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Hiding in plain sight, *Ficus desertorum* (Moraceae), a new species of rock fig for Central Australia

Brendan C. Wilde and Russell L. Barrett

National Herbarium of New South Wales, Royal Botanic Gardens and Domain Trust, Mrs Macquaries Road, Sydney, New South Wales 2000, Australia
brendan.wilde@rbgsyd.nsw.gov.au; russell.barrett@rbgsyd.nsw.gov.au

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Abstract

A new species of lithophytic fig, *Ficus desertorum* B.C.Wilde & R.L.Barrett, endemic to arid Central Australia, is described and illustrated. It is distinguished from other species in *Ficus* section *Malvanthera* Corner by having stiff lanceolate, dark green, discolorous leaves; many parallel, often obscure lateral veins; petioles that are continuous with the midrib; with minute, usually white hairs and non- or slightly sunken intercostal regions on the lower surface. Previously included under broad concepts of either *Ficus platypoda* (Miq.) Miq. or *Ficus brachypoda* (Miq.) Miq., this species has a scattered distribution throughout Central Australia on rocky outcrops, jump-ups (mesas) and around waterholes. This culturally significant plant, colloquially referred to as the desert fig, grows on elevated landscapes in central Australia, including Uluru (Ayers Rock), Kata Tjuṯa (The Olgas) and Karlu Karlu (Devils Marbles), three of Central Australia's best-known natural landmarks. Evidence is provided to show these plants are geographically and morphologically distinct from *Ficus brachypoda*, justifying the recognition of *F. desertorum* as a new species. Taxonomic issues with *F. brachypoda* and *F. atricha* D.J.Dixon are also discussed. Lectotypes are selected for *Urostigma platypodum* forma *glabrior* Miq. and *Ficus platypoda* var. *minor* Benth.

Introduction

Figs are a globally recognisable and highly culturally significant plants. Figs are significant as objects of human spirituality, as major structural components of natural ecosystems providing both habitats and food, and they are dependent on elaborate mutualisms with wasps in the family Agaonidae for pollination (Wilson and Wilson 2013). Around two thirds of the world's 750 fig species are found in Asia and Australasia (Berg and Corner 2005). Australia is relatively poorly represented, with about 43 native species (Atlas of Living Australia 2020), but has a remarkable radiation of species into seasonally arid and arid environments (Dixon 2001a; Bruun-Lund 2019). Figs are a very important plant group for Australian Aboriginal people, providing critical resources, especially in more arid environments where seasonal availability of food becomes most critical, recorded in a considerable body of literature (Kemp 1891; Cleland 1932; Cleland and Johnston 1933, 1937, 1939; Tindale 1941, 1981; Johnstone and Cleland 1943; Sweeney 1947; Mountford 1950, 1962; Cleland and Tindale 1954, 1959; Meggitt 1957; Maconochie 1970; Latz and Griffin 1978; O'Connell *et al.* 1983; Nash 1984, 1993; Low 1991; Latz 1995, 2007; Brand-Miller and Holt 1998; Everard *et al.* 2002; Clarke 2007, 2008, 2012).

The most recent treatments or summaries of Australian *Ficus* that cover most species are those by Corner (1965) and Chew (1989). More recent papers have only dealt with select species groups. The rock figs of northern and central Australia (*Ficus* section *Malvanthera* Corner) have been, and continue to be, difficult for taxonomists to circumscribe (Chew 1989; Henderson 1993; Dixon 1999, 2001a, 2002, 2003; Dixon *et al.* 2001). Many species occur in remote, poorly botanically explored locations across the rocky ranges of northern and inland Australia, are poorly represented in herbarium collections, and commonly display considerable morphological variation. Delimitation of species based primarily on herbarium specimens has remained challenging and a classification reflecting diversity observable in the field is yet to be achieved.

Following the taxonomic revision and determination of specimens by Dixon (2001a), the most frequently collected species of fig for north, west and central Australia is a broadly defined *Ficus brachypoda*.

Dixon (2001a) used two key features to distinguish *F. brachypoda*; plants with parts being variously hairy, and the intercostal [regions] not strongly sunken. Following Dixon's (2001a) taxonomic concepts, these two characters allow nearly any hairy Australian fig to be included in *F. brachypoda*, resulting in a highly morphologically variable species concept (Fig. 1). This is also reflected by the wide distribution of the species, from western Queensland, Northern Territory, northern Western Australia and northern South Australia. Dixon (2003) later also included collections from the Lesser Sunda Islands and Timor within this species. Thus defined, *Ficus brachypoda* is the most widely distributed of all Australian figs (Fig. 2A) and sympatric with five other figs in section *Malvanthera* Corner; *F. atricha* D.J.Dixon (2001a) (Fig. 2B), *F. cerasicarpa* D.J.Dixon (2001a), *F. lilliputiana* D.J.Dixon (2001b), *F. platypoda* (Miq.) Miq. (Miquel 1867–8) and *F. subpuberula* Corner (1960).

Considerable morphological variation can be seen in Herbarium collections of *F. brachypoda sensu* Dixon (2001a). Plants with large, almost glabrous, heart-shaped leaves (Fig. 1 A), others with small, obviously hairy, elongated leaves (Fig. 1 B), and much variation in between, are currently assigned to this species. Geographically, the concept includes populations spanning from the wet tropical north (>1400 mm rainfall p/a), to the arid interior of Australia (<250 mm rainfall p/a). At the time of writing, more collections were attributed to *F. brachypoda* (1522) than all five other north-west species in section *Malvanthera* combined: *F. atricha* (359), *F. cerasicarpa* (311), *F. lilliputiana* (71), *F. platypoda* (476), *F. subpuberula* (194); totalling 1411 records (Atlas of Living Australia, 14 Jan. 2020; http://www.ala.org.au).

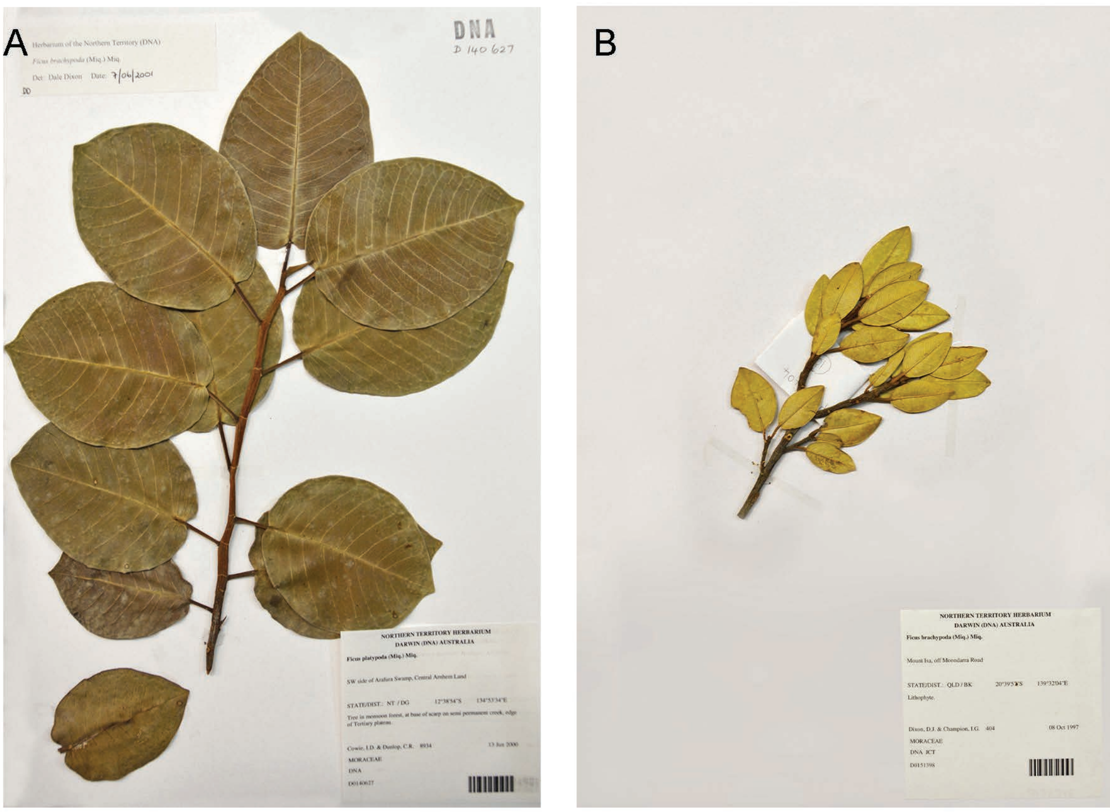

Fig. 1. Two specimens that have been determined by D.J. Dixon as *Ficus brachypoda.* A: From tropical Northern Territory; with large leaves and obvious veins (DNA D0140627). B: From western Queensland; with small narrow hairy leaves and barely visible veins (DNA D0151398). The right-hand collection is allied to *F. cerasicarpa*.

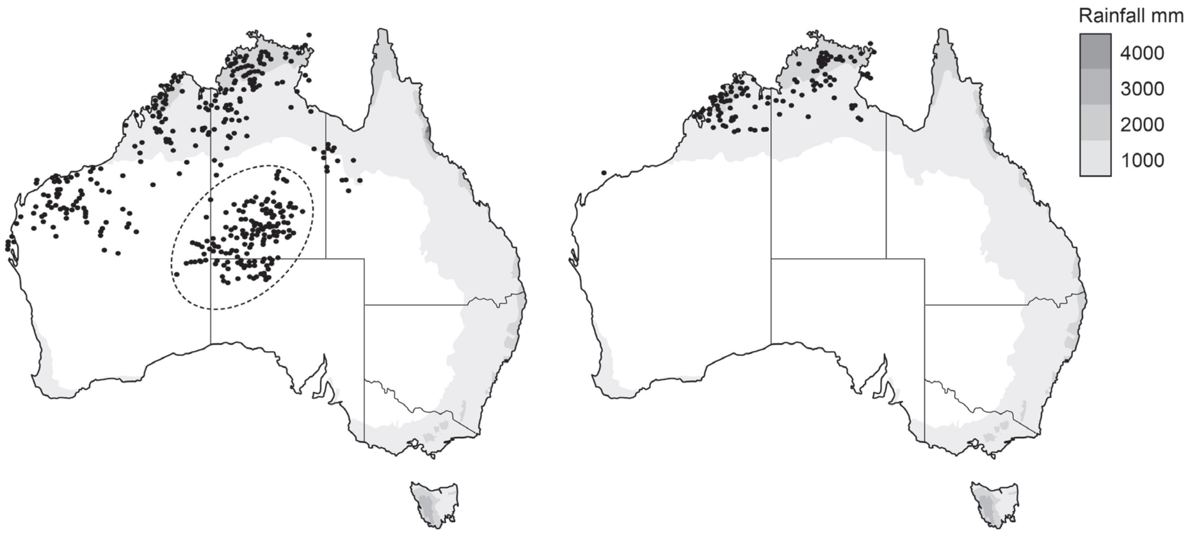

Fig. 2. The '*Ficus. brachypoda*' complex showing all collections for A: *F. brachypoda* (dashed ellipse covers specimens here separated as *F. desertorum*) and B: *F. atricha.* Map shows annual precipitation from bioclim12 (http://www.worldclim.oeg/bioclim) averaged over the period 1983–2012. Occurrence records downloaded from Atlas of Living Australia (http://www.ala.org.au). Accessed 22 January 2020.

The type specimen of *Ficus bachypoda* was collected from York Sound on the north coast of Western Australia by the French expedition of 1800–1803 to map the coastline of New Holland, led by Nicolas Baudin. Specimens from the vicinity (<100 km) of the type location are illustrated in Fig. 3.

Ficus brachypoda was included as a synonym of *F. obliqua* var. *puberula* (Benth.) Corner by Chew (1989), but Dixon (2001a) reinstated the species, and considerably altered the concept of *F. platypoda* at the same time. Dixon (2001a) reinstated *F. brachypoda* based on measurement of 25 morphological characters from 133 herbarium specimens. The 133 specimens were split into 2 groups based on unexplained gross morphology; the '*F. platypoda* complex' and '*F. leucotricha* complex'. The 2 datasets, containing mixed, variable morphotypes, missing data and multiple correlated variables, were log-10 transformed, an Euclidean distance matrix was created and presented as UPGMA (unweighted pair group method with arithmetic mean) dendrograms. Dixon found that both the '*F. platypoda* complex' and '*F. leucotricha* complex' further divided into 2 sub-groups.

Table 1. Dixon's (2001a) divisions of *F. platypoda* and *F. leucotricha* complexes into 4 species. The decision to not use the species name *F. platypoda* for specimens in the *F. platypoda* complex is explained in the nomenclatural notes of Dixon (2001a).

Complex	Group	Delimiter	Species
F. platypoda	*A*	variously hairy	*F. brachypoda*
F. platypoda	*B*	all parts hairless	*F. atricha*
F. leucotricha	*A*	syconia bracts 2.5–7.8 mm	*F. cerasicarpa*
F. leucotricha	*B*	syconia bracts 6.6–28.5 mm	*F. platypoda*

Six hair variables were found to be the main delimiting factors for the '*F. platypoda complex'*, with the following characters responsible for the division with coefficient values of 0.85 or greater from UPGMA; Leaf pubescence abaxial surface (0.94); Fig pubescence (0.93); Leaf petiole pubescence (0.91); Young stem pubescence (0.90); Stipule pubescence (0.90); Leaf pubescence adaxial surface (0.90); and Leaf width (0.89). Though differences among the groups were statistically significant, there is no practical significance (Kirk, 1996) for taxonomic recognition of these groups. The division of Dixon's '*F. platypoda* complex' into the two species *F. brachypoda* and *F. atricha* based on the presence of hairs is too general to categorise the scope of variation found within the complex. Further, populations of morphologically distinct central Australian figs, which have, among other differences, narrower leaves compared to the tropical figs, were grouped with *F. brachypoda*. It is clear from examining herbarium specimens and from field work that *F. brachypoda* and *F. atricha* as defined by Dixon (2001a) represent unresolved species complexes needing further investigation. With the two species complexes growing intermixed at some locations and no practical delimiting characters, the two species are treated herein as the '*F. brachypoda* complex'.

Fig. 3. *Ficus brachypoda* specimens from the vicinity of the type location in the north-west Kimberley. A: small plant from the Artesian Range. B. lower surface of leaves showing sunken intercostal regions (left), and smooth upper surface (right). C: fruiting stem and petioles with characteristic hairs. D: branchlet apex with fruit and apical bracts with characteristic hairs. E: fruiting branchlet with floral bracts. F. longitudinal section of fruit. Voucher: B–F from Boongaree Island, *P.G. Wilson 11395* (CANB). Photos by R.L. Barrett.

The task of re-circumscribing the '*F. brachypoda* complex' begins here with segregation of the desert figs of Central Australia. Central Australian figs are recognisable as a single meta-population having long, narrow, almost hairless leaves, while the Pilbara and tropical populations of *F. brachypoda* show a multitude of variations. As well as obvious climatic difference between the tropical and desert populations of *F. brachypoda*, there appears to be a geographic gap of at least 150 km between the closest neighbouring desert and tropical collections. Though wind has been shown to transport pollinator wasps over 100 km, Nason *et al*. (1998) found most pollinators travel less than 14 km between individual figs.

Prior to the central Australia figs being grouped under *F. brachypoda*, they were commonly included in a loosely defined concept of *F. platypoda* A.Cunn. ex Miq. (Miquel 1847). The names *F. platypoda* var. *platypoda* (Miq.) Miq. and *F. platypoda* var. *minor* Miq. ex Benth. (1873) have both been applied to the desert figs. Dixon (2001a) noted that Corner considered *F. platypoda* var. *platypoda* from the inland of Northern Territory to be the most distinct form of *platypoda* and approached the appearance of *Ficus platypoda* var. *minor.*

The type specimens of *F. brachypoda* and *F. platypoda* both come from the Kimberley region of Western Australia, and the main concept of *Ficus platypoda* var. *minor* (sensu Bentham 1873) applies to plants from the Pilbara. There is currently no name available for the Central Australian desert fig, and as a newly defined species, it requires a new name.

The aims of this study were to:

1. Provide a diagnostic, morphological delimitation of the desert fig as a distinct species.
2. Test if a MaxEnt species range predication for the desert figs was restricted to central Australia or includes the Pilbara.
3. Test if morphological measurements from Dixon (2001a) could be used to successfully delimit the central Australian desert figs from all other figs in Dixon's data set.

Materials and Methods

Herbarium specimens have been examined at CANB, DNA, MEL, NSW and PERTH. Images of specimens (marked *) have been examined through JSTOR Plants (https://plants.jstor.org/; accessed July 2020), Kew Herbarium Catalogue (http://apps.kew.org/herbcat/gotoHomePage.do; accessed July 2020), Naturalis (https://bioportal.naturalis.nl/; accessed July 2020), and Muséum national d'Histoire naturelle (https://science.mnhn.fr/all/search; accessed July 2020).

Dixon's *Basal bract length* and *Internode length* were excluded because they lacked some data for both complexes. Where available, the latitude and longitude for each specimen was sourced from the *Atlas of Living Australia* (http://www.ala.org.au).

Specimen selection

Data for 25 morphological measurements of 133 figs from both Dixon's '*F. platypoda* complex' and '*F. leucotricha* complex' were acquired from Dixon (2001a). Study of voucher specimens used by Dixon (2001a) suggested that names had been applied to mixed taxonomic concepts, warranting reanalysis of morphological variation. For this study, Dixon's '*F. platypoda* complex' and '*F. leucotricha* complex' were combined into a single group. Any samples lacking latitude and longitude co-ordinates or missing data for any of the final variables were removed. Some records supplied by Dixon with 'PHD' numbers could not be found on ALA and were also excluded, while the locations for other 'PHD' numbers are given in Dixon's PhD thesis (Dixon 1999). This left 106 specimens from the original 133 in Dixon's study (see supplementary data) and included specimens variously identified as *F. atricha, F. brachypoda, F. cerasicarpa* and *F. platypoda.*

Variable Selection

Rather than attempting to delimit all taxa potentially present in Dixon's (2001a) study, we aimed to determine if central Australian populations formed a distinct group separate to Dixon's *F. platypoda* and *F. leucotricha* complexes. All of Dixon's variables were used except for Internode length (IL for '*F. platypoda*' group only) and Basal bract length (BBL for '*F. leucotricha*' group only), this left 22 variables (Table 2). Intercostal region sunken was added to the data set of Dixon (2001a).

Data Analysis

Original data from Dixon (2001a) contained 999 to show missing data, this was replaced with NA in the current study. Data analysis was performed using RStudio (RStudio Team 2015). Data was read in with the function read.csv with the na.strings option set to NA to prevent variable types being converted. Individuals with NA for any variable were removed with the na.omit function, this left a final set of 106 out of 133 specimens. A matrix containing the final variables was standardised with the scale command (centre true, scale true). Principle Component Analysis data was generated with the R function princomp and visualised as a scree plot to help decide on the most appropriate k value for the count of species clusters, in this case k = 4, which matched Dixon's conclusion that there were 4 species in the dataset.

In an attempt to recreate Dixon's results, data was explored with PCA and 2 clustering libraries 'pvclust' (Suzuki and Shimodaira 2006) and 'phangorn' (Schliep 2011); which contains a UPGMA function. All distance options were tested for pvclust (average, centroid, complete, mcquitty, median, single and ward.D) and UPGMA (average, complete, mcquitty, median and ward.D) to see which provided results that best matched Dixon's expected species clusters. Dendrogram results presented here were achieved by transposing the standardised data matrix to suit the pvclust command which was run with the Euclidean distance method, ward.D cluster method and nboot of 10,000 to create the AU (approximately unbiased) P values (%) for each node. Individual specimens from each cluster were then mapped with the R package Oz (Venables and Hornik 2016) and the points function.

Table 2. Data variables used in this study. All data except latitude and longitude (sourced from ALA 2020) are from Dixon (2001a). * marks the variables Dixon (2001a) found to most strongly separate *F. brachypoda* and *F. atricha.* Bolded variables were not used in the final analysis of this study. #Hair types: 0 = glabrous, 1 = clear, 2 = brown, 3 = clear and brown. Boolean 0 = false, 1 = true.

Variable	Abbreviation	Measurement Type
Specimen number		
Latitude decimal	Lat	decimal
Longitude decimal	Long	decimal
Leaf length	LL	mm
*Leaf width	LW	mm
Petiole length	PL	mm
Petiole width	PW	mm
Basal bract length (‘*F. leucotricha*’ only)	**BBL**	**mm**
Fig length	FL	mm
Fig diameter	FD	mm
Fig peduncle length	FPL	mm
Internode length (‘*F. platypoda*’ only)	**IL**	**mm**
Number of lateral veins	LV	count
Leaf shape	LS	decimal
Fig shape	FS	decimal
Basal vein angle	BVA	degrees
Lateral vein angle	LVA	degrees
Leaf apex	LA	degrees
Leaf base	LB	degrees
Basal bract pubescence	BBP	#0/1/2/3
*Fig pubescence	FP	#0/1/2/3
Peduncle pubescence	PP	#0/1/2/3
*Leaf pubescence adaxial surface	LPAD	#0/1/2/3
Leaf pubescence abaxial surface	LPAB	#0/1/2/3
*Leaf petiole pubescence	LPP	#0/1/2/3
*Stipule pubescence	SP	#0/1/2/3
*Young stem pubescence	SYP	#0/1/2/3
Intercostal region sunken	IR	boolean

Ecological Niche Modelling was performed in Maxent version 3.4.1 (Phillips *et al.* 2006; Phillips and Dudik 2008) via the spatial portal of Atlas of Living Australia (Atlas of Living Australia (http://www.ala.org.au). Accessed 30 December 2020). All *F. brachypoda* records were downloaded from Atlas of Living Australia (http://www.ala.org.au, Accessed 22 January 2020). A subset was created comprising specimens with “Coordinate Uncertainty in Metres” ≤ 100m. Specimens from the southern half of the Northern Territory regions of Alice Springs, Central Desert and MacDonnell Ranges along with the and north-west of South Australia were included in the model, with most records occurring in the Burt Plain, Central Ranges, Finke and Great Sandy Desert biogeographic regions (IBRA v7.0; Auricht 2014). Layers bio01 – bio19 (https://www.worldclim.org/data/bioclim.html) were selected to test each variable’s contribution to the maxent prediction. The top 5 contributing bioclim variables were then used to create the final maxent prediction. This included: Bio09 (el875) Temperature - driest quarter mean (35.8%), Bio04 (el892) Temperature - seasonality (15.3%), Bio07 (el862) - Temperature annual range (11.2%), Bio12 (el893) Precipitation - annual (9.4%), Bio17 (el889) Precipitation - driest quarter (6.9%). The prediction was created using 77 *F. brachypoda* collection records, 38 used for training, 4 for testing. 10038 background points and presence points were used to determine the Maxent distribution. Regularization values: linear/quadratic/product: 0.227, categorical: 0.250, threshold: 1.620, hinge: 0.500, Feature types used: hinge linear quadratic.

Results

For consistency with the study of Dixon (2001a), we discuss the two dendrograms presented in Fig. 4, where dendrogram A represents analysis of 22 variables and 106 individuals from Dixon (2001a) (dendrogram A); and data used to create dendrogram B includes an additional variable IR. Cluster 1 contains the same individuals in dendograms A and B. All 33 are from Dixon's *F. platypoda* group, including 30 that he identified as *F. atricha* and three as *F. brachypoda.* Cluster 2 contains the same seven individuals from Dixon's *F. leucotricha* group for both dendrograms, six that he identified as *F. platypoda* and one as *F. cerasicarpa.* Cluster 3 contains individuals from Dixon's *F. leucotricha* and *F. platypoda* groups for both dendrograms. For dendrogram A, cluster 3 contains 22 individuals including 16 from Dixon's *F. platypoda* group, all identified by Dixon as *F. brachypoda* and one which (though we determined one (*P03*) as the new species *F. desertorum*) and six individuals identified by Dixon as *F. cerasicarpa.* For dendrogram B, cluster 3 contains 32 individuals from Dixon's *F. leucotricha* and *F. platypoda* groups, 26 identified by Dixon as *F. brachypoda* and six identified as *F. cerasicarpa.* Cluster 4 for both dendograms contains individuals all from Dixon's *F. platypoda* group. In dendrogram A, cluster 4 contains 34 individuals identified by Dixon as *F. brachypoda,* 26 of which we determined as *F. desertorum.* In dendrogram B, cluster 4 contains 25 individuals, all from Dixon's *F. platypoda* group. Dixon identified all of these as *F. brachypoda,* but we determined all as *F. desertorum.* Samples in cluster 4 in dendrogram B are restricted to Central Australia, while clusters 1–3 for both dendograms are sympatric across northern and western Australia. Maxent Ecological Niche Modelling defines the highest probability envelope (>80%) for *F. desertorum* as localised to Central Australia (Fig. 6).

A pilot study using DArT sequencing, following the methods of Wilde *et al.* (2020), clearly separated multiple samples of *Ficus desertorum* from *F. brachypoda s.lat.* and a specimen of *F. atricha* (B.C. Wilde, unpubl. data).

Discussion

Using most of the morphological variables from Dixon (2001a) and an additional new variable (IR) we were able to separate a cluster (Fig. 4 B to cluster 4) of central Australian figs from other collections identified as *F. brachypoda*, *F. cerasicarpa* and *F. platypoda*. We note that sunken intercostal regions are diagnostic for the *F. brachypoda* complex as we define it (which remains highly variable even after the removal of *F. desertorum*), in contrast to the definition provided by Dixon (2001a) in his key and description. We consider a number of specimens included in *F. brachypoda s. lat.* by Dixon (2001a) to be better placed in *F. platypoda s. lat.*, so our concepts are not entirely equal, even in a broad sense of these species. The typical form of *F. brachypoda* has been examined in the field by RLB, along with images of the type collections, which each clearly show the sunken intercostal regions. The typical form is probably restricted to the north-west Kimberley region, but other forms with sunken intercostal regions still included in *F. brachypoda s. lat.* are very widespread from the southern Pilbara in Western Australia, north and east to central Queensland.

The other 3 clusters identified in Fig. 4 A and B may or may not represent valid groupings. No further analysis of these clusters was attempted, though there does appear to be some morphological order to these clusters that will be explored in future studies.

Within Cluster 1, most individuals identified by Dixon as *F. atricha* grouped together, though this study found no evidence for the absence of hairs as a delimiter for the species, with *F. brachypoda* sensu Dixon (2001a) also included within the cluster. Based on field observations by the authors, there is likely no single fig species spanning this distribution and this cluster probably represents multiple species. Cluster 2 contains all *F. platypoda* specimens and one individual of *F. cerasicarpa*. Dixon (2001a) considers these species to be allied and the cluster appears to make morphological sense with all individuals having large-leaves. Cluster 3 contains all the remaining *F. cerasicarpa* and some *F. brachypoda* specimens, with individuals spread over a wide range of WA, NT and western QLD. This cluster is unlikely to represent a single species. Individuals identified as *F. brachypoda* are found in three out of the four clusters, suggesting the species, as defined by Dixon (2001a), is not a natural taxon. No support was found for the separation of individuals into Dixon's '*F. leucotricha*' and '*F. platypoda*' complexes, with Cluster 3 including a combination of both complexes. Novel morphological measurements are likely to be required to delimit tropical Australian *Ficus* sect. *Malvanthera* species and there is likely no 'one size fits all' approach that will successfully delimit all species.

Though the results of these morphological analyses suggest that *F. desertorum* does not extend into the Pilbara region of Western Australia, plants from that region do appear very similar in leaf shape and petiole length, though differing in abaxial lamina venation (see Fig. 5). It is possible that the Pilbara meta-population is genetically isolated from the Central Australian plants by physical distance but it is considered more likely that it originated from an independent dispersal from northern Australia, and appears morphologically similar due to convergent evolution as an adaptation to the arid environment. It is also possible that the Pilbara *F. brachypoda* populations have ongoing gene flow with disjunct fig populations along the Kimberley coastline of Western Australian.

The results of the current study are consistent with a molecular phylogenetic study by Bruun-Lund (2019). A specimen of *F. brachypoda* from central Australia (*Bruun-Lund 799*) included in his analysis did not resolved as sister to another *F. brachypoda* specimen from Litchfield National Park in tropical NT (*Bruun-Lund 791*), that instead grouped with two other tropical figs *F. cerasicarpa* and *F. subpuberula*. The central Australian *F. brachypoda* specimen (=*F. desertorum*) was strongly supported as a lineage sister to all three of these samples. A significant amount of work is still required to delimit species boundaries within the *F. brachypoda* species complex, including broad-scale collecting and sampling for genetic analyses.

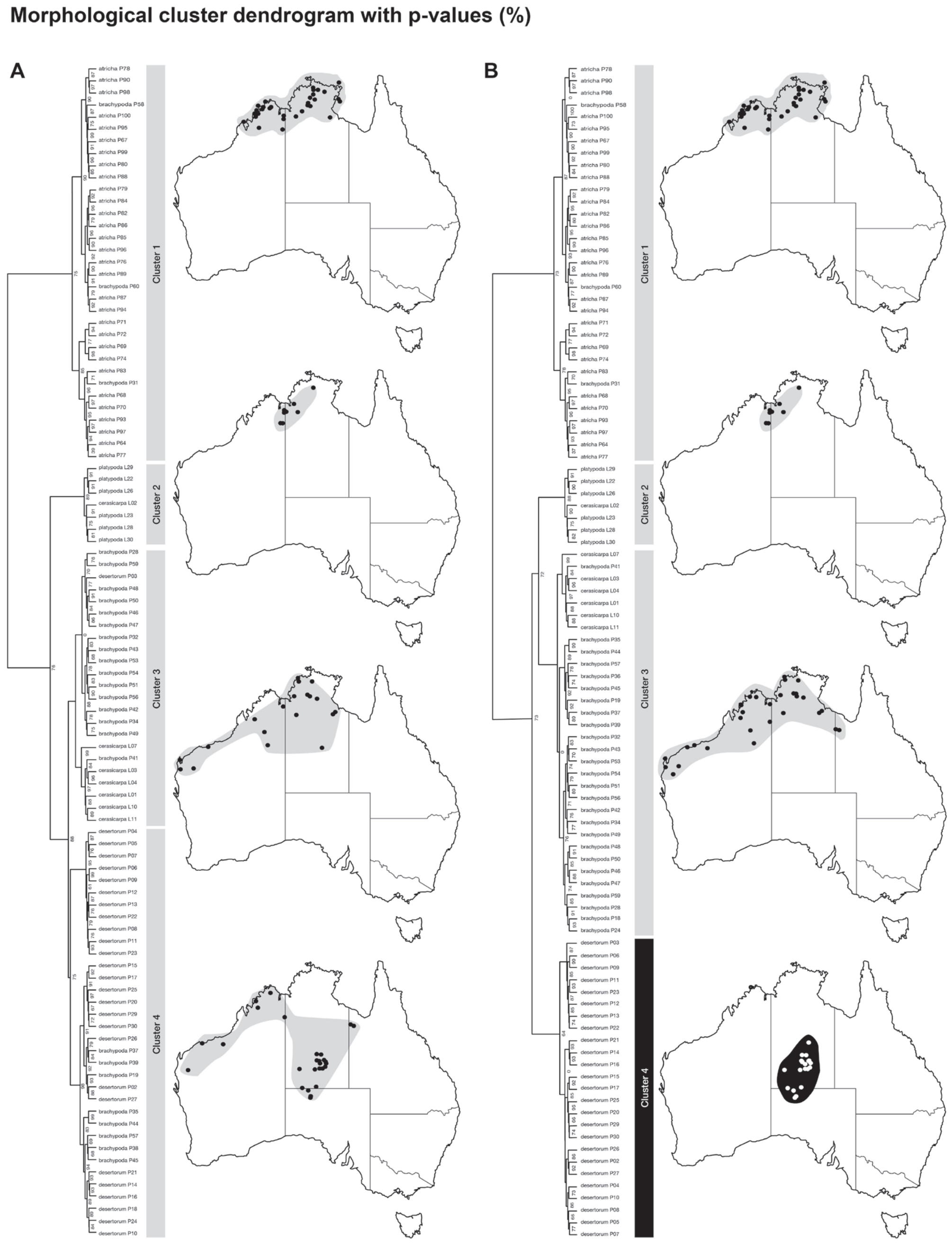

Fig. 4. Results of cluster analysis of the *Ficus brachypoda* and *F. platypoda* complexes based on morphological characteristics defined by Dixon (2001a). Dendrograms labelled with p-values on nodes and sample numbers from Dixon (2001a). Maps show distribution of individuals in each cluster. Dendrogram A with all of Dixon's morphological variables, Dendrogram B with an additional variable of sunken intercostal region.

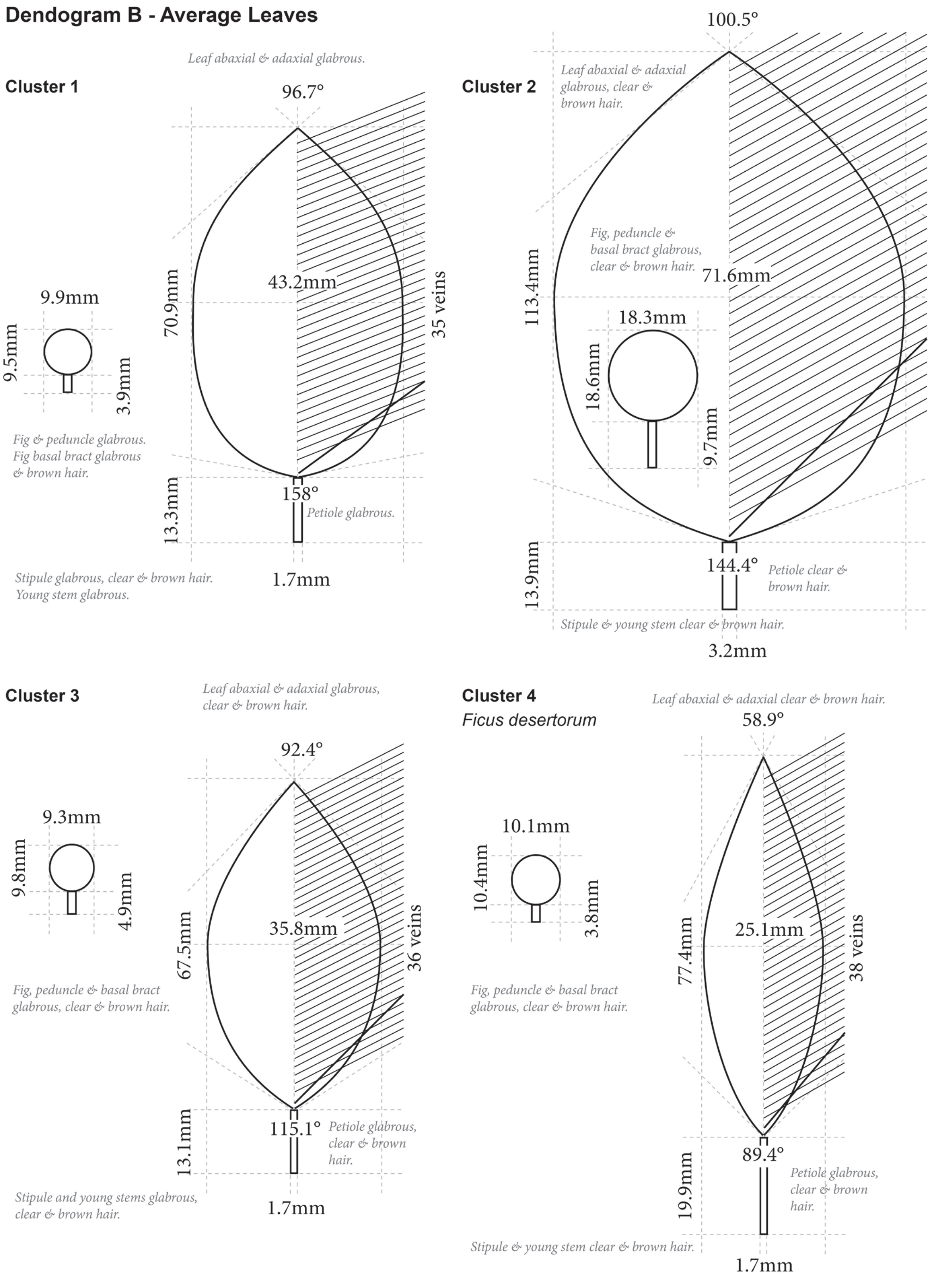

Fig. 5. Illustrations of the average leaf for each cluster of Dendrogram B representing the *Ficus brachypoda* and *F. platypoda* complexes using data from Dixon (2001a). Cluster 4 corresponds to *F. desertorum* as defined here.

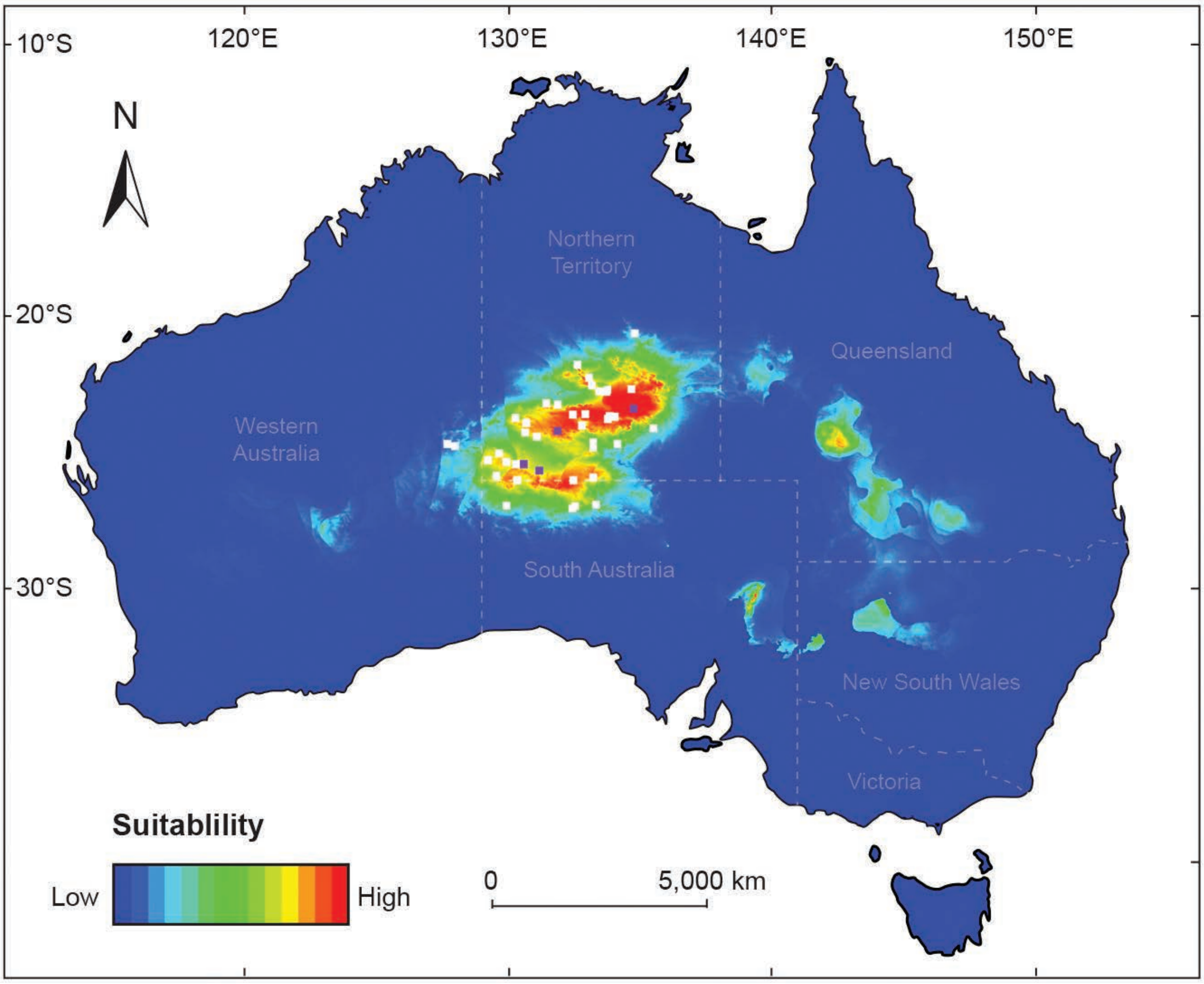

Fig. 6. Ecological Niche Modelling for *F. desertorum*. White dots represent the *F. brachypoda* occurrence records used to create the model, Violet dots are locations used by Maxent for testing (refer to Materials and Methods).

Taxonomy

While no name exists for the central Australian *Ficus* taxon at the rank of species, a single collection of this entity was included as a syntype of *Urostigma platypodum* forma *glabrior* by Miquel (1861) and the name *Ficus platypoda* var. *minor* (Bentham 1873) has also been applied with a similar circumscription. As no lectotypes have been previously designated for these names, we do so here to taxonomically exclude these names from our concept of *F. desertorum*.

Urostigma platypodum forma *glabrior* Miq., *J. Bot. Néerl*. 1: 236 (1861).

Type citation: '*Novae Hollandiae ora bor. occid*.: W. BYNOE, in *Herb. Hook*., *itineratores francogalli* in *Herb. Mus. Parisin*. – *Nova Holl. centralis* in tractu montium *M'Donnell*: STUART.'

Lectotype (here designated). 'Novae Holl. or. occ.' [Western Australia: N.W. coast, *B. Bynoe s.n.*] (lecto: K 001050896*; isolecto: U 0066831 [U.1424548]*, U 0066820 [U.1424547]*).

Residual syntype: 'Neu. holl. cot. occid., Voyage du Capitaine Baudin' (P 06762560*).

Excluded syntype (representing *Ficus desertorum*): Northern Territory: Brinkleys Bluff, MacDonnell Ranges, 1861, *J. McDouall Stuart s.n.* (syn: MEL 0239508, 239508!, U 0141619 [U.1424550]*).

Ficus platypoda var. *minor* Miq. ex Benth., *Fl. Austral*. 6: 169 (1873)

Type citation. 'N. Australia. N.W. Coast, *Bynoe*; Nicol Bay, *Gregory's* and *Ridley's* Expeditions.'

Lectotype (here designated). 'Novae Holl. or. occ.' [Western Australia: N.W. coast, *B. Bynoe s.n.*] (lecto: K 001050896*; isolecto: U 0066831 [U.1424548]*, U 0066820 [U.1424547]*).

Residual syntypes: Western Australia: Shark Bay, *F.T. Gregory s.n.* (syn: U 0142275*); Nicol Bay & De Grey River, 1863, *J.B. Ridley s.n.* (syn: K 001050895*).

Urostigma platypodum forma *minor glabrior* Miq. in Hooker, W.J., *London J. Bot.* 6: 562 (1847), *nom. illeg.*

Typification. We here select the *Bynoe* specimen at K as lectotype for both *Urostigma platypodum* forma *glabrior* Miq. and *Ficus platypoda* var. *minor* Miq. ex Benth. as it is a good fruiting specimen and it has Miquel's annotation as 'forma glabrior'. Bentham attributed his var. *minor* to Miquel, so it seems logical to choose a collection seen by both Bentham and Miquel as the lectotype of that name.

Notes. We currently include *Urostigma platypodum* forma *glabrior* and *Ficus platypoda* var. *minor* within a broadly defined *Ficus brachypoda*, with further research required to define taxon boundaries within this variable complex. We recommend not recognising this taxon at the rank of forma or variety.

Ficus desertorum B.C.Wilde & R.L.Barrett, **sp. nov.**

Type: Uluru (Ayers Rock-Mt Olga) National Park: Uluru (Ayers Rock), Mutitjulu (Maggie Springs) walk, on the ring road, 1.7 km NE of Ranger Station, 19 May 1988, *M. Lazarides & J. Palmer 252* (holo: CANB 385988; iso: DNA D0046821).

Illustrations: Laramba (Napperby) Community Women (2003; pl. p. 17, as *F. brachypoda*); Chew (1989; pl. 3, as *Ficus platypoda* var. *minor*); Jessop (1986; fig. 60, as *F. platypoda*); King (1986; fig. p. 41); Kutsche and Lay (2003; pls p. 85, as *F. brachypoda*); Latz (1995; fig. p. 196, pls p. 197, as *F. platypoda* var. *minor*); Low (1991; pl. p. 175, as *F. platypoda*); Moore (2005; pl. p. 192, as *F. brachypoda*); Urban (1990; pl., fig. p. 19); Womersley (1981; fig. 30, as *F. platypoda*).

Lithophytic multi-stemmed shrub, without buttresses; to around 4 m tall, branches spreading, 3–10 m wide; aerial roots usually absent, but sometimes rooting from decumbent branches. *Twigs* 2.0–6.5 mm diam. in fruit, ribbed when dry, often with a thin glaucous coating, puberulous with ascending hyaline hairs when young, soon glabrescent. *Leaves* alternate, loosely spirally arranged, often only persisting near branch tips and held erect to spreading. *Petiole* 9–34 mm long, 1.2–2.7 mm wide, flat to distinctly grooved above, commonly flattened below and ribbed when dry, finely puberulous with ascending hyaline hairs when young, soon glabrescent. *Lamina* coriaceous, (40–)46–120 mm long, (15–)19–44 mm wide; entire, lanceolate, occasionally broadly lanceolate or elliptic (widest point 30–50% along leaf blade from petiole); lateral veins (10–)12–18 pairs, looped at margin, 33.0–84.0°; basal veins sometimes indistinct, 24.0–119.0°, up to 1/10–1/6 the length of the lamina, tertiary venation reticulate to sub-scalariform; base acute to slightly obtuse, symmetric to slightly asymmetric; apex acute to obtuse; darker green when young (newest growth sometimes densely rusty-pubescent but usually white-pubescent if not glabrous), discolorous; *adaxial surface* glabrous or soon glabrescent, dark green, semi-glossy, not or lightly pruinose, midrib slightly raised, lateral veins flat to slightly sunken, sometimes indistinguishable, major and minor secondary veins similar in width, similar in colour to the blade, forming an indistinct reticulum, the surface appearing slightly spongy or blistered; cystoliths only on upper surface (hypergenous); *abaxial surface* glabrous or soon glabrescent, paler, mid-green to dark green, midrib flattened but distinctly raised, continuous with the petiole, yellow or cream, distinctly contrasting with the leaf lamina,; lateral veins ± flat or slightly raised. *Stipules* terminal, in pairs (10–)14–43(–62) mm long, lanceolate, caducous, sparsely puberulous with ascending hyaline hairs, glabrescent. *Basal bracts* 3, 2.2–6.2 mm long, free, imbricate, caducous, puberulous with ascending hyaline hairs. *Peduncle* (0–)1.5–9.7(–12.0) mm long, slender, 1.1–2.5 mm thick, ribbed when dry, pale green to green or yellow, sparsely to densely puberulous with ascending hyaline hairs. *Syconia* axillary, solitary or in pairs, 8.3–14.9 mm long, 7.8–16.3 mm diam.; obloid to spheroid, reddish brown when ripe, minutely pubescent at 40× magnification (appearing glabrous to the eye), punctate. *Ostiole* triradiate, prominent, 1.0–2.3 mm long, 2.2–4.8 mm wide, open, pubescent; *ostiolar bracts* 3, ovate, up to 1.0 mm long; internal ostiolar bracts ovate or deltoid, 0.8–1.0 mm long, glabrous; internal papillae abundant but minute; *interfloral bracts* ovate to lanceolate, 0.6–1.1 long, 0.3–0.5 mm wide, brown, glabrous, margins hyaline. *Female florets* embedded in wall of receptacle, sessile or pedicellate, 0.6–3.3 mm long; tepals 3 or 4; ovary ovoid or globose, 0.4–1.3 mm long; style 0.9–1.7 mm long, pale or whitish, glabrous; stigma bifid, papillose. *Male florets* very few, interspersed with the female and gall florets, ± sessile, *c.* 1 mm long; tepals 3 or 4, completely united, rarely free, spatulate, 0.8–1.2 mm long, reddish or whitish, glabrous; anther 1, *c.* 0.3 mm long, ovoid or oblong, dehiscence crescentic and longitudinal, filament *c.* 0.3 mm long. *Gall florets* sessile or pedicellate, 1.4–1.7 mm long, pedicel up to 0.4 mm long; tepals 3 or 4, free or united, ovate, *c.* 1.6 mm long, glabrous; ovary obovoid, 0.6–0.8 mm; style lateral, *c.* 0.3 mm long, glabrous; stigma simple. *Achenes* ovoid or sub-tetragonous, 0.8–1.5 mm in diam., surface ± smooth, very finely reticulate at 40× magnification. (Figs 7–9).

Fig. 7. *Ficus desertorum*. A: fruiting branch. B: detail of leaf venation, abaxial surface. C: detail of stem and petiole. D: leaf, abaxial surface. E: leaf base and petiole detail. F: mature fruit lateral view. G: longitudinal section of fruit. H: habit and habitat. Vouchers: A from *G. Chippendale s.n.* (NSW 927786); B, C, E-G from cultivated material; D from *G. Chippendale s.n.* (NSW 452252). Scale bar: A = 30 mm, b = 10 mm, c, e, f = 15 mm, d = 20 mm, g = 5 mm, h = no scale. Illustration by Lesley Elkan.

Fig. 8. *Ficus desertorum*. A: habit on Uluru, NT. This individual has a decumbent habit and flows down the face of Uluru. B, C: foliage and young figs showing typical upright branches and leaves, Karlu Karlu, NT. D: variation in leaf shape. This individual is growing in sand, Simpsons Gap, NT. E: Fruiting branchlet on cultivated plant. F: Figs, petioles and apical bracts on cultivated plant. Photos: A–D by B.C. Wilde; E, F by R.L. Barrett.

Diagnostic characters. Distinguished from other Australian species in *Ficus* section *Malvanthera* by having stiff lanceolate, dark green, discolorous leaves; many parallel, often obscure lateral veins; petioles that are continuous with the midrib (not constricted); leaves with minute, white or rusty hairs and not or slightly sunken intercostal regions on the lower surface (the aeroles appearing very slightly raised). The leaves of this species separate it from most other native Australian figs, with petioles 9–34 mm long, 1.2–2.7 mm wide, and the lamina lanceolate (occasionally broadly lanceolate or elliptic), (40–)46–120 mm long, (15–)19–44 mm wide, a distinctive length/width ratio (Fig. 5). Some populations of *F. brachypoda s. lat.* from the Pilbara region of Western Australia do have a similar leaf shape, but all specimens assigned to *F. brachypoda s. lat.* differ in the strongly sunken, finely reticulate intercostal regions (or intercostal veins appearing raised) on the lower surface.

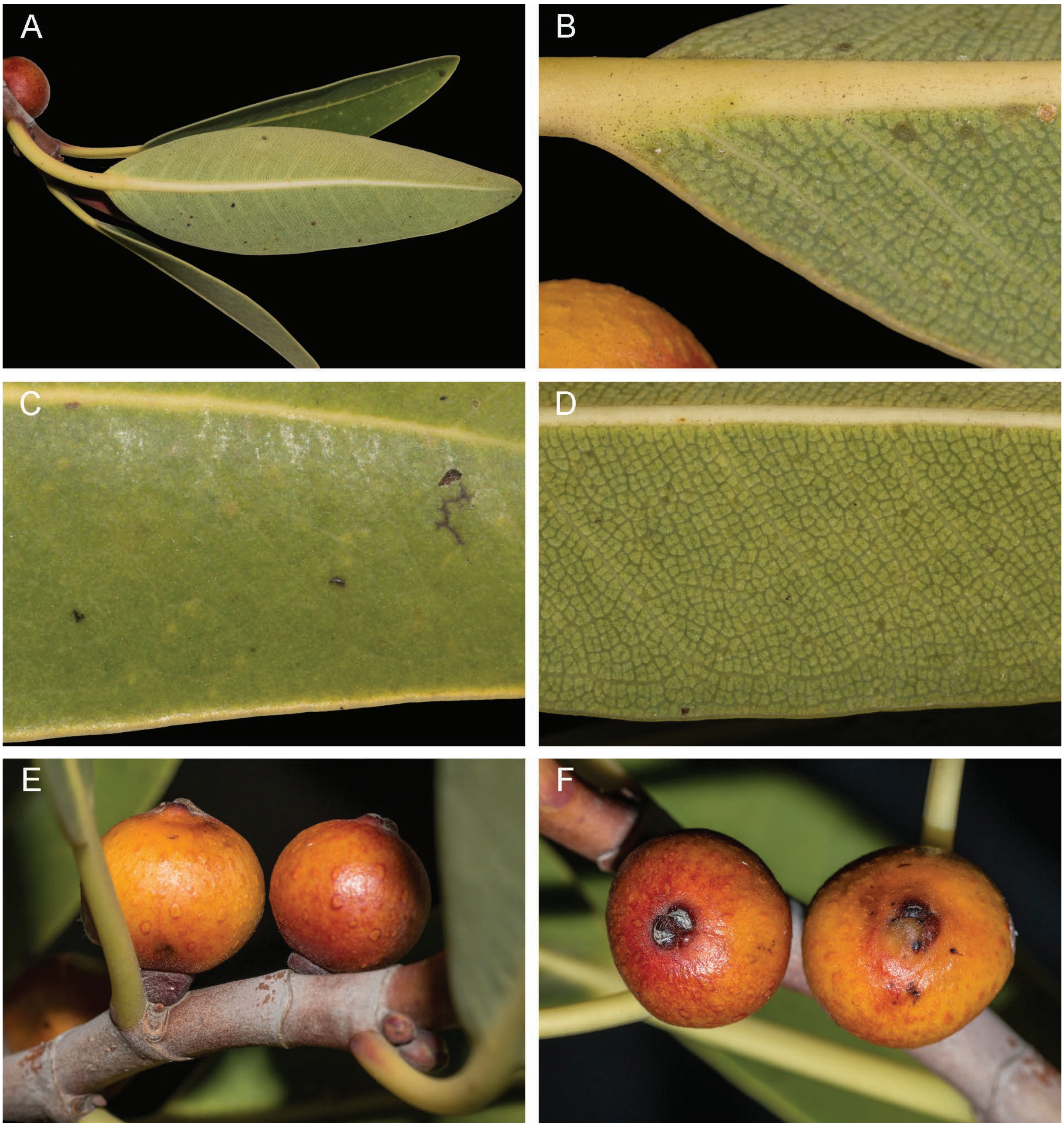

Fig. 9. *Ficus desertorum*. A: abaxial leaf surface. B: abaxial leaf surface at junction with petiole. C: close-up of smooth adaxial leaf surface. D: close-up of abaxial leaf surface with flat or scarcely sunken intercostal regions (pale areas surrounded by reticulate veins). E, F: fruit. Photos by R.L. Barrett from a cultivated plant.

Selected specimens examined: (30 of c. 450): WESTERN AUSTRALIA: Blackstone Ranges, 2 Aug. 1967, *R.C. Carolin 6032* (AD, *n.v.*, L*); Mount Eveline, E of Warburton Mission, 27 Aug. 1961, *A.S. George 2924* (PERTH); Pangkupirri Rockhole, Walter James Range, 22 Sept. 2006, *H.P. Vonow, V.T. Clarke, W.A. Thompson HPV 3073* (AD, PERTH); Rawlinson Range, 400 m W of Yirrima Springs, 46 km NW of Giles Meteorological Station, 17 Aug. 2012, *N.G. Walsh 7613* (MEL, PERTH). NORTHERN TERRITORY: Devils Marbles, *c.* 63 miles [101.3 km] S of Tennant Creek, 16 June 1967, *B.G. Briggs 1205* (NSW); 53 km E by N [from] Alice Springs, 6 Oct. 1978, *J.C. Cardale s.n.* (CANB 278054); 32 km WNW Alice Springs, 8 Oct. 1978, *J.C. Cardale s.n.* (CANB 278053); Palm Valley National Park, Palm Creek, 25 June 1974, *G.W. Carr 2095* (DNA, MEL, NSW); Alice Springs, 25 Nov. 1954, *G.M. Chippendale 683* (DNA, NSW); Jessie Gap, MacDonnell Ranges, 30 May 1997, *L.A. Craven, C.L. Brubaker & J. Grace 9652* (CANB); 800 m by road from Ormiston Gorge campground towards Namatjira Drive, West MacDonnell Ranges, 21 Sept. 2018, *M.D. Crisp 11793* (CANB); Alice Springs, May 1939, *Mrs Dale s.n.* (NSW 452254); Ross Highway, E of Alice Springs, Mt Benstead creek crossing, 21 Oct. 1997, *D. Dixon & I. Champion PHD484* (CANB, DNA, JCT); MacDonnell Ranges, 23 Mar. 1911, *G.F. Hill 121* (MEL); Finke River, 1880, *F.A.H. Kempe 211* (MEL); 45 km W of TiTree Roadhouse, 22 July 1992, *P.K. Latz 12370* (CANB, DNA, NT); 10 miles NE of Woodgreen Station, 23 May 1955, *M. Lazarides 5278* (AD, CANB, MEL, NSW); Tephrina Gorge, 10 Feb. 1985, *G.J. Leach 520* (CANB, DNA, K, MEL, NSW, UPNG); Yalkipi / Alkipi, *c.* 11.4 km due SW of Papunya, 21 Jan. 1984, *D. Nash 25* (CANB); Umbeara (Alice Springs District), Nov. 1965, *J.C. Newman s.n.* (CANB 00829250); 15 miles NE of Yambah Station, 10 Mar. 1953, *R.A. Perry 3381* (CANB); Prowse Gap, Stuart Hwy, 12 April 1979, *M.O. Rankin* 1912 (AD, DNA, MEL, PERTH); by SE base of Ayers Rock which is c. 350 km SW of Alice Springs, 31 Aug. 1957, *R. Schodde 419* (AD, CANB); Vaughan Springs, 4 July 1954, *R.E. Winkworth 422* (CANB). SOUTH AUSTRALIA: Cheesman Peak, N face, below and to the W of the summit, 28 Aug. 1978, *W.R. Barker 2927* (AD, MEL); Everard Ranges, Everard Park. Betty Well area, 25 June 1965, *A.C. Beauglehole 10186* (AD, MEL, NSW); NW of Watarru Rock; *c.* 5 km E of Watarru Community, 15 July 2000, *A. Christie 80* (AD, CANB, DNA, NT); 20 miles W of Tieyon Homestead, *P.L. Milthorpe s.n.* (CANB 831889); Mount Lindsay, 6 Aug. 1962, *D.E. Symon 2578* (AD, PERTH); between Betty and Ronalds Well, Everard Park Station, Everard Ranges, Feb. 1965, *D.E. Symon 3346* (AAU, AD, CANB, K).

Distribution. Most common in the greater MacDonnell Ranges of the Northern Territory, from the Devils Marbles, south to the Everard Ranges in South Australia and west to the Rawlinson and Walter James Ranges in Western Australia (Fig. 2A, within dashed ellipse).

Ecology. Usually on rocky sandstone, quartzite, or siliceous slopes, ridges and cliff faces, or on large granite or sandstone boulder fields, often associated with drainage lines, water-accumulation points and waterholes, the roots commonly following rock fissures. While mostly growing in rock fissures with little or no soil, it has occasionally been recorded growing in alluvial sand or in rocky red soil adjacent to rocky outcrops. Commonly growing in isolation on rock faces with few directly associated species, but recorded in association with *Acacia aneura*, *A. kempeana*, *A. olgana*, *A. tetragonophylla*, *A. victoriae*, *Atalaya hemiglauca*, *Callitris glaucophylla*, *Cheilanthes sieberi*, *Corymbia opaca*, *Cymbopogon ambiguus*, *Cyperus cunninghamii*, *C. iria*, *Dodonaea viscosa*, *Eragrostis sterilis*, *Eriachne mucronata*, *Eucalyptus camaldulensis*, *Laurentia* (*Isotoma*) *petraea*, *Livistona mariae*, *Macrozamia macdonnellii*, *Ptilotus obovatus*, *P. polystachyus*, *Santalum lanceolatum*, *Senna* spp., *Themeda triandra*, *Triodia irritans*, *Tripogonella loliiformis*, and the introduced grass *Cenchrus ciliaris*.

Phenology. Flowering and fruiting all year round following rainfall, but the main fruiting time appears to be August to January.

Conservation status. The species is widespread and present in a number of national parks and other conservation reserves, but it is usually only found as small populations, so threats such as fire may have localised impacts.

Etymology. The epithet refers to the unusual habitat of this species (for *Ficus*) in the arid centre of Australia, dominated by desert environments.

Indigenous names. *tywerrk* (Alyawarr; Anmatyerr); *tjurrka* (Arrente); *utyeerk*, *utyeerke* (Eastern Arrente); *tywerrke* (Western Arrente); *iḻi*, *witjirrki*, *yiḻi* (Pintupi); *iḻi* (Pitjantjatjara / Yankunytjatjara); *wÿirrki* (Warlpiri). The figs as a food are known as *mai puḻka* (Yankunytjatjara). (See Kemp 1891; Cleland and Johnston 1933, 1937, 1939; Johnstone and Cleland 1943; Meggitt 1957; Cleland and Tindale 1959; Maconochie 1970; Hale 1975; Hansen and Hansen 1977; O'Connell *et al.* 1983; Latz 1995; Everard *et al.* 2002.)

Common names. Desert fig (preferred); Wild fig; Rock fig; Native fig.

Ethnobotany. Desert figs are an important traditional food source for many Aboriginal people in Central Australia, being rich in both calcium and potassium (Low 1991). Only ripe figs are picked by Anmatyerr people, immature figs being left to mature (Laramba (Napperby) Community Women 2003). Around Mount Liebig, the desert fig fruit grow in summer and are eaten when yellow and still raw (Nash 1984). Desert fig has the advantage of providing tens of thousands of fruit (each c. 2.5 g fresh, 1 g dry) from a single tree, and early European settlers even used the fruit to make jam (O'Connell *et al.* 1983; Latz 1995). Fruit not eaten when ripe (by people, birds or wallabies), fall to the ground and dry hard and intact, providing a long-lasting food source that can be ground up with water and / or wild honey (Latz 1995; Moore 2005). Dry figs that are ground with water can be formed into balls that can then be re-dried and stored for long periods for consumption when other foods are scarce (Latz 1995). Dried figs were traditionally gathered during the winter months of June to August in some areas north of Alice Springs (Tindale 1981; Specht and Specht 1999). This species was traditionally a critical food source during dry periods due to the abundance of fruit, and habitat around waterholes which are critical environments during periods of drought (Latz 1995). An increase ceremony, intended to maximise fruit production, is described by Mountford (1950) and the fact that a ceremony has been dedicated to fruit production in this species indicates its cultural significance.

In addition to utilisation for food, the leaves of this species were used for children's games, women's leaf games, and love potions (Latz 1995).

The desert fig features prominently in local oral histories and is a totemic species for the eastern Pitjantjatjara people, of sufficient importance that damaging a plant could result in a death penalty (Tindale 1941; Womersley 1981; Low 1991; Latz 1995). In more recent times, seedlings and cuttings have been transplanted to local communities as an ongoing source of traditional food (Nash 1993). Seedlings were also historically transplanted to important waterholes as a source of food (Nash 1993), so at least some of the present populations are likely due to human-mediated dispersal.

Notes. Latz (1995) records that roots form on lateral branches in good seasons, and main roots can extend up to 50 m down cliff faces, following rock fissures to moisture. Sensitivity to both fire and frost is noted by Latz (1995). Around Lake McKay, fires would not be lit near culturally valuable fig trees to protect the valuable fruit (Edwards and Allan 2009).

Plants cultivated in Sydney stay true to type and form ripe fruit, possibly pollinated by wasps that normally pollinate *F. obliqua* G.Forst. Hybrid seedlings from cultivated plants have been grown for >5 years and most are healthy and strong. They appear morphologically intermediate between *F. desertorum* and *F. obliqua*. Plants of *F. obliqua* and *F. desertorum* cultivated together set fruit at the same time.

The fruit of *F. desertorum* is eaten by the Western bowerbird *Ptilonorhynchus guttatus guttatus* (Gould) (Fig. 10). The distribution of this bowerbird subspecies is very similar to that of the desert figs in Central Australia and it has a strong (though not exclusive) ecological link to the fig trees as fruit are available all year round, the fig trees often grow near water, and the dense cover offers excellent sites for bower construction (Frith and Frith 2008). This somewhat mutualistic association was documented by Eylmann (1911), with more detailed observations provided by McGilp (1931). A summary of known observations is provided by Higgins *et al.* (2006). The Western bowerbird might be the vector of desert figs growing on inaccessible cliffs and located many kilometres away from their nearest neighbours through consumption of fruit.

While most specimens here included in *Ficus desertorum* were determined as *F. brachypoda* by D.J. Dixon, some specimens were determined as a range of other *Ficus* species.

Fig. 10. Western Bowerbird with the foliage of *Ficus desertorum* in the background and fruit in its beak. Photo by Tim Rudman (CC BY-NC-ND 3.0).

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