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Comparative leaf morphology and cuticular anatomy of *Akania bidwillii* (Akaniaceae)

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Abstract: Leaf morphology and cuticles of *Akania bidwillii* (Akaniaceae) are described and illustrated in detail for the first time and compared with leaves of *Bretschneidera sinensis* (Akaniaceae) and Tropaeolaceae. The most distinctive features of the cuticle are the discrete clusters of stomata on the abaxial surface which are both surrounded and covered by clumps of highly ornamented, coronulate papillae. The leaves were also compared to previously described fossil Akaniaceae leaves from South America. Leaf fossils from the early Miocene-aged New Zealand Foulden Maar site, from where *Akania* flowers were recently described, were also compared to the highly distinctive leaves and cuticles of *A. bidwillii*, but to date no matches have been found from there or any other New Zealand or Australian fossil sites.

Keywords: *Akania*, Akaniaceae, Brassicales, leaf cuticle, *Bretschneidera*, Tropaeolaceae

Introduction

Akaniaceae (turnipwoods) are a family of flowering trees in the order Brassicales consisting of two monotypic genera: *Akania* Hook.f. endemic to eastern Australia; and *Bretschneidera* Hemsl. in China (including Taiwan), Vietnam and India, each with a single species (Bayer & Appel 2003a; Kumar *et al.* 2017). The latter genus is sometimes placed in its own family (Lu & Boufford 2001), but was found to be sister to *Akania* in molecular studies (Gadek *et al.* 1992; Andersson & Andersson 2000), the expanded family forming a basal lineage with Tropaeolaceae, sister to the remainder of Brassicales (Cardinal-McTeague *et al.* 2016). *Akania bidwillii* (R.Hogg) Mabb. is an uncommon small rainforest understorey tree that occupies a narrow zone in coastal lowland and adjacent ranges from north-east New South Wales to south-east Queensland (Fig. 1) (Hewson 1985).

Fossils of *Akania* of Palaeocene age have been reported from South America, based on leaves with distinctive marginal tooth morphology and venation, but which lack cuticle (Romero & Hickey 1976; Gandolfo *et al.* 1988; Iglesias *et al.* 2007). Akaniaceae wood of Miocene age has also been described from South America (Brea *et al.* 2017). Recently, the first fossil *Akania* inflorescence and flowers with *in situ* pollen were described by Conran *et al.* (2019) from earliest Miocene lacustrine sediments at the Foulden Maar *Konservat-Lagerstätte* site near Middlemarch in southern New Zealand (45.5271° S, 170.2218° E), representing the first fossils of Akaniaceae from Australia or New Zealand. However, to date no examples of the distinctive fossil leaves have been reported from Australasia.

The leaf epidermal anatomy of *Akania* was described briefly by Solereder (1899), but not illustrated. In this paper we provide the first detailed systematic and illustrated description of the leaves and cuticles of *Akania* using both light microscopy and SEM. This will allow comparison with previous studies of its sister genus *Bretschneidera* (Qiao *et al.* 2010; Tu *et al.* 2012) and the related family Tropaeolaceae, as well as to determine if any leaves with similar epidermal features are present amongst fossils collected previously from Foulden Maar, or from other sites in New Zealand and elsewhere.

Materials and methods

Reference leaves of *Akania bidwillii* (*D.J. Mcauliffe s.n.*, AD98142330; *J.B. Williams s.n.*, NE20021; *J.G. Conran 3965*, AD, NE) were examined and comparative cuticular preparations are held in the Department of Geology Museum (OU), University of Otago, Dunedin, New Zealand. Leaf fragments for

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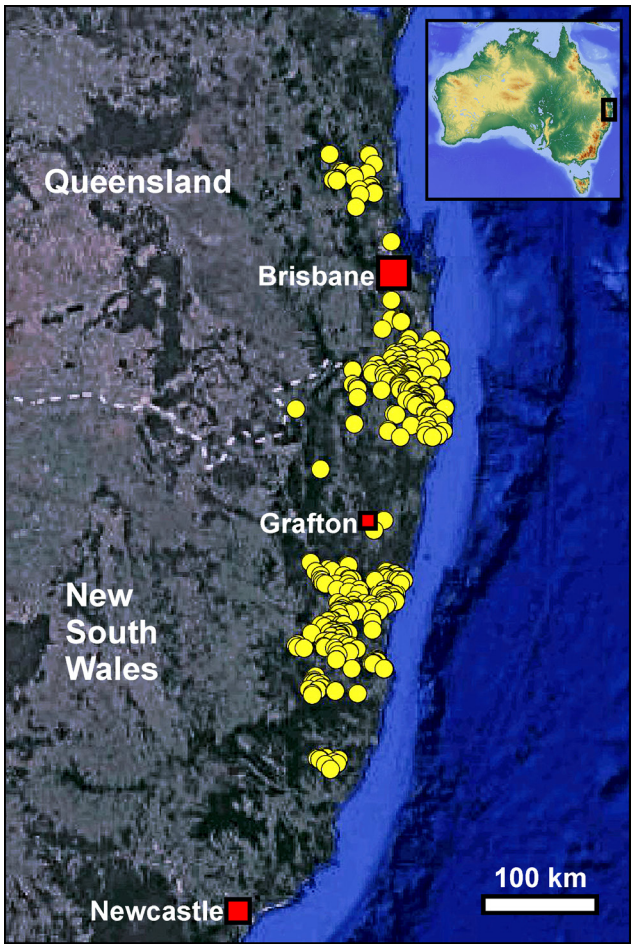


Fig. 1. Distribution map of localities for *Akania bidwillii* in eastern Australia. Source: AVH (2018).

venation were cleared by cutting small pieces from the midsection of desiccated leaves and soaking in 30% hydrogen peroxide at c. 60°C until cleared (24–48 h). The fragments were then stained in 0.5% aqueous Safranin O, differentiated to the desired transparency in 95% ethanol before slide-mounting in thymol-glycerin jelly. The cleared leaves were photographed using a Nikon D80 DSLR camera (Nikon Corporation, Tokyo, Japan). Venation features were illustrated and described following Ellis *et al.* (2009).

Akania cuticle preparation involved soaking small desiccated leaf pieces in 30% hydrogen peroxide with a few crystals of tetra-sodium pyrophosphate, warming gently and, once cleared, rinsing in distilled water. The cuticle layers were separated and debris removed with fine paintbrushes before staining with 0.1% aqueous crystal violet for c. 60 s, washing in RO water and slide mounting in thymol-glycerine jelly. Cuticles were photographed with a Leica digital camera attached to a Leica DM1000 LED microscope (Leica Microsystems GmbH, Wetzlar, Germany) using LAS software (Leica Microsystems 2015). Where appropriate, images were stacked using Picolay (Cypionka 2015). SEM of platinum-coated and stub-mounted cuticle fragments used a JEOL 6700F Field emission Scanning Electron Microscope (JEOL Ltd, Tokyo, Japan). Cuticles features were described following Wilkinson (1979). Comparative Tropaeolaceae cuticles were also prepared for *Tropaeolum majus* L. (*J.G. Conran 4006*, ADU: Adelaide University plant reference collection).

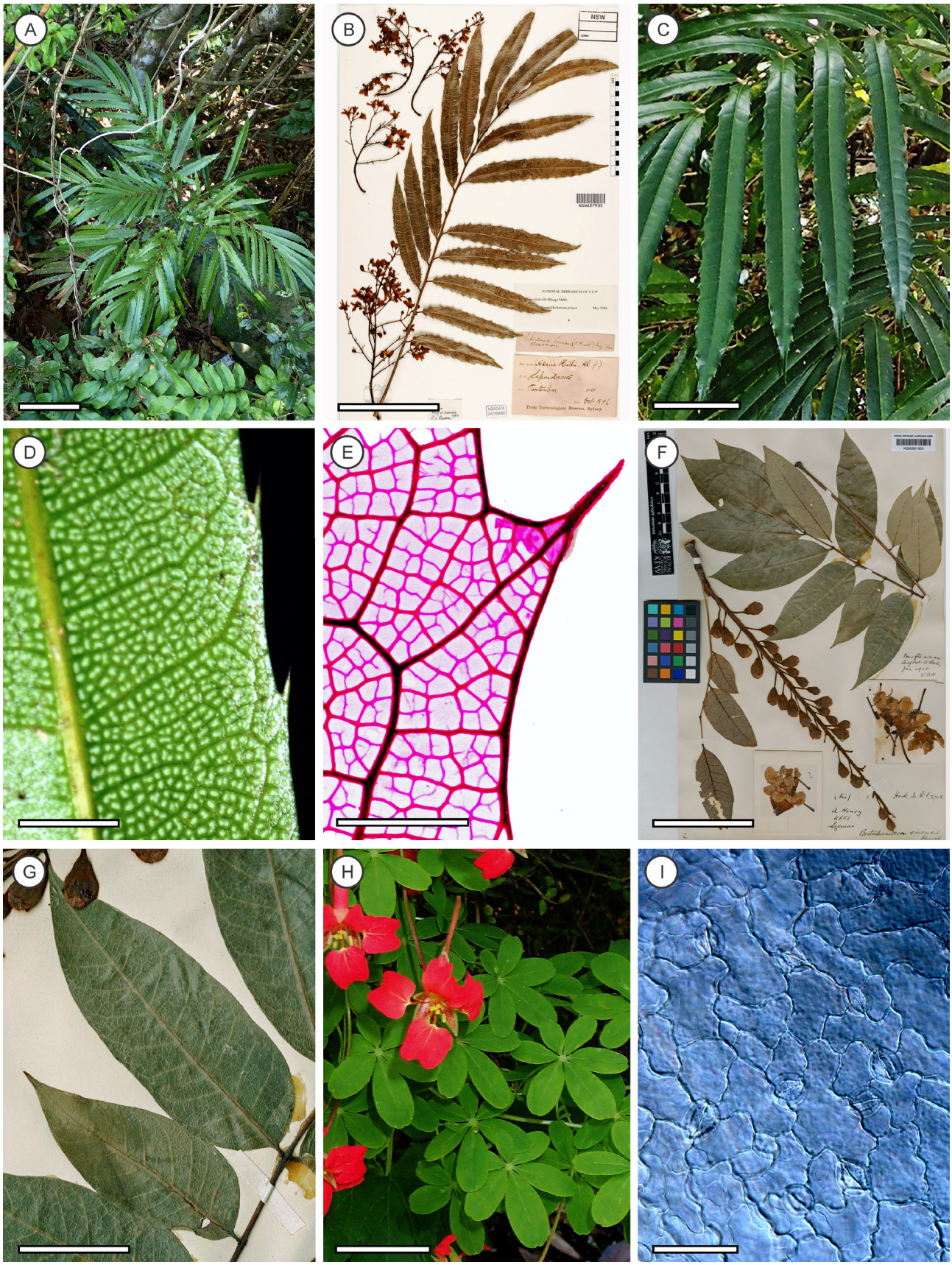
Results

Although leaves of *Akania* have not been recovered from Foulden Maar, the presence of fossil flowers there, fossil leaves and wood in South America and living plants in Australia suggests that they should be found in other Southern Hemisphere Cenozoic fossil deposits. Some of the distinguishing features of leaf teeth and venation that allowed placement of their fossils into *Akania* were illustrated by Romero & Hickey (1976) and discussed further by Gandolfo *et al.* (1988) and Iglesias *et al.* (2007). However, although Solereder (1899) gave a brief account of the leaf epidermis, there is currently no illustrated account of the venation and cuticles of the genus.

Leaves. Leaves up to 75 × 25 cm alternate, once-pinnate, petiolate, petiole to ~8 cm long, terete; leaflets 9–31, opposite, imparipinnate (Fig. 2A); blade attachment marginal; petiolules to 10 mm long, swollen-terete (Fig. 2B). Leaflets lanceolate to oblanceolate, 10–30 × 1–2 cm, coriaceous, toothed; apex bluntly acuminate; base cuneate, acute; adaxially more or less glabrous (Fig. 2C), abaxial surface areolate, white-dotted with clumps of papillae concealing stomata (Fig. 2D); margins pungent-toothed, one order of teeth, tooth spacing regular, ~1 cm^{-1}, sinus rounded, tooth shape CC/CC (concave/concave sensu Ellis *et al.* 2009); principal vein terminating at the tooth apex (Fig. 2E). Venation simple, pinnately brochidodromous, raised abaxially, forming a network of sunken areoles; secondary vein spacing regular, uniform, excurrent, interior secondary and intersecondary veins absent, marginal secondary veins present; tertiary and higher vein orders irregular reticulate; areolation prominent, free vein endings absent (Fig. 2E).

Cuticle. Adaxial cuticle thin, epidermal cells irregularly isodiametric, 16–44 µm wide (average 26 µm); outer surface of epidermal cells smooth, periclinal walls slightly raised (Figs 3A, 4A); inner surface anticlinal walls straight/curved to slightly undulate with relatively broad short flanges, appearing as slightly raised walls (Fig. 4B), inner periclinal walls granular (Fig. 4B),

Fig. 2. *Akania* (**A–E**), *Bretschneidera* (**F**, **G**) and *Tropaeolum* L. (**H**, **I**) habit and leaves. **A *Akania bidwillii*** habit, growing in rainforest at Hayters Hill Nature Reserve, N.S.W. (*JGC 3965*, NE); **B** Herbarium specimen showing 1-pinnate leaves and paniculate inflorescences (NSW627935); **C** Linear-lanceolate leaflets with prominent teeth (*JGC 3965*); **D** Portion of a leaf showing venation, areolate papilla clusters and distinctive marginal spines (*JGC 3965*); **E** Portion of a cleared leaf to show venation detail and characteristic marginal spine (NE20021). **F *Bretschneidera sinensis*** herbarium specimen showing 1-pinnate leaves and racemose inflorescences (K000681003);



G Broadly-lanceolate leaflets showing entire margins and slightly asymmetrical bases (K000681003). **H** ***Tropaeolum speciosum*** Poepp. & Endl., habit showing peltate leaflets, adventive in the Town Belt, Dunedin, New Zealand. **I** ***Tropaeolum majus*** L., abaxial cuticle with unornamented anomocytic stomata (*JGC 4006*). Herbarium specimens reproduced with permission: B The Royal Botanic Gardens & Domain Trust, http://plantnet.rbgsyd.nsw.gov.au/ (photo: B. Araghi, PlantNET); F, G Board of Trustees of the Royal Botanic Gardens, Kew, http://specimens.kew.org/herbarium/K000681003. Scale: A = 20 cm; B, E, F = 5 mm; C, H = 20 mm; D = 10 mm; G = 1 mm; I = 50 µm.

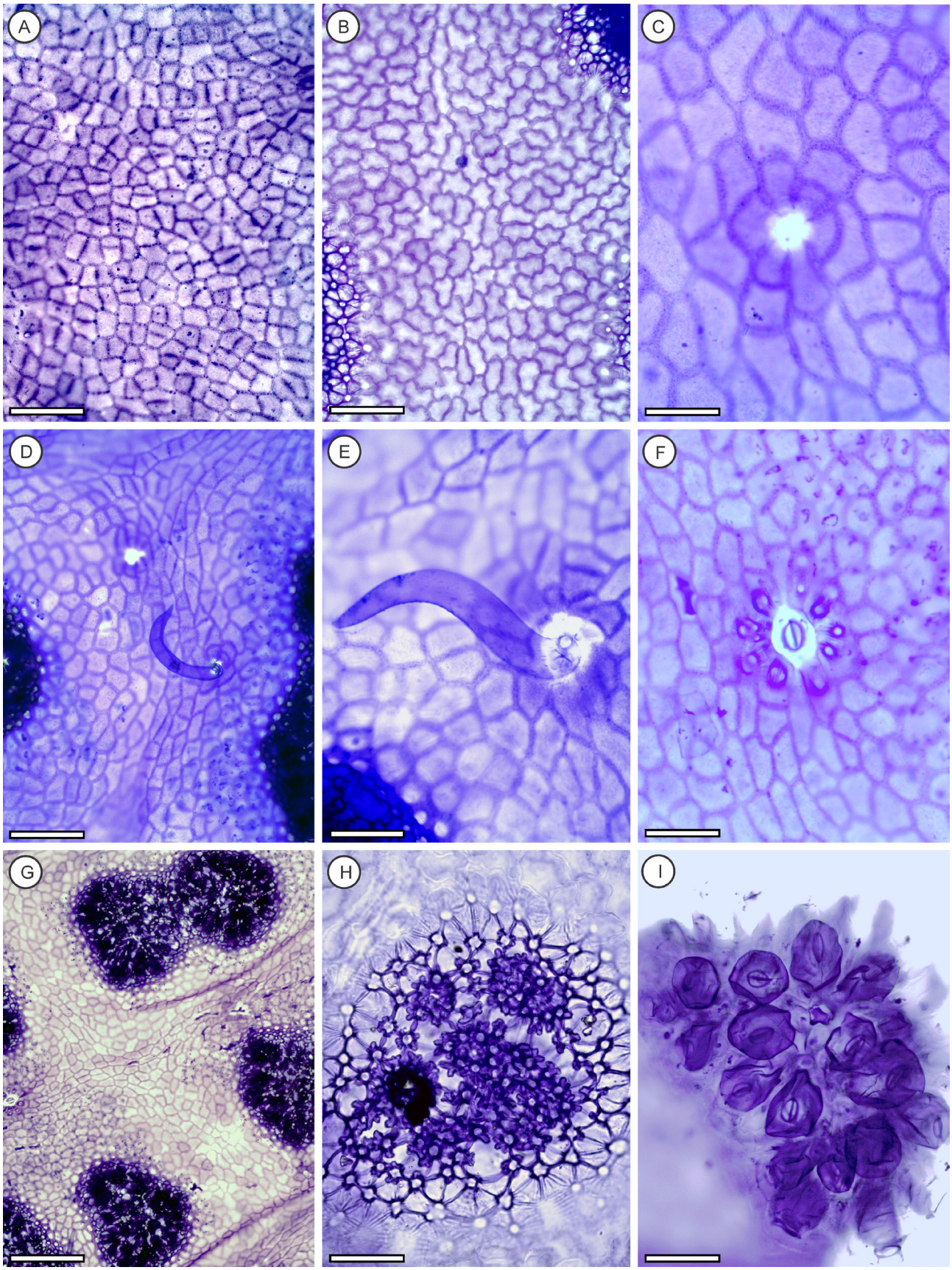


Fig. 3. Light microscopy of ***Akania bidwillii*** cuticles (NE20021). **A** Adaxial surface (appearing 'fuzzy' due to finely granular inner periclinal walls); **B** Abaxial surface away from papillate clusters; **C** Porate adaxial trichome base with surrounding cells; **D** Abaxial trichome and trichome base close to vein; **E** Detail of simple abaxial trichome; **F** Hydathode with papillate surrounding cells; **G** Arrangement of papillate (stomatal) clusters on abaxial surface; **H** Single enlarged cluster showing outer simple and inner coronulate papillae; **I** Detail of H. Scale: A, B, D = 100 µm; C, E, F, H = 50 µm; G = 200 µm; I = 20 µm.

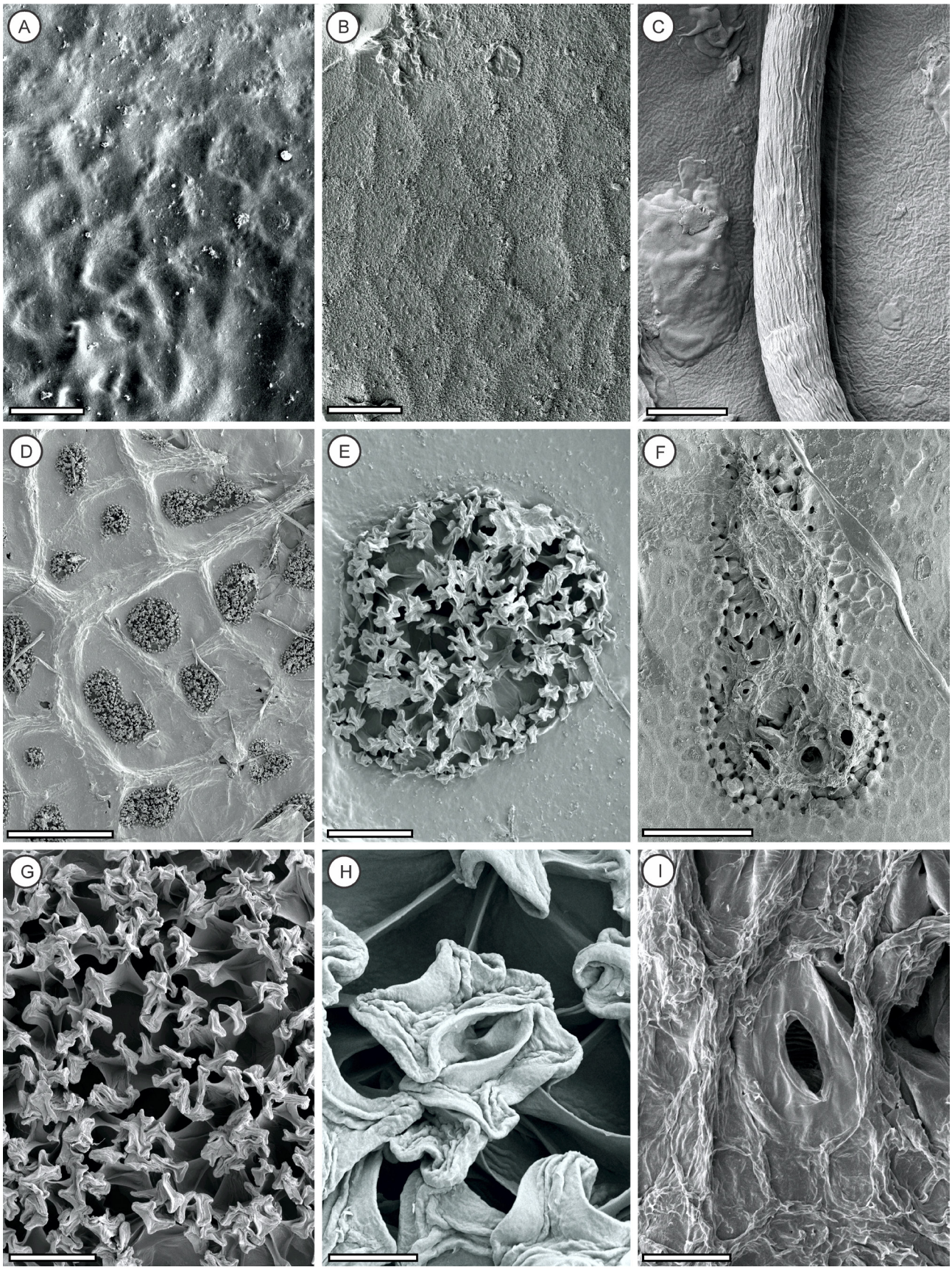


Fig. 4. SEM of ***Akania bidwillii*** leaves (NE20021). **A** Adaxial outer surface showing raised periclinal walls; **B** Adaxial inner surface showing short flanges (appearing as slightly raised walls) and fine periclinal granulation; **C** Detail of trichome with sculpturing of fine ridges; **D** Abaxial areolar surface to show stomatal groups; **E** Single cluster showing central coronulate papillae with simpler surrounding papillae; **F** Inner abaxial surface showing a few indistinct stomata and papilla bases; **G** Coronulate papillae; **H** Detail of lobed and striated papilla head with interconnecting ridges; **I** Inner surface of abaxial surface showing a single stoma. Scale: A–C = 25 µm; D = 500 µm; E, G = 50 µm; F = 100 µm; H = 10 µm; I = 20 µm.

making the cuticle appear 'fuzzy' under TLM (Fig. 3A). Trichomes short (<1 mm), simple, non-septate (Fig. 3C, E), thin walled with fine striations (Fig. 4C); trichome base slightly sunken in the epidermis, consisting of a pore and about six surrounding cells (Fig. 3C).

Abaxial cuticle thin, veins raised to form a network of sunken areoles; cuticle over the veins ridged, but smooth over the areolar surface (Figs 3D, E, 4D). Anticlinal epidermal cells irregularly isodiametric, 23–50 μm wide (average 35 μm), walls undulate, flanges short, wide and granular, appearing as slightly raised walls (Fig. 3B); periclinal walls granular. Trichomes few, similar to those present on the adaxial surface. One hydathode was seen with nine surrounding simple papillae (Fig. 3F).

Stomata in tight clusters surrounded by coronulate papillae, usually only 1–2 clusters per areole (Figs 3G, 4D); hidden by the papillae; anomocytic (Fig. 4F, I), small (10–14 μm, average 12 μm). Central papillae in the stomatal clusters coronulate, the large heads are irregularly lobed and striated (Figs 3H, I, 4E, G, H), the lower part of these papillae also striated; adjacent papillae connected by ridges (Fig. 4H). In some places coronulate heads coalesce to form a central cover with simpler papillae at the periphery (Figs 3H, 4E).

Discussion

Akania leaves resemble those of *Bretschneidera* in being alternate, imparipinnate and in having papillate cuticles (Bayer & Appel 2003a); however, *Bretschneidera* leaflets are broadly lanceolate with entire margins (Fig. 2F, G), whereas *Akania* leaflets are linear-lanceolate with prominent marginal teeth (Fig. 2B–E) and have papillae that form macroscopic clumps on the abaxial lamina (Fig. 2D; Solereder 1899). The leaves of *Tropaeolum* are also alternate, but vary from digitately pinnate to lobed, entire, or peltate (Fig. 2H) and unlike Akaniaceae, stipules are sometimes present (Bayer & Appel 2003b).

The cuticles of *Akania* are similar to those reported for *Bretschneidera* by Qiao *et al.* (2010) and Tu *et al.* (2012), particularly in the presence of distinctive, interconnected papillae surrounding the anomocytic stomata and the presence of simple unicellular trichomes and hydathodes derived from modified stomata. However, *Akania* bears macroscopic papilla clusters that cover the stomata (Figs 3G–I, 4E–H), whereas *Bretschneidera* has scattered stomata, each surrounded by microscopic papillae. Tropaeolaceae cuticles share anomocytic stomata (Fig. 2I), simple few-celled trichomes and vein-associated hydathodes with Akaniaceae, but lack the characteristic stomatal-associated papillae seen in the latter (Metcalfe & Chalk 1950; Weber & Kenda 1952; Bayer & Appel 2003a).

Despite more than 25 years of fossil collection at Foulden Maar by Pole (1993, 1996) and the current research team led by Assoc Prof. Daphne Lee at Otago University, including anatomical investigations of over 1000 mummified leaves (see summaries in Lee *et al.* 2012, 2016), no cuticle-bearing leaves or dispersed cuticle samples that match *Akania* have been reported to date, or any other fossil site in New Zealand, South America or Australia. This may be due to the leaves possessing very thin cuticles that are not easily preserved as fossils.

Leaflet impressions of extinct fossil *Akania* species (without cuticle) matching closely to those of the living species described here have been preserved at several sites in South America (Romero & Hickey 1976; Gandolfo *et al.* 1988; Iglesias *et al.* 2007). These Paleogene leaflet fossils were identified using a combination of the distinctive teeth, as well as shared characteristics of the secondary and higher-level venation, areolation, veinlet and intercostal areas. In particular, they share pinnately brochidodromous secondary venation, a fimbrial vein, keeled and ribbed midvein and spinose, irregularly spaced, CC/CC teeth (Gandolfo *et al.* 1988). These features were considered in combination to be characteristic of *Akania* leaflets by Romero & Hickey (1976), Gandolfo *et al.* (1988) and Iglesias *et al.* (2007). In contrast, although the basic venation pattern in *Bretschneidera* is also pinnately brochidodromous with similar higher vein order orientation to *Akania*, it has broader, asymmetrical and entire-margined leaflets and lacks all of the tooth-related characteristics of the latter (Fig. 2F, G).

Fossil Akaniaceae pollen is only known from the flowers found at the Miocene-aged Foulden Maar site in New Zealand, possibly because the thin walls of the fossil pollen makes fossilisation less likely (Conran *et al.* 2019). As summarised in Conran *et al.* (2019), the pollen of the fossil has a more well-defined reticulum, especially in polar areas, the colpi are short and narrow, with indistinct margins. The exine and sexine of the fossil is thinner than in the living *A. bidwillii* and has a much finer reticulum with more evenly sized luminae than *Bretschneidera* and lacks luminal granulae. Nevertheless, both living genera share medium sized tricolpate pollen with short colpi and a well-defined reticulum with variable-sized luminae. In contrast, Tropaeolaceae pollen is tricolporate with a reticulate to partially striate exine and granulate luminae (Erdtman 1986; Bayer & Appel 2003b), agreeing with the placement of these families in the lower Brassicales. The fossil *Akania* pollen does somewhat resemble the palynomorph *Tricolpites densipunctatus* D.J.McIntyre of unknown affinity from the early Miocene of New Zealand (McIntyre 1968; Raine *et al.* 2011). However, although the pollen of the latter is tricolpate with a microreticulate and punctate exine, its grains are approximately half the size and the colpi are long and narrow with straight, well-defined margins.

Akaniaceae are thought to have diverged from Tropaeolaceae in the Late Cretaceous (Cardinal-McTeague *et al.* 2016), with subsequent dispersal to Australia and New Zealand and then on to China

(Wang *et al.* 2018) and India (Kumar *et al.* 2017). The differentiation of the two living genera and the fossil history and biogeography of Akaniaceae was summarized by Conran *et al.* (2019), where the reasons for the family's disjunct distribution were explored. Based on molecular studies of the lower Brassicales (Cardinal-McTeague *et al.* 2016) and the presence in South America of leaf impressions possessing the characteristic marginal teeth of *Akania* (Fig. 2F) going back to the Palaeocene (Romero & Hickey 1976; Gandolfo *et al.* 1988; Iglesias *et al.* 2007), a South American origin for the family is suggested. The discovery of Miocene-aged fossil *Akanioxylon* Brea, Zucol, Bargo, Fernicola & Vizcaíno wood (Brea *et al.* 2017) in Argentina further supports this, with Carlquist (1996) and Brea *et al.* (2017) both noting that the wood anatomy of *Akania* and *Bretschneidera* is almost identical. The apparent wide Southern Hemisphere distribution of the family throughout the Cenozoic and its subsequent expansion into Asia means that further fossils displaying the distinctive leaves and cuticles of Akaniaceae could well be collected South America, Australasia, China and possibly India.

However, because this South American origin hypothesis is conditional on older, unequivocal Akaniaceae fossils not being found elsewhere, the ability to identify fossilised leaves of *Akania* and *Bretschneidera* is critical for evolutionary and biogeographic studies of the lower Brassicales. The present study suggests that in addition to a woody habit and large, pinnately-compound leaves, the presence of interconnected coronulate abaxial papillae on the leaves are a synapomorphy for Akaniaceae, distinguishing them anatomically from their herbaceous sister family Tropaeolaceae, which has unornamented abaxial cuticles. Within Akaniaceae, the two living *Akania* and *Bretschneidera* species can also be distinguished easily, both by the lack of teeth on the leaflets of the latter, but more importantly (as leaflet toothing may be different in extinct taxa) by the scattered papillae of *Bretschneidera* in contrast to the tightly clustered and stomate-associated papilla clumps in *Akania*. Because both the family and the two extant genera can be recognised readily from leaf cuticles, this will assist in the definitive identification of any new Akaniaceae macrofossils or dispersed cuticle samples.

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