

## A TOOTHED LAURACEAE LEAF FROM THE EARLY EOCENE OF TASMANIA, AUSTRALIA

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*Bandulskaiia aestuaria* gen. et sp. nov. is described from Early Eocene estuarine sediments in Tasmania. It is represented by an incomplete leaf with a finely toothed margin and well-preserved cuticle. Despite the absence of such teeth in more than 2500 known species of fossil and extant Lauraceae, the fossil cuticle exhibits traits that in combination are found only in the family. These include the derived characters of sunken, paracytic stomata with small, apparently embedded guard cells, stomata confined to small areoles, and stomatal positions that are marked by slitlike abaxial surface apertures, as well as the presence of persistent resin bodies and simple, uniseriate trichomes with thickened, poral bases. Although monimiod teeth occur widely in other lauralean families, the teeth in *B. aestuaria* are not monimiod, and it is most parsimonious to infer that the teeth were derived independently within Lauraceae, possibly in response to the physiological demands of a warm, waterlogged, high-latitude “greenhouse” environment.

**Keywords:** Early Eocene, Lauraceae, Laurales, leaf cuticle, leaf teeth, stomata.

### Introduction

The Lauraceae is one of the largest subtropical to tropical families of woody plants, with more than 50 genera and 2500–3000 species (Rohwer 1993). Phylogenetically, the family forms a monophyletic group with Monimiaceae and Hernandiaceae in the Laurales. Although morphology-based interpretations place Hernandiaceae as sister to Lauraceae (Doyle and Endress 2000), the most recent molecular studies using multiple genes show Hernandiaceae + Monimiaceae as the sister (Qiu et al. 2006). Despite this topological disparity, Laurales is clearly understood on both molecular and morphological evidence to also include Atherospermataceae, Calycanthaceae/*Idiospermum*, *Gomortega*, and Siparunaceae (Renner 1999, 2004; Doyle and Endress 2000; Renner and Chanderbali 2000). Laurales are sister to Magnoliales, and these orders form a near-basal angiosperm clade with Canellales and Piperales (Qiu et al. 2006). Relatively abundant fossilized foliar and reproductive structures of Lauraceae are known from widespread mid- and Late Cretaceous localities in the Northern Hemisphere (Drinnan et al. 1990; Upchurch and Dilcher 1990; Eklund and Kvacek 1998; Frumin et al. 2004), and well-preserved leaves of Lauraceae are obvious and common components of Cenozoic floras across the globe, where they are widely accepted indicators of warm and wet climates.

The current distribution of Laurales suggests a Gondwanic origin (Rohwer 2000). Australasia is a center of diversity for Lauraceae, with 115 species in seven genera (Hyland 1989), including a strong representation of taxa within “basal” clades (Rohwer 2000; Chanderbali et al. 2001), especially *Cryptocarya*.

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Also, numerous leaf and dispersed cuticle records suggest that the family has had a long history in Australia since at least the Paleocene (Vadala and Greenwood 2001). Fossil leaves assigned to Lauraceae occur across Australia, where they appear to be most abundant and diverse in Eocene assemblages. For example, 13 species have been described from the Middle Eocene Nerriga site (Hill 1986; Conran and Christophel 1998), and at least nine taxa were recognized from leaf and cuticular fragments in the Early Eocene Hotham Heights assemblage (Carpenter et al. 2004).

All known extant species of Lauraceae have simple, entire-margined leaves, apart from lobing in *Sassafras* and *Lindera* and young foliage of *Parasassafras* and *Sinosassafras* (Li and Christophel 2000; J. Rohwer, personal communication). Lauraceae leaves show a wide diversity of venation, including acrodromous, brochidodromous, and camptodromous types (Wolfe 1977; Christophel and Rowett 1996). Overall, this means that fossil leaf impressions cannot be placed in the family with any confidence, and although some fossils with lobes and large, lobelike teeth have been assigned to Lauraceae (Johnson 1996), no toothed species have been described that are supported by cuticular evidence.

Hill (1986, p. 328) summarized the history of taxonomic approaches with respect to fossil leaves that might be referable to Lauraceae and concluded that the form genus *Laurophyllum* Goeppert “should be used for all fossil leaves which belong to the Lauraceae, but which cannot be placed in a living genus.” Hill’s (1986) emended diagnosis for the genus emphasized the following cuticular features: (1) paracytic stomata with cuticular scales between the small, embedded guard cells and overarching subsidiary cells (following Bandulskai 1926) and (2) slitlike stomatal openings on the outer abaxial surface. A further, nonobligatory inclusion in the diagnosis was the presence of resinous secretory cells that can often be

observed as yellowish to dark spherical bodies that adhere to the cuticle (Berry 1916; Bandulska 1929; Dilcher 1963). Although the presence of such distinctive cuticular features is strong evidence for Lauraceae, little research has evaluated the phylogenetic worth of these characters. Thus, only Upchurch and Dilcher (1990) attempted to identify whether foliar characters in Lauraceae were derived (and therefore helpful in excluding extinct or unknown lineages). They postulated that within Laurales extant Lauraceae show a unique, derived combination of two features that could be interpreted from leaf cuticles: the type of stomata previously described and relatively strong higher-order vein areolation.

Apart from the need to further explore the utility of cuticular traits with respect to phylogenies published since the work of Upchurch and Dilcher (1990), it is apparent that some aspects of Lauraceae stomatal anatomy require clarification. In particular, Bandulska (1926), Hill (1986), and Christophel et al. (1996) all presented stylized diagrams that are incorrect in showing the guard cells positioned entirely below the subsidiary cells and without inner cuticular ledges. In fact, transverse sections of Lauraceae stomatal complexes show that the guard cells are embedded in the midregion of the ventral walls of the overarching subsidiary cells and have quite prominent inner ledges (Faggetter 1987; Edwards 1990; see fig. 1).

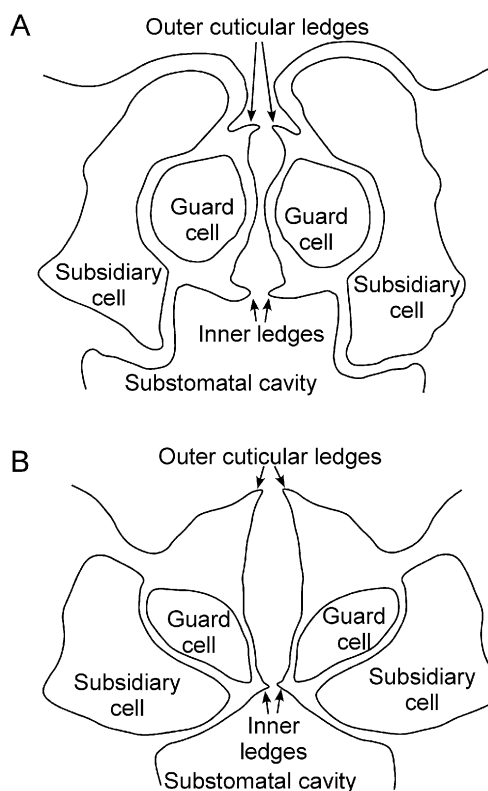
In this article, we further assess aspects of leaf and cuticular morphology pertaining to phylogeny in Lauraceae and related taxa to justify the placement of a toothed leaf from the Early Eocene of Tasmania in Lauraceae. The fossil is assigned to a new genus because the diagnosis of *Laurophyllum* prescribes entire margins (Hill 1986).

## Material and Methods

### *Setting, Age, and Nature of the Fossil Assemblage*

Early Eocene sediments containing plant fossils are widespread in the Strahan region of Macquarie Harbor, western Tasmania, Australia (Pole 1998; Jordan and Hill 2002). The specimen was recovered from a new site on Lowana Road, Regatta Point, as part of a collection of fossil material made by G. J. Jordan in 2003. Microfossils in this material include saltwater dinoflagellates and an extremely diverse pollen/spore flora dominated by angiosperms (Macphail 2005). These offer correlative evidence for the age of the sediments from both marine and terrestrial microfossil schema. On the basis of these, the sediments containing the fossils are most likely to belong to the Upper *Malvacipollis diversus* Zone of Stover and Partridge (1973) and more or less correlate with the mid-Ypresian or Planktonic Foraminiferal Zone P7 of Hardenbol et al. (1998) (Macphail 2005). This implies that the sediments were deposited ca. 52–51 million years ago, at or near the height of the Early Eocene Climatic Optimum, when “greenhouse” conditions are considered to have prevailed worldwide (Zachos et al. 2001). At this time, Australia was connected to Antarctica through the Tasmanian region, and western Tasmania would have represented the eastern extent of a long, shallow embayment between these landmasses.

The fossils are currently the subject of a wider study but include *Lygodium* (Schizaeaceae), *Bowenia* (Zamiaceae), Cupressaceae, several species of Araucariaceae and Podocarpaceae,



**Fig. 1** Stylized transverse sections through stomata. *A*, Lauraceae (general form). Note the guard cells sunken below the leaf surface and embedded in the subsidiary cells, and the way that each guard cell bulges between the inner and outer cuticular ledges. The extent of cuticularization is variable and not shown, but the cuticle between the guard cells and subsidiary cells is typically obvious in the region of the outer ledges as laterally extending flanges. *B*, *Atherospermataceae*; Laurales, showing features widespread in other angiosperms. Note that the guard cells are not embedded in the subsidiary cells and do not bulge markedly between the inner and outer cuticular ledges.

and *Gymnostoma* (Casuarinaceae), *Ripogonum* (Ripogonaceae), Proteaceae, and other Lauraceae (R. J. Carpenter, G. J. Jordan, and R. S. Hill, unpublished data). Pollen of the mangrove palm *Nypa* is common (Macphail 2005), and as for other sites in the Strahan region (Pole and Macphail 1996; Pole 1998), this strongly suggests that the sediments were deposited in a quiet-water estuarine setting with tidal influence. The association of *Nypa* and other taxa with nearest living relatives in modern tropical lowlands has been used as evidence that coastal vegetation in the region had a megatherm character (Macphail et al. 1994). According to Nix's (1982) model, megatherm elements now dominate rain forests in the Australia/Papua New Guinea region where mean annual temperatures exceed 24°C, having optimal temperatures for photosynthesis of 26°–28°C.

### *Analysis of the Fossil and Comparable Extant Taxa*

The specimen that is the subject of this study, LO 49, was recognized as lauraceous by examination of its well-preserved

cuticle. Fragments of organic material were first placed in hydrofluoric acid overnight to remove adherent siliceous material. Cuticles were then prepared for both light microscopy (LM) and scanning electron microscopy (SEM) by placing the leaf fragments in 10% chromium trioxide to clear the mesophyll, followed by a rinse in water. These cuticles were then either further rinsed with dilute ammonia, stained with safranin O, and mounted on glass slides in phenol glycerin jelly for LM or mounted flat on double-sided adhesive tape on an aluminum SEM stub and gold/carbon coated. SEM was performed using a Philips XL 30 FEGSEM operated at 10 kV. For LM, cuticles were photographed using an Olympus DP11 digital camera attached to a Zeiss Axioskop microscope. The leaf specimen was photographed with a Nikon Coolpix 5000 digital camera.

Leaf architectural description is based on Hickey and Wolfe (1975), Hickey (1979), and the Leaf Architecture Working Group (1999). Leaves and cuticles from numerous taxa of Lauraceae were studied using fresh material and the collection that is housed in the School of Earth and Environmental Sciences, University of Adelaide (table 1). Pieces of leaf of some species (table 1) were also cut using a freeze microtome to obtain transverse sections ca. 20  $\mu\text{m}$  thick. Longitudinal sections of photosynthetic stems of the almost leafless parasite *Cassytha pubescens* were obtained with the same methods. These sections were stained with a saturated ethanolic solution of the cuticle specific stain, Sudan III. Overall, the species examined occupy widely divergent positions across extant clades of Lauraceae, according to the most recent phylogenetic analyses (Rohwer and Rudolph 2005). Some comparisons of tooth and cuticle morphology were also made using leaves of other Laurales (table 1) to help determine whether the characteristic cuticular character states of Lauraceae are plesiomorphic or apomorphic. This approach essentially follows that of Upchurch and Dilcher (1990), so that unique combinations of apomorphic states are assumed to be good evidence for identifying fossils.

## Results

### Systematics

#### Order—Laurales

#### Family—Lauraceae

#### *Species—Bandulskaiia aestuaria* Carpenter, Jordan, and Hill gen. and sp. nov.

*Generic and specific diagnosis.* Leaves toothed, hypostomatic. Teeth nonglandular. Stomata paracytic with small, sunken guard cells associated with pronounced cuticular development between guard cells and overarching subsidiary cells. Stomatal openings on outer cuticular surface slitlike. Resin bodies present.

*Type species.* *Bandulskaiia aestuaria* Carpenter, Jordan, and Hill sp. nov.

*Etymology.* Genus named for Helena Bandulska, whose detailed work highlighted the distinctiveness of Lauraceae stomata. Species named with reference to the presumed estuarine habitat of the source plant.

*Holotype.* LO 49 here designated (only specimen).

*Repository.* Specimen: Department of Plant Science, University of Tasmania; cuticle slides and SEM stubs: School of Earth and Environmental Sciences, University of Adelaide.

*Type locality.* Lowana Road, Macquarie Harbor, Tasmania, Australia. Early Eocene mudstone of Macquarie Harbor Formation (Pole 1998).

*Description of type.* Architecture (fig. 2). Leaf incomplete, 62 mm long, but estimated to be ca. 100 mm long, 28 mm wide, ovate. Margin regularly serrate, at least in the apical portion that is preserved (fig. 2A, 2B). Teeth (fig. 2C) robust, nonglandular, approximately two teeth per secondary vein. Tooth apical angle acute, apical side concave, basal side acuminate. Venation indistinct, but secondary veins appear eucamptodromous, diverging at moderate acute angles from the primary vein, and curved uniformly upward, with all visible secondary veins running directly into teeth. Intersecondary and higher-order veins not visible.

Cuticular morphology (fig. 3). Abaxial surface. Stomata confined to very small areoles, randomly oriented (fig. 3A). Stomatal positions marked by longitudinal surface slits ca. 21  $\mu\text{m}$  long, with evidence of overarching cuticle associated with subsidiary cells (fig. 3B). Cuticle outer surface otherwise smooth. Stomatal complexes paracytic (fig. 3C–3E), ca. 16  $\mu\text{m}$  long. Guard cells sunken below overarching subsidiary cells, cuticle with prominent polar extensions (fig. 3D, 3E). Massive cuticular thickenings face pore between guard cells. Irregular-edged cuticular flanges extend laterally between guard and subsidiary cells (fig. 3E). Inner cuticular anticlinal extensions between epidermal cells straight or rounded, weakly developed except in tooth regions, much more pronounced associated with subsidiary cells (fig. 3D). Poral trichome bases with thickened margins infrequent, mostly along veins (fig. 3A). Trichomes simple, uniseriate, thin walled, ca. 90  $\mu\text{m}$  long (fig. 3F). Resin bodies abundant, darkly stained (fig. 3G). Adaxial surface. Cuticle outer surface smooth. Inner cuticular anticlinal extensions between epidermal cells straight or rounded (fig. 3H, 3I). Glandlike poral trichome bases present, with thick cuticle around pore extending along radial walls of surrounding cells, giving stellate appearance (fig. 3H). Regions of connected periclinal cuticular thickenings present, especially near leaf margin (fig. 3I).

## Discussion

### *Characters Used in Identifying Fossil Lauraceae*

The features usually used to identify fossil leaves of Lauraceae are best interpreted as being a mixture of apomorphic and plesiomorphic states. Paracytic stomata are well known to occur throughout the family, but this state alone is of little use for identifying fossils because it is widespread in angiosperms, including Magnoliales and other Laurales (e.g., data in Doyle and Endress 2000). However, as recognized by numerous authors, the stomata of Lauraceae are quite distinctive. Our transverse leaf sections show that with the exception of *Hypodaphnis*, Lauraceae stomata follow the general arrangement of being paracytic with sunken guard cells embedded in the ventral walls of the subsidiary cells and bulging between prominent inner and outer cuticular ledges (table 1; figs. 1A, 4A). These results support previous work by Faggetter

**Table 1**  
**List of Laurales Species Examined in Detail**

	1	2	3	4	5	6
Atherospermataceae:						
<i>Atherosperma moschatum</i> Labill.	E/CM/010	No	No	Anomocytic	Simple	
<i>Daphnandra micrantha</i> (Tul.) Benth.	M. Pole OPH1323	No	No	Anomocytic	Simple	
<i>Doryphora sassafras</i> Endl.	E/DO/037	No	No	Anomocytic	Simple	
<i>Laureliopsis philippiana</i> (Looser) Schodde	E/3128	No	?Yes	Paracytic	Simple	
Calycanthaceae:						
<i>Idiospermum australiense</i> (Diels) S. T. Blake	M. Pole OPH1615	No	No	Paracytic	Simple	
Hernandiaceae:						
<i>Gyrocarpus americanus</i> Jacq.	CANB 464883	Yes <sup>a</sup>	No	?Paracytic	Simple	
<i>Hernandia albiflora</i> (C. White) Kubitzki	Cultivated Brisbane	No	No	?Anomocytic	Glandular	
<i>Hernandia bivalvis</i> Benth.	Adelaide Botanical Gardens	No	No, TSN	Paracytic	Glandular	
Lauraceae:						
Fossil <i>Bandulskia aestuaria</i>		Yes <sup>a</sup>	Yes	Paracytic	Simple	Yes
<i>Beilschmiedia bancroftii</i> (F. M. Bailey) C. T. White	LAE 230499, E/0158	Yes <sup>a</sup>	Yes	Paracytic	Simple	
<i>Beilschmiedia dilmyana</i> Kosterm.	E/0162	Yes	Yes	Paracytic	Simple	
<i>Beilschmiedia gemiflora</i> (Bl.) Kosterm.	E/0163	Yes	Yes	Paracytic	Simple	
<i>Beilschmiedia obtusifolia</i> (F. Muell. Ex Meisn.) F. Muell.	Sydney Botanical Gardens	Yes	Yes, TSE	Paracytic	Simple	
<i>Cassytha pubescens</i> R. Br.	University of Tasmania	No	Yes, TSE	Paracytic		
<i>Cinnamomum archboldianum</i> C. K. Allen	LAE 19224, E/0177	Yes	Yes	Paracytic	Simple	
<i>Cinnamomum culilawan</i> Bl.	LAE 2632, E/0216	Yes	Yes	Paracytic	Simple	
<i>Cinnamomum hentyi</i> Kosterm.	LAE 112121, E/0179	Yes <sup>a</sup>	Yes	Paracytic	Simple	
<i>Cinnamomum oliveri</i> F. M. Bailey	LAE 230867, E/0187	Yes	Yes	Paracytic	Simple	Yes
<i>Cryptocarya angulata</i> C. T. White	E/0204	Yes	Yes	Paracytic	Simple	
<i>Cryptocarya glaucescens</i> R. Br.	LAE 222127, E/0237	Yes <sup>a</sup>	Yes	Paracytic	Simple	
<i>Cryptocarya meissneriana</i> Frodin	E/DO/030	Yes	Yes	Paracytic	Simple	
<i>Cryptocarya obovata</i> R. Br.	E/1125	Yes	Yes	Paracytic	Simple	
<i>Cryptocarya triplinervis</i> R. Br.	Sydney Botanical Gardens	Yes	Yes, TSE	Paracytic	Simple	
<i>Endiandra crassifolia</i> C. T. White and W. D. Francis	M. Pole OPH1300	Yes	Yes	Paracytic	Simple	
<i>Endiandra glauca</i> R. Br.	LAE 221745, E/0332	Yes	Yes	Paracytic	Simple	
<i>Endiandra virens</i> F. Muell.	E/1129	Yes	Yes	Paracytic	Simple	
<i>Hypodaphnis zenkeri</i> (Engl.) Stapf	HBG G. Zenker 3033	Yes	No, TSN	Paracytic	Simple	Yes
<i>Laurus nobilis</i> L.	Adelaide Botanical Gardens, E/1167	Yes <sup>a</sup>	Yes, TSE	Paracytic	Simple	
<i>Lindera benzoin</i> (L.) Blume	KUN 0049334, E/3856	Yes	Yes	Paracytic	Simple	Yes
<i>Litsea bindoniana</i> (F. Muell.) F. Muell.	Sydney Botanical Gardens	Yes	Yes, TSE	Paracytic	Simple	
<i>Litsea leefeana</i> (F. Muell.) Merr.	LAE 230944, E/0422	Yes <sup>a</sup>	Yes	Paracytic	Simple	
<i>Neolitsea dealbata</i> (R. Br.) Merr.	E/BB/024	Yes	Yes	Paracytic	Simple	
<i>Persea borbonia</i> (L.) K. Spreng.	LAE 83340, E/0453	Yes <sup>a</sup>	Yes	Paracytic	Simple	
<i>Sassafras albidum</i> (Nutt.) Nees	K. Holland 42, E/M/130	Yes	Yes	Paracytic	Simple	
Monimiaceae:						
<i>Hedycarya angustifolia</i> A. Cunn.	Adelaide Botanical Gardens	No	No, TSN	Paracytic	Simple	Yes
<i>Levieria acuminata</i> (F. Muell.) J. R. Perkins	JCT/S7114	No	No	Paracytic	Simple	Yes
<i>Palmeria scandens</i> F. Muell.	E/BB/027	No	No	Anomocytic	Stellate	Yes
<i>Steghanthera laxiflora</i> (Benth.) Foreman and Whiffin	JCT/S994	No	No	Paracytic	Simple	Yes
<i>Wilkiea hugeliana</i> (Tul.) A. DC.	JCT/s 6152a	No	?Yes	Paracytic	Simple	Yes

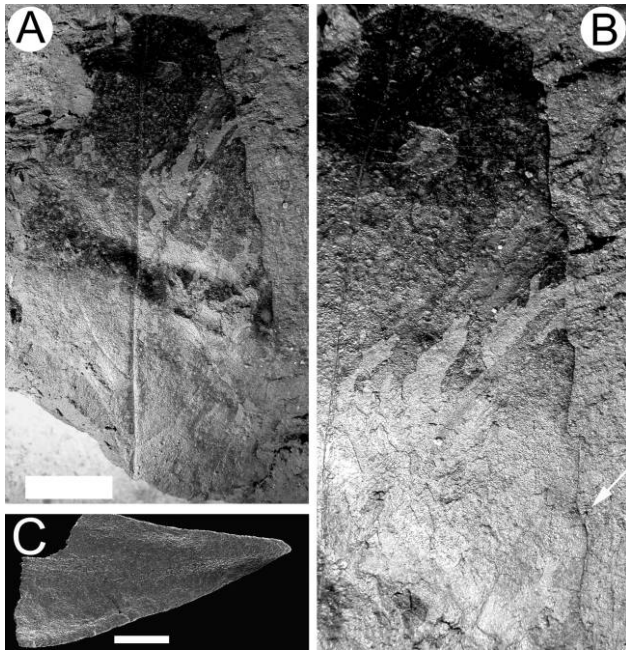
Note. 1, Source/University of Adelaide cuticle number; 2, well-defined areoles; 3, prominent cuticular development between guard and subsidiary cells (TSE = transverse section clearly shows guard cells embedded in subsidiary cells; TSN = not embedded); 4, subsidiary cell arrangement; 5, trichome type; 6, resin adherent to cuticle.

<sup>a</sup> Very small, ca. 0.1 mm<sup>2</sup>.

(1987, her fig. 47E) and Edwards (1990). There are many variations in the organization of the stomatal complex in Lauraceae (Bandulskia 1926; Dilcher 1963; Hill 1986; Faggetter 1987; Christophel and Rowett 1996), including that further cuticular development is often obvious as variably extensive flanges between the guard cells and overarched subsidiary cells (fig. 4B). These flanges have previously been referred to as scales (e.g., Hill 1986) or lamellae (Upchurch and Dilcher 1990). They appear markedly butterfly-like in many species of *Cryptocarya* (Christophel and Rowett 1996). Given that the gen-

eral stomatal arrangement is unknown elsewhere in Laurales (see also Upchurch and Dilcher 1990) and not found in *Hypodaphnis*, which is best interpreted as sister to the rest of Lauraceae (Rohwer and Rudolph 2005), then the most parsimonious interpretation is that this arrangement is a synapomorphy for Lauraceae, excluding *Hypodaphnis*.

A potential problem in conclusively determining fossil stomata as lauraceous is that stomatal anatomy and cuticularization is best interpreted through appropriately stained transverse sections, and it is unlikely that these can be obtained from



**Fig. 2** Holotype of *Bandulskaiia aestuaria*. Scale bars = 1 cm for A, 500  $\mu\text{m}$  for C. A, Whole specimen showing upwardly curving secondary veins. B, Enlargement showing positions of leaf teeth. Arrow indicates a preserved robust tooth apex. C, SEM image of detached tooth apex. Note absence of glandular tip.

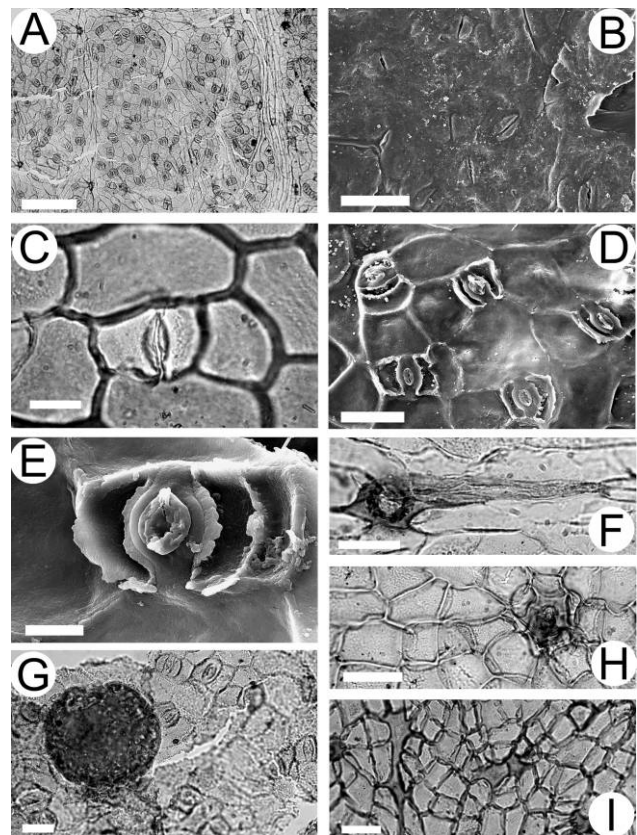
fossil material. Also, stomatal anatomy somewhat similar to that of Lauraceae occurs in some nonlauralean angiosperms. Metcalfe (1987) described the stomata of Myristicaceae as paracytic, with guard cells more or less embedded in the subsidiary cells. However, Myristicaceae have complex, distinctively nonlauralean trichome bases (Upchurch and Dilcher 1990). Sunken guard cells embedded in the subsidiary cells and bulging between prominent inner and outer cuticular ledges are also present in *Simarouba glauca* DC (Simaroubaceae; Sapindales) and many monocots. However, the stomata in *S. glauca* are anomocytic, and monocots can differ from Laurales in many other features.

Our studies support the findings of Upchurch and Dilcher (1990) and Christophel and Rowett (1996) that Lauraceae (apart from *Cassytha*) have relatively strong higher-order vein areolation, with stomata confined to regions sometimes as small as 0.1 mm<sup>2</sup> (table 1). Such areolation only occurs elsewhere in currently recognized Laurales in Hernandiaceae subfamily Gyrocarpoideae (table 1; Upchurch and Dilcher 1990). Following the topology of Qiu et al. (2006), we therefore conclude that it most parsimoniously arose independently in Lauraceae and Gyrocarpoideae. Similar areolation occurs widely among other angiosperms.

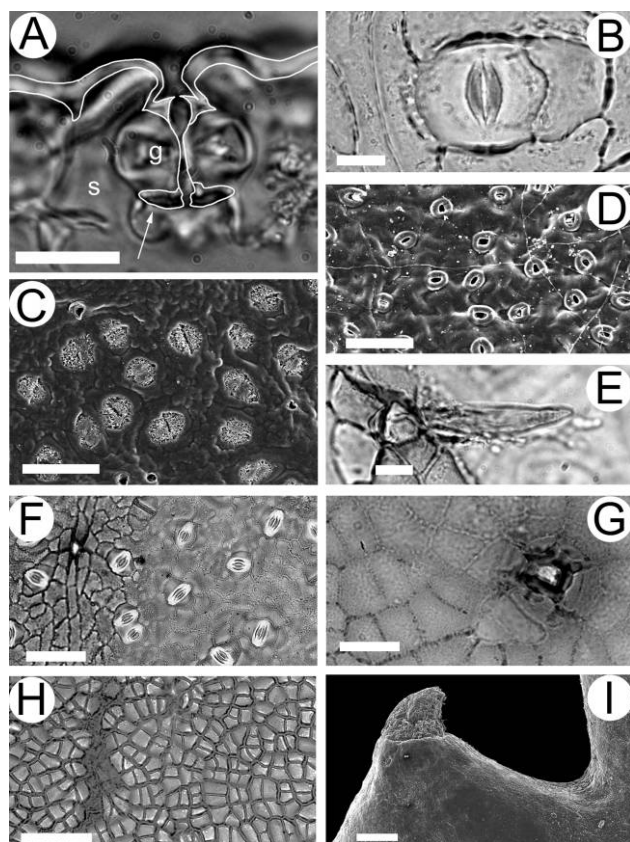
The presence of stomata with slitlike external apertures was included in the diagnosis of *Laurophyllum* by Hill (1986). Unlike most angiosperms, which have stomatal apertures associated with raised, elliptical regions (or peristomatal rims) formed by the guard cell outer cuticular ledges (see fig. 1B), the apertures in Lauraceae generally lack rims (fig. 4C) and

appear as slits formed between cuticular extensions of each subsidiary cell (overarching cuticular scales *sensu* Hill 1986; see fig. 1A). This character is associated with the synapomorphy for Lauraceae (excluding *Hypodaphnis*) of embedded guard cells and has not been observed elsewhere in Laurales (see also Metcalfe 1987). Elliptical external rims are evident in some species of Lauraceae (fig. 4D; Hill 1986, his fig. 6d), and these are probably secondarily derived from subsidiary cell cuticle.

Secretory cells are widely observable in Lauraceae and Monimiaceae as spherical globules adhering to isolated cuticle



**Fig. 3** Light microscopy (A, C, F–I) and scanning electron microscopy (B, D, E) images of *Bandulskaiia aestuaria*. Scale bars = 100  $\mu\text{m}$  for A; 50  $\mu\text{m}$  for B; 10  $\mu\text{m}$  for C; 20  $\mu\text{m}$  for D, F, G; 5  $\mu\text{m}$  for E, 25  $\mu\text{m}$  for H, I. A, General view of abaxial cuticle showing stomata in an areole and several poral trichome bases on veins. B, Outer abaxial cuticle showing slits that lead to stomata and evidence of overarching subsidiary cells. C, Individual paracytic stoma, showing stomatal slit and cuticular development between guard and subsidiary cells. D, Inner surface of abaxial cuticle showing stomata. Anticlinal cuticle flanges of epidermal walls are well developed only where associated with subsidiary cells. E, Detail of inner stomatal complex showing evidence of sunken guard cells and overarching subsidiary cells. Note polar cuticular extensions, inner thickenings surrounding pore, and cuticular flanges with irregular edges between guard and subsidiary cells. F, Thin-walled simple trichome arising from poral base on abaxial vein. G, Dense resin body adherent to inner abaxial cuticle. H, Adaxial cuticle showing thickened poral trichome base with stellate appearance. I, Adaxial cuticle showing connected regions of periclinal thickenings.



**Fig. 4** Light microscopy (A, B, E–H) and scanning electron microscopy (C, D) images of extant Lauraceae cuticle and SEM image of *Laureliopsis philippiana* leaf tooth (I). Scale bars = 20  $\mu\text{m}$  for A; 5  $\mu\text{m}$  for B; 50  $\mu\text{m}$  for C, D, F, H; 10  $\mu\text{m}$  for E; 25  $\mu\text{m}$  for G; 200  $\mu\text{m}$  for I. A, Transverse section through *Laurus nobilis* stomatal complex. Regions stained red with Sudan III (i.e., cuticularized) are outlined. Note that the subsidiary cells (s) extend both above and below the embedded guard cells (g). Also note outer and inner (arrow points to one of pair) guard cell cuticular ledges. B, Individual paracytic stoma of *Beilschmiedia gemiflora* showing cuticular development between guard and subsidiary cells. C, Outer abaxial surface of *Beilschmiedia bancroftii* showing a small areole with stomatal positions marked by slitlike apertures and poral trichome bases on veins. D, Outer abaxial surface of *Cryptocarya angulata* showing raised elliptical rims surrounding stomata. E, Thin-walled simple trichome arising from poral base on abaxial vein of *Cryptocarya glaucescens*. F, General view of stomata of *Endiandra virens* with a poral trichome base on vein at upper left. G, Adaxial cuticle of *Endiandra crassifolia* showing thickened poral trichome base with stellate appearance. H, Adaxial cuticle of *Cryptocarya obovata* showing connected regions of periclinal thickenings. I, Tooth apex showing prominent monimoid glandular cap.

(table 1). Oil cells in the mesophyll are also recorded throughout other Laurales and other basal angiosperms, excluding *Amborella* (Metcalf 1987; Doyle and Endress 2000). We therefore presently regard the presence of these structures in leaves of Laurales as plesiomorphic. The phylogenetic significance of the phenomenon of resin adherence to the cuticle in Lauraceae and Monimiaceae is unclear and may merely reflect oil cell abundance. Simple, nonglandular trichomes occur

throughout Lauraceae (fig. 4E), where they are often found on veins. They arise from poral bases (fig. 4E–4G) that occur at the junction of several cells and that are variously thickened surrounding the pore. The range of base types for Australian species was illustrated by Christophel and Rowett (1996). This type of trichome occurs widely in at least other Laurales (Metcalf 1987; table 1), suggesting that it is another plesiomorphic trait in Lauraceae.

Overall, our studies support Upchurch and Dilcher's (1990) proposal that extant Lauraceae show the derived traits of paracytic stomata with embedded guard cells, overarching subsidiary cells, and strong cuticular development between guard and subsidiary cells, as well as relatively well-developed higher-order vein areolation. By implication, the identification of a fossil leaf as Lauraceae should at least demonstrate these features. The presence of slitlike surface apertures is associated with the stomata, but resin bodies and simple, poral-based trichomes are plesiomorphic.

#### *Bandulskaia* as Lauraceae

Despite not being observable in transverse section, the stomata of *Bandulskaia* clearly show evidence of a synapomorphy for Lauraceae (excluding *Hypodaphnis*) in being paracytic with very small guard cells overarched by subsidiary cells and pronounced cuticular development between guard cells and subsidiary cells (cf. figs. 3C, 4B). The fossil stomata also have other derived states in Lauraceae: They are restricted to small, high-order areoles and open into slitlike apertures on the cuticle surface. While, individually, each of these features may occur in other angiosperms, we argue that it is very unlikely that all of these structures would occur together in living or extinct lineages outside of Lauraceae. The stomatal anatomy provides evidence that *Bandulskaia* is nested within extant Lauraceae because the apparent sister taxon to the rest of the family (*Hypodaphnis*) expresses the plesiomorphic state.

All other cuticular features of *Bandulskaia* are consistent with Lauraceae (table 1). The fossil exhibits relatively unthickened poral trichome bases on the abaxial surface (fig. 3A, 3F) and more heavily thickened bases on the adaxial surface (fig. 3H). Both base types were observed in extant species (fig. 4E, 4G). Similarly, a simple, nonglandular trichome found on the abaxial surface of the fossil (fig. 3F) is clearly comparable with the trichomes of extant species (fig. 4E). Abundant resin bodies adherent to the cuticle are also highly typical of extant Lauraceae. A further, unusual feature of the fossil is that there are regions of irregular but connected, thickened (dark-staining) cuticle on the adaxial surface (fig. 3I). Again, near identical regions were found in the cuticle of an extant species of *Cryptocarya* (fig. 4H).

#### A Toothed Lauraceae

Leaf teeth are unknown in extant Lauraceae, but monimoid teeth occur widely in most other Laurales (data from Doyle and Endress 2000; Sauquet et al. 2003) and are probably synapomorphic for Laurales, given that Eklund et al. (2004) reassessed the teeth of *Trimenia* (Trimeniaceae; Austrobaileyales) as chloranthoid and not monimoid, as first determined by Hickey and Wolfe (1975). Monimoid teeth have an opaque, sometimes persistent glandular cap having an

acute apex, with the shape of the tooth being acuminate-convex and its venation showing a secondary or tertiary vein entering the tooth medially, the tooth not being joined by lateral veins (Hickey and Wolfe 1975; also see fig. 4J). However, the leaf teeth in *Bandulskia* lack the glandular caps of monimoid teeth (fig. 2C). Although nonglandular teeth could have evolved from monimoid teeth, they could also have evolved independently. Overall, the latter hypothesis is more parsimonious, given the evidence that *Bandulskia* is nested within Lauraceae.

Toothed leaf margins are overrepresented among woody plants of wet habitats in general (Kowalski and Dilcher 2003), probably related to teeth being sites that can enable the release of guttation sap during root pressure, thus promoting the avoidance of mesophyll flooding (Feild et al. 2005). This seems an attractive hypothesis for explaining the teeth in *Bandulskia*, especially given that the source plant was probably growing in the close vicinity of tidal channels and thus in wet soil.

Aspects of past climates have been predicted by simply assessing the margin types of leaves in fossil assemblages (e.g., Wing and Greenwood 1993; Greenwood et al. 2004), based on the long-standing observation of a positive correlation be-

tween mean annual temperature (MAT) and the proportion of extant woody dicotyledonous species with nontoothed leaf margins (Bailey and Sinnott 1916). Increasingly sophisticated techniques and more data sets derived from modern floras (e.g., Royer et al. 2005) offer the possibility of reducing the magnitude of the inherent limitations (Jordan 1997) associated with this approach. Also, there is greater recognition that climate variables such as growing season length probably influence leaf physiognomy more than MAT per se (Jordan 1997; Royer et al. 2005). Our demonstration of the presence in the Early Eocene of Tasmania of a species of toothed margined Lauraceae associated with cycads and mangroves at 65°S serves as a reminder for paleoclimatologists that unusual leaf forms are to be expected in past environments that have no modern equivalent (e.g., Hill and Scriven 1995).

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