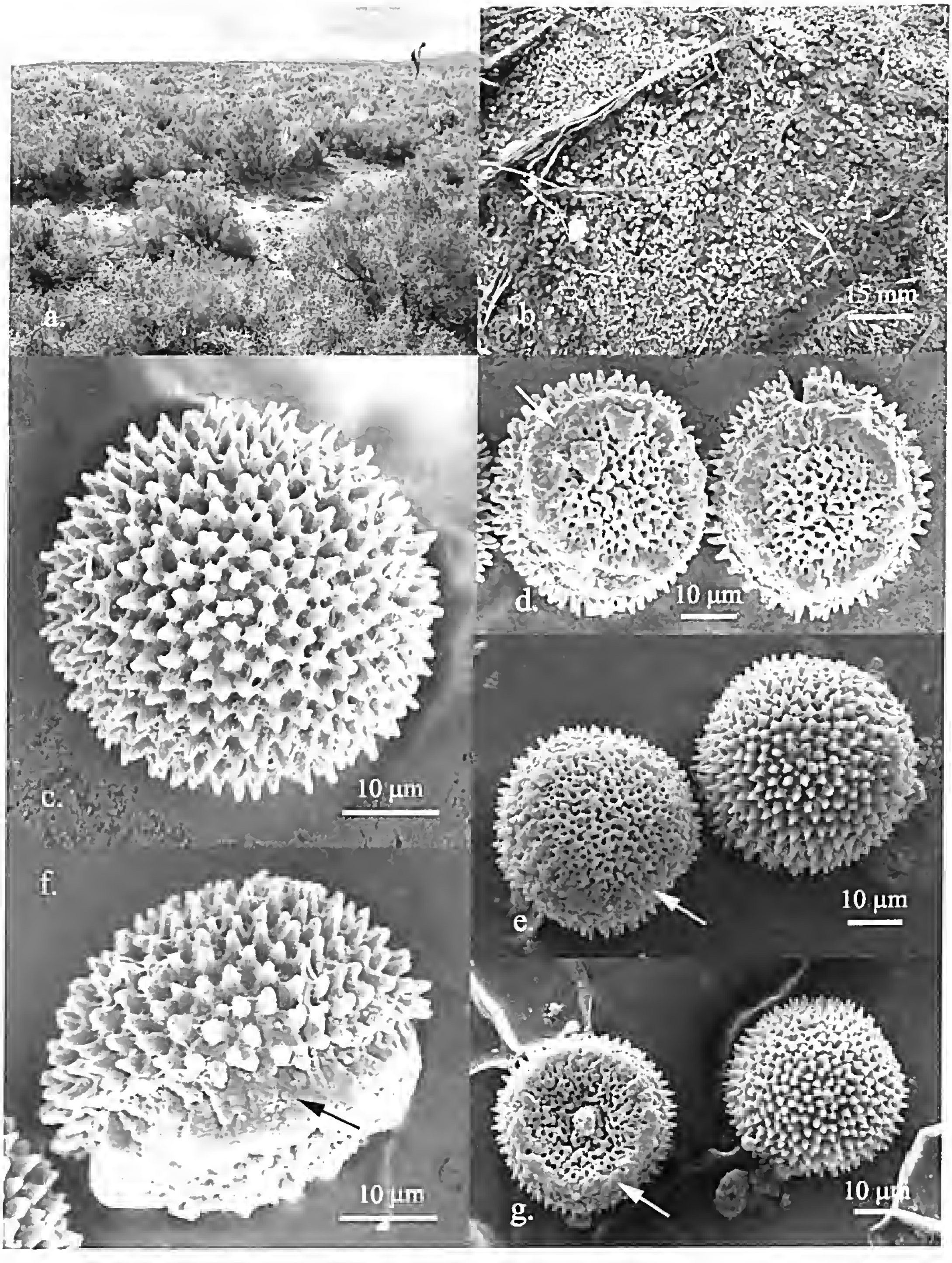

**Figure 2. a.** Habitat of *Monocarpus sphaerocarpus* at Winninowie CP, South Australia; **b.** plants *in situ* at Port Augusta mud flats, South Australia; **c.** distal view of spore from *Carr s.n.* collections from Victoria; **d.** proximal views of spores from *Carr s.n.* collections from Victoria; **e.** proximal and distal view of spores from Western Australian collections, *Jolley & Milne 171*; **f.** equatorial view of spore showing the cylindrical shape of the proximal cingulum from *Carr s.n.* from Victoria; **g.** proximal and distal view of another two spores from the same capsule as *e.* from Western Australian collections, *Jolley & Milne 171*. All arrows indicate position of cingulum on the proximal face of spore.

in the liverwort *Frullania asagrayana* Mont., although the plastid loci that were sequenced proved invariant, the use of microsatellite markers allowed detection of reproductively isolated groups (Ramaiya et al. 2010).

In contrast, when we looked at within-species sequence variation in a second Sphaerocarpalean genus, *Sphaerocarpos*, only one of the four species sampled had DNA sequences identical for all loci of all accessions (*Sphaerocarpos texanus* Austin from France, Portugal, Turkey and the United Kingdom – no variation for *rbc*L and *rpo*C1, one base change in *psb*A-trnH). Within the three other morphologically defined species we sampled, the sequences from all three loci were variable (*S. stipitatus* Bisch. ex Lindenb. from South Africa and Nepal — one base change in *rbc*L; one base change in *rpo*C1; four base changes in *psb*A-trnH; *S. drewei* Wigglesw. from California, USA — two base changes in *rbc*L; three base changes in *rpo*C1; one base change in *psb*A-trnH; *S. michelii* Bellardi from France, Portugal and the United Kingdom — up to nine base changes in *rbc*L; up to seven base changes in *rpo*C1; up to five base changes in *psb*A-trnH). As well as being phylogenetically related, species in *Sphaerocarpos* share some ecological features with *Monocarpus*, including a tendency to occur in ephemeral habitats.

For *Monocarpus sphaerocarpus*, we consider that the spore differences observed by Forrest et al. (2015) are more than likely due to maturity of spores or natural variation within the species (Figs 2d, e). In combination, both the lack of variation within five plastid loci and the lack of clear spore morphological differences across Australian populations are consistent with the recognition of a single species. The occurrence of a single chloroplast haplotype across Australia is indicative of either the lack of any barrier to gene flow between populations (i.e. long distance dispersal), or recent range size expansion from a small ancestral population. Population-level markers (e.g. microsatellites) would need to be identified to explore the genetic structure among the widely separated Australian populations of *M. sphaerocarpus*.

As currently sampled, this species has a rather disjunct distribution on the Australian continent. However, it is rarely collected due to its small size and ephemeral nature, and we have limited knowledge of the duration of its colonies and its life history. Of the 37 collections in Australian herbaria, most were collected in late winter to early spring. Only two sites in Victoria, the Raak Plain and Lake Duchembegarra, have been re-visited and the species relocated and recollected after a period of approximately 50 years. One of these sites, the Raak Plain, was re-visited again the following November (2016) with no sign of the plant (Milne, pers. obs.). Therefore, there is evidence that the lifespans of individuals are most likely brief and their occurrence in time and space sporadic, with all collections probably the result of opportunistic encounters. Known populations may not be truly disjunct, but may form part of a continuous distribution range comprising yet-to-be-discovered populations across southern Australia, stretching from western Victoria through South Australia, along southern Western Australia and finishing up along the mid-west coast region of Western Australia near Carnarvon.

## Acknowledgements

The authors would like to thank Graham Bell of AD herbarium and Alison Downing from Macquarie University for providing live plants collected from a recent and new location in South Australia to include in our molecular dataset. They would also like to thank David Long for help sampling *Sphaerocarpos*, and Lan Li (CANB herbarium) for technical support with the DNA work. The Scottish Government's Rural and Environment Science and Analytical Services Division supports research at the Royal Botanic Garden Edinburgh.

We also thank the reviewers, Matt Renner and an anonymous reviewer, and subeditor, Neville Walsh, whose comments improved this paper.

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ROYAL
BOTANIC GARDENS
VICTORIA

# The origins of botanic gardens and their relation to plant science, with special reference to horticultural botany and cultivated plant taxonomy

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> *On ne connait pas complètement une science tant qu'on n'en sait pas l'histoire*
>
> *Cours de Philosophie Positive 1835; Auguste Comte (1798–1857)*

## Introduction

Botanic gardens are versatile institutions whose objectives depend on both local circumstances, and the more general social, economic and environmental needs and concerns of the day. As they are diverse and evolving institutions, the provision of a precise formal definition would be both contentious and misleadingly prescriptive.

The oldest existing botanic gardens date back to the early modern period, to the educational physic gardens associated with the medical faculties of universities in 16th-century Renaissance Italy. Today's botanic gardens have little to do with these early and highly specialised medicinal gardens whose narrow academic and scientific goals and formal designs have subsequently taken on additional economic, environmental, aesthetic and other values. Collectively the world's botanical gardens have come to reflect the many-sided relationship between humans and plants and, though science provides a common underlying theme, they may emphasise other objectives and social values.

## Abstract

This paper explores the origin and development of botanic gardens including consideration of the beginnings of plant cultivation and domestication and the emergence of botanical science. We suggest that the origins, history and functions of modern botanic gardens pre-date the European Renaissance and that they reflect the social, economic and environmental circumstances of their times.

ISSN: 0077-1813 (print) · ISSN: 2204-2032 (online)

Our approach is to examine the evolving family of shared characteristics that have, over time, drawn botanic gardens into a global community. We see today's botanic gardens as having much in common with the ornamental and utilitarian gardens of ancient civilisations and the first truly scientific garden established in ancient Athens. The characteristics associated with today's botanic gardens include: public plant displays labelled and thematically arranged in designed landscapes; the presence of some kind of botanical institution; the emphasis on a diversity of plants grown for their utility, beauty, rarity, curiosity and scientific value; and the connection with plant knowledge and education. Many of these factors, and more, relate to general garden history that pre-dates the European Renaissance.

To understand today's cultural landscapes in general, and botanic gardens in particular, we must go back to the very beginnings of plant cultivation and the origins of domesticated plants. What were the social forces that gave rise to our present-day configuration of urban and rural space, the familiar everyday cultivated surroundings of gardens, parks and fields?

## Prehistory

### The beginnings of plant cultivation and domestication

We know that there must have been a time, many millennia ago, when tending plants became more than the simple husbandry of plants growing naturally in the wild. In all likelihood discarded pips and other plant remnants left over from feasting around camp fires sprouted into food plants that could be harvested when sites were revisited. Plants could be grown easily enough from seed, transplants or cuttings in special areas dedicated to their cultivation. Then, over long periods of time, the process of continuous selection of plants with desirable characteristics gave rise to new kinds of plants with combinations of characters not found in their wild ancestors.

The large-scale domestication of animals and plants that we call agriculture did not arise from a single region and tradition. Archaeological evidence suggests that agriculture arose independently in more than ten major centres across the world over a period spanning about 6000 years and referred to as the Neolithic Agricultural Revolution. The earliest of these centres occurred in the Ancient Near East dating back about 12,000 years, probably a product of the conducive climate and growing conditions in this region after the last Ice Age and the presence of both animals and plants amenable to domestication, although the precise reasons are disputed (Rindos 1986; Smith 1986; Diamond 1997; Tudge 2003). In Europe the Agricultural Revolution gradually spread from the Ancient Near East, taking about 8000 years to reach the British Isles in the north-west (Cunliffe 2013).

Worldwide it appears that there were many different kinds of proto-farming leading to the fields and pastures that we are familiar with today (Holmes 2015). In New Guinea, for example, a form of shifting agriculture was practised while in Australia food plants were managed in many different ways (Clarke 2007): there was the carefully managed burning of natural vegetation to flush out animals and induce succulent new shoots, now known as 'firestick farming' (Jones 1969; Gammage 2011), while wild cereals were sometimes harvested *in situ* (Gerritsen 2008) and yams and other plants were propagated and managed in a horticulture-like manner (Gott 2002).

Agriculture provides the big-picture backdrop to the history of botanic gardens not only because it now underpins all human existence as a source of sustenance, but because it produced the surplus wealth that facilitated the urbanisation and civilisation from which botanic gardens would emerge.

Agriculture fed the body but less certain is the way that plants nourished the 'soul'. What were the attitudes and beliefs of our ancestors and how did these influence their plant management?

So far as we know, societies in prehistory attributed nature with human characteristics; it was anthropomorphised, and the spiritual world was one of temporal continuity, extending from past to present and future through ancestors, the living and the afterlife. Underlying the human relationship to plants would have been innate and universal factors: our fascination with their beauty, novelty, utility and the way they teased our intellectual curiosity. But the plant world of our ancestors would have been far richer in symbolism, mystery and religious meaning than that of today.

Plant knowledge was gained by determining which plants were safe to eat, which had medicinal properties, which affected the mind, when and where they grew, as well as their relationship to cultural beliefs. This knowledge entailed precise observation, experimentation and the transmission of cumulative knowledge down the generations as rudimentary science; empirical knowledge whose detail was likely only mastered by special individuals (such as a shaman or medicine man).

Hunter-gatherers lived in small nomadic bands within nature. They were a part of nature itself, much as non-human primates are a part of nature today; they depended on unpredictable weather and other uncertain environmental factors to secure their seasonal sources of food. Their fate, they believed, depended on spiritual forces from an unseen world and it was probably this spiritual realm that dictated plant practices. Perhaps special attention was given to those plants growing in areas set aside for ceremony and ritual, especially areas associated with ancestors and the dead – maybe around a burial mound, sacred tree, sacred grove, spring or a shrine of some kind (Hooke 2010; Nielsen 2013; Turner 2013). Simple shrines dedicated to local deities are found the world over.

We must look to early human settlements to tell us more about the developmental path that led to today's cultivated spaces and the particular plant interests that would later become the special concerns of botanic gardens.

## The Neolithic Revolution and ancient civilisations

### Agriculture and early civilisation

Living together in ever-increasing numbers required the careful management of both people and physical space as more and more land was appropriated from nature for human use.

The Agricultural Revolution altered for all time the relationship between humans and nature in at least three critical ways: it changed the human evolutionary environment; it created a world consisting of new physical spaces (including gardens, parks and fields) with a corresponding new world of associated words and ideas that emphasised a distinction between nature and culture; and it produced the conditions necessary for the emergence of new forms of social organisation and development.

### Human evolution

The natural forces of evolutionary selection that had forged human bodies and minds were being replaced by human-derived selective forces: humans had moved out of their environment of evolutionary origin into an environment of their own making. From this time on, changes in human social circumstances would, for the most part, be a consequence of rapid cultural change, rather than slow biological change.

Paradoxically, though humans were the domesticators, it is as though they were themselves being domesticated. And insofar as agricultural crops were determining lifestyles, humans were being domesticated by plants. The coevolution of humans and plants had entered a new phase.

### Urbanisation – physical and mental space

City dwellers now lived behind walls that both separated and protected them from what lay beyond. The distinction between nature and culture (as civic space) had been literally set in stone. Though nature was accessible outside city walls, plant cultivation in urban surroundings would become more and more the way of engaging with nature and the natural seasonal biological rhythm of growth, maturation, death, decay and renewal.

Even in the earliest phases of urbanisation we can recognise at least seven kinds of special human spaces – all potentially containing cultivated plants and all with counterparts today. These are structural or bounded spaces that suggest values as well as functions:

- space for domesticated plants and animals as grazing land and cereal crops, also orchards, vegetable plots and vineyards
- space for domestic housing and private gardens
- communal space: a city square or forum for discussion generally including a place for trade
- places for recreation, relaxation and entertainment
- an administrative centre, usually the ruler's palace and its grounds
- religious space for temples and various monuments associated with the dead
- connecting space for the passage of people and goods.

What is not so obvious is that urbanisation created not only functional physical enclosures but a new set of words, categories and ideas that were absent from the Palaeolithic mind. The new mental categories expressed a dialectic between objects of nature and objects of culture. Those relating directly to plants included: natural/man-made, wild/cultivated, urban (town)/rural (country). Other distinctions that related to cultivated plants were public/private, formal/informal, sacred/secular, work/pleasure and utility/luxury.

As cities grew, so too did the corresponding agricultural space needed to feed them and this produced a trichotomy urban/rural/wild in which enclosure, a feature of urban space, would become of increasing historical significance to rural space, eventually even applying to wild space through national parks and bounded wilderness areas.

All these themes, collectively subsumed under the distinction between nature and culture, arose largely as a consequence of the advent of agriculture.

### Social organisation

Social order in cities was maintained by government based on strong social hierarchies. The community was usually headed by a single, often religiously sanctioned, god-like ruler. Matters of state were then overseen by the ruler and court from a royal palace. Spiritual matters were the concern of a priest class operating from a temple. Palace and temple precincts were used to gain the support of the gods, to inspire citizen pride, and to instil visitors with both admiration and fear. The management of space would become critical as legal systems defined public and private places, systems of ownership and acceptable social behaviour. Cities were an opportunity to produce the best a society could offer, to specialise, compete and excel in architecture and sculpture, engineering, trade, warfare and more. Demonstrations of civic pride would include the acquisition and display of exceptional and interesting curios from nature including impressive collections of animals and plants.

Agriculture catalysed the process of social and economic development that accelerated human control of nature. Cities prospered and grew on the resources provided by trade, fostered through political interaction with other cultures. Warfare generated the competition and conquest that would benefit victors. With urban growth came not only an increase in population but an increase in social complexity and organisation that could take advantage of the benefits of scale and specialisation that permit the development of more elaborate technologies, larger armies and so forth. It is this faltering but inexorable cycle of growth that has created today's global economic community as, in 2007, UNESCO announced that worldwide city dwellers outnumbered people living in the country and that by 2030 nearly two-thirds of the world population would be living in urban areas (United Nations 2007). The human journey from early cities like Uruk in Mesopotamia in about 4500 BCE to the modern megalopolis has taken about 6500 years.

It was during the phase of city-building facilitated by agriculture that the category 'garden' comes to us as an enclosed (sometimes sacred) and cherished artificial space dedicated to cultivated plants. Classics professor and garden historian Katherine von Stackelberg (2013, p. 120) suggests that it was in the Bronze Age interaction of trade, diplomacy and military conquest that occurred between Mesopotamia, Egypt and the Aegean during the third to second millennia BCE that '... *gardens emerge as distinctly meaningful spaces*'. These ancient civilisations all had cities with imposing royal gardens and artistically inspired religious precincts. Here we see the first large-scale parks and gardens associated with royal palaces, temples and tombs.

An examination of some of these early gardens provides us with an insight into not only the factors that distinguish botanic gardens from other gardens, but also the important scientific and aesthetic features linking particular gardens of the ancient world with botanic gardens of the modern era (see also Hill 1915).

## Ancient gardens

### Egypt

In ancient Egypt, built on the fertile soil of the river Nile, there is evidence for an academic interest in the medicinal use of plants that dates back to at least the Third Dynasty pharaoh Imhotep (2667–2648 BCE). Imhotep was revered as the founder of Egyptian medicine, the first great physician, and was worshipped as a god. Later, ancient Greek physicians would identify Imhotep with Asklepios, the God of Greek medicine, and they would use his Egyptian temples as learning centres for trainee Greek physicians (Osler 1913).

We know about Egyptian medicine via famous papyrus manuscripts such as the Hearst Papyrus (c. 2000 BCE), Kahun Gynaecological Papyrus (c. 1800 BCE), Edwin Smith Papyrus (c. 1600 BCE) and London Medical Papyrus (c. 1325 BCE). The best-known is the Ebers Papyrus which dates from the reign of pharaoh Amenhotep I (c. 1534 BCE). The Egyptian Ebers papyrus is a 110-page scroll about 20 m long and likely copied from earlier texts. It is one of the oldest preserved medical documents and is probably the world's earliest surviving list of medicinal plants. Some 30 herbal remedies inscribed on this scroll suggest herbs and spices that are in common use today (Bryan 1930).

Egyptian medicine set a precedent for civilisations that followed. Homer's *Iliad* and *Odyssey* written in about 800 BCE make reference to Egyptian expertise in medicine as does the Greek historian Herodotus in about 440 BCE.

The herbal remedies written on Egyptian papyri are a mix of empirical medicine, magical formulas, incantations and inhalations. No doubt the strong aromas and flavours of herbs and spices had attracted spiritual associations, a legacy of prehistory handed on to the ancient Egyptians. Herbs and spices had many uses. Cinnamon, especially, from today's Sri Lanka, was used for embalming. The Egyptian tradition of matching plant and animal characteristics to the symptoms of the patient *simila similibus* (similar with similar) has passed down history, most obviously in the Medieval Doctrine of Signatures.

In the period of the New Kingdom from 1500 to 1250 BCE the Nile floodplain allowed year-round irrigation for vegetables, palms and fruit trees. Design elements in cities at this time included complex enclosed estates, elaborate architecture, groves of trees, pavilions, temples, and pools for lotus and birds. From about 1500 BCE *'native trees and flowers were being steadily augmented by foreign introductions from the east and south-east of the Mediterranean'* and included the pomegranate, *Punica granatum* L. (Caspian Sea region), also Cornflower, *Centaurea depressa* M.Bieb., and Poppy, *Papaver rhoeas* L. (eastern Mediterranean) (Hobhouse 1994, p. 12).

Religious precincts of this period contained temples dedicated to various gods and these were frequently decorated with formally designed gardens. Pharoah Hatshepsut (1508–1458 BCE) was a much-revered and progressive pharaoh. The temple constructed in her reign is recognised today as a masterpiece of landscape architecture. She restored former trade with Punt which was a source of gold, aromatic resins, African blackwood, ebony, ivory, slaves and wild animals. One expedition to the land of Punt, on the Horn of Africa, consisted of five ships and a complement of over 200 men including 30 rowers, each ship about 21 m long with several sails. The expedition returned with 31 live myrrh trees transported with their roots in baskets; the cargo including people from Punt who were treated as either trophies or slaves. This appears to be the first recorded transplantation of trees from a foreign expedition. Hatshepsut planted the trees in the courtyard of the Deir el-Bahari tomb complex that she dedicated to the god Amun (von Stackelberg 2013, pp. 122–123).

Hatshepsut's successor was Tuthmosis III (1479–1425 BCE) whose military victories were celebrated by the construction of a Festival Hall at the Temple of Amun at Karnak, its entrance carved with a list of conquered territories in Syria, Palestine and Lebanon. On a wall in a sacred space at the back of the Hall is a finely detailed relief, known as the 'botanic garden', depicting native Egyptian plants like figs, dates, vines and lotus, but also plants from Syria and Palestine such as *Iris* L., *Arum* L. and *Kalanchoe* Adans., presumably trophies of war taken for their medicinal and religious significance as well as their natural beauty (von Stackelberg 2013).

A copy of the most famous (now destroyed) painting of an Egyptian garden is that of wealthy official Sennufer in the reign of Amenophis III (1450–1425 BCE); it shows a walled garden where visitors arrived by boat along a tree-lined canal. A gated lodge opened into a central vine-shaded courtyard with trellised arbours, awned pavilions and shady colonnaded courtyards. Garden pools were decorated with flowering plants and potted lotus (Hobhouse 1994, p. 32).

In the reign of pharaoh Akhenaten (1352–1336 BCE) a garden city was built at el-Amarna in Middle Egypt, with sunken gardens which had decorative tiles illustrating individual plants (perhaps a guide to identification) and a vineyard, while just outside the city centre was a sacred area, Maru-Aten, with a central lake, avenues of trees, garden beds and temples. Wealthy citizens and important officials lived in walled villa estates, often as retreats situated outside the city limits, while workers lived on the outskirts of the city, growing vegetables in their home gardens (Wilkinson 2001, p. 418; Baines & Whitehouse 2006). Gardens as sanctuaries feature in Egyptian art, literature and poetry at this time, often with strong symbolic associations (Joyce 1989, pp. 7–8).

These accounts from ancient Egypt indicate an intellectual interest in herbs, spices and plants of medicinal value, as well as an appreciation of the botanical benefits of trade and conquest. Exploratory voyages yielded plant trophies, often edible or useful, but sometimes also of ornamental value as lessons of plant transportation over long distances were learned.

Public parks and gardens were carefully designed with elaborate architecture and other ornamentation; they were used as sanctuaries, public meeting places or sites of religious observance. Home gardens, vegetable patches, market gardening, avenues of trees and luxurious suburban estates (often with water features) as retreats for the wealthy were all well established by 1500 BCE.

## Mesopotamia

In Mesopotamia, a land irrigated by the Tigris and Euphrates rivers, Sargon the Great (c. 2333–2279 BCE), founder of the Akkadian dynasty, was the son of a gardener in an association between kings, courts and horticulture that echoes down the ages. Sargon accumulated exotic plants collected on military campaigns. Similar collecting expeditions are recorded for subsequent magnificent palace gardens of the kings Tiglath-Pileser I (1114–1076 BCE), Assurnasirpal II (883–859 BCE), Sargon II (721–704 BCE), Sennacherib (704–681 BCE) and Ashurbanipal (668–627 BCE) (Leslie & Hunt 2013).

On stone tablets Assyrian king Tiglath-Pileser I speaks of his herds of deer, gazelle, ibex, oxen and asses that he has assembled as trophies of war to stock his park-like hunting grounds along with '*... such trees as none among previous kings, my forefathers, had ever planted ... I took rare orchard fruit which is not found in my land and filled the orchards of Assyria*' and he lists among his new trees the cedar, box-tree and Kanish Oak (von Stackelberg 2013, p. 123).

King Assurnasirpal II brought back plants from a military campaign, incorporating them into an elaborate landscape modification:

> *I made gardens in the upper and in the lower town, with the earth's produce from the mountains and the countries round about, all the spices from the land of the Hittites, myrrh (which grows better in my gardens than in its native land), vines from the hills, fruits from every country; spices and Sirdu-trees have I planted for my subjects. Moreover, I have cut down and levelled mountain and field from the land about the town of Kisiri unto the country near Nineveh, so that the plants may thrive there, and I have made a canal; one and a half hour's journey from the Chusur river have I brought water to flow in my canal, and between my plantations for their good watering. I have set a pond in the garden to keep water there, and in it I have planted reeds.* (Dalley 1993, p. 3)

From a library of tablets assembled from all over Mesopotamia, written in cuneiform and curated by King Ashurbanipal II (668–627 BCE) in his royal palace at Nineveh (the tablets now stored in the British Museum), it is clear that medicinal herbs were grown in special gardens, the plants being carefully listed on clay tablets as a *materia medica*, or herbal, complete with synonymy and described by botanical historian Alan Morton as '*the earliest truly botanical work at present known*' (presumably because it deals with taxonomic and nomenclatural issues) (Morton 1981, p. 9). The king's knowledgeable physicians at Nineveh worked with about 250 different medicinal plants. Records in the library trace the Mesopotamian herbal back to at least the second half of the third millennium BCE (Wallis Budge 2011).

The culmination of horticulture in antiquity was almost certainly the Mesopotamian Hanging Gardens of Babylon, one of the seven wonders of the ancient world, constructed at the dawn of Mediterranean Classical civilisation (Fig. 1). Greek and Roman writers such as Strabo (c. 64 BCE–c. 24 CE) and Diodorus Siculus (fl. 60–30 BCE) describe the Hanging Gardens as a vast amphitheatre, reaching toward heaven and terraced in tiers with a cleverly engineered system of irrigation that raised water to the top (probably an Archimedes screw built before Archimedes lived!) – a towering and impressive architectural masterpiece with cool recesses and pavilions for entertainment, and a lake at its base. The precise location of these gardens has only recently been determined as being not at Babylon, but at Nineveh or 'Old Babylon' located about 400 km to the north, during the rule of King Sennacherib (reigned 705–681 BCE) (Dalley 1993).

In this record from Mesopotamia we can discern not only advanced horticulture and landscape design but hunting parks, zoos, the use of water features and an economic botany that exploited plants from foreign lands, placing special emphasis on spices. Plant knowledge was incorporated into a vast reference library. As in Egypt there is the specialised study of medicinal plants administered by a class of physicians – ancient academics who pre-date the apothecaries and professors of early modern medicinal gardens by at least 3500 years.

## Asia and the Axial Age (c. 800–200 BCE)

By the sixth and fifth centuries BCE peoples across the world had entered what is now known as the Axial Age, subjecting old beliefs to critical examination and developing new social structures, religions and philosophies. In this period of intellectual introspection we see the emergence in the East of Chinese Taoism and Confucianism, in India Buddhism and Jainism, and in Persia Zoroastrianism. In the Near East there was the Hebrew religion of Judaism that existed before the rise of the later Abrahamic religions Christianity and Islam.

Chinese historical records indicate that interest in plants was, from the earliest times, herbal in character, but in a written tradition that first dates to about the time of Confucius (551–479 BCE). Dictionaries and encyclopaedias included lists of medicinal plants and

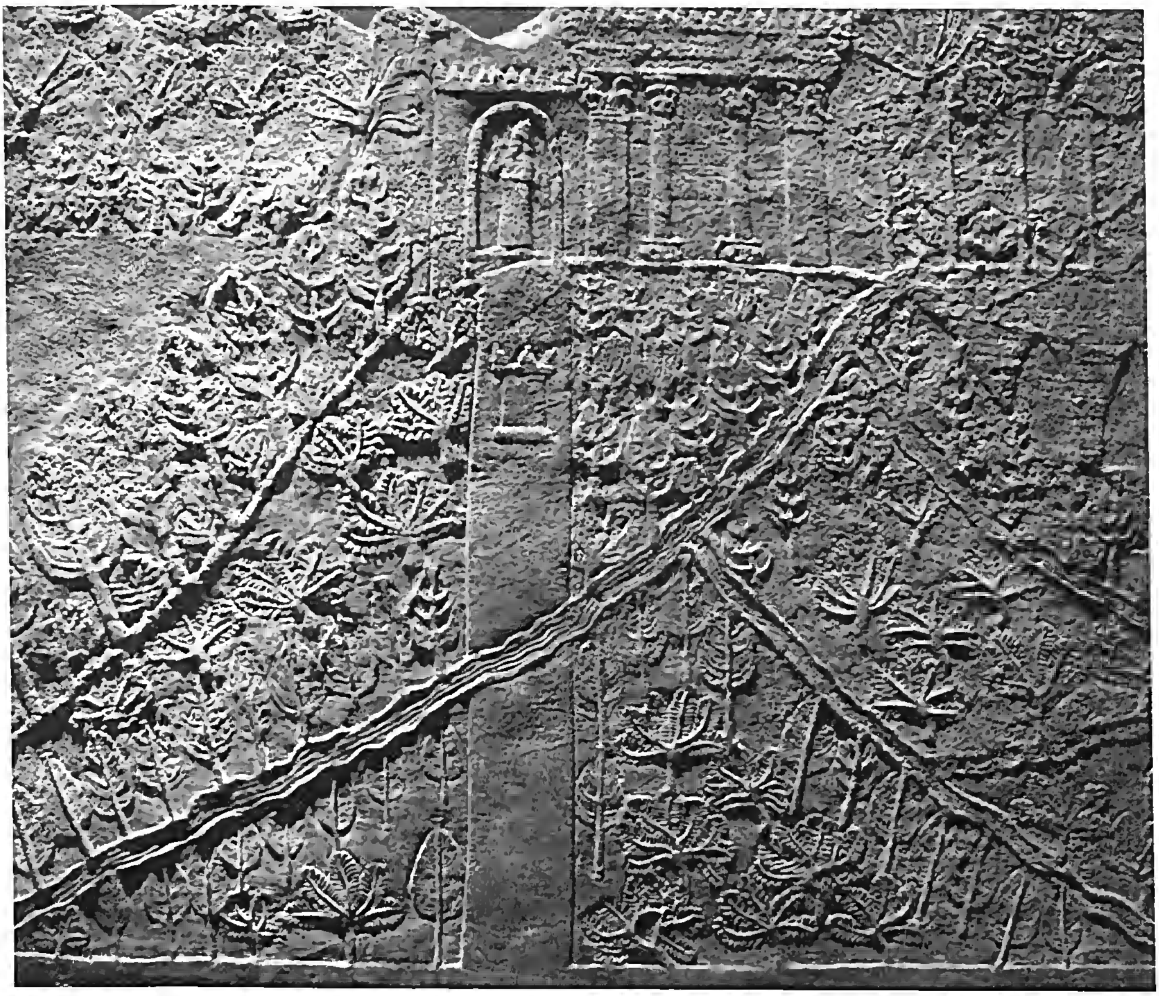

**Figure 1.** Bas-relief sculpture of Sennacherib's Hanging Gardens at Nineveh (Old Babylon) from the palace of Sennacherib's grandson Assurbanipal (668–627 BCE); believed to represent the gardens when mature. The palace is at the top and the terraced gardens were irrigated by Archimedean screws that sourced water from a cistern fed by mountain river water that passed over an aqueduct (top right). Relief now held by British Museum. (Photograph: Owen Jarus)

their properties. When an imperial decree of 659 CE ordered the synthesis of this knowledge the result was what probably constituted the first pharmacopeia of any nation (Morton 1981, p. 11).

Indian Vedic writings are based on an oral tradition presumed to date back to at least the second millennium BCE and the medical and mystical properties of plants, but the earliest written texts of any substance appear to be almost exclusively medical in character. The Susruta-Samhita, associated with surgeon Susruta at about the time of the Gauthama Buddha (560–480 BCE), probably derives from much earlier documents and it lists about 700 plants with their medicinal properties. However, botanical features do play some part in their classification (Morton 1981, p. 12).

### Persia

Following the great ancient empires of Egypt and Mesopotamia there emerged a vast Persian Eastern empire that, at its height in about 490 BCE engulfed both Mesopotamia and Egypt in the west and extended to the Himalayas in the east. Persians excelled in hydraulic engineering used to great effect in their carefully constructed gardens that were especially sensitive to climatic conditions.

The ancient Persian word *pairidaēza* refers to an enclosure, park or hunting ground (no doubt connected with the hunting parks of the Assyrians and Babylonians) and is related to the later Greek word *paradeisos* and English 'paradise'. Persian ideas derived in part from Egypt and Mesopotamia would be incorporated into private and public space in the new Hellenistic Greek Empire that followed Alexander's military conquests, most notably in the planning of the new city of Alexandria and design of villa retreats built by his generals. It was these villas whose style would be later emulated and embellished by the Roman elite and passed on within the general Western gardening tradition.

## The origin of botanical science in the classical era

### Ancient Greece

One Western branch of thought that emerged from the melting pot of ideas in the Axial Age was the school of naturalistic pre-Socratic philosophers (c. 624–430 BCE) of Ionia (today's western Turkey) and the Eleatics of southern Italy. They are regarded as the first natural scientists since they developed explanations for phenomena in nature that did not depend on supernatural causes. Following this tradition were the later classical philosophers Socrates, Plato, Aristotle and Theophrastus who would have a major influence on subsequent Western culture and science. It is Theophrastus (c. 371–c. 287 BCE) who laid the foundations of today's plant science, the critical study of plants for their own sake as well as for their utility (Morton 1981; Thanos 2005).

Ancient Greek public gardens were founded on former traditions. A *kēpos* was a formal temple enclosure while an *alsos* was a sacred grove as an unbounded natural space, like a wildlife reserve, where grazing and cutting were forbidden (von Stackleberg 2013, p. 132).

Gardens of ancient Athens were modest in comparison with the horticultural grandeur of Mesopotamia, Egypt and Persia. According to Roman chronicler Pliny the Elder (23–79 CE) it was Epicurus (341–270 BCE) who was the first to create a garden in ancient Athens. By 'garden' he probably meant something substantial: '*... up to this time it had never been thought of, to dwell in the country in the middle of a town*' (Pliny, *Historia Naturae* 19, 19). Epicurus had purchased a property which he called *The Garden* by the main gate into Athens and it had a reputation for great beauty. Here Epicurus and his followers worked on their philosophical ideas. He considered that philosophy was, first and foremost, a form of therapy for life, since '*philosophy that does not heal the soul is no better than medicine that cannot cure the body*' (Usener 1887), and no doubt his garden contributed to a tranquil state of mind.

While Epicurus nurtured his soul with garden beauty, philosopher Theophrastus fed his soul in a different way, by indulging his intellectual curiosity in plants. Theophrastus succeeded Aristotle as head of ancient Athens' *Lyceum* gymnasium, a university-like all-male educational establishment teaching academic subjects, sport and military training (Fig. 2). The mornings were for discussion as he walked with students around the *Lyceum* garden while public talks on plants were given later in the day (Leroi 2014, p. 345). From Theophrastus's lecture notes we now have *Historia Plantarum* and *Causa Plantarum* (c. 345–342 BCE) which, together with Aristotle's *Historia Animalia* are, in effect, the first recorded scientific treatises on plants and animals.

Theophrastus had little interest in medicinal plants. The systematisation of medicinal plant knowledge in the Athens of his day had been completed efficiently by his contemporary, the physician Diocles of Carystius (c. 375–c. 295 BCE) whose work, subsequently lost, probably formed the foundation of later lists attributed to Pedanius Dioscorides (c. 40–90 CE) and Pliny the Elder (23–79 CE) (Morton 1981, pp. 64–66). Theophrastus regarded many plant remedies, those based on hearsay rather than observation, with great suspicion. He was less concerned with the utility of plants – instead his curiosity was focused on the plants themselves, their relationship to one another, their classification, structure, function, reproduction, interaction with the environment and geographic distribution. His knowledge was always based on proven experience, reason and logic. In fact Theophrastus's approach hardly differed from that of modern evidence-based plant science. He clearly regarded gardens as potential places for experimentation and the close observation of nature (Morton 1981, pp. 51, 67).

However, the *Lyceum* was not an academic ivory tower; it was also affected by affairs of state, and plant utility was not ignored. Theophrastus lived in a time when the independent Greek city-states, following Macedonian Alexander's conquests, were preparing for possible imperial unification under a Macedonian monarchy, so the *Lyceum* was being used '*to train the leaders, officials and experts of the new era*' (Morton 1981, p. 49). Theophrastus was the son of a fuller and aware that the *Lyceum* could improve its public profile by raising revenue and engaging with the world of economics. The kind of economic ambitions he pursued would be remarkably similar to those of colonial Europe in the 17th and 18th centuries. Theophrastus expressed particular interest in:

> *... increasing the productivity of agriculture, the study of native and colonial plant resources, the acclimatisation of*

**Figure 2.** Excavation of the Ancient Greek *Lyceum* of peripatetic philosophy in Athens made famous by Aristotle and Theophrastus, founders of zoological and botanical science respectively. (Photograph: Roger Spencer 2014)

> *plants in new habitats, an intense interest in the production of timber and tar for shipbuilding, especially for the navy, linen for sails, charcoal for metallurgy and metal-working.* (Morton 1981, p. 29)

The garden at the *Lyceum* was, first and foremost, an adjunct to an educational institution. The *Lyceum* and Plato's *Academy* served as models for the later universities and the first modern botanic gardens. Theophrastus had extended the study of plants from that of utility to that of science – to the study of the plants themselves. The living plant collection was the subject of close scientific observation. The garden, set within designed parkland, benefitted from both local plants and those obtained through trade, foreign exploration and warfare. His plant science included consideration of the benefits that could accrue to Athenian citizens from economic botany and many of the plants grown in the garden were received from outside Greece – from exploratory expeditions, a few donated by merchants, and others sent to Athens by soldiers on military campaigns. Among the latter were believed to be some collected by the famous military hero Alexander the Great (356–323 BCE), a former student of Aristotle (Thanos 2005). The *Lyceum* survived until closed in 529 CE by Byzantine Emperor Justinian who considered it a threat to Christianity.

The idea of the *Lyceum* garden as a place for reflection, education and science was not forgotten by posterity '*... the perception of the garden as a suitable location for philosophical investigation became entrenched*' and '*... philosophers inspired the lasting associative tradition between gardens, classical education, and higher thought that persisted into the eighteenth century*' (von Stackelberg 2013, pp. 131–132).

The analytical scientific spirit of the ancient classical world and its search for naturalistic explanations would pervade the thinking of later European Renaissance and Enlightenment intellectuals.

## Physic gardens

The intellectual and cultural centre of the ancient world passed from Athens to Egyptian Alexandria (founded 331 BCE and named after its conqueror) with its famous library, museum and beautifully designed public space, but it too fell into decline in the seventh century CE. After the dissolution of the Classical world, ancient learning and manuscripts, including the works of Aristotle and Theophrastus, were lost to Western Christendom although fortunately preserved and extended in the Arab world through the Middle Ages, mainly in Persia, Syria and Arabia, eventually returning to the West where they were translated from Arabic back into Latin and Greek. Throughout this period, academic interest in plants was confined once again to their medicinal properties and a staggering 1200 years would pass before the return of Greek-spirited analytical plant science (Morton 1981, pp. 49, 123).

As the old Roman trade routes and institutions crumbled, communal life and learning in Europe of the Middle Ages took on its feudal and religious character. Plant interest had now reverted again to the practical concerns of food and herbal medicine and this was a period especially rich in folklore, alchemy, sorcery, witches, potions, magic and the like. Herbal medicine was practised within the family, by local physicians, and in the Christian monasteries which had become community centres and a focus for learning.

While Christendom languished, the Arab world prospered through an Islamic Golden Age that lasted from the eighth to the 13th centuries. The study of medicinal plants and ornamental gardens flourished in Spain, Turkey and the Levant. The first capital of the Islamic world was in Damascus during the Umayyad Caliphate of 661 to 750 CE before transfer in the 760s to Baghdad as a trade centre with magnificent gardens, floristry, perfumery, education and science. In 711 CE Moorish armies captured Cordoba in Spain, the city rising to prominence until, by 950 CE, its universities, libraries, medical schools, vineyards, orchards, gardens and commercial vibrancy proclaimed it as Europe's centre of intellectual activity and one of the most populous cities in the world before its role was overtaken by Seville (Morton 1981, pp. 86–89; Lehrman 1986) (Fig. 3). During this period new crops were introduced and distributed through Muslim gardens managed by leading pharmacists and physicians like Ibn Bassal (fl. 11th century) of Toledo and Seville, and Ibn al-Wafid (997–d. c. 1074) of Toledo. Gardens of the Muslim world combined art and ornamental display with economic botany and science, networking in a manner that would not be seen in Christendom for several centuries.

Many of the symbolic and aesthetic aspects of gardens come to us through this tradition. One aspect of the creation of impressive gardens at this time was the evocation of a terrestrial paradise (Prest 1981). Persian gardens especially accentuated fertility, abundance and beauty. Later Islamic charbagh gardens, like their Persian predecessors, would also associate gardens with paradise as an idealised place of eternal serenity and bliss, a retreat from civic duty, a heaven on earth, much like the Christian Garden of Eden. They were laid out in a quadripartite formal symbolism typical of the mystical numerology of the times – four directions, four seasons, four elements, four corners of the earth and the four rivers of Eden. This four-part design would later be used in the very first early modern botanic gardens like that in Padua (est. 1545).

Frankish King Charlemagne was crowned Holy Roman Emperor in 800 CE, the first emperor of Western Europe since the Roman collapse. One of his decrees was the *Capitulare de Villis* (*On the Management of Estates*, c. 771–800) which attempted to revive a Roman villa-type garden- and money-based market economy using the Lords of manorial estates. The document contained detailed recommendations for the construction and contents of gardens (Mobbs et al. 2008). The *Capitulare de Villis* lists over 70 species of flowers, herbs and vegetables and 16 kinds of fruit and nuts, giving us a synoptic account of the commoner cultivated plants at that time (Darryl 2010).

Medicinal plants were cultivated in the monastery gardens where some Roman garden traditions were retained, like the cloisters as a colonnaded peristyle, and enclosed gardens, the *Hortus conclusus*, itself further divided into garden 'rooms'. The *hortus* was a garden used mostly for vegetables while the *herbularis* or *hortus medicus* was a physic garden of labelled medicinal plants, the pharmacy of its day as a source of plant remedies for the ailing patients who were being cared

**Figure 3.** The enclosed colonnaded *Patio de los Naranjos* (Garden of Oranges), of the *Mezquita de Córdoba* (the Great Mosque of Còrdoba, now the Cathedral of Còrdoba). The Moorish architecture of the *Mezquita* reflects Córdoba's importance in the Islamic world when it controlled much of the Iberian Peninsula. (Photograph: Rob Cross 2015)

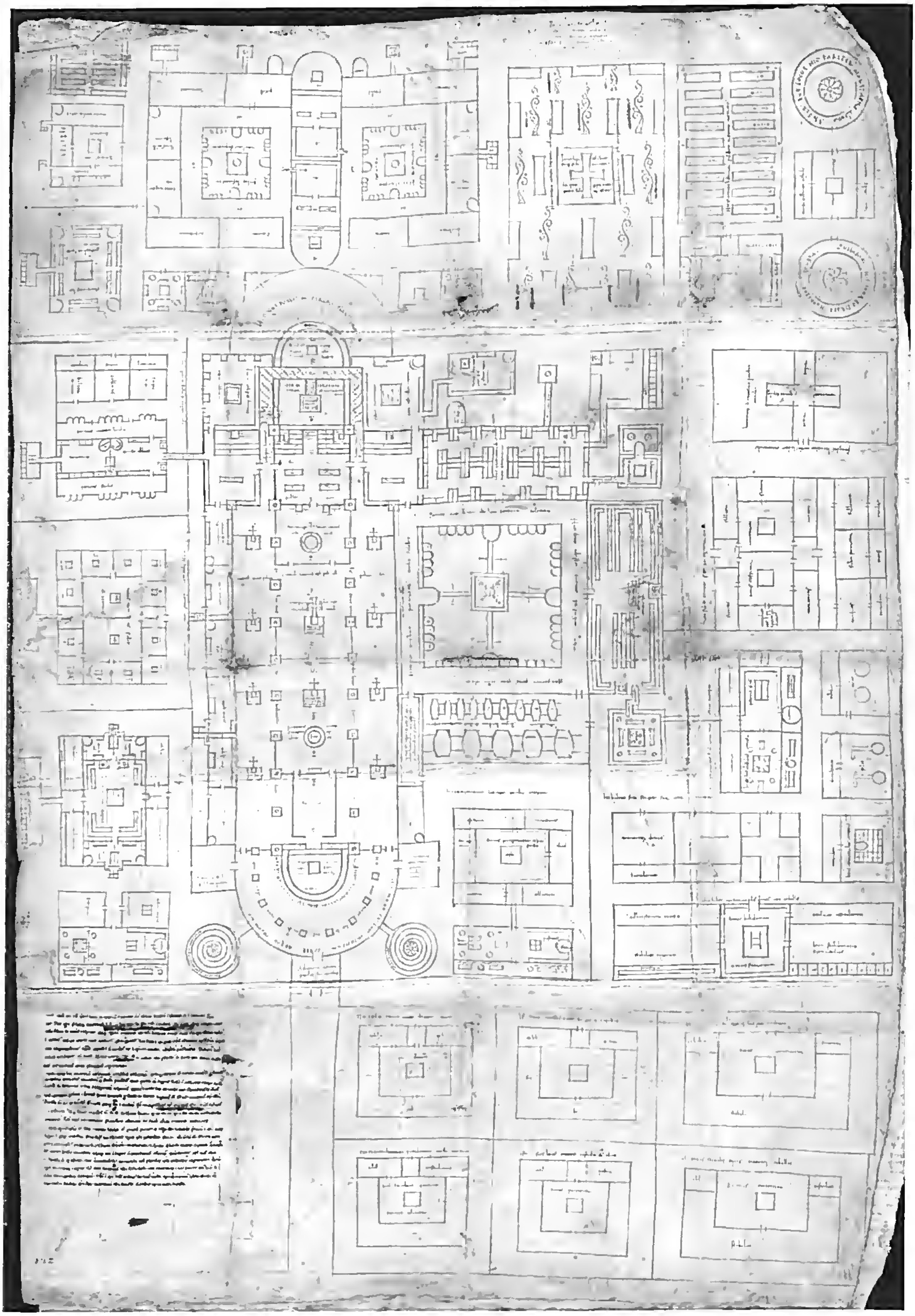

Figure 4. An original medieval architectural drawing for the Abbey of St Gall in Switzerland c. 830 CE. Stored in the monastery library, the plan was never realised but it shows the proposed structure of the herb gardens. (Image: Reichenau-St. Gall Virtual Library – http://www.stgallplan.org/en/index_plan.html)

for in the monastery dormitories (Holmes 1906). An 830 CE architectural plan of the famous *Abbey of St. Gall* in Switzerland shows 16 herb beds in a formal design as precursor to the later university physic gardens (Fig. 4).

Education was gradually becoming more secular in character. Universities evolved out of church schools in about the 12th century with lecturers known as scholastics. The typical Master of Arts degree took six years to complete during which students learned the seven liberal arts (arithmetic, geometry, astronomy, music theory, grammar, logic and rhetoric) all in Latin and combined with Aristotelian philosophy. Students were expected to be fluent in Latin which was the international language of scholarship and the reason why today's plant names are in Latin. Higher education could then be pursued in the disciplines of theology, medicine and law (Fig. 5). Bologna University was founded in 1088, Paris in 1150, Oxford in 1167, Cambridge in 1209 and Padua in 1222. Medicinal plant remedies were no doubt studied as a major part of the curriculum in those universities with medical faculties and here, for many years, medical students would be taught what little remained of the honoured work of classical physicians Hippocrates (c. 460–c. 375 BCE) and Galen (129–c. 216 CE).

In the London of 1180 wholesale merchants formed a pepperers' guild which later merged with the spicers' guild and much later still, in 1429, the Grocers' Company. These guilds were the forerunners of apothecary associations – the term 'apothecary' combining the vocations of botanist, chemist, druggist, herbalist, merchant and physician and reinforcing the persistent vital role of herbs and spices in Western medicine (Purseglove et al. 1981, p. 12).

The evolution of the modern botanic garden can now be placed within the broad historical context of its antecedents.

## The modern era

### 250 years of social transition

The years between the establishment of early modern botanic gardens in Italy and the settlement of Australia, roughly 1550–1800, witnessed a series of momentous interconnected social transitions that were all European in origin but which would become of global significance. They are generally described using a cluster of historical categories: Renaissance, Scientific Revolution, Age of Discovery, Enlightenment, Commercial Revolution, Age of Revolutions and Industrial Revolution. Collectively these social transformations have been referred to as The Great Divergence. This was a time when the West surged ahead of the rest of the world in political and economic power. Eventually Britain, as centre of the

**Figure 5.** Matthaeus Silvaticus teaching his students about medicinal plants in his physic garden in Salerno, southern Italy. From the frontispiece to a 1526 edition of his pharmacopoeia *Opus Pandectarum Medicinae*, which he completed in 1317 (see http://www.interzone.com/~cheung/SUM.dir/med43.html).

Industrial Revolution and mechanised agriculture, would create the world's largest ever empire embracing over a quarter of the world's population as European commerce followed the path of maritime trade routes from the Mediterranean to the Atlantic, Indian and Pacific Oceans. Economic power would eventually pass from Britain to America in the 20th century (Nunn & Qian 2010).

Between 1650 and 1800 the world population doubled and European commercial and cultural impetus shifted from the Mediterranean, with its cultural and trading hubs in Egypt, Greece, Italy and the Levant, to the countries and cities of Western Europe. Cities situated on the Atlantic seaboard were geographically ideally situated to reap the economic and political benefits of the maritime expansion into the New World and beyond.

All of these social changes impacted on the objectives and general character of botanic gardens.

## Renaissance botanic gardens

Of the many precursors to contemporary botanical gardens, the scientific *Lyceum* garden of Theophrastus certainly stands out, although, in retrospect, it seems likely that ornamental horticulture would also, eventually, become part of a botanic garden mix of science and education, art and utility. But, for a while, it would be medicine that would still hold sway.

Renaissance intellectuals recovering the ancient literature of the Greco-Roman world were impressed by descriptions of ancient royal gardens, carefully designed with architectural elements, maintained and irrigated in an urban setting. They were also aware of the continuity between the Greek and Roman cultures.

Pliny (*HN* 19.4.19) regarded the Greek *Lyceum* garden and gymnasium as a model for the gardens of the Roman upper class (Nielsen 2013, p. 53). Cicero (106–43 BCE) owned a Tuscan villa that boasted two gymnasia that were named, following the Greeks, the *Lyceum* and *Academy* (named after Plato's gymnasium in Athens). In the second century CE Emperor Hadrian's retreat, the Villa Adriana at Tibur (Tivoli), combined features of Egyptian, Greek and Roman architecture (including his own *Academy*), to create a sacred landscape (Littlewood & von Stackelberg 2013, p. 149).

Influential Renaissance figures persisted with the Greek theme of philosophers' gardens. The 14th-century Florentine Medici family dynasty initiated a new era of wealthy private villa gardens. Cosimo de Medici 'The Elder' (1389–1464) had made a fortune as a banker and became a famous patron of the arts and learning during the Italian Renaissance. In 1439, he named one of his gardens the *Academy*.

The origin of botanic gardens is usually dated to the early modern Italian Renaissance of the 16th century. These botanic gardens arose at a time when science itself was in its infancy. Theophrastus's works, written in Greek and probably derived from copies in the libraries of Alexandria and Byzantium, were held in the Vatican library and, on the instruction of Pope Nicholas V, they were translated into Latin by Theodore Gaza (Morton 1981, p. 100). This pope also, in 1447, set out a medicinal garden in the grounds of the Vatican where students were taught the rudiments of botany (Hyams & MacQuitty 1969, p. 16).

Appointments to university chairs as professors of botany were often combined with a botanic garden directorship as these medicinal gardens were maintained as educational adjuncts to the medical faculties of universities. The first university chair in botany, styled *Professor Simplicium* (professor of medicinal plants or 'simples'), was awarded to Francesco Bonafede at Padua in 1533 while the first botanic garden of the modern era was founded by a different Medici, Cosimo I de Medici (1519–1574) in Pisa in 1544. The establishment of botanic gardens was thus linked to the appointment of university chairs in botany (Morton 1981, pp. 120–121).

Botanical gardens were founded at Pisa, Padua and Florence in the 1540s (Hill 1915; Hyams & MacQuitty 1969, pp. 19–23; Hepper 1986, p.67; Morton 1981, pp. 120–121). Then, from Italy, the institution of the botanic garden spread to Northern and Western Europe taking about 35 to 100 years to do so as traced through the foundation dates of major city botanic gardens: Pisa est. 1544, Padua and Florence 1545, Bologna 1568, Valencia 1567, Montpellier 1593, Leiden 1587, Leipzig 1597, Oxford 1621, Paris 1635, Berlin 1646, Uppsala 1655, Edinburgh 1670, Chelsea Physic Garden 1673 and Amsterdam 1682 (Stearn 1971).

Padua was situated close to Venice and could therefore access goods from Constantinople, Egypt, Syria, Crete and Cyprus. However, the importation of exotic plants, networking of *giardini dei semplici* and *praefecti horti* (gardeners and curators of physic gardens) would become most in evidence at *Hortus Academicus Leiden* which assumed the role of repository for plants returned to Holland by the Dutch East India Company. It is probably the Leiden Botanic Garden under Clusius (Director 1593–1609) that was among the first of the early modern period to grow plants for their ornamental interest rather than their medicinal use *'to make a true* hortus botanicus *rather than a* hortus medicus' (Hobhouse 1994, p. 104).

## The Scientific Revolution

The Scientific Revolution arose in Western Europe during the period 1550 to 1750 before it passed to the rest of the world: it ended the pervasive deference to ancient learning and mounted a major assault on superstition. Expressed crudely it marked a transition from alchemy to chemistry, magic to medicine and botany, astrology to astronomy, and mystical numerology to mathematics.

At first, the *'primary objective of Renaissance intellectuals was to recover the lost culture of the past, not to establish new knowledge of their own'* and *'... the further back in time one went, the nearer one approached to the truth'* (Wootton 2015, pp. 73, 76). These men looked back to the philosophy of Aristotle and interpretation of the Holy Scriptures as sources of truth. It would take the effrontery of men like scientist-philosopher Englishman Francis Bacon (1561–1626) to establish a sense of a progressive forward-looking science building on the hard-gained advances of an imperfect past (Wootton 2015, pp. 83–85). Francis Bacon in his Novum Organum Scientiarum (1620) outlined a new scientific method that attacked the Aristotelian emphasis on deductive logic and offered a more practical experimental approach, a strict empiricism backed by inductive logic.

Scientific knowledge fed into new technologies that, in turn, produced social change. The German Gutenberg printing press of 1440 greatly facilitated communication and among the first, most popular and well-illustrated books were the herbals that, from 1470 to 1670, delivered the information needed for household pharmacy. Improved instrumentation, notably the microscope, launched the discipline of plant anatomy and other precision instruments set experimental physiology in train.

Above all, maritime exploration was revolutionised by improved navigational instrumentation that included precision chronometers, telescopes that aided astronomical and other observation, and improved compasses. Sophisticated cartography rapidly expanded the European view of the world while skilled shipbuilding techniques created vessels that sailed faster and further than ever before (Jardine et al. 1996).

One consistent claim of botanic gardens throughout their modern history has been that they are, above all, scientific gardens. What then has been their contribution to science in the period up to the 19th century?

At first botany remained in the thrall of the ancients as herbals were largely popular and derivative compilations of former works. Among these early compilations were the *Hippocratic Corpus* attributed to Hippocrates of Cos (c. 460–c. 370 BCE), Theophrastus's (c. 371–c. 287 BCE) works, the *Naturalis Historia* of Pliny the Elder (23–79 CE) and the *De Materia Medica* by Dioscorides (40–90 CE). The *De Materia Medica* was itself a derivative work slavishly copied again and again for 1500 years up to and including the first printed herbals.

The greatest scientific advance in botany was in plant taxonomy as exotic plants were introduced to European gardens. Gradually lists included plants from parts of the world unknown to the scholars of antiquity. Much of this new activity required an institutional focus and although the new science was practiced by men of universities and learned societies, it was mostly in botanic gardens that this work would flourish.

### Herbals

In the late 15th century Western European lists of medicinal plants appeared for the first time, not in copied manuscript form, but as printed herbals.

From Spain and Portugal came the herbals of de Orta (1490–1570), Monardes (1493–1588) and Hernandez (1514–1580), and mention of plants from the New World and Asia. From Germany the works of Brunfels (1489–1534), Bock (1498–1554) and Fuchs (1501–1566), from the Low Countries Dodoens (1517–1585), appointed Professor of Medicine in Leiden in 1582, Lobel (1538–1616) and Clusius (1526–1609). From Italy Mattioli (1501–1577), who studied at the University of Padua in 1523, and Alpino (1553–1617), who assisted the establishment of the botanic garden at this university in 1545. From England came the herbals of Turner (c.1508–1568), Gerard (1545–1612), Parkinson (1567–1650) and Culpeper (1616–1654).

John Parkinson (1567–1650) was physician to James I and Charles I and an outstanding botanist awarded the title *Botanicus Regius Primarius* (King's First Botanist) for his *Paradisi in Sole Paradisus Terrestris* (1629). He described over 1000 plants, many of these being new introductions, the descriptions embellished with woodcut illustrations. Significantly, Parkinson's *Paradisi* was subtitled 'A garden of pleasant flowers', this probably being *'the first English work to consider flowers for their beauty rather than their use as herbs'* (Hobhouse 1994, p. 104). In his later years Parkinson was neighbour to John Tradescant (the Elder) (c. 1570s–1638), another eminent collector of Lambeth, London. Tradescant travelled to the Low Countries, Russia and North Africa, exciting public interest in plant collection. He wrote to the Secretary of the British Admiralty requesting that British merchants should *'procure all manner of curiosities from abroad'* (Drayton 2000, p. 34). His nursery business produced an impressive plant catalogue in 1634 and his son John (the Younger) (1608–1662) continued the tradition by collecting in Barbados and Virginia (Arber 1986). The father and son business named their collection of travel curios The Ark, which became the first public museum in England. These collectables passed to the Ashmolean Museum in Oxford. The church at Lambeth where the Tradescants worshipped, with the family tomb in the grounds, was converted into a Garden Museum in the 1970s and, after refurbishment, will house a new gallery called The Ark, probably including some of the original collection (Emma House pers. comm. 3 Aug. 2016)

Though derivative, the herbals were useful textbooks for the students of physic gardens and the growing number of wealthy private garden owners: they mark the dawn of organised plant knowledge that was spreading from local centres of learning, the first modern era botanic gardens. Herbals gradually included more and more wild plants collected from ever more distant places including the New World. Over time they exemplified the origins of botany as a discipline distinct from medicine by diverging on the one hand into the medicinal pharmacopeia and, on the other, into the regional descriptive accounts of wild plants that we now know as Floras. Beautiful and increasingly botanically accurate plates also stimulated the art of botanical illustration.

## Taxonomy

Herbals were an extension of the old world of medicine, but the many new plant introductions resulted in ever longer lists of names and descriptions that cried out for system and order.

Luca Ghini (1490–1556) was a physician and *Lector Simplicium* at the University of Bologna before becoming the *Professor Simplicium* in 1538. It was he who was invited by Cosimo 1 de Medici to take the chair of botany at the new botanic garden of Pisa in 1544. It was also Ghini who probably began the preservation of dried and labelled plant collections (*hortus siccus* or 'dried garden') using a plant press, the pressed specimens then shelved systematically in a building called a herbarium. The exchange of dried specimens between botanists became commonplace at this time. This link between descriptive botany, botanic gardens and herbaria – with the active exchange of both live plants, mainly as seed, and dried herbarium specimens – has persisted to this day (Morton 1981, pp. 120, 153). Most taxonomic studies were based at botanic gardens. For example, Italian Andrea Caesalpino (1519–1603) also studied at Pisa, becoming Director of the Botanic Garden from 1554 to 1558. French Swiss Gaspard Bauhin (1560–1624) studied at, among other places, Padua and Montpellier where a *Jardin des Plantes* was established on the Mediterranean in 1593, the earliest botanic garden in France.

English botanist John Ray (1623–1705), the son of a village blacksmith, worked outside the world of medicine and botanic gardens. He was educated at Cambridge and formed a close association with the Royal Society. His passion for plant inventory led to *Synopsis Methodica Stirpium Britannicarum* (1690), essentially the first British Flora, and his travels on the continent and beyond contributed to more widely applicable lists. His interests extended from foundational work in taxonomic theory to interest in the distinction between phenotype and genotype and physiological experimentation. *Historia Plantarum* (1686) (the same title as Theophrastus's work) can be regarded as a synthesis of botanical knowledge to that time. Ray '*... influenced both the theory and the practice of botany more decisively than any other single person in the latter half of the seventeenth century*' (Morton 1981, p. 195).

It was the desire for precise botanical description and comparable lists of plant names that ended the preoccupation with the medicinal properties of plants that had persisted from antiquity. In step with Theophrastus's exhortation to cast the botanical gaze beyond human utility to the plants themselves, the new discipline of botany began by putting order into the world of plants. Prompted by the deluge of new plant introductions in the Age of Discovery there began a phase of identification, classification, nomenclature and description that, in this early modern phase, culminated with the publications of Carl Linnaeus (1707–1778) who was Professor of Medicine and Botany and Director of the botanic garden in Uppsala, Sweden. Though generally remembered for his association with the system of binomial nomenclature, Linnaeus's consummate skill lay in making botany accessible by providing an internationally acceptable methodology for descriptive plant inventory. His artificial (based on characters of convenience) 'sexual system' (1735) of plant classification was easily understood and, by his own admission, would soon be improved – but it got things going.

Linnaeus's system was resisted by botanists in both England and France where strong independent taxonomic traditions had developed. Thus the principles and characters used to classify plants came under ever closer scrutiny by the new botanists. The story of the development of plant taxonomy is covered in great detail in student text books but less well known is the institutional and social background to these developments.

French botany, in particular, produced an impressive line of accomplished taxonomists. Pierre Magnol (1638–1715) was Professor of Botany and Director of the Royal Botanic Garden of Montpellier. In Paris Joseph Pitton de Tournefort (1656–1708), who first studied at Montpellier, was appointed Professor of Botany at the *Jardin des Plantes* in Paris in 1683 and here he was followed by outstanding taxonomists Bernard de Jussieu (1699–1777), Bernard's nephew Antoine-Laurent de Jussieu (1748–1836), and Michel Adanson (1727–1806). Antoine and Bernard de Jussieu studied under Magnol, and Antoine followed Tournefort as Director of the *Jardin des Plantes*.

## Anatomy and physiology

Francis Bacon's influence was apparent in the 17th-century emergence of experimental botany that accompanied the more descriptive taxonomy. Interest was gathering in plant function, nutrition and reproduction. The advent of the microscope (1590) heralded the beginning of anatomy as scientific interest in plants took a physiological turn. Joachim Jung (1587–1657), Professor of Natural Sciences at the Akademisches Gymnasium in Hamburg, was an outstanding taxonomist who also asked tentative questions about plant nutrition as, at the same time, chemists began delving into the chemical constituents of matter by challenging the classical elemental framework of Earth, Air, Fire and Water. Englishman Robert Hooke (1635–1703), closely associated with the Royal Society, published stunning examples of plant microscopy in his *Micrographia* of 1665 and pioneering work in anatomy was developed by Englishman Nehemiah Grew (1641–1712) of Cambridge and Leiden universities, and Italian Marcello Malpighi (1628–1694) working at the universities of Bologna and Pisa. Rudolf Camerarius (1665–1721), professor of medicine and director of the botanic garden at Tübingen, Germany in 1687, was the first to present scientific proof of plant sexuality (Morton 1981, pp. 167–220).

In the 18th century plant physiology made major strides. English clergyman Stephen Hales, elected a fellow of the Royal Society in 1718, had published pioneering work on the flow of sap and water as well as measurements of the gaseous components of the air and the proposal that they could become 'fixed' as solids, his most notable work being his *Vegetable Staticks* of 1727. Later, the Dutch botanist Jan Ingenhousz, who had studied at Leiden, demonstrated that it was only the green parts of plants that gave off 'dephlogisticated air' (oxygen) and Genevan Jean Senebier (1742–1809) correlated oxygen release with light intensity. Building on this and other work Théodore de Saussure in his *Chemical Researches on Vegetation* (1804) showed experimentally that carbon dioxide is emitted from plants in the light and the dark (respiration) and that absorption of carbon dioxide results in the 'fixing' of carbon and release of oxygen. Collectively these studies led to the demystification of photosynthesis (Morton 1981, pp. 246–340).

## The Age of Discovery

The illustration on the title page of Bacon's *Novum Organum Scientiarum* (1620) shows galleons departing the security of the Mediterranean through the Strait of Gibraltar and setting out for the New World. This clever symbolism signified both the intellectual release from the Classical world and the momentously significant opening up of new economic and other opportunities in the wider world beyond, not only across the Atlantic where Columbus had made landfall in the West Indies of the Americas in 1492, but also along the trade routes to the East Indies, and eventually Australia.

The strongest early European connection with the Australian region relates to plants of economic significance, the spices that grew only in the Moluccas, small islands to north of Australia just west of New Guinea. Spices were objects of ancient desire, used to enhance food and, when burned like incense, they would awaken and summon up the gods. Archaeologists have found cloves in a pantry jar excavated in Terqa, Syria dating to around 1721 BCE (Potts 1997, p. 269) suggesting an extremely early trading route from the distant Spice Islands (Fig. 6). Exasperatingly the source of the extremely expensive and tantalising nutmeg and cloves remained unknown to the West.

When Constantinople was captured by Ottoman Turks in 1453, Muslims gained control of the lucrative spice trade that passed between China and the Mediterranean along the Silk Road that crossed the steppes of Central Asia. With the prospect of exorbitantly high prices resulting from prohibitive levies and taxes imposed by numerous middle-men, European countries were forced to seek alternative trade routes, but this time by sea. It was Spain and Portugal that led the spice race in the early stages of the Age of Discovery that followed.

### The Portuguese and Spanish

The search for an eastern sea route to the mysterious Spice Islands began with the Portuguese and Spanish seizure of Atlantic islands, notably Madeira, off the west coast of Africa. Here they established sugar plantations, the islands becoming important staging posts for the Portuguese slave trade. This was followed by the rounding of Africa's southern cape by Bartholomew Diaz in 1488 and the first direct sea voyage to Asia across the Indian Ocean to India's spice-rich Kerala west coast where Vasco Da Gama landed in Calicut in 1498. Beyond, on the Malay Peninsula, lay Malacca which was a trading hub visited by ships from both the west (India, Persia, Arabia and Egypt) and east (Sumatra, Java and the

**Figure 6.** The islands of Ternate and Tidore. The natural distribution of cloves was restricted to these northern Moluccan islands as well as Moti, Makian and Bacan, which were the sites of spice wars between the Portuguese, Dutch and indigenous people. (Photograph: Roger Spencer 2015)

**Figure 7.** Fresh cloves are the unopened flower buds of *Syzygium aromaticum* (L.) Merr. & L.M.Perry, which, when sun-dried, produce the spice cloves. (Photograph: Roger Spencer 2015)

Moluccas). Malacca was a vital link in the Lisbon–India (Goa)–China–Spice Islands chain. Accordingly, Malacca was seized by Portuguese forces in 1511, a small fleet of three ships under Antonio de Abreu continuing on to the fabled Banda Islands with their nutmeg and cloves, arriving in 1512 and ending the millennia-old European quest to find their source (Fig. 7). By 1514 Portugal had ruthlessly gained control of the spice trade on both the western Indian coast and the Moluccas, building forts to ward off competitors (Burnet 2013, pp. 82–96).

Between about 1500 and 1550 Antwerp was the commercial capital of northern Europe, being the trade centre for sugar (known as 'sweet salt') grown on the Atlantic islands especially Madeira. It was also the chief emporium for spices like pepper, cloves and cinnamon, brought to Europe by the Portuguese fleet – although there was competing trade in Marseilles, Alexandria, and the Italian city-states. In India, the Portuguese cultivated food plants from Brazil like the cashew, pineapple, sweet potato and cassava, and, from the West Indies, the custard apple, chili peppers, averrhoa and groundnut. Influential Portuguese physician Garcia de Orta (c. 1501–1568) established a tropical medicinal garden in the Indian Portuguese colony of Goa, his herbal of 1563 achieving wide acclaim (Ly-Tio-Fane 1996).

Spain, as a dominant European power, mounted an expedition to the New World in 1570–1577, Hernandez bringing back, among other botanical treasures, pineapples, cocoa and maize. At this time there were also reports of gardens maintained by the great Incan and Aztec civilisations of the 13th to 16th centuries although little can be told with certainty (Granziera 2005). What we do know is that:

> *Thousands of manuscripts … treasured in great libraries and in the private houses of individuals, were committed to the flames by authorities of the Christian Church or by the Inquisition … [and that] The independent testimony of many contemporary Spanish observers concurs that at the time of the conquest the Mexicans had a number of botanical and zoological gardens, which in extent and arrangement were said to be far in advance of any then existing in Europe.* (Morton 1981, p. 13)

In 1592 the English captured a Portuguese spice ship off the Azores. It contained:

> *425 tonnes of pepper, 45 tonnes of cloves, 35 tonnes of cinnamon, 3 tonnes of mace, 3 tonnes of nutmeg, 25 tonnes of cochineal and 2.5 tonnes of benjamin (an aromatic resin), as well as ebony, ivory, pearls and precious jewels. The cargo value of this single ship was estimated at half a million pounds, almost half of England's treasury at this time.* (Burnet 2013, pp. 122–123)

Control of the spice trade guaranteed fortunes: nutmeg and cloves acted as a global currency which, at their peak value, rivalled the value of gold. Columbus, Da Gama and Magellan were spice hunters first and discoverers second. Spanish and Portuguese trade had created a network of trade routes that spanned the world – the beginnings of today's global economy. South American gold and silver passed to China and the East Indies while laquered goods, porcelain, silk, spices and other fancy goods flowed into Europe.

### The Dutch

Portuguese and Spanish exploration, at first confined to the Atlantic, had shifted to the Indian and Pacific Oceans. With changes in European political fortunes there followed a Dutch Golden Age – a flowering of Dutch culture and political influence across the world that lasted from about 1580 to 1670. During this time plant collection and the return of plants to botanic gardens began in earnest, only to be eclipsed by the ascendancy of France and Britain in the 18th century.

When Spanish and Portuguese power declined the Dutch began a merciless campaign to wrest the lucrative spice market monopoly from the Portuguese.

In 1602 the Dutch East India Company (Vereenigde Oost-Indische Compagnie, or VOC) was formed with its colonial headquarters in Batavia (now Jakarta) on the north-west coast of today's Java in Indonesia. The VOC was a vast private enterprise of Amsterdam merchants determined to monopolise the spice trade. At its height the VOC comprised about 50,000 employees, a fleet of 200 ships based in Rotterdam, and an army of 30,000 fighting men (Purseglove et al. 1981). This was an extremely powerful joint stock company (effectively the world's earliest multinational corporation) with its shares traded on the Amsterdam Stock Exchange, the world's first stock market. Between 1605 and 1621 the Portuguese and native traders were driven ruthlessly out of the Spice Islands.

While the VOC was setting up provisioning and trading hubs, sometimes with associated botanic gardens, questions arose concerning the economic potential of the land to the south of Batavia. This prompted the VOC to send out Abel Tasman on two voyages in 1642–3 and 1644 to reconnoitre the mysterious *'Terra Australis'.* Tasman returned from these voyages with a negative report having first inspected the north coast and then circumnavigated Australia in an extremely wide arc that only closed in on land on the north coast and southern tip of today's Tasmania.

Tasman's opinion of Australia as an inhospitable land without commercial potential probably delayed for another 180 years the European occupation of the region he called *Hollandia Nova* (New Holland).

## Dutch botany

During the Dutch Golden Age, Leiden was the intellectual centre of Europe (Morton 1981, p. 237). Dutch botanists were among the first colonial scientists in an era when strategic colonial outposts were established in the East Indies at Batavia in 1619, at Cape Town in 1679, in India, and elsewhere.

*Hortus Botanicus Leiden* was one of the earliest modern botanic gardens, established in 1587, with the first *Praefectorius* (Curator) being the eminent Flemish physician-botanist Charles de l'Écluse, better known as Carolus Clusius (1526–1609). He had studied at Montpellier before being appointed Prefect to the imperial medicinal garden in Vienna and subsequently professor at the University of Leiden in 1593. At Leiden he assembled a herbarium of dried specimens and a living collection that included plants returned to Holland by sea captains, and his publications included translations of De Orta's herbal and other Portuguese medicinal works as well as his own research on the floras of Spain, Portugal, Austria and Hungary. His plant catalogue *Rariorum Plantarum Historia* (1601), which includes both Spanish and Austrian plants, was a precursor to the many plant compendia to come. The title page of the book is an engraving that depicts the 'first gardener', Adam, and the Classical botanical scholars Theophrastus and Dioscorides. In Europe he was well-known for the distribution of bulbs like tulips and hyacinths, and he was closely associated with the fashionable craze known as 'tulipomania'.

Paul Hermann (1646–1695), who was Professor of Botany and director of the gardens from 1680 to 1695, had trained at the medical school in Padua before being employed by the VOC, working in Ceylon (Sri Lanka) in the 1670s where he grew custard apple, guava, cashew nut, capsicum and cotton, all introduced from the Americas (Rice 2010, p. 60). By 1672 he had built up a large herbarium with collections from the Indies, Cape and America (later acquired by Englishman Hans Sloane). Between 1678 and 1693 he was overseer of van Reede's 12-volume *Hortus Indicus Malabaricus* (1678–1693) an early tropical flora covering coastal south-west India and published in Amsterdam (Jardine 1999, p. 266).

A Company Garden was established at the Cape by Governor Simon van der Stel and by 1680 it had become an exceptional botanic garden, the VOC using 54 male and female slaves to maintain crops of exotic fruits and vegetables, a beautifully presented collection of indigenous plants, as well as rare and unusual species assembled from Dutch exploration. From 1679 to 1706 it was a popular source of plants for Amsterdam, Leiden and other gardens (Ly-Tio-Fane 1996; Jardine 1999).

At first, botanical interest was directed towards the pharmaceutical and therapeutic properties of Asian plants but interest soon moved to garden ornamentals and curiosities as Germans Andreas Cleyer and George Meister (former gardener to the Duke of Saxony) joined forces in Java in 1677 to uncover botanical and horticultural rarities and fruit trees suitable for export to Europe. Travelling to Japan they collected plants that were sent to the Cape botanical garden for acclimatisation, Meister returning to Holland in 1682 with nine chests of trees for the *Hortus Botanicus Amsterdam* (founded by Jan Commelin (1629–1692)), which was a showcase for plants collected by the VOC including, at one time, over 200 species from the Cape. Imports also included Asian bulbs and hothouse plants (Jardine 1999, pp. 236, 246).

An insight into the stirrings of colonial botany and horticulture during this period is provided through the life of German-born Rumphius (Georg Rumpf, 1627–1702) who was employed by the VOC to study the flora of the Moluccas, the company presumably expecting some botanical discoveries with commercial benefit. He arrived in Batavia in July 1653, moving to the Ambon archipelago in 1654. In 1657 he became 'junior merchant' studying the flora and fauna on Hitu Island north of Ambon. His botanical reputation grew and earned him the title Plinius Indicus (Pliny of the Indies). Rumphius is best known for his *Herbarium Amboinense* (1741–1755), a catalogue of the plants of today's island of Ambon and a book that is still referred to today. The work was completed before the universal acceptance of Linnaean binomial nomenclature. Despite the vast distance, Rumphius maintained communication with scientists in Europe and he was a member of the Scientific Society of Vienna. He provided illustrations and descriptions for several hundred new species (Ly-Tio-Fane 1996). *Herbarium Amboinense* finally arrived in the Netherlands in 1696 but the VOC considered its contents so economically sensitive, presumably in relation to the spice trade, that it was not published until 1741, after Rumphius's death (Jardine 1999).

Dutch botany reached its zenith in the early 18th century with the international fame of Leiden's Herman Boerhaave (1668–1738) and Amsterdam's Johannes Burman (1707–1779). Both had living collections close at hand in their botanical gardens which, at that time, contained more plant species than any other European garden. Hermann Boerhaave, by transforming Leiden into Europe's centre for medical education, became the most influential European physician of the early 18th century. Typical of the times he stated in his *Index Alter Plantarum ...* (1720), a list of plants held at Leiden, '*practically no captain, whether of a merchant ship or man-of-war, left our harbours without special instructions to collect everywhere seeds, roots, cuttings, and shrubs and bring them back to Holland*'. Boerhaave also worked with Joseph II of Austria sending missions to explore the tropics and enhance the natural history collections at the Palace of Schönbrunn in Vienna.

Dutch influence, and especially that of the VOC, had captured international attention. Russia's Peter the Great (1672–1725), a progressive leader wishing to reform and modernise Russia, planned a modern navy based at St Petersburg on the Baltic coast. In 1697, with a Russian delegation, he spent 18 months in Europe, four of these in the Netherlands including time spent at the VOC shipyards. In 1714 he founded the Saint Petersburg Botanical Garden (the first botanic garden in Russia), as a medicinal garden, later visiting the Dutch master of scientific medicine Boerhaave in 1716–1717, then, following Enlightenment tradition, in 1724 he decreed a Russian Academy of Sciences, Saint Petersburg State University, and Saint Petersburg Academic Gymnasium.

European presence in the Pacific and the Dutch entrepôt at Batavia had heightened interest in the mysterious land mass, *Terra Australis*, to the south.

By the middle of the 18th century Holland's botanic gardens at Leiden and Amsterdam were brimming with new plants curated by some of the most brilliant physicians in Europe. Amsterdam was Europe's publishing centre and Dutch botanists were leading the world in tropical botany and the taxonomy of plants growing beyond Europe's boundaries. Holland was therefore extremely attractive to the brilliant Swedish naturalist Carl Linnaeus (1707–1778) who travelled there to obtain a doctorate and visit the Leiden and Amsterdam botanic gardens.

## The Commercial Revolution

When Constantinople was seized by the Turks in 1453 many artists, intellectuals and merchants fled from the city to northern Italy. Here they not only headed the translation of ancient manuscripts and revival of learning, they also set up trade networks and banking infrastructure. Portuguese exploration was financed mostly by merchant bankers from Antwerp and the Italian city-states of Venice, Florence, Genoa and Milan but, in the Dutch Golden Age large-scale banking, insurance and finance moved to Amsterdam with an exchange bank created in 1609, only two years after the establishment of a bourse, and a lending bank opened in 1614. Then, from the 19th century, business shifted to London, which became the financial centre of the British Empire.

With the trade generated from resources of the New World, given impetus by the new science and its technology, European commerce and finance flourished as never before. This was the age of mercantilism, the government control of national commercial interests as a way of increasing state power, especially by maintaining a positive balance of trade. Mercantilism evolved into the global capitalism that flourished during Britain's Industrial Revolution and colonial empire.

Two private corporations stand out in these times: the British East India Company (est. 1600) and the Dutch East India Company (VOC est. 1602), the former through its trade with India setting Britain on the path to global power, and the latter being the world's first joint-stock company with steady trade in company stock on the Amsterdam Exchange. These changes would have far-reaching consequences with these companies, at times, controlling international finance and, in the case of the British East India Company, even assuming government of India's Bengal, with Calcutta named the capital of British India in 1772. The new buying and selling of shares in joint stock companies, the development of expensive insurance schemes, and the public financing of government debt to fund costly colonial wars were integral parts of imperial conflict and ascendancy, all linked into the world of economic botany.

World trade in plants would transform society by providing new foods, beverages and distractions, all with their associated economies and social rituals: tea, coffee, cocoa, tobacco, rubber, sugar, cotton and more.

## The Enlightenment and its voyages of scientific exploration

Botanical historian William Stearn notes of the 18th century, the century of Australian settlement, that:

> *... attention is narrowed to the development and influence of a few botanic gardens, since in their history and in the achievements of the men associated with them can be traced most of the botanical history of the 18th century ... increase in the number and diversity of living plants available for study was the most important single factor affecting eighteenth century botany.* (Stearn 1961, p. xliii)

At the start of the 18th century the Dutch were occupied with the tropics and Cape, the English with Virginia in America, and the French with the fur trade in Canada, but European attention would soon turn from the Atlantic and Indian Oceans to the Pacific.

Political fortunes took another turn as maritime power passed to the French and English, and Enlightenment thinking within the European intelligentsia became preoccupied with science and rational thought. This brought with it the questioning of traditional wisdom, the time-honoured royal and religious social institutions. We associate this time with the democratic principles and reforms expressed during the American War of Independence (1775–1783) and the rejection of absolute monarchy that prompted the French Revolution of 1789.

With the VOC and Dutch West India companies, Holland had established a trading empire with botanic gardens and trading hubs at the Cape, Malabar, Java, Ceylon and Brazil all linked to the finest living and dried botanical collections in Europe held at the botanic gardens and Rijksherbaria of Leiden and Amsterdam (Drayton 2000, p. 18). Here in Holland Linnaeus had, in the 1730s, completed his foundational work on botany. However, by the third decade of the century the Dutch grip on European politics and botany was weakened as France and Britain came to the fore.

Linnaeus was an advocate of mercantilist natural history and acclimatisation. He harnessed international commerce by ensuring that each year a student of natural history (one of his 'apostles') should receive a free passage on a trading ship of the Swedish East India Company (Stearn 1961, p. cxix). Between 1746 and 1773 he sent ten students out into the world to collect plant treasures in China, North and South America, and Egypt. Other European cities soon joined the race for botanical booty as more botanists and horticulturists hunted for plant trophies in the newly established colonies.

Plants and plant exploration ranked high on the scientific agenda although no country was above combining a little espionage with their science. There was now a pronounced change in the focus and content of Europe's botanic gardens. From the 16th century there had been a steady increase in numbers of plants arriving from foreign lands but now new plants flooded into Europe and the former physic gardens were transformed into repositories, not for medicinal plants,

**Figure 8.** Avenue, *Jardin des Plantes*, Paris – Plane trees were used in ancient Greece and Rome to mark sacred or public meeting places (Photograph: Roger Spencer 2014)

but for plants that were described using the adjectives 'beautiful', 'curious' and 'new'.

The romance of mysterious and exotic foreign lands captured the imaginations of all sectors of society. Travelogues, especially, drew public attention to the new era of voyages of scientific discovery and exploration. Tales of intrepid explorers were reminders of heroic ages past like the Mesopotamian *Epic of Gilgamesh* (2700 BCE) and Egyptian *Tale of the Shipwrecked Sailor* (c. 2000–1700 BCE). On Cook's first circumnavigation of the world in the *Endeavour*, his naturalists Banks and Solander returned to England as heroic plant collectors who had faced the gruelling test of global circumnavigation interspersed with the tropical delights and diversions of the enchanted islands of Otahiti: they were Enlightenment 'Shipwrecked Sailors' repeating deeds and exploits recounted in epics written over 3000 years before. After the magnificent botanical haul in Botany Bay, and with paper for the plant presses running out, Banks resorted to using unbound sheets of a copy of Milton's *Paradise Lost* that he had brought to read on the voyage (Finney 1984, p.16). This may have been the reason that, many years later, Charles Darwin kept a copy of *Paradise Lost* in his library on his world-changing voyage of the *Beagle* (1831–1836).

Under the curatorship of Philip Miller, the Chelsea Physic Garden became England's – and the world's – foremost plant collection until this honour passed to Kew Gardens in London at the end of the century. At Kew Joseph Banks groomed many botanical adventurers for work overseas – as botanists, horticulturists or garden administrators. Collectors were also sent from Edinburgh Botanic Gardens in smaller numbers.

In Paris the *Muséum d'Histoire Naturelle* was headed by the world-renowned natural historian the Comte de Buffon, the museum incorporating the *Jardin des Plantes* (called the *Jardin du Roi* before the Revolution; Fig. 8) whose head gardener was the outward-looking André Thouin. Significantly, in 1718 the name had been changed from *Jardin Royal des Plantes Médicinales* to *Jardin Royal des Plantes* indicating the change in emphasis from medicine to botany (Hyams & MacQuitty 1969, p. 83).

In Vienna there were the gardens, menagerie and heated glasshouses of Joseph II of Austria at the Palace of Schönbrunn that were constructed and managed with Dutch botanical expertise.

Then there were also the gardens of Empress Catherine the Great (1729–1796) of Russia, as well as the many estates of the aristocracy and Europe's social elite.

Enlightenment voyages of scientific exploration by Britain and France included not only astronomers, geologists, zoologists, botanists and other scientists, but also landscape artists and biological illustrators. The status of botany in scientific, social and economic circles had never been higher. Botanists needed herbarium specimens to describe these strange and wonderful plants and a craving for natural history specimens among European high society was unleashed, especially living plants and seed from New Holland. This lust for ornamental plants from across the sea became an obsession referred to as 'botanophilia', gripping the wealthy and influential, including botanists and nurserymen, and it was fed by new illustrated periodicals, plant dictionaries, encyclopaedias and travelogues (Williams 2001). Plant treasures were proudly displayed as rarities in the gardens and state-of-the-art heated glasshouses (hothouses) that protected the precious warm-climate botanical novelties from the severe European winters.

Both France and England set up networks of coastal outposts in the tropics to act as provisioning ports and holding stations for new crops and other plants of economic or ornamental value. Attention was given to acclimatisation, the plants trialled in different climates and soils, as these hubs became experimental stations and botanic gardens dedicated to economic botany. The botanical bounty was eagerly shared between colonies, especially those of the tropical Indo-Pacific and Caribbean regions (Ly-Tio-Fane 1996). Directors of these gardens, often trained in Paris or London, were highly skilled gardener-botanists who produced catalogues of the gardens under their care and engaged in international plant and seed exchange.

Major British gardens were established at St Vincent and Jamaica in the Caribbean (1765), and in St Helena in the Atlantic off the west coast of Africa (1787) as a stopping-station on the way to Indian Calcutta (1786) and Malaysian Peninsula Penang. From the 1790s the British Admiralty initiated hydrological surveys that employed salaried naturalists that were paid to complete their work onshore. Among the later beneficiaries of this source of revenue would be Thomas Huxley, Charles

Darwin and Joseph Hooker (Drayton 2000, pp. 126–127).

The following list gives an impression of the geographic range of these trading hubs: National Botanic Garden, Kirstenbosch, South Africa, formerly the Company Garden of VOC, (1658); Pamplemousses, Mauritius, now Sir Seewoosagur Ramgoolam Botanical Garden (1745); St Vincent and St Thomas, Caribbean (1764); Calcutta, India (Acharya Jagadish Chandra Bose Indian Botanic Garden, previously the Indian Botanic Garden) (1786); St Helena, South Atlantic (1787); Rio de Janeiro, Brazil (Jardim Botânico do Rio de Janeiro) (1808); Bogor, Java, Indonesia (Kebun Raya Bogor) (1817); Sri Lanka (Royal Botanic Gardens, Peradeniya, Fig. 9) (1821); and Singapore (Singapore Botanic Gardens) (1822).

Paris already had a maritime base in Madagascar in 1642 but other outposts were established in the Mascarenes (Mauritius and Réunion, then called Île de France and Île Bourbon). Pamplemousses on the Île de France was a Paris garden specialising in plants from Africa and Asia and famous for its acclimatisation of Brazilian manioc as food for plantation slaves. Pierre Poivre (1719–1786) had founded the botanic garden near Port Louis on Mauritius but he introduced spice plants to both islands, notably pepper and cinnamon, cloves and nutmeg. He was succeeded at Île de France by botanist Jean-Nicolas Céré (1737–1810) who continued the distribution of economic plants. Focus was also on the French Caribbean with gardens on the extremely lucrative settlements that had been founded at Saint Domingue and Guadeloupe. Coffee was soon cultivated on the Île Bourbon and by 1723 had reached the Antilles; other crops included pepper, cinnamon and breadfruit.

**Figure 9.** Local visitors enjoying the Royal Botanic Gardens Peradeniya, near Kandy in Sri Lanka. Joseph Banks encouraged the establishment of a strong network of botanic gardens throughout the British Empire, including in tropical locations where Europeans had already exploited the economic benefits of spices and other plants. Although the earlier Dutch colonisers had established a botanic garden in Colombo, in 1810, Joseph Banks advised the colonial government to establish a new one. Sri Lanka's history clearly represents the waves of European interest in exploring for spices, the Portuguese having arrived in 1505. (Photograph: Rob Cross 2014)

Colonial economic botany and the excitement of botanophilia played a major role on the path to European empires, a global economy, and the character of today's botanic gardens (McCracken 1997).

### Enlightenment and liberal democracy

The Enlightenment was, in part, an assault on kings and queens, wealth and privilege. In the latter quarter of the century Europe passed through yet another historical phase, an Age of Revolutions. From 1774 to 1848 revolutionary movements in Europe and the Americas were changing the form of government from absolute monarchy to constitutional states and republics: the groundwork for Western liberal democracy was being laid. This was a social change as never before with political power steadily withdrawn from its former royal base. The world of horticulture and botanic gardens would also be democratised as, through the 19th and 20th centuries, horticulture would be slowly handed over to the people.

Since the time of the royal dynasties of antiquity there had been an intimate connection between royalty, hierarchy and gardens. In the 18th century this connection would achieve its grandest expression in a final royal gasp of horticultural exuberance by the kings of the two most powerful countries in the world at this time, France and Britain.

In France the 18th-century kings were Louis XIV, XV and XVI of the House of Bourbon, who reigned from 1638 to 1792. The gardens were at the palace of Versailles and environs where the extravagant opulence of the Sun King Louis XIV, drawing on the genius of landscape architect André Le Nôtre, created what is arguably the world's greatest ever artistic garden masterpiece. Associated with Versailles was Louis XIV's retreat, the Grand Trianon, within whose grounds Louis XV later built another garden retreat, the Petit Trianon. In Paris, at the medicinal *Jardin du Roi*, it was learning and not art that was on display. After the Revolution the royal garden was renamed *Jardin des Plantes*, its goals becoming more scientific and educational, flourishing for many years and producing some of Europe's most outstanding biologists.

In England the kings were George I, II and III of the House of Hanover, who reigned from 1713 to 1811. The royal garden of England was at Kew. More modest in scale than royal gardens in France, Kew was a late-developer but it would ultimately have a greater impact on the world than its counterparts in France. The English secret to horticultural ascendancy was the scrupulously organised regime of economic botany promoted by Joseph Banks (1743–1820) in the years 1772 to 1820. The genius of Banks had been built on his early experiences with the internationally renowned Chelsea Physic Garden and its curator Philip Miller (1691–1771).

### Royalty

From antiquity came the common understanding that rulers were religiously sanctioned. Royalty set the standards for competitive fashionable society and in the 18th century gardens were a place where social competition was at its keenest. The tradition was an old one, the nobility and intelligentsia were intent on keeping up with, and thus gaining the support of, their social superiors, keeping in step with royal interests and foibles. Fashions and fads would then trickle down to the lower orders of society.

Perhaps the *Lyceum* had an influence on the well-to-do intelligentsia. The opulent estates of Roman Pliny the Younger (61–112 CE) had provided the model for Roman villas and *'played a part in formulating the principles of seventeenth and eighteenth century landscape gardening'*, while his letters *'... established the tradition, later drawn upon by Renaissance and Enlightenment humanists, whereby a man of letters should also be interested in the content and layout of his garden'* (Littlewood & von Stackelberg 2013, p. 147).

While rich and powerful husbands dealt with affairs of state and other important matters, it was conventional for their wives to manage their estates (like the wives of their Greek and Roman upper class predecessors). Two titled women will serve as examples of royal interest in gardens at this time: in England, Mary Duchess of Beaufort (1630–1715), and in France, Empress Joséphine de Beauharnais (1763–1814).

England's Duchess of Beaufort's vast family home at Badminton could boast a stove house to rival that of Queen Mary and it was filled with the latest exotic fruits and other novelties collected from the South African Cape, West Indies, Virginia, India, Ceylon, China and Japan, sourced via her botanical contacts including her London neighbour Hans Sloane. Hans Sloane (1660–

1753) had joined the Royal Society in 1685, following Isaac Newton as President in 1727. Sloane was a society physician, his patients including Queen Mary, George I and George II. He was a wealthy and influential traveller and collector of natural history specimens who had purchased the site of the Chelsea Physic Garden in 1712, hiring it out to the Society of Apothecaries for £5 a year in perpetuity. Sloane would later found the British Museum based on his vast collection of specimens. The botanical enthusiasm of the Duchess was so great that she had accumulated a personal herbarium that was donated to Sloane and housed in London's Natural History Museum. There was also a two-volume florilegium of drawings of her favourite garden treasures by Everhardus Lychicus, which was kept in the library at Badminton. British gardening can thank the Duchess for the introduction of several new plants including the zonal pelargonium, *Pelargonium zonale* (L.) L'Hér., and passionfruit, *Passiflora caerulea* L. (Uglow 2005, p. 109). The Duchess is commemorated in the Australian genus *Beaufortia* R.Br.

In France the Château de Malmaison was an extravagance in grand style. Situated just outside Paris the château was purchased in 1799 by Joséphine while her husband General Napoléon Bonaparte was away fighting an Egyptian Campaign. Napoléon's Egyptian army, in keeping with Enlightenment ideals, had included a staggering 167 savants (scientists and academics). At Malmaison Empress Joséphine competed with the *Jardin des Plantes* for botanical bounty and any other curiosities returned to France from the Pacific voyages of scientific exploration. The Malmaison menagerie contained Australian animals like the kangaroo (collected on Kangaroo Island during the Baudin expedition) and black swans. Also on display was a collection of ethnographic artefacts purchased from George Bass (Duchess of Hamilton 1998).

The Malmaison garden included Australian plants, some collected by gardener-botanist Félix Delahaye who was assistant to the botanist Jaques-Julien Labillardière on the D'Entrecasteaux expedition of 1791–1794. Delahaye had been selected for the expedition from students at the botany school of the *Jardin des Plantes* by Head Gardener André Thouin and he was the only gardener of this period to survive the voyage to the antipodes. Back in Paris Delahaye eventually became Joséphine's head gardener. Tasmanian plants cultivated in the Malmaison garden were illustrated by one of the world's greatest botanical illustrators, Pierre Redouté. Redouté, the 'Raphael of flowers' was court artist to Marie Antoinette when Paris was still the fashionable centre of Europe following Louis XIVs reign when, from 1798–1837, botanical illustration was thriving and adding to the excitement of botanophilia.

From this voyage also came the first ever extended account of the continent's plants written by Labillardière, whose 7 kg *Novae Hollandiae Plantarum Specimen*, published between 1804 and 1807, contained 265 black-and-white engravings by artist Pierre Antoine Poiteau. The subsequent Baudin expedition of 1800–1804 was the most lavishly equipped and ambitious of all the Enlightenment voyages of scientific exploration, supported by Napoléon and returning more scientific specimens to Europe than any other expedition, though at great human cost.

To Napoléon's irritation Joséphine communicated with Joseph Banks at Kew and eagerly sought advice and plants from London nurseryman Lewis Kennedy of The Vineyard nursery of Hammersmith, in the development of her *Jardin Anglais*. Her social standing ensured that her unsurpassed collection of roses would create a revitalised desire for roses that would sweep across Europe.

With gathering political uncertainty, the privileged were looking for diversions in their vast gardens. European admiration for the formal landscape splendour of the French court gave way to the non-geometrical English landscape style, and horticultural interest in plant novelties became the vogue. The new fashion in aristocratic gardening arrived in France as *Le Jardin Anglais*, in Germany as *Der Englischer Garten*, and in Italy as *Il Giardino Inglese* (as at the royal palace of La Reggia at Caserta just north of Naples). Catherine the Great of Russia enthusiastically summarised the new trend as follows:

> *I passionately love gardens in the English style, the curved lines, the gentle slopes, the ponds pretending to be lakes ... and I deeply disdain straight lines ... I should say my anglomania gets the better of planimetry.* (Hobhouse 1994, p. 190)

The English landscape style, evident in a number of modern botanic gardens, including the Royal

Botanic Gardens Victoria, was an aesthetic statement that combined Classicism and Romanticism. It was a rejection of formalism and a return to the evocation of a terrestrial paradise or sacred garden. As a movement in art it was related to the Greek idea of Arcadia, an ancient Golden Age of man in an idyllic time of peace, harmony and prosperity that existed either within a garden wilderness or state of pastoral bliss. No doubt it was sources like these that helped promote the idea of a botanic garden as a sanctuary for rest and relaxation (Prest 1981).

Much of English (and therefore 'Western') garden history falls under royal headings: Tudor, Elizabethan, Jacobean, Regency, Edwardian and so on. But the days of royal precedence in horticulture, as in pubic governance, were numbered. Certainly the change from patronage to people would be gradual, but by the 1830s the scale of gardens was diminishing. Garden designers like Capability Brown had worked on expansive and picturesque gentlemen's estates; now designers like Humphrey Repton were employed on smaller-scale gardenesque country manors. The 'garden' was growing again and the 'park' shrinking.

As governments became more powerful so royal and wealthy patronage was reduced. It was a combination of royalty, government and intelligentsia that added science to the usual economic and strategic reasons for colonial expansion. The gardens of kings, the wealthy elite and intelligentsia would gradually decline under the weight of new taxes. There would never be resident ruling kings or queens in North America or Australia and garden traditions named after royalty would go.

Also, the days of vast private enterprises like the VOC commanding vast armies were over – or at least they would take a different form. By the time of Empress Victoria in Britain, royal political power had long gone and royal social prestige was on the wane, although the great estates and royal traditions still remain as an echo of past royal horticultural glories adored by the public.

Enlightenment trade generated a new and affluent merchant class, a *nouveau riche*, to challenge the aristocracy, and the lower orders of society could now access a multitude of plants from overseas as they appeared in the proliferating commercial plant nurseries. Western horticulture was changing from privilege to populism as the many traditions that entrenched social stratification began to break down and social mobility became a possibility: but power over nations and gardens would not be given away lightly.

## France

The development of French and English royal gardens followed very similar paths, starting out as medicinal gardens, then becoming involved with science and associated botanical and horticultural education. The gardens of London and Paris provided the gardeners who would collect and care for plants on the great Enlightenment voyages of scientific exploration.

The medicinal *Jardin du Roi* in Paris was founded in 1626 but before too long its botanical interests extended beyond medicine. From 1670 to 1704 the Sun King Louis XIV sent scientific missions to Canada (1670), China (1685) and the French West Indies (1689). In 1700 botanist Tournefort was sent on a mission to Greece, Asia and Egypt, and a subsequent expedition was sent to Abyssinia in 1704 (Drayton 2000, pp. 16–17). Guy Fagon (1638–1718), who was an important early figure in the development of this garden, became personal physician to Louis XIV in 1669. He was Professor of Botany and Chemistry at the *Jardin du Roi* and produced a catalogue of its stock, *Hortus Regius*, in 1665, also instigating a series of exquisite, engraved plant illustrations based on its collections, an early example of impressive florilegia associated with botanic gardens (Chalmers 1812). Fagon was elevated to Superintendent of the garden in 1698 and was made an honorary member of the French Academy of Sciences in 1699.

In 1772 Louis XV, who ruled from 1715 to 1774, supported the Comte de Buffon in his renovation of the *Jardin du Roi*, adding a botany school. Plants in botanic gardens were now sometimes arranged according to the preferred classification systems of their associated botanists: they were becoming systems gardens. Linnaeus's 'sexual system', first published in 1735, had used artificial (convenient) characters. He acknowledged the taxonomic strength of natural systems but found his artificial system more practical. French and English taxonomists had persisted with their natural systems. In 1759 Bernard de Jussieu arranged the plants in the royal garden at Trianon according to his own natural system of classification, then, from 1774 to 1787, a new system garden demonstrating botanical families arranged according to the natural system of Antoine de Jussieu (Fig. 10) was established in the *Jardin du Roi* (Drayton 2000, pp. 19, 77).

During the reigns of Louis XV and Louis XVI from 1715 to 1792, three scientific voyages reached the South Seas and Nouvelle Hollande (Australia). Louis de Bougainville's expedition (1766–1769) pre-empted James Cook by being the first to circumnavigate the world with professional naturalists and geographers aboard, including the Montpellier-trained botanist Philibert Commerçon (Commerson) but there was only a brief sighting of the Great Barrier Reef. Then followed two ill-fated expeditions, the first by Marc-Joseph Marion Dufresne (1769–1772), who was sent to the South Pacific in search of *Terra Australis Incognita* and made landfall in Tasmania (hence the eponymous Marion Bay) but was later killed in conflict with New Zealand Maoris. In 1772 Louis de Saint Aloüarn was sent in search of new territories for France, his ship making a formal claim of French sovereignty over the west coast of Nouvelle Hollande (Cook had only claimed the east coast) before later dying at Port Louis in Mauritius on the way home.

**Figure 10.** Antoine Laurent de Jussieu (1748–1836) – Sculpture in the Museum at the *Jardin des Plantes*. De Jussieu devised a natural classification of flowering plants that was displayed as a systems garden in the Jardin: it extended the work of his uncle, the botanist Bernard de Jussieu whose system had been displayed at Trianon. (Photograph: Roger Spencer 2014)

France's major contribution to the natural history of the Pacific region was the result of three scientific voyages that occurred between 1785 and 1804, and which followed the Western Australian route of Saint Aloüarn – by Jean-François de la Pérouse (1785–1788), Brunl d'Entrecasteaux (1791–1794) and Nicolas Baudin (1800–1804). These expeditions span years when Paris was in the grip of both a political revolution and botanophilia.

Gardeners for these expeditions were provided by horticultural botanist André Thouin (1747–1824), who held the position of Head Gardener at the *Jardin des Plantes* from 1764 to 1793. Thouin was the foremost French horticulturist of the late 18th century and he exemplifies well the spirit of the times. The famous Enlightenment figure Jean Jacques Rousseau corresponded with Thouin, whose family lead a simple Rousseauesque lifestyle, his family home an annex to the hothouses at the *Jardin du Roi* (Spary 2000, pp. 40, 49).

Thouin, like other naturalists of his day, built up a wide correspondence network that included more than 400 people of assorted backgrounds, from botanists to the wealthy elite. His correspondence generally included a *Desiderata* (list of plants required) accompanied by a catalogue of plants and seed he could offer in exchange. This was an effective way of organising the exchange of plants and seed from around the world for the botanical gardens and their greenhouses, which now acted as acclimatisation centres (Williams 2001, p. 46). Under his charge from 1774 to 1786 the number of taxa

**Figure 11.** A specimen container or vasculum used by botanists to keep specimens fresh, *Jardin des Plantes.* (Photograph: Roger Spencer 2014)

sown in the nursery doubled from 1096 to 2200 (Spary 2000, p. 58). Thouin prepared journals for his travelling gardeners with detailed instructions for the collection, packaging, preservation and care of specimens (Fig. 11). He recommended that they read the works of Linnaeus and various travelogues while on the voyage. French use of miniature glasshouses on board preceded the British use of Wardian cases by several decades (Spary 2000, pp. 86, 120–121).

The botanical-horticultural school produced a generation of *Jardin* protégés sent on voyages or given senior posts in France's regional gardens, with one gardener, Schweykert, even being posted to the rival Kew Gardens under William Aiton (Spary 2000, p. 95).

In the 1790s, Thouin became a key figure in French agricultural improvement, being appointed Professor of Culture in 1793, his reputation requiring him to give talks to eager landowners and plant lovers at six o'clock in the morning (Spary 2000, pp. 86–87). He was elected to the Académie in 1786 and awarded the cross of the Légion d'Honeur (Williams 2001, p. 152).

**Figure 12.** Neoclassical entrance to the Museum of Botany and Geology at the *Jardin des Plantes*, Paris. (Photograph: Roger Spencer 2014)

The French botanical legacy is substantial. The men who worked in the *Muséum National d'Histoire Naturelle* and *Jardin des Plantes* (Fig. 12) in the early 19th century '*... were virtually the founding fathers of the modern natural sciences ...*' and it was '*... Frenchmen at the* Jardin des Plantes *rather than Britons at Oxford, Chelsea and Kew, who founded modern botany*' (Hyams & MacQuitty 1969, p. 84). But this was not the case for horticulture.

## Britain

Dutch horticultural expertise was brought to Britain in the 17th century when the co-regency of Dutch Prince William and Queen Mary acceded to the British throne in 1689. Bemoaning the lack of interesting plants, the Dutch collection of potted exotic plants was brought across the English Channel to be displayed formally at the royal residence of Hampton Court where state-of-the-art Dutch hothouses were built using underfloor heating that emulated the hypocaust of Roman baths and buildings. Garden beds in the hothouses were kept warm with manure and tanners bark, thus allowing the cultivation of plants from Barbados, Canaries, East Indies and the Cape. The potted warm-climate plants were aired outside in summer (Uglow 2005, p. 120).

Many of the newly introduced plants had found their way into prestigious gardens through the exploits of reckless adventurers. English privateer William Dampier made landfall on the north-west coast of New Holland on 14 January 1688, careening his ship, the *Cygnet*, and doing repairs in a 'sandy cove'. These pirates were the first British to set foot on New Holland, some 80 years before Cook and his men. Dampier stored the record of his voyage in waterproof bamboo cylinders sealed with wax and, when he arrived back in England in 1691, published them as *A New Voyage Round the World*. Within two years of its first publication in London in 1697 his travelogue had run to four editions, being translated into Dutch (1698), French (1698) and German (1702) (George 1999, p. 7).

Dampier's scientific enthusiasm so impressed the Royal Society that, when he requested a ship from the British Admiralty for a return to the South Seas, his request was granted. His brief was to investigate the uncharted eastern coast of New Holland, perhaps solving the mystery of the fabled *Terra Australis Incognito*. This was the first British Admiralty expedition dedicated to both exploration and scientific study: it was to survey '*all islands, shores, capes, bays, creeks and harbours, fit for shelter as well as defence*', to also bring back specimens of animals and plants, and to have with him an artist to '*sketch birds, beasts, fishes and plants*'. He was also asked to bring back a sample native person '*providing they shall be willing to come along*' (Hill 2012, p. 46).

Dampier departed England in 1699 and arrived in New Holland the same year. Using a chart of the western coast drawn up by Abel Tasman 50 years before, he named Shark Bay and sailed north, collecting as he went, pressing plants between the leaves of a book. Plants, birds and fish were sketched by a crew member following a procedure first encouraged by the Royal Society in 1665. However, the *Roebuck* foundered and Dampier arrived back in England without his ship in 1701 to be court-marshalled by the navy for, among other things, loss of the *Roebuck* and cruelty to his Lieutenant and a boatswain. As a penalty his pay for the voyage was docked and he returned to writing travelogues; his account of this second 1699–1701 expedition to New Holland was published in 1703 and 1709 as *A Voyage to New Holland*. The sketches and descriptions published together were the first recorded graphic representation of plants and animals of New Holland (Finney 1984, p. 11).

Botanical specimens from the Roebuck expedition were presented to the Royal Society and about 40 are now held by the Fielding-Druce Herbarium at Oxford University (George 1971; Olde & Marriott 1994, p. 11). Nine of his Australian specimens were described by leading English botanist John Ray, the 'father of British botany', in his *Historiae Plantarum* (1704), and others by Leonard Plukenet, who was Royal Professor of Botany and gardener to Queen Mary (George 1999, p. 22). Those published before Linnaeus's *Species Plantarum* (1753) were given 'phrase names' as brief Latin descriptions, also referred to as polynomials.

Dampier was the first person to circumnavigate the world three times, and he made the first fully authenticated plant collections in New Holland. His travelogues were the inspiration for Daniel Defoe's *Robinson Crusoe*, Swift's *Gulliver's Travels* and Coleridge's poem *Rime of the Ancient Mariner*, which were recommended reading for subsequent voyages of scientific exploration.

The direction of botanic gardens, and indeed Western horticulture, owes much to Scotsman Philip Miller (1691–1771) of the Chelsea Physic Garden and Joseph Banks (1743–1820) of Kew Botanic Gardens. Miller was a key figure in international horticulture at a time when Chelsea, not Kew, was the pre-eminent garden in England.

As early as 1680 merchant apothecary and former curator of the Chelsea Physic Garden, John Watts, was instructed to grow both native and exotic plants in addition to the medicinal ones, and he sent gardener John Harlow to collect plants in Virginia, America. Then, in 1682, the Chelsea garden was visited by Leiden's Paul Hermann. Watts's subsequent return visit to Amsterdam in 1683 initiated not only an exchange of seed and plants, but the tradition that would become known as 'the international botanic gardens seed exchange', a free exchange network that persists to this day (Minter 2000, pp. 5–6, 102). The exchange of a seed catalogue (*Index Seminum*) has been, historically, a major means of global plant distribution but it is waning today due to concerns about genetic piracy and the danger of innocently spreading environmentally invasive plants (Aplin & Heywood 2008).

Philip Miller was appointed *Praefectorius* of London's Chelsea Physic Garden in 1722 and in 1727 he visited Leiden, admiring the garden and greenhouse displays, the greatest living plant collections in Europe. After meeting Boerhaave he returned to London determined to increase the Chelsea collection, and by the 1730s the Chelsea Physic Garden could boast a collection of plants that would rival any in Europe (Hadfield et al. 1980). Then, in 1732, letters arrived from Boerhaave himself requesting trees and shrubs: *'I know of no one in your country who is more capable to identify and distinguish them'* and *'Remember, I beg you, my garden'* (Wulf 2009, p. 40), this being, to all intents and purposes, an acknowledgement by Boerhaave of the transition of European horticultural pre-eminence from Holland to Britain.

Linnaeus travelled from Holland to London in 1736 visiting the Chelsea Physic Garden on three occasions, describing Miller as *'Hortulanorum Princeps'* (Prince of gardeners) and Miller's *Dictionary* as *'Non erit lexicon hortulanorum sed etiam botanicorum'* (not just a dictionary of horticulture but a dictionary of botany too) (Huxley 1992, p. 240). Miller was best known for his compendium *Gardeners Dictionary*, first published in 1731 but with many later editions. This work was like an encyclopaedia of garden plants and it has continued in various guises right up to the present day. Publications following Miller's tradition include the *New RHS Dictionary of Gardening* (Huxley 1992) and *RHS Plant Finder*. William Stearn described the *Gardeners Dictionary* as *'the most important horticultural work of the eighteenth century'*, especially the eighth edition of 1768, the first to use the Linnaean system previously resisted by Miller (Stearn in Le Rougetel 1990, p. 169). Covering the period 1731 to 1804, each edition of the *Dictionary* was not only a horticultural encyclopaedia, it was a record of plant introduction through the century as it included approximate dates of introduction as well as additional historical and botanical information. In 1764, notable English merchant and plant collector Peter Collinson stated that Miller *'has raised the reputation of the Chelsea Physic Garden so much that it excels all the gardens of Europe'* (Paterson 1986). From this time in the mid-18th century to the present day, horticulture has remained an English obsession, prompting a remark in the preface to the German translation of the encyclopaedic 1750 edition of Miller's *Gardeners Dictionary* referring to the English as *'All, more or less, gardeners'* (Wulf 2009, p. 310).

In the latter half of the 18th century Europe was captivated by the voyages of Captain James Cook (1728–1779) who had completed three circumnavigations of the globe (1768–1771, 1772–1775, 1776–1779). The first voyage included the now famous eight-day extravaganza of botanical collecting at Botany Bay in April 1770 by the naturalists Joseph Banks and Linnaeus's favourite student Daniel Solander (1733–1782) who, Linnaeus had hoped, would marry his daughter (Moyal 1976). The exotic adventure along the east coast of New Holland proved so popular that, back in Europe, Banks and Solander were widely acclaimed and decorated. From 1778, Banks held the position of President of the Royal Society for 41 years, and was a founding member of the (Royal) Horticultural Society. After stepping off HMS Endeavour, he had effectively become Director of the Royal Botanic Gardens Kew in 1772 to preside over a golden era that ended rapidly following his death in 1820.

Kew, though having a long royal history, was at this time virtually an offshoot of the Chelsea Physic Garden.

George III needed a garden that might rival those in France although it could not possibly compete with the art of Versailles. Kew was selected and in 1772 Banks was put in charge, immediately opening up communication with Bouffon and Thouin.

Kew's first head gardener was Scotsman William Aiton, formerly of the Chelsea Physic Garden, who was appointed in 1759 on Miller's recommendation. The first nine acres were laid out according to Linnaeus's sexual system of classification (Stearn 1961, p. xcix).

Major landmarks of plant cataloguing were achieved over the next few decades. Clearly Europe's leading gardens were competing to hold the greatest number of different plants. In the 1660s the *Jardin du Roi* claimed about 4000 species (Stafleu 1969), probably the most extensive at this time, but by 1720 giving way to Leiden under Boerhaave with 5846 different kinds (Boerhaave 1720). Between 1730 and 1770 both the reputation and collection at the Chelsea Physic Garden grew until the species totalled about 5000 (Uglow 2005, p. 147). John Hills's *Hortus Kewensis* of 1769, an inventory of Kew's stock, listed only about 600 species. Then, following the 1768 edition of Miller's *Gardeners Dictionary*, came Aiton's three-volume *Hortus Kewensis* in 1789, a monumental descriptive inventory of Kew's living collections assembled under Banks's influence and totalling over 5500 species. This was an invaluable horticultural record that included Linnaean Latin diagnoses (much of it was written by botanists Solander, Dryander and Brown) and was annotated with dates of introduction etc. It included '... *almost all the species then cultivated in England*' (Stearn 1961, pp. cvii–cviii). The 1813 edition of *Hortus Kewensis* had swelled to five volumes and over 11,000 species, including about 300 from Australia indicating the further impact of Banks's acquisitiveness (Drayton 2000, p. 125). Though all these new plants arriving at Kew embellished His Majesty's collection (Kew only became public in 1840), George III actually expended very little in their acquisition.

When, as a young man, Banks had moved from his country estate to London his new home was situated near the east corner of the Chelsea Physic Garden, which became one of his favourite haunts. Here he met Philip Miller who acted as a horticultural mentor, explaining about plant collections and the excitement of introducing new species into cultivation while at the same time introducing Banks to the circle of eminent horticulturists, nurserymen and collectors of the day, among whom were botanist Daniel Solander and well-known The Vineyard nurseryman James Lee (colleague of Lewis Kennedy), John Bartram in America, Hans Sloane and many others (Minter 1994). Miller's herbarium specimens, including copper-plate coloured engravings made by outstanding botanical artist Georg Ehret (1708–1770) completed during Miller's curatorship, were purchased in 1774 by Banks and are now housed at the Natural History Museum, many serving as voucher specimens for plants cultivated in Britain for the first time (Uglow 2005, p. 146; Stearn in Le Rougetel 1990, pp. 185–186).

Banks, like Thouin in Paris, groomed enterprising young gardeners as plant collectors, several later finding their way to posts in colonial gardens including in Australia, where Kew-trained gardeners and botanists have found employment to the present day. Gardeners sailed on ships attached to various government and private organisations (Fig. 13). Examples include Christopher Smith, who worked with Bligh before taking charge of the Calcutta Botanic Gardens, and Peter Good, previously a foreman gardener at Kew, who eventually died in 1802 on Matthew Flinders's *Investigator* mission of 1801 while serving as gardener to botanist Robert Brown during a detailed charting of the Australian coast. William Kerr, a Scottish gardener to the British East India Company and a Kew gardener selected by Banks, worked in Canton and Java before taking charge of the Ceylon Botanic Garden in 1810 (Drayton 2000, p.86). There are many others.

Banks never met Linnaeus and Linnaeus himself never saw plants collected by Banks and Solander on the *Endeavour* voyage. Solander eventually ceased correspondence with his old master. Banks had circumvented the need for internationally recognised botanical authority by poaching Linnaeus's favourite student, Solander, and later another student, Dryander. Linnaeus had even magnanimously suggested the name Banksia for the southern continent that would eventually become known as Australia, as he wished to commemorate the work of the *Endeavour's* naturalists in 1770 (Moyal 1976).

When Linnaeus died in 1778 his entire collection of natural history specimens, including an extensive

**Figure 13.** *Araucaria columnaris* (G.Forst.) Hook., indigenous to New Caledonia, making a magnificent avenue at the Royal Botanic Gardens Peradeniya, Sri Lanka. James Cook recognised the potential of these 'pines' as masts for ships of the British navy. (Photograph: Rob Cross 2014)

herbarium, was put on the market for 1000 guineas. As Linnaeus had used these collections for the reclassification of the natural world they were of inestimable value as 'type' specimens and in much demand from, amongst others, Catherine the Great of Russia, botanists in Denmark, Holland, France and Switzerland, and even Sweden's King Gustav. Banks managed to acquire the collection for Britain by persuading Scottish botanist James Smith to make the purchase. This effectively placed Britain and Banks in charge of the botanical world:

> *With Linnaeus's collection in Chelsea, Banks's collection at Soho Square, Sloane's bequest at the British Museum and the living plant entrepôt at Kew, London had become the botanic centre of the world. Nowhere else was there such an accumulation of foreign plants – dried and living – as well as of botanical knowledge. The purchase of Linnaeus's collection, one of Smith's friends wrote, 'most decidedly sets Britain above all other nations in the Botanical Empire'.* (Wulf 2009, p. 223)

Imperial powers were well aware of the economic opportunities presented by plants. Fortunes built on spices were a reminder that plants were economic resources as well as ornaments. From his imperial botanical hub at Kew, Banks set out to exploit the full commercial potential of tropical and other crops. A globally respected plant celebrity and father-figure, he was a master of economic botany and a supreme administrator and communicator, orchestrating events from the centre of a vast scientific, botanical, horticultural, political, economic, aristocratic and royal network. He initiated foreign employment on the brink of an era of salaried positions for scientists. His legacy is summarised by horticultural historian Andrea Wulf:

> *One of the most influential men of the Enlightenment ... who was the engine of scientific progress for more than four decades and who believed that science was the future of both Britain and humankind ... Banks was generous because he believed that the sharing of knowledge would bring progress ... one of the most fascinating men of Georgian England.* (Wulf 2007)

> *... he consolidated practical horticulture, systematic botany and imperial expansion into a coherent enterprise. As President of the Royal Society, Member of the Privy Council, confidant of King George III and founder of the Horticultural Society, he, more than anyone before or after him, saw how the three elements could bring pleasure and prosperity to a nation.* (Wulf 2009, p. 241)

In the 18th century, botany was like a thick fibre woven into the fabric of society. Banks facilitated the linking of botany and horticulture, science and economics, nurseries and botanic gardens, even the Royal Society, government, and British high society, all united into an international network engaged in the collection, distribution and exchange of living and dried plants. With Kew a strategic centre of economic botany for the world's largest-ever empire, it is not surprising that its activities in botany and horticulture would have a profound influence on future global plant distribution and management.

## Biological globalisation and economic botany

The Great Divergence that placed Europe at the centre of a new global order and economy would also have global implications for the world's flora and fauna.

Claudius Ptolemy (c. 100–c. 170 CE) was a Greco-Egyptian natural scientist and geographer who worked in Alexandria. For well over a millennium his map of the classical world had served European mariners as an operational map of the known world. However, from 1482, European exploration and charting of the Atlantic, Indian and Pacific Oceans rapidly outlined the familiar world map of today. The Age of Discovery, and especially the first circumnavigation of the globe in 1519–1522, had established the spatial limits of the world. By locating the boundaries of the world's land masses, humanity was confronted for the first time with the physical reality of a finite planet. An inventory of the world's resources, including its biological organisms, thus became a meaningful pursuit for the logical and scientific mind.

By the end of the 15th century botanists were speculating about the possible number of different plants in the world. The herbals had described 500–1000 species, this being the legacy of Classical and Medieval knowledge (Morton 1981, p. 145). In 1613 Jean Bauhin (1541–1613) (son of Jean Bauhin (1511–1582) who was physician to Jeanne d'Albret, Queen of Navarre) described about 4000 species. Jean's brother Gaspard, in the *Pinax* of 1623, increased this number to 6000, his account including synonymy, references and binomials over a century before they were used by Linnaeus. John Ray's three-volume *Historia Plantarum* (1686, 1688, 1704) lists some 18,700 different kinds of plants.

Linnaeus in 1753, less than 40 years before Australian settlement, believed that the total number of plant species in the world was unlikely to exceed 10,000 (Stearn 1959). Today the total number of naturally occurring seed plant taxa in the world is estimated to be about 369,000 (RBG Kew 2016).

The dangers and risks of exploration might be rewarded by the discovery of new and valuable resources. Fortunes made from spices had alerted merchants to the commercial potential of plants as new foods, beverages, condiments, ornaments and other as-yet-unknown but lucrative uses. Like spices, new crops might be luxury items rather than essentials.

Colonial powers introduced European institutions, technology, trade and people to the Americas, Asia and southern Africa. But the expansion of Europe was also a two-way process, a contraction of the world (Drayton 2000, p. xiv), and part of this process was the reciprocal exchange of animals and plants between the Old and New Worlds. This began in earnest after Columbus's discovery of the New World and therefore became known as the 'Columbian Exchange' (Crosby 1972). The Columbian Exchange announced an acceleration of biological globalisation.

Botany became an arm of international economics as botanic gardens outside Europe became holding, provisioning and trading hubs as well as experimental stations, and bases seeking out plant novelties. These activities linking botanic gardens to the politics and economics of the day, and the increasing distribution of ornamental plants to commercial nurseries as well as to private individuals and the major botanical centres, meant that botanic gardens were moving away from academia, royalty and narrow interests to become instruments that also served the state and their local communities.

Prospecting for economic plants would lead to a global redistribution of the world's vegetation out of native habitats into cultivated land, and then sometimes escaping into the wild. Two world wars would draw attention to the need for self-sufficiency in plants of economic importance and this encouraged their wider distribution (or the introduction of suitable substitutes).

The kinds of commercially and culturally important plants that are the focus of human plant redistribution fall into four broad groups. First, there was an early phase associated with the mystical and medicinal herbs and spices managed mostly by specialist physicians. Then there were three groups mostly distributed in the modern era: staple agricultural crops, mostly the cereals that were the mainstay of temperate European agriculture transferred as part of the process of European colonisation; horticultural crops, foods grown to enhance diets and nutrition, often cultivated *en masse*; and garden plants grown as ornamental plant luxuries.

An early phase of plant globalisation was the East–West exchange of herbs and spices between China, India and the great cities of the Mediterranean.

### Herbs and spices

From earliest history, apart from food plants, it was herbs and spices in particular that commanded human respect and study.

According to Indian, Persian, Greek and Roman traditions of medicine, especially those espoused by Hippocrates and the Islamic physicians, the body had four humours (black and yellow bile, phlegm and blood) corresponding to four temperaments (sanguine, choleric, melancholic and phlegmatic): herbs and spices could be used to adjust these humours.

The distinction between herbs and spices is not clear-cut but, in general, relates to both the part of the plant being used and also its geographic origin. Culinary herbs consist of the leafy green part of a plant, and are mostly temperate and Mediterranean in origin. Spices are sourced from other parts of the plant than the leaf such as the root, stem, bulb, bark, resin or seeds, and most spices are native to the Asiatic tropics. Following Purseglove et al. (1981), the major spices are: cardamom, cinnamon and cassia, chillies, cloves, coriander, ginger, nutmeg and mace, pepper, pimento, turmeric and vanilla; lesser ones would be caraway, cumin, dill, fennel, garlic, frankincense, juniper, liquorice, mustard, myrrh, onion, sandalwood and sesame. Some plants have the distinction of being used as both herbs and spices – like coriander, fennel and dill.

Though the numbers of species transported to be grown elsewhere was small, trade along the Incense Route and Silk Road provided a foretaste of the East–West spice and plant trade that would gather momentum in the Age of Discovery. Leading this early trade were the spices frankincense (the aromatic resin of four species in the genus *Boswellia* Roxb. ex Colebr.) and myrrh (an aromatic resin from species of *Commiphora* Jacq.), almost always traded together and often associated with gold. Gold symbolised royalty, frankincense divinity, and myrrh was an aromatic oil with a bitter taste and symbolised death. Being in limited supply these were luxury goods that commanded high prices among the well-to-do. Frankincense and myrrh were accessed from Arabia by all the ancient civilisations including those of India and China. India's reputation as a land of spices had attracted ancient Babylonians, Assyrians and Egyptians to the Malabar Coast as early as c. 2000–3000 BCE. Many spices now popular and widely grown in the tropics were traded from the south-west coastal region of Kerala in India (India itself well-deserving its title Land of Spices), which was a centre for both land and sea trade from both East and West (Purseglove et al. 1981, pp. 1–9).

Greco-Roman trade in the period c. 700 BCE to 200 CE passed between North Africa (including the Horn of Africa, today's Ethiopia and Somalia, which provided rare woods, animal skins, feathers and gold), the Eastern Mediterranean and the Arabian Peninsula, where frankincense and myrrh were obtained and traded along what is sometimes known as the Arabia to Damascus Incense Route. But there were also goods from India: spices, silk and textiles, precious stones, pearls and ebony, as well as from the Horn of Africa. Desire for spices did not diminish as is amply demonstrated by the demands of Alaric the Goth who, to call off the Visigoth siege of Rome in 408 CE, called for a bounty of gold,

Nutmeg (*Myristica fragrans*), also a source of mace, growing at the Royal Botanic Gardens Peradeniya, near Kandy in Sri Lanka. European exploration into the the Indian Ocean and ultimately to the Spice Islands of Indonesian was stimulated by the search for rare and highly desired spices like Nutmeg. Although the Dutch had established an earlier botanic garden in Colombo, the English closed it establishing a new one at Slave Island, moving it to Kalutara and ultimately to where it was thought the climate was more favourable at Peradeniya in 1822. The site was originally a Royal Garden established during the reign of King Kirthi, 1747-1780.

**Figure 14.** Nutmeg. (Photographs: Rob Cross (tree and gardens 2014); Roger Spencer (nutmeg 2015))

silver and 3000 pounds of pepper (Purseglove et al. 1981, pp. 1–9).

Initially inspiring the whole enterprise of economic botany and plant prospecting were the nutmeg and cloves from the Indonesian Molucca islands in the Banda and Molucca Seas.

The herbs and spices that have figured in world trade can be divided into two groups based on the climate of the countries where they grow. The temperate and Mediterranean (some extending to India) herbs and spices include coriander, cumin, dill, fennel, frankincense, garlic, juniper, mint, myrrh and thyme, and, to a lesser extent, caraway, fenugreek, liquorice, marjoram, mustard, onion and parsley. Then there were the Indian and Far Eastern tropical spices that became so pivotal for world trade and global politics in the Age of Discovery: cardamom, cinnamon, cloves, mace, nutmeg, pepper and, to a lesser extent, ginger, henna, sandalwood and sesame (Fig. 14).

Once France and England had obtained nutmeg plants, plantations were set up in Ceylon (Sri Lanka) and Granada, and these and other spices became commonplace and relatively cheap, much as they are today. Through the 17th and 18th centuries the one-time mystery and magic of spices that enhanced the exotic cuisine of the aristocracy faded as their use passed into broader society.

## Agricultural subsistence crops

Staple cereal crops have had more impact on humanity than any other plants: for their cultural transformation, life-sustaining nutritional energy, their influence on the human economy, and the expanse of land and resources required for their cultivation.

Agriculture, now a specialist applied science treated separately from botany, began to diverge from botany and botanical gardens through the 18th and 19th centuries. Cereals are quite difficult to display, and in botanical gardens their significance is often passed over. However, for a while in the 18th century, botanical gardens, being a major source of general plant knowledge, were also a source of agricultural knowledge.

Agriculture was both a scientific and moral priority of the Enlightenment since it was perceived as a means of 'improvement' of land, society and non-European peoples, as well as '*a synonym for the laying out of parks and gardens*' (Stroud 1986). It therefore gained royal patronage across Europe in the 1760s (Drayton 2000, p. 89). From its earliest days the Royal Society had ranked agriculture and forestry among its major concerns, forestry being essential for the timber needed to build and maintain the royal navy (Drayton 2000, p. 52).

Economies at this time were essentially agrarian and France and England competed in the development of scientific agriculture. French physiocrats promoted agricultural labour as the source of surplus energy and, therefore, the wealth needed to drive society forward. Today's *Académie d'agriculture de France* was founded as a royal society in 1761 by Louis XV. In 1784 the *Annals of Agriculture* was first published in Paris.

In England of the early 18th century there were '*... great strides in land fertility and reclamation from the heath, bog, and scrub with which more than half the countryside is estimated to have been covered*' (Stroud 1986).

In 1787 merino sheep were imported by England's George III from Spain to roam the royal gardens at Windsor and Kew, and it was from these flocks that the first merino sheep were selected for the Colony of New South Wales in 1804 (Drayton 2000, p.87). Banks was a wealthy landholder, a Lincolnshire squire in the tradition of the Roman farmer-statesman, and agriculture was close to his heart.

Colonising Europeans preferred comfortable temperatures, settling mainly in temperate regions where they introduced the familiar domesticated animals and plants of temperate agriculture, although associated with these came unwanted pests, diseases and invasive organisms. The temperate Afro-Eurasian cereals barley, oats, wheat, millet and rice (which had found its way from China to south-east Asia and India in the third millennium BCE), along with assorted pulses, were introduced by the European settlers to temperate regions of the world, which became 'Neo-Europes' (Crosby 2004). Maize (corn) was introduced to the wider world from South America.

The energy provided by agricultural and horticultural crops, and the wealth generated by trade in crops like sugar, cotton, tea and coffee, would feed into the accelerating growth of the world population. During the 19th century, vast tracts of the planet's land surface would be turned over to crops and agricultural rangeland. The first indications of large-scale environmental impact were appearing that would later become topics to be addressed by botanic gardens. Demand for wood had already depleted the supply of native timber prompting the demand for more organised forestry. Seizure of arable land for agriculture was transforming landscapes and was a common reason for indigenous dispossession.

### Horticultural crops

Over time horticultural crops would become the concern of specialist arms of government, but botanic gardens played a vital role in the discovery, introduction and distribution of these socially transforming plants. Only a little of this story can be touched on here.

Between the fall of Rome and the voyages of Columbus it was mainly Arab merchants who were the agency for worldwide plant exchange. For example, sugarcane, which is native to south-east Asia, had passed in ancient times from south-east Asia to India, then to Egypt, Syria and Arabia, and from there to Europe and the Atlantic islands. Columbus introduced sugarcane to the New World from the Canaries in 1493. Sugar plantations were soon part of European wealth accumulation as part of a circular Atlantic trade route for goods and people running between Britain, West Africa, the New World and back, a trade based mainly on African slaves taken to work plantations in Brazil and the Caribbean. Plantation crops like sugar, tobacco and cotton, though generating vast wealth and benefit for their colonial overseers, were maintained by slavery and often involved cruel mistreatment of indigenous peoples.

Horticultural food crops obtained from the New World of South America and the Caribbean included avocado, cashew, cassava, chili peppers, cocoa, Jerusalem artichoke, peanuts, pineapple, pumpkin, French and runner beans, squash, sunflower, sweet potato, tomato, vanilla and the staple cereal maize (corn).

From the Old World and Asia passing to the New World were apples, aubergines (eggplant), citrus, coffee, grapes, mango, olives, onions, peaches, pears, spinach and tea, and from Africa especially came sorghum, henna and watermelons. From south-east Asia came the banana, breadfruit, coconut, sugar, taro, yams and plantains.

There were additional economically important non-food plants, including tobacco from tropical America, the rubber plant from Brazil, quinine from Bolivia, Ecuador and Peru, opium from Eurasia, the fibres hemp and jute from Asia and sisal from South America, and cotton from the tropics and beyond.

Portuguese traders introduced many economic plants to India, the *Jardin des Plantes* introduced coffee to the West Indies from a plant sent to Louis XIV as a gift from the Dutch government in 1714, the plant itself derived in turn from one sent to the Amsterdam Botanic Gardens from Java in 1706 (Standage 2007). Miller of the Chelsea Physic Garden excelled in his cultivation of melons, paw-paws and pineapples in glasshouse 'hot beds' (Minter 2000). Kew introduced quinine to India, and rubber to the world.

The links between botanic gardens, horticultural crops and taxonomy were many. For example, a banana plant from Surinam was grown in the private glasshouses of Clifford's estate at Hartekamp. While working here Linnaeus was the first European to coax the plant into flower and fruit. Linnaeus in his excitement sent a fruit to Antoine de Jussieu at the Paris *Jardin du Roi* (Jussieu was also trying to get the plant to fruit), Jussieu being most impressed. When naming the plant Linnaeus chose the genus name *Musa* L., almost certainly commemorating Antonius Musa, a Greek freedman botanist-physician to Rome's first emperor Augustus. It was believed by Linnaeus and others that the Tree of Knowledge, whose forbidden fruit was eaten by Adam and Eve in the Garden of Eden, was in fact a banana and, accordingly, Linnaeus erected the names *Musa sapientum* L. and *Musa paradisiaca* L. (Koerner in Jardine et al. 1996, p. 147). In the 16th century the banana was introduced to the Americas by the Portuguese via West Africa and the Canaries, but it would remain an exotic luxury novelty in temperate Europe until the advent of rapid transport and refrigeration in the 20th century.

Various commercial enterprises were initiated by the French in the tropical French West Indies including the first introduction of breadfruit, considered a French triumph, especially after the initial failure of Britain's Captain Bligh and the *Bounty* expedition (Fig. 15).

The voyage of Captain Bligh, who would later become an Australian governor, was legendary. The Royal Society had offered a prize for the successful transfer of breadfruit from Tahiti to the Caribbean where it was to be used as a staple food for the thousands of slaves working in the English sugar plantations. On the first voyage of 1787–1790 with gardeners William Brown and David Nelson (selected by Banks), the *Bounty* called in to Adventure Bay in Tasmania (where the gardeners set up a small food garden) but the mission later ended in mutiny, with the plants thrown overboard. Bligh and 18 loyalists, including David Nelson, were cast adrift with a meagre supply of food and water in an open boat just 7 m long. In a staggering feat of endurance and navigation, the small boat covered the 5822 km to Timor in six weeks, even charting part of the north-east coast of New Holland on their way. Ironically, a few days after arriving in Timor, Nelson, who was always keen to botanise, could not resist spending a day in the mountains where he caught a cold and died of 'inflammatory fever' (St John 1976). Nelson was buried in a grave in Timor that would later be also used for French gardener Anselme Riedlé of the Baudin scientific expedition (1800–1804), and Alexander Zippelius, a Dutch gardener-botanist and assistant curator of the Buitenzorg Botanic Gardens (now Bogor Botanical Gardens), who died in Timor in 1828. Bligh's second breadfruit voyage in the *Providence* from 1791 to 1793, with illustrators, artists, and Kew gardeners James Wiles and Christopher Smith, was successful although, ironically, the breadfruit was rejected as a food source by the plantation slaves.

**Figure 15.** Breadfruit, *Artocarpus altilis* (Parkinson ex F.A.Zorn) Fosberg, was transported by France and Britain from the eastern to western tropics. (Photograph: Wikimedia Commons)

## Ornamental plants

Crops serviced basic human needs while ornamental plants were socially prestigious luxuries. It was mostly botanic gardens that spearheaded the early introduction and exchange of plant novelties by sending out plant hunters, herbarium specimen collectors, botanists and gardeners. After settlement, new plants could be accessed by direct exchange supplemented by the botanic garden international seed exchange program.

As with the spices before them it was to the wealthy and powerful that these plants would go first. Gardener-botanists on voyages of exploration and discovery sought out horticultural delights for the estates of the European wealthy, a duty that required specially designed cabinets and equipment like the Wardian Case to protect the living cargo. The gardeners assisted with the collection, transport, cultivation and distribution of the plants, working as assistants to the naturalists, collecting live plants, cuttings and seed, as well as plant specimens for herbarium collections. They often maintained journals and records of their collections and made observations on the vegetation encountered during the voyage.

The global exchange and flow of ornamental plants that began in the modern era as part of the accelerating process of globalisation turned into a flood in the 18th century.

Plants were, of course, passing both in and out of Europe but, on the inward path of ornamental plant introduction, Gregor Kraus (1894) recognised six phases as the geographic area available for plant collection widened through colonial expansion (Stearn 1965, 1971):

| | |
|---|---|
| • To 1560 | European-Mediterranean Period |
| • 1560–1620 | Near East (mostly bulbs) |
| • 1620–1686 | Herbaceous plants from Canada and Virginia |
| • 1687–1772 | Cape of South Africa |
| • 1687–1772 | North American trees and shrubs |
| • 1772–1820 | Australian plants. |

Stearn increased the number of periods to nine, his additional three periods being:

- 1820–1900 Tropical glasshouse plants and hardy plants from Japan and North America
- 1900–1930 Plants from West China
- 1930s Genetics and plant breeding producing new garden varieties.

To this list can be added a tenth period:

- 1980–present Genetically engineered plants.

The number and variety of plants introduced to Europe from overseas in the 16th and 17th centuries was dwarfed by the industry of plant collection and redistribution that occurred in the 18th century. Colonial expansion was feeding the plant lust sometimes referred to as botanophilia (Williams 2001) that had gripped both scientists and the fashionable gardening elite. As international commerce thrived, a new affluent middle class of merchants and professionals joined the upper echelons of society in the socially prestigious activity of gardening, and the number of market gardens increased.

Manorial gardens in England of the Middle Ages had become progressively more estate-like and horticulturally adventurous over time, looking to classical models for inspiration. On Europe's grand estates the English landscape style had increased in popularity through the late 18th century. Plant exchange with America had brought to England the delight of autumn foliage colours of the deciduous liquidambars, maples and other trees that now adorned these properties, all feeding the desire for more. Gardening was becoming more a part of daily life for all.

It is difficult to quantify this social change in gardening habits. However, in England, small nursery concerns had begun in the reign of Charles I (1600–1649) and trade in ornamental plants was largely confined to London where, in 1691, there were about five nurseries and seed suppliers, the total rising to about 15 in 1690–1700, and 35 in 1700–1730, when nurseries were beginning to open up in the provinces. In Georgian England (1713–1830) by 1730–1760 there were around 42 nurseries in London and 40 in the provinces including distant places like Edinburgh and Yorkshire (Harvey 1974, pp. 4–6). A survey in 1760 by the London Gardeners' Company produced the following estimates for professional and commercial gardeners in England and Wales: 10 garden designers, 150 nobleman's gardeners, 400 gentleman's gardeners, 100 nurserymen, 100 florists, 20 botanists and 200 market gardeners.

By 1780 printed directories were being produced and had become available outside London which, by 1825, allowed more precise estimations of the increasing number of plant taxa in cultivation (Harvey 1974, p. 6). In late Georgian England the number of commercial plant nurseries soared, with plant exchange possibly facilitated by the improvement of the canal system. The later development of railways would further improve transport and communications as the Industrial Revolution progressed so that by 1839 garden chronicler John Loudon could list 18,000 species in cultivation in Britain (Harvey 1974, p. 128) and similar developments were taking place on the continent. American ornamental plants were now coming into the country in large shipments, and nurseries in the Netherlands, especially those providing bulbs, were sourcing plants from across Europe (Webber 1968).

From this period on, ornamental plant introduction by Europeans would radically change the plant composition and appearance of both urban and rural landscapes in a cultural tradition that would flow on to the Neo-Europes. Britain, more than any other country, exemplifies this change. Here more than 120,000 different garden plants have been recorded in cultivation in recent decades (J. Armitage pers. comm. 2015), while plants in the wild number only about 3850, about half of these being naturalised. About 13 per cent of the total Australian flora is naturalised and about 60 per cent of these naturalisations are garden escapes. The account of human dispersal of plants across the globe is both fascinating and important, but at present piecemeal and incomplete. What part did biological globalisation play in the doubling of world population between 1650 and 1850? Botanic gardens can assist in providing answers to such questions.

Today we face the difficulty of distinguishing and defining what we mean by natural landscapes and natural plant communities: the distinction between natural and man-made or man-altered plants is also increasingly blurred. The deliberate management of hybrid and novel ecosystems as synthetic vegetation at the interface between natural and artificial systems is a topic for current debate (see Bridgewater 2016), while the expensive problem of exotic plants invading and sometimes breeding with indigenous plants has been with us for many years.

In retrospect, it is clear that the sharing of the world's botanical bounty was an inevitable consequence of globalisation though the way this occurred and its long-term consequences are yet to be fully assessed and experienced.

Cultivated plant taxonomy applied to ornamental plants is an important aspect of botanic garden horticultural botany and has been a major component of the horticultural botany at gardens like the Royal Botanic Gardens Victoria (RBGV). Cultivated plant taxonomy is practised mostly in botanic gardens and has its own important history.

## Cultivated plant taxonomy

In this paper we define cultivated plant taxonomy as the scientific study of the classification of plants modified by humans and, for convenience, we define horticultural botany as a special occupation that helps distinguish botanic gardens from other gardens. We will extend this discussion in a later paper.

Theophrastus distinguished between wild and cultivated plants and shared with pre-Socratic philosopher Hippo (fl. fifth century BCE) the view that it was human action, not divine intervention, that had transformed wild plants into domesticated kinds with desirable characteristics (like high yield, disease resistance or double-flowers) – a controversial view for his day. He had noticed what we might call anthropogenic or human-modified plants. Botanical historian Morton (1981, pp.38–39) notes how Theophrastus In his *Historia Plantarum* iii,2,2 and *Causa Plantarum* i,9,3 '*had an inkling of the limits of culturally induced (phenotypic) changes and of the importance of genetic constitution*' because he had observed that cultivated varieties of fruit trees would degenerate if propagated from seed.

As a consequence of the Agricultural Revolution, humans shifted from a plant diet of wild greens, fruits, seed and root vegetables to a modern diet comprised almost exclusively of man-made plants.

Over many millennia, and across the world, humans have steadily replaced natural landscapes with man-made or cultural landscapes. Continual Aboriginal burning in some areas of Australia, for example, is believed to have changed both the species and structural composition of plant communities (Gammage 2011). More obvious though were the cultivated crops first appearing about 12,000 years ago as monocultures deliberately cultivated in demarcated areas that displaced naturally occurring plants. These cereal crops were generally the result of human selection: they were kinds of plants that no longer grew naturally in the wild and in this sense they were anthropogenic or man-made. In some cases the wild ancestors of these plants are not just different, they are unknown and possibly extinct, this being the case for the broad bean, date palm, ginger, lentil, turmeric and onion.

In the 20th century, with the advent of genetics and plant breeding, the production of these plants was greatly accelerated, and further accelerated by today's genetic engineering. Not surprisingly our rural landscapes consist mostly of man-made plants. Ornamental cultigens – garden plants produced by selection and breeding – are also becoming more common than plants taken directly, unchanged, from the wild. The global phase of food and ornamental plant discoveries is essentially over; novelties are now more likely to arise from genetic experimentation than as new discoveries.

All-in-all the number of different cultigens and the area of land dedicated to their cultivation is steadily increasing as is the need to distinguish, list and name the different kinds. This is the task for cultivated plant taxonomy and it is not unlike the situation facing plant taxonomists of wild plants in the 17th and 18th centuries, but this time it is anthropogenic plants that need to be placed in order.

### Cultigen

For simplicity, man-made or anthropogenic plants are now referred to collectively as cultigens (Spencer 1999; Spencer & Cross 2007, 2008). Included under this category would be the following:

- Ancient selections of crops often of uncertain origin and unknown in the wild
- Simple selections of variants taken from plants in the wild or in cultivation
- Artificial hybrids produced both by accident and intention

- Clonal material reproduced by cuttings, grafting, budding, layering, etc
- Graft-chimaeras
- Selections of aberrant growth such as witches' brooms
- The progeny of deliberate repeatable single crosses between two pure lines that produce plants of a particular phenotype that is desirable for horticulture, but which are not genetically identical
- Plants produced by genetic engineering.

The word 'cultigen' (Latin *cultus* – cultivated, and *gens* – kind) was coined in 1918 by Liberty Hyde Bailey (1858–1954), an American horticulturist and botanist who realised that plants altered by humans needed special classification categories because they did not fit neatly into the hierarchical system devised by Linnaeus (Bailey 1918). Bailey was again echoing Theophrastus's distinction between 'wild' and 'man-made' or 'cultivated' plants. He called 'wild' plants indigens and 'man-made' plants cultigens, the latter being:

> *... a domesticated group of which the origin may be unknown or indefinite, which has such characters as to separate it from known indigens, and which is probably not represented by any type specimen or exact description, having therefore no clear taxonomic beginning.* (Bailey 1918, p. 306)

The first cultigens were probably the agricultural cereals that arose about 12,000 years ago (Stearn 1965) but we have no record of any special names given to cultigens until Roman times. Morton notes that Theophrastus refers to wheat varieties (HP VIII, 1, 2–7) and Roman agricultural writer Columella (4–c. 70 CE) mentions selections of carrots in his *De Re Rustica* ix,4,6. Botanical historian William Stearn attributes the first record of named cultigens to the Roman statesman Cato the Elder (234–149 BCE) who, writing in *De Agri Cultura* in about 160 BCE, named 120 kinds (what we would now call cultivars or *culti*vated *var*ieties) of figs, grapes, apples and olives (Stearn 1986).

While devising his system of plant classification and nomenclature Linnaeus was constantly frustrated by the multicoloured and other ornamental cultigens so adored by the non-scientific gardening community. He disparagingly labelled these people 'anthophiles' (flower lovers):

> *... botany has been overborne by the system of varieties for long enough ... few, if any, agree as to what constitutes a species, or what a variety; ... I wish the system of varieties were entirely excluded from Botany and turned over entirely to the Anthophiles, since it causes nothing but ambiguities, errors, dead weight and vanity ...* (Linnaeus 1737)

He added much later '*... no botanist in his senses will enlist in their camp*' (Linnaeus 1751, aphorism 310, transl. Stafleu 1971). Like many scientists of his day Linnaeus believed in natural theology – that the order of the plant kingdom was evidence for the order placed in nature by God and species were immutable. Cultigens were not really a part of the natural order.

> *All the species recognized by Botanists came forth from the Almighty Creator's hand, and the number now and always will be exactly the same, while every day new and different florist's species arise from the true species recognized by botanists, and when they have arisen they eventually revert to their original forms.* (Linnaeus 1751, aphorism 310, transl. Stafleu 1971)

Further order was put into the chaos of plant nomenclature when the *Lois de la Nomenclature Botanique* (Laws of Botanical Nomenclature) were established at an International Botanical Congress convened in Paris in 1867. This system of nomenclatural rules has been regularly updated and is now known as the *International Code of Nomenclature for algae, fungi, and plants* (ICN), this particular title coined at a Botanical Congress in Melbourne in 2011. Although the difficulties with cultigens noted by the acerbic Linnaeus persisted, it would take until 1953, a date we can assign to the beginning of cultivated plant taxonomy, before his wish for a separate code would be granted with the publication of the first, Wageningen, *International Code of Nomenclature for Cultivated Plants* (ICNCP), abbreviated to *Cultivated Plant Code*. This was followed by seven subsequent editions – in 1958 (Utrecht), 1961 (update of 1958), 1969 (Edinburgh), 1980 (Seattle), 1995 (Edinburgh), 2004 (Toronto), and the latest in 2009 (Wageningen) (Brickell et al. 2009).

Cultigens are specified in the *Cultivated Plant Code* as plants '*... whose origin or selection is primarily due to the intentional actions of mankind*', and they require use of the special classification categories cultivar, Group and grex, which are rank-like names akin to ranks like family, genus and species in the ICN. In practical terms cultigen taxonomy serves a particular community of people – those requiring non-Latin names for plants available in the commercial worlds of agriculture, forestry and horticulture, so it is farmers, foresters, horticulturists, nurserymen and gardeners who are the most frequent users of these names. Wild plant taxonomy and cultigen taxonomy are both about the science of plant names, but the former is plant-centred and the latter is human-centred, recalling the theme of studying plants either for their own sake or for their utility, as pure and applied science.

### Cultivar

In a subsequent paper Bailey referred to indigens as '*those that are discovered in the wild*' and noted that cultigens '*arise in some way under the hand of man*'. It was also here that he coined the term 'cultivar', a contraction of 'cultivated variety', to be used as a taxonomic category ('cultigen' is a general-purpose term) for plant variants arising in cultivation (Bailey 1923). 'Cultivar' (defined today as '*... an assemblage of plants that (a) has been selected for a particular character or combination of characters, (b) is distinct, uniform and stable in those characters, and (c) when propagated by appropriate means, retains those characters*' (Brickell et al. 2009, p. 6)) is now the most widely used taxonomic term in cultigen taxonomy, introduced to the wider horticultural community with the first *Cultivated Plant Code* in 1953.

Across the world, natural landscapes made up of wild plants have been progressively transformed into cultural landscapes consisting mostly of cultigens. Among the many and complex historical reasons for these landscapes are: the appropriation of vast areas of arable land for the cultivation of food crops; the desire for ornamental plants as society luxuries; the international transmission of ornamental plants as part of a global plant exchange that began in the 17th century, facilitated by botanic gardens; the commercialisation of plants through plant nurseries; and the advent of genetics, plant breeding and genetic engineering.

### Horticultural botany

Horticultural botany is an important topic that is closely related to botanic gardens because, as its name suggests, many of its interests lie between those of botany and horticulture, and therefore help to distinguish botanical from other kinds of gardens.

Nowadays the expression 'horticultural botanist' is used in many ways, loosely indicating people with a broad knowledge of cultivated plants who are usually employed by botanic gardens, large plant nurseries, associations like the English Royal Horticultural Society and, occasionally, university departments and government agencies. Their duties vary according to the missions and priorities of the institutions that employ them but the kinds of activities they perform find a focus in the special operations generally found in botanic gardens and can include: seeking out new plants for cultivation; liaising with the general public on matters of plant identification, description, classification and nomenclature, including concerns about plant intellectual property; describing and studying the cultivated plants of particular regions, possibly resulting in the publication of an inventory or Flora; recording new plant introductions; maintaining databases of cultivated plants; curating cultivated plant herbaria, seed banks, images, information and artefacts; and the conservation of cultigens and indigens.

Most of the world's 3270 botanical institutions, botanic gardens and arboreta, seed banks and zoos are engaged in at least a few of these activities (BGCI 2015).

Major Australian city botanic gardens, at least in Melbourne, Sydney, Adelaide, Canberra and Hobart, have all supported horticultural botanist positions (or equivalent) on their staff in recent decades, associated mainly with the scientific documentation of their collections and to provide scientific input to the accessions and collections policies.

At RBGV, horticultural botany has been associated with cultivated plant taxonomy; the nomenclature, identification and documentation of the living collections; the maintenance of an associated horticultural herbarium including standards (similar in role to types); and the conservation of indigens and cultigens. Public outreach has included an identification service, talks and publications, and the completion of original research. All these activities and more will be discussed in greater detail and in relation to the RBGV in subsequent articles.

## Discussion

How do we account for the totally different attitudes to plants and land management that were juxtaposed when, at Botany Bay in 1788, Europeans of the First Fleet stood face-to-face with Australia's First People, the two groups observing one another from the '... *opposite side of the Neolithic Revolution*' (Crosby 2004, p. 18)? In Australia this is the first key question to answer if we are to truly understand the establishment of botanical gardens in Australian and other European colonies (Fig. 16).

European settlers observed Aboriginal people taking food directly from nature. This begs the question: why are plants cultivated in the many ways that we do today, indeed, why do we need to cultivate plants at all? What was the historical experience from which plant cultivation, gardens and, more specifically, botanic gardens emerged? To answer this question has meant going back to origins, to the first plant cultivation and domestication, the beginning of gardens and gardening, and the foundations of botany and botanic gardens.

Prehistoric nomadic hunter-gather societies like those of Australian Aboriginal people associated plants with a spiritual world acknowledged in rituals, beliefs and customs passed down through generations. Traditional empirical plant knowledge would have related to the use of plants as food, materials like fibre and tools, and medicine (Clarke 2007). We may glimpse a little of this world through remnant ceremony, mythology, folklore, religion, rock art, archaeological remains and traditions hidden deep in language. We know, for example, that there is a close connection between the myths and legends of India and those of Western Europe, but the details are unsurprisingly diverse and obscure. Nature, it seems, was deeply personified and anthropomorphised and there was temporal continuity between the lives of ancestors, the living and the afterlife. We can surmise the existence of sacred sites of different kinds with their associated plants, the simple beginnings of plant husbandry, and the special urgency and mystery of medicinal knowledge.

Hunter-gatherers lived within nature but they also changed it. The extent to which Australian Aboriginal people modified Australia's landscapes remains uncertain but in all probability many of the sites first settled by Europeans had been modified by human activity before their arrival (Gammage 2011). Even so, modified nature was totally unlike the man-made surroundings that were constructed in urban environments.

Ancient urban environments, made possible by agriculture, were structured into functional physical spaces very similar to those of today. Plants were brought from the wild into all of these spaces where they were managed or 'cultivated'. From these urban

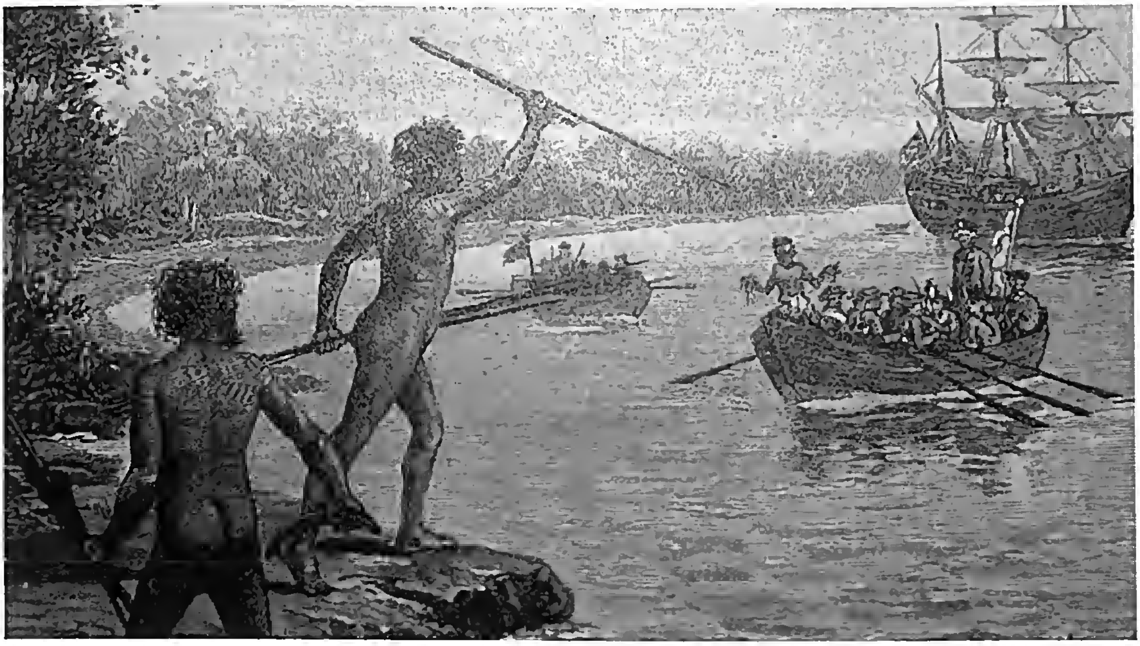

**Figure 16.** *'Natives Opposing Cook's Landing'.* Reproduced from the *Picturesque atlas of Australasia* edited by the Honourable Andrew Garran and published by the Picturesque Atlas Company Limited (Sydney, Melbourne, London) in 1886.

cultivated spaces of the Bronze Age emerged places specifically dedicated to plants – the kinds of spaces we now know as 'gardens'. Among these Bronze Age gardens were those containing medicinal plants that were the subjects of study by academic physicians. These spaces were the precursors to, if not the first, 'botanic gardens'. The early core of special mystical and medicinal plants worthy of study were the herbs and spices, their flavour and scent suggesting that they were touched by the spiritual and divine giving them social prestige and high commercial value as luxury goods. Greeks and Romans referred to these plants as *aromata* and the ones of greatest fascination came from distant paradise-like places.

The human modification of plants also began in prehistory, with the selection of forms of cereals that are now staples of our modern diet. Stearn has claimed that '*cultivated plants are mankind's most vital and precious heritage from remote antiquity*' (Stearn 1965, p. 282). Our Paleolithic and Neolithic forbears bequeathed to us the first domesticated crops – plants with man-induced characteristics that distinguished them from their wild ancestors.

The inhabitants of early civilisations were aware of the enormity of the transition they had made from nature to culture and were ambivalent about its benefits. Mythology, religion and historical accounts sometimes characterised the former life in nature as a romantic age of innocence, a paradise, or a lost Garden of Eden before the advent of civilisation, which was the source of misery, toil and a fall from grace. On the other hand, others, like philosopher Aristotle (see his *Nicomachean Ethics*), regarded these early times as an era of savagery and ignorance: civilisation and progress had arrived with the first cities, which were the only places where humans could reach their full potential as social animals. European settlers assumed that their lifestyle was both morally and materially superior to that of Aboriginal Australians. Agriculture was a 'higher' mode of existence and a means of human 'improvement'. Today's attitudes to 'progress' are more ambivalent.

The theme of a garden as a primordial place of peace and relaxation is frequently associated with the modern botanic garden.

Other echoes of prehistory can be found in ancient civilisations. The stone columns and colonnades so popular in the architecture of antiquity, especially the Greek Corinthian columns whose capitals were decorated with foliage, probably served as symbols of the trunks of trees that grew in ancient sacred groves (Hooke 2010, p. 9). The first public park of ancient Rome, opened in 55 BCE, consisted of a porticus (colonnade) surrounding a *nemus* (sacred grove) with avenues of plane trees and a parkland temple precinct dedicated to the goddess Venus. The park proved so popular that, by the first century AD, the word 'porticus' was being used to describe all the urban parks of central Rome and this particular porticus was similar to the lavish suburban *horti* (gardens) of wealthy Roman generals on the outskirts of the city (Gleason 1994). Roman villas had peristyle gardens, which were inner open courtyards with a surrounding colonnade supporting a shade-roof beneath which was often a shrine dedicated to the household gods. The gardens of royal courts were often linked to wilderness. Their use for hunting, up to the present day, suggests perhaps a glance back to distant hunter-gatherer ancestors.

In antiquity we already see the strong association between useful and interesting plants, trade, and the heroism of exploration and military conquest. Ancient texts from Bronze Age cities indicate the spiritual significance of plants through their symbolism but special attention is given to their medicinal properties. Records include registers of plant names, sometimes with brief descriptions, but mostly as herbal remedies. In Egypt this tradition dates back to the third millennium BCE. Always, though, the interest is anthropocentric; it is about the relationship between plants and humans, not about the plants themselves.

Though horticulture was well established in antiquity, it is only in the classical era that we see the emergence of plant science as we would recognise it today.

The *Lyceum* in Athens (a site named after its temple dedicated to Apollo Lyceus the 'wolf-god') headed by Theophrastus had much in common with the modern botanic garden and university. As a centre of learning it was situated in designed parkland that incorporated sacred sites with shady groves of trees, a sanctuary dedicated to the Muses, a library, and a garden devoted to the study of plants. Lectures were delivered to both students and the general public and plant studies were part of a general educational program within the gymnasium as a whole. At the *Lyceum* we see the birth of botany in a clear break from the former tradition of medicine. Philosopher Theophrastus used objective analytical thinking to lead the study of plants in a completely new direction, one that, so far as we know, was not previously apparent in either the West or the great ancient civilisations of India and China. His plant studies were about the plants themselves as well as their utility. He wrote about their identification, relationships, structure, function, reproduction and ecology. Plants grown in the *Lyceum* garden were collected not only from local sources but from the then-known world: they were both a valuable collection and a living resource for the students. The sheer diversity of plants facilitated detailed observation, comparison and description. Theophrastus's research was incorporated into his lecture notes that became *Historia Plantarum* and *Causa Plantarum*, the world's first scientific treatises on plants. The *Lyceum* was a property that Aristotle had rented and it enjoyed a degree of academic freedom. Royalty was not a part of democratic ancient Athens and state interference was limited, although both Aristotle and Theophrastus were metics (foreigners without citizen rights).

The ancient Greeks had added a new subject to the educational curriculum, plant science, with the combination of Theophrastus's plant research and Aristotle's work on animals laying the foundations of biological science. Sadly this beginning to botanical science was a brief flame of intellectual curiosity that would be extinguished for about 1200 years.

With the Renaissance revival of ancient learning came the recovery of Theophrastus's works which were '... *certainly known and read by botanists; he was frequently referred to and quoted* ...' (Morton 1981, p. 121). Though the medicinal Renaissance botanic gardens are often treated as the first botanic gardens, we can now see how they harked back thousands of years to an ancient social class of academic physicians. There is a continuity of tradition and function that runs from the medicinal gardens and libraries of antiquity, of Egypt and Mesopotamia, including the *rhizotomi* (herbalists) of ancient Athens, to the monastic physic gardens of the Christian scholastics, and the apothecaries and botanical professors of the early modern university botanic gardens of Italy. Perhaps this history can even be traced back to the medicine man or shaman of prehistory. Only with the *Lyceum* teaching garden in classical Athens did this tradition take a brief but crucial turn into a study of the science of plants.

The geometric designs (generally quadripartite) of the early modern botanic gardens allowed beds to be numbered and medicinal plants listed but this stock was soon supplemented by additional plants that were beautiful, curious and new. So began the transition from *hortus medicus* to *hortus botanicus*, the latter combining education with academic botanical interests and the pleasing displays that we associate more with the botanic gardens of today. The new elements reflected, on the one hand, the educational and academic objectives evident at the *Lyceum* of ancient Athens and, on the other hand, the magnificent designed landscapes of the royal and aristocratic gardens of Egypt and Mesopotamia that culminated in the Hanging Gardens of Babylon and later the grand architectural gardens of ancient Rome.

With the unprecedented and extremely rapid social, economic, scientific and intellectual change that occurred in the modern era came an equally dramatic change in the character of botanic gardens and the work done within them. In the period up to the 19th century, a relatively short 250 years (c. 1550–1800), the influx of new plants to Europe during the Age of Discovery initiated a prolonged phase of plant classification, nomenclature and description. Plant knowledge was synthesised in the taxonomic work of Linnaeus, culminating in the publication of his magnum opus of known plants, *Species Plantarum*, in 1753, the first edition published on 1 May 1753 marking the starting point for modern botanical nomenclature. Past debts were recognised, as it was Linnaeus who anointed Theophrastus with the sobriquet 'Father of Botany'.

The early stages of this taxonomic journey were facilitated by the advent of printing and the publication of herbals that lasted from about 1470 to 1670. These books gradually changed from simple lists of plants and their medicinal and other properties into academic compendia of scientific botanical descriptions. The Scientific Revolution and its technology also facilitated the beginnings of plant anatomy and the first scientific investigations of plant function as physiology.

The momentum of change increased dramatically in the 18th century as European colonial expansion gathered pace, uniting scientists and intellectuals, royalty and the social elite, as well as government, into an economic and political force that would be felt across the world. Under the influence of Enlightenment reason and science, two generations of naturalists were launched on scientific voyages of discovery. European political ascendancy began with Portugal and Spain as countries leading Europe across the world, lured by a spice race that promised personal, royal and public fortunes. Holland, similarly motivated, would follow. A gathering interest in economic and ornamental botany would reach its height in the Pacific voyages of scientific exploration and discovery sent out from the great capital city gardens of Paris and London, initiated by the monarchs of France and Britain. It would be the horticulturally obsessed Britain that would eventually set up a colony on the world's largest island continent located on the opposite side of the world.

Theophrastus's writings no doubt stimulated the revitalisation of plant science and hinted at the lucrative economic botany that would eventually drive so much of the scientific and economic activity of 18th-century Europe. In retrospect this was a pivotal period in global plant history, and Britain was at its centre with its increasing number of nurseries, horticultural commerce, its gardens and gardening, landscaped country estates, the frenzy of plant collection, the worldwide distribution of seed and plants, its dominance of economic botany and agriculture, and general botanical curiosity. Humanity at this time was beginning to take charge of the planet, its land and its biodiversity. Plant commerce and nurseries played a major role in the historical acceleration of ever-increasing numbers and kinds of plants being distributed more rapidly over greater distances across the globe. Merchants, adventurers, missionaries, naturalists and chartered companies were now repeating on a global scale the pattern of local foreign forays and plant hunting exhibited by the Egyptian pharaohs Hapshetsut and Tuthmosis III, ancient Assyrian kings Tiglath-Pileser I and Assurnasirpal II, and Macedonian warrior Alexander the Great.

Enlightenment intelligentsia of the European empires, including those scientists who communicated in Latin, had received a classical education. Theophrastus was a part of the Greco-Roman ethos that inspired leaders of the British Empire in their heroic search for the resources needed to fuel Britain's growing population and gathering Industrial Revolution. This was still an age of royalty, patronage and privilege. Banks had paid for his place on Captain Cook's voyage of the *Endeavour*, taking with him eleven servants (two were Africans) and two greyhounds. The efforts of Enlightenment gentlemen would build the world's largest ever empire and generate a global economy. It would also accelerate a redistribution of world vegetation that had gathered momentum in the New World Columbian exchange. Temperate crops were spread to other temperate regions of the world, now 'Neo-Europes'. Tropical crops were distributed between eastern and western hemispheres; ornamental plants would be shipped around the world; and native floras would be invaded by the unanticipated escape into the wild of plants growing in fields and gardens. Increasing wealth and the escalation in numbers of plant nurseries would increase the flow of plants through social strata thus meeting the demands of an increasingly affluent and numerically expanding middle class trying to emulate the lifestyles of their social superiors; plant exchange was not confined to packets of seed and exchange between a few individuals but involved substantial shipments and major enterprises; the global homogenisation of garden floras was beginning; technology like glasshouses helped overcome the constraints of climate; horticultural crops were transforming daily life as plants like cotton, rubber, quinine and tobacco supercharged economies; there was an internationalisation of beverages based on grapes, tea, coffee, cocoa, sugar and cereals; and, associated with agriculture, the massive appropriation of land for crops and pastoralism combined with the global spread of invasive organisms and pathogens.

Botanic gardens of the early modern period, often regarded as the first botanic gardens, were limited in their content, objectives and audience. Their content was medicinal plants, their objectives were instructive and scientific, and their audience were students of university medical faculties. Over time these gardens, though some retained the old formal layout, would for the most part become broader in scope until today their collections might include any member of the plant kingdom. Their objectives have extended beyond the narrow goals of science and education to include a wide range of additional aesthetic and utilitarian considerations. The audience is no longer the specialised physician (university student) but the general public whose diverse interests have resulted in gardens that are a '… *mixture of meditative retreat, scientific collection, menagerie, public playground, palace, and experimental station'* (Drayton 2000, pp. xii–xiii).

Just as the character of botanic gardens has changed over time, so too has the character and role of the people in charge of the plants. We can trace a loose historical path and connection between shaman-medicine-man, priest, physician, philosopher, herbalist, apothecary, pharmacist, professor of botany, the intellectually curious man of means and leisure, professional botanist … to general managers with botanical, horticultural or other administrative background.

The expectations and demands of non-academic audiences have reconfigured the early botanic garden paradigm of instructive science and medicinal garden to that of a pleasure ground, albeit a thoughtful one. The most obvious change in botanic gardens was the incorporation of art and design into a public (not just scientific or academic) space, although there is still often a class of academic physicians, as scientists, working in the institutions associated with the gardens. Mostly this has meant fewer regimented and rectilinear features announcing the scientific order of nature, and more visually pleasing elements borrowed from an eclectic garden history – the ancient Western design elements synthesised by the Romans and subsequently resynthesised repeatedly on a world scale.

In their recent form botanic gardens more closely resemble the grandiose gardens of antiquity than the medicinal botanic gardens of the Italian Renaissance. There is still an emphasis on intellectual curiosity and science, but with room for individualism and the broader currents of global social, economic and environmental history.

Collectively, botanic gardens today explore the connection between plants, people and our planet in all its richness and complexity.

## Acknowledgements

We are grateful to the referees for their valuable comments, and the editors, Teresa Lebel and Alison Vaughan, for their constructive suggestions.

The history of science has a considerable literature devoted to physics and mathematics with botanical science receiving much less attention. The most comprehensive and readable overview of the history of botanical science is a 1981 account by Alan Morton, Emeritus Professor of Botany at the University of London and Fellow of the Royal Society of Edinburgh. This little-quoted but valuable work has provided the historical framework for the arguments developed in this paper.

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# Correction to the 'Key to Australian species of *Microseris*' in Walsh (2016), *Muelleria* 34, pp. 63–67

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## Correction

Within the key to the Australian species of *Microseris* (p. 65), 'mm' has been inadvertently inserted after the value for each mention of pappus scales. The value should be read as the number rather than the length of pappus scales per cypsela, i.e. 30–66 scales per cypsela for *M. scapigera*, 10–20 for *M. lanceolata* and c. 10 for *M. walteri*.

## Acknowledgement

Thanks to Brian Bainbridge for bringing this unfortunate error to my attention.

# MUELLERIA INSTRUCTIONS FOR CONTRIBUTORS

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ISSN 0077-1813

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