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Cuticular features of *Cryptocarya* (Lauraceae) from Peninsular Malaysia, Thailand and Indo-China and its taxonomic implications

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Abstract

Cuticular features potentially offer valuable information on phytotaxonomy, especially for plants that are difficult to classify or identify. *Cryptocarya* is one such difficult and poorly known genus, and we investigated its cuticular features to evaluate their taxonomic implications. We examined cutinized leaf epidermis and the stomatal complex for 21 species from Peninsular Malaysia, Thailand and Indo-China, as well as one species endemic to Borneo and one to Sumatra, and compared features among members of this group, between this group and congeners in the other countries, and between this group and the other genera of Lauraceae. Many of the *Cryptocarya* species studied have straight to slightly curved anticlinal epidermal walls and butterfly-shaped stomatal ledges, although some variation was seen in the ornamentation of the periclinal epidermal walls and the appearance of the stomatal complex. Based on these results, we recognized four groups and two subgroups among the South-east Asian species. Comparison with congeneric taxa in the other countries indicates that butterfly-shaped stomatal ledges are often shared among the species across the regions. However, no cuticular features occur exclusively in any of the species groups of *Cryptocarya* studied here, nor in the genus as a whole. We consider that cuticular features are useful in the recognition of infrageneric groups within Lauraceae, bearing in mind that they might have evolved in parallel in different genera.

Key words: cuticle, epidermis, morphology

Introduction

The genus *Cryptocarya* Brown (1810: 402) is rather poorly known due to the large number of species, difficulties in their identification, and the lack of an intra-generic classification. It is one of the largest genera in Lauraceae, consisting of more than 300 species (van der Werff 2001), many of which are important components of tropical and subtropical forests (e.g., Celis-Diez & Bustamante 2005; Nizam *et al.* 2008) and/or have economic uses (e.g., Kochummen 1989; van Balgooy 1998). The recognition of the genus is relatively easy, mainly because it is one of the few laurel genera whose fruits are completely enclosed in receptacular tissue and appear to be inferior. This character is only shared with five small other genera: *Aspidostemon* Rohwer & Richter (1987: 71), with 26 species endemic to Madagascar (van der Werff 2006), plus the monotypic genera *Dahlgrenodendron* van der Merwe & van Wyk (1988: 80) from South Africa, *Hypodaphnis* Stapf (1909: 185) from tropical Africa, *Eusideroxylon* Teijsmann & Binnendijk (1863: 292) and *Potoxylon* Kostermans (1978: 143), both endemic to Borneo and Sumatra. The classification of the genus is, however, far from complete. This is mainly because many species share similar vegetative and reproductive macro-morphological characters, such as alternate leaves with entire margins and mostly pinnate venation, trimerous flowers with nine small stamens, two-locular anthers, and a single pistil enclosed in a long receptacular tube. A recent molecular phylogenetic study by Rohwer *et al.* (2014) supported its monophyly, but this result was based on a sample of only 20 species representing the entire genus, as their main aim was to investigate relationships among the various genera in the *Cryptocarya* group, not those within the genus itself. The taxonomic relationships within the genus are still underexplored and no infrageneric classification yet exists.

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Cryptocarya is an almost pantropical genus (absent from central Africa), with the majority of species in tropical Asia (van der Werff 2001). Peninsular Malaysia harbours a moderately large number of species for its small size, as 17 were recorded in a recent taxonomic study (de Kok, in press), while in Thailand and Indo-China, 16 species are recognised (de Kok 2015). In his recent revision of the Brazilian taxa, Moraes (2007) was unable to identify clearly distinguishable morphological groups. Hyland (1989) organised Australian *Cryptocarya* into ten groups based on a series of morphological characters, although they were, however, not consistently used throughout the classification. Characters he used included: bark colour; size and venation of the leaves and the presence/absence of a glaucous coating on them; floral scent; presence/absence of a ribbed endocarp in the fruits; cotyledons ruminate or not; presence/absence of cataphylls in the seedlings. Although the author argued that each group contains closely related species, he also commented that while the relationships can be substantiated by obvious morphological similarities in most cases, in others, the similarities are not obvious and certain groupings were made somewhat intuitively (Hyland 1989). Hyland's (1989) system has not been taken up by other researchers.

In the recent revisions of the genus for Peninsular Malaysia, Thailand and Indo-China (de Kok 2015; de Kok, in press), species are assembled in three groups based on two morphological characters and geographical distribution. The first group is characterised by having triplinerved leaves, i.e. *C. densiflora* Blume (1825: 556), *C. laevigata* Blume (1825: 556), and *C. wrayi* Gamble (1910a: 142). The first two species are widespread (from South China or Peninsular Malaysia to Australia), while the last one occurs on mountain tops in Peninsular Malaysia. This group is also likely to include the Sumatran endemic *C. nana* Kostermans (1970: 78) and the Bornean endemic *C. tuanku-bujangii* Kostermans (1970: 79), which are very similar to *C. wrayi* in their macro-morphology, and also occur on mountain tops, in North Sumatra and Sarawak respectively.

The second group, which is the biggest, has pinnately veined leaves and small bracteoles, i.e., *C. amygdalina* Nees (1831: 69), *C. chanthaburiensis* Kostermans (1974: 33), *C. concinna* Hance (1882: 79), *C. costata* Blume (1825: 558), *C. diversifolia* Blume (1851: 335), *C. enervis* Hooker (1886b: 119), *C. ferrea* Blume (1825: 557), *C. hainanensis* Merrill (1922: 343), *C. impressa* Miquel (1855: 923), *C. kurzii* Hooker (1886b: 119), *C. nitens* (Blume 1851: 375) Koorders & Valeton (1904: 220), *C. pallens* Kostermans (1974: 34), *C. pustulata* Kostermans (1974: 35), *C. sublanuginosa* Kostermans (1974: 36), and *C. teysmanniana* Miquel (1861: 360). This group is widespread on the Sunda plateau and in Thailand and Indo-China. The third group, i.e. *C. bracteolata* Gamble (1910a: 143), *C. griffithiana* Wight (1852: 12) and *C. rugulosa* Hooker (1886b: 118) has pinnate leaf venation and linear to lanceolate bracteoles that are markedly longer than those of the other *Cryptocarya* species. This group is centred in Peninsular Malaysia, Peninsular Thailand and Borneo. Here we study the cuticular features of species in these three groups to determine whether these additional characters support the recognition of these groups.

The cuticular features we studied are observed in cutinized cell walls of the epidermis and stomatal complexes of leaves (Christophel *et al.* 1996). They potentially offer a suite of characters that are independent of flowers and fruits (Nishida & van der Werff 2007), and they have long been used in the identification of the fossil remains of angiosperms and in recognizing relationships among extant taxa (e.g., Baranova 1972, 1987, 1992; Carpenter *et al.* 2010; Upchurch 1984a, 1984b; Yang & Lin 2005). With reference to the taxonomy of Lauraceae, they have been intensely studied since Christophel & Rowett (1996) published a comprehensive cuticular study for the Australian species, and they are presumed to be useful when recognizing groups at generic level (Christophel *et al.* 1996) or sub-generic level (Nishida & Christophel 1999). Recently they were used to reveal the generic identity of a poorly known species, *Beilschmiedia scintillans* (Kostermans 1939: 113) van der Werff & Sach.Nishida (Nishida & van der Werff 2007: 1236), and to classify *Syndiclis* Hooker (1886a: plate 1515) and its allies (Yang *et al.* 2012). A comparison of the relationships suggested by cuticular features with those revealed by molecular phylogeny suggests that cuticular features, especially the appearance of the stomatal complex, are useful in establishing relationships between taxa in Lauraceae (Nishida & van der Werff 2011).

In this study, we examined cuticles of species from Peninsular Malaysia, Thailand and Indo-China, plus one each from Borneo and Sumatra. The last two species were included in this study given their close relationship to *C. wrayi*. We observed the cuticles under both light microscope and scanning electron microscope (SEM), and determined whether cuticular features enable us to group species. We further looked for associations between these features and macro-morphological characters, and we compared the cuticular features observed with those of congeners from other regions and of other laurel genera to determine their wider taxonomic implications.

Materials and Methods

For each species, one or two (if available) leaves were taken from a specimen at K, except a sample of *C. laevigata* from Australia (QRS) (Table 1). Leaves were arbitrarily selected, but only matured leaves were used.

The procedure for examining the cuticles largely followed that of Nishida & Christophel (1999). A piece of leaf blade ca. 1 x 1 cm was cut out of a lower right side of each leaf (with the adaxial surface upward), and kept in 90% of ethanol for more than 10 h. The leaf fragment was then put in a test tube with ca. 2.5 ml of 30% H_2O_2 and 2 ml of 90% ethanol, and heated in a heat block at ca. 120°C for ca. 2 h. When the sample became soft and turned whitish yellow, it was taken out of the test tube and put into a Petri dish with water. After cleaning with a fine paint brush, both adaxial and abaxial epidermis was picked out from the water and kept in 90% ethanol overnight.

For observation under the light microscope, the pieces of epidermis were rinsed with 3% ammonium solution to adjust its pH, put into a Petri dish with water and cleaned again with a fine paint brush. They were then stained in 0.1% Crystal Violet, washed in water to remove extra stain, placed in a droplet of glycerol on a glass slide, and covered with a coverslip.

For examination with SEM, pieces of lower epidermis were subjected to the same procedure as above until the point at which they were rinsed with ammonium solution. They were then dehydrated in a t-butanol series (90% ethanol : t-butanol = 3:1; 1:3; 100% t-butanol twice), freeze-dried using a JFD-310 (JEOL, Tokyo, Japan) at -3°C, then placed on an aluminum stage. The sample on the stage was finally coated with platinum and observed under a JSM-6060B microscope (15 kV; JEOL).

TABLE 1. List of the samples examined. Specimens are deposited in K.

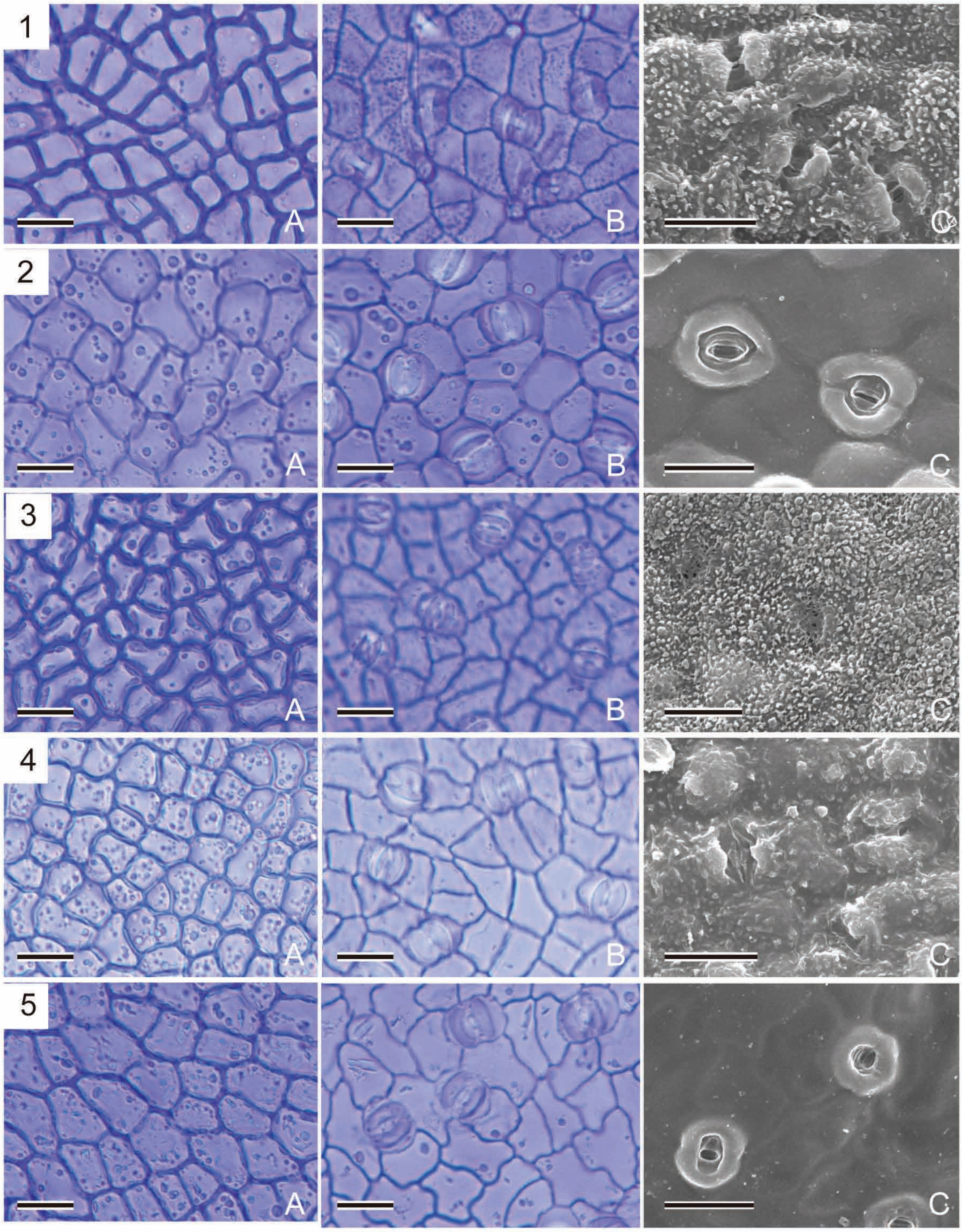
Species	Collection no.	Locality
C. amygdalina Nees	*Whitmore FRI 8675*	Peninsular Malaysia, Kluang Forest
C. amygdalina Nees	*Kochummen FRI 23111*	Peninsular Malaysia, Ginting Highland road
C. bracteolata Gamble	*Kamarudin FRI 31491*	Peninsular Malaysia, Kota Tinggi
C. chanthaburiensis Kosterm.	*Collins 1421*	Thailand, Si Racha
C. chanthaburiensis Kosterm.	*Kerr 17712*	Thailand, Chantaburi, Khao Kuap
C. concinna Hance	*Poilane 13181*	Vietnam, Cha-pa
C. costata Blume	*Corner 29289*	Peninsular Malaysia, Mawai-Jemaluang Rd.
C. densiflora Blume	*Kochummen FRI 16412*	Peninsular Malaysia, Fraser Hill
C. densiflora Blume	*Poilan 2026*	Laos, Sam Neua
C. diversifolia Blume	*Kiah 32356*	Peninsular Malaysia, Sungai Kayu
C. enervis Hook.f.	*Burkill 6567*	Peninsular Malaysia, Klang
C. enervis Hook.f.	*Cockburn FRI8312*	Peninsular Malaysia, Trengganu, Ulu Besut FR
C. ferrea Blume	*Ngadiman SFN 34754*	Peninsular Malaysia, Mawai
C. griffithiana Wight	*Damanhur FRI 36010*	Peninsular Malaysia, Teluk Kemang
C. hainanensis Merr.	*Poilane 7583*	Vietnam, Liên Chiêu
C. impressa Miq.	*Corner 36978*	Peninsular Malaysia, Sungai Sedili
C. impressa Miq.	*Ngadiman SFN 36835*	Peninsular Malaysia, Johor, Sungai Sedili
C. kurzii Hook.f.	*Lesmy FRI 35940*	Peninsular Malaysia, Linggiu-Sindora Forest
C. kurzii Hook.f.	*Corner 25972*	Peninsular Malaysia, Johor, Sungai Sedili
C. laevigata Blume	*Corner 28958*	Peninsular Malaysia, Sungai Berassau
C. laevigata Blume	*Chua et al. FRI 38578*	Peninsular Malaysia, Kelantan, Sungai Pergau
C. laevigata Blume	*Forster 27628*	Australia, (detailed locality unknown)*1
C. nana Kosterm.	*de Wilde & de Wilde 13003*	Sumatra, Atjeh
C. nana Kosterm.	*de Wilde & de Wilde 19186*	Sumatra, Near Camp Aceh
C. nitens (Blume) Koord. & Valeton	*Denny s.n.* (May 1953)	Peninsular Malaysia, Sungai Pelek
C. pallens Kosterm.	*Kerr 17963*	Thailand, Kao Sabap
C. pustulata Kosterm.	*Kerr 12496*	Thailand, Pak Sai
C. rugulosa Hook.f.	*Whitmore FRI 15760*	Peninsular Malaysia, Ulu Perak
C. sublanuginosa Kosterm.	*Poilane 377*	Cambodia, Montagne de l'Éléphant
C. sublanuginosa Kosterm.	*Collins 1975*	Thailand, Sriracha Forest
C. teysmanniana Miq.	*Kochummen KEP 99384*	Peninsular Malaysia, Ulu Gombak
C. tuanku-bujangii Kosterm.	*Rene et al. S. 63323*	Malaysia, Sarawak
C. tuanku-bujangii Kosterm.	*Yahud, Mahmud et al. S88321*	Malaysia, Sarawak, Gunung Murud
C. wrayi Gamble	*Nur SFN 32583*	Peninsular Malaysia, Cameron Highlands

*1 Sample was from outside of South-east Asia, but examined for comparison.

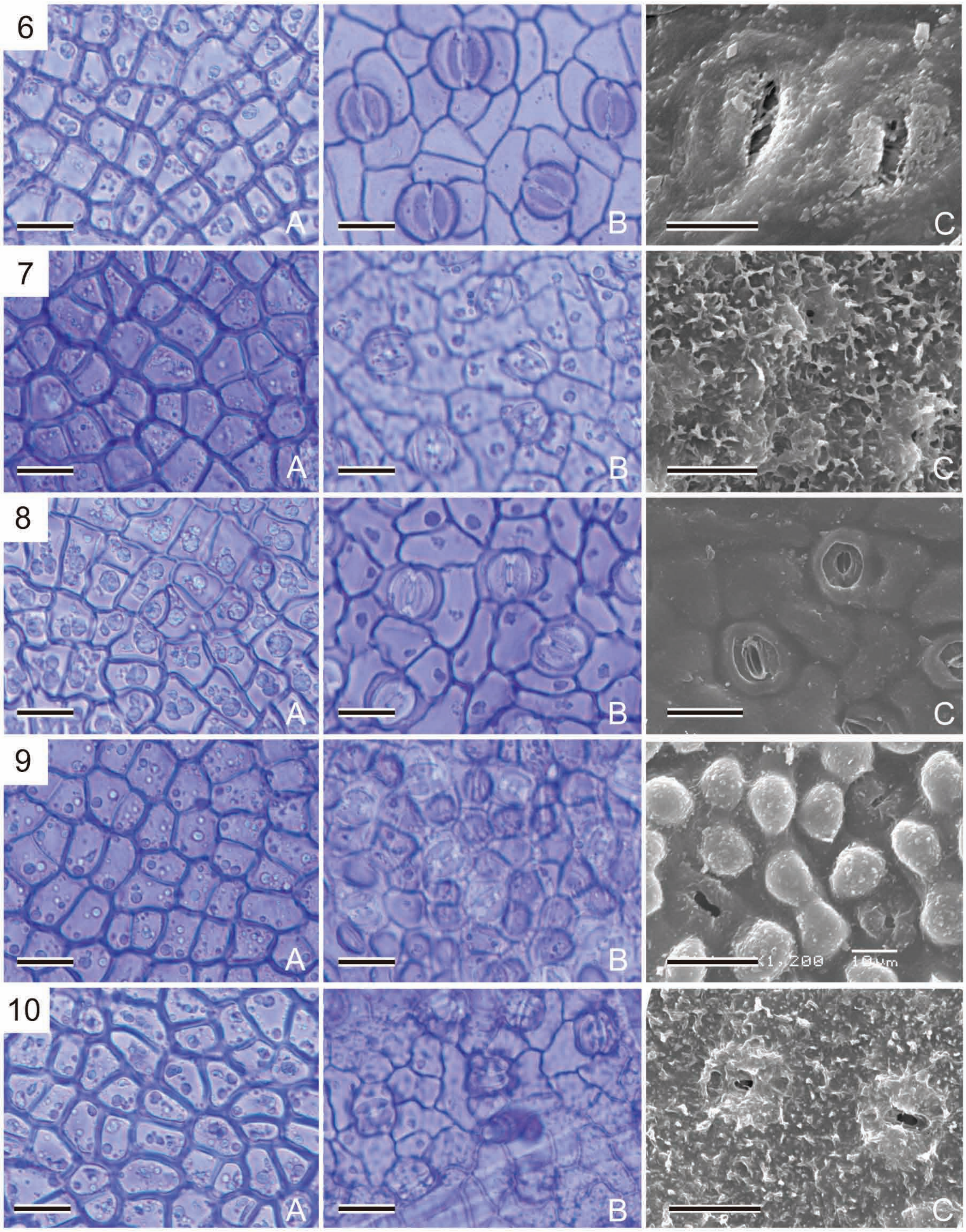
Results

The cuticular features in the *Cryptocarya* species studied are listed in Table 2 and shown in Figs. 1–26. They were consistent within each species for which two samples from different specimens were examined, except for the periclinal wall ornamentation on the abaxial surface in *C. kurzii* (see below).

The cuticular features differed between the adaxial and abaxial leaf surfaces. Those of the adaxial epidermis were more or less similar for all the species: i.e. the samples had smooth periclinal cell walls, smooth to beaded anticlinal cell walls, and lacked stomata. The only feature of the adaxial leaf surface that showed a certain amount of variation was the straightness of the anticlinal cell walls.

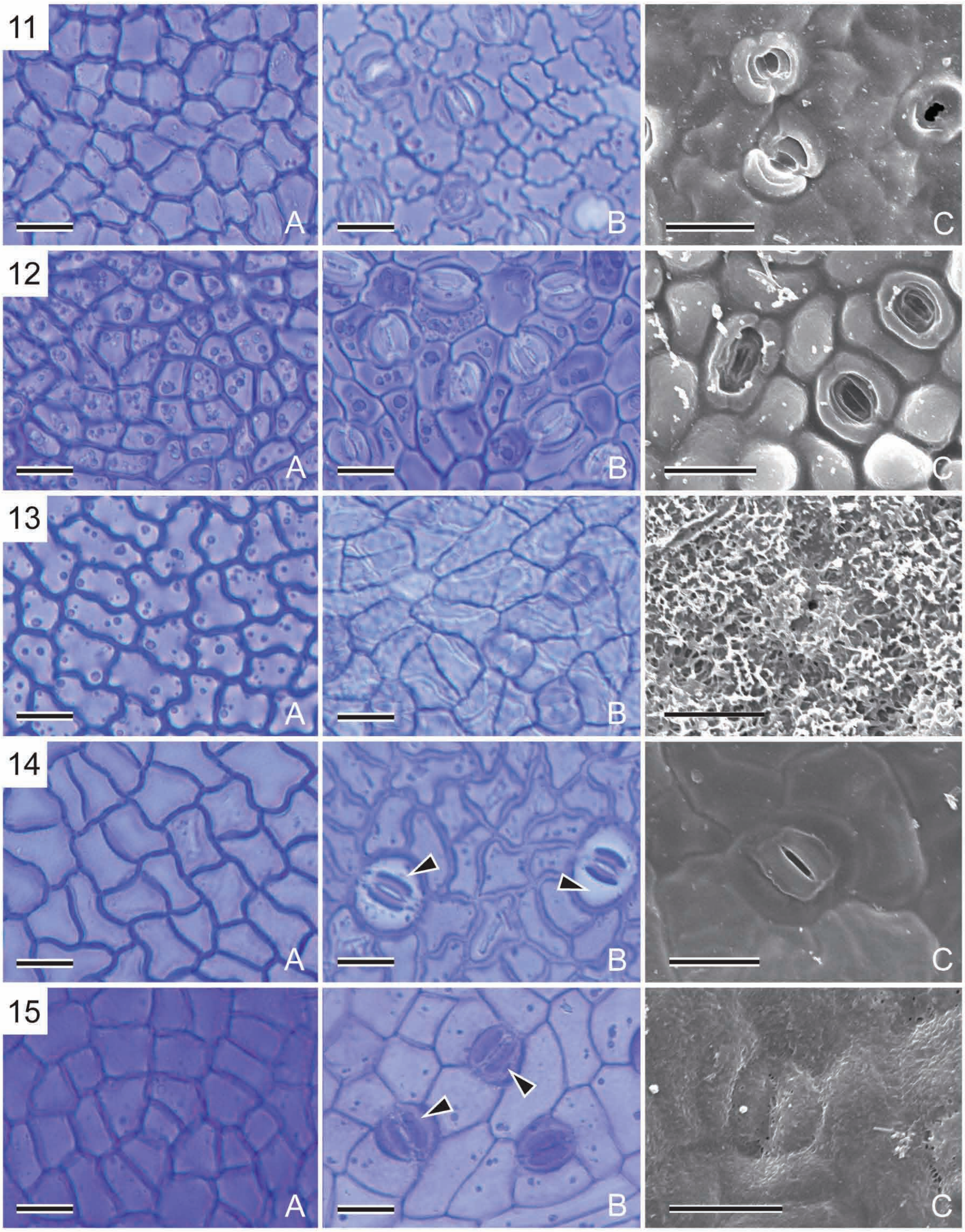


FIGURES 1–5. Optical micrographs of the adaxial cuticles (A), abaxial cuticles (B) and SEMs of the stomatal complex (C) of the *Cryptocarya* species.—1. *C. amygdalina*.—2. *C. bracteolata*.—3. *C. chanthaburiensis*.—4. *C. concinna*.—5. *C. costata*. Scale bars = 20 µm.



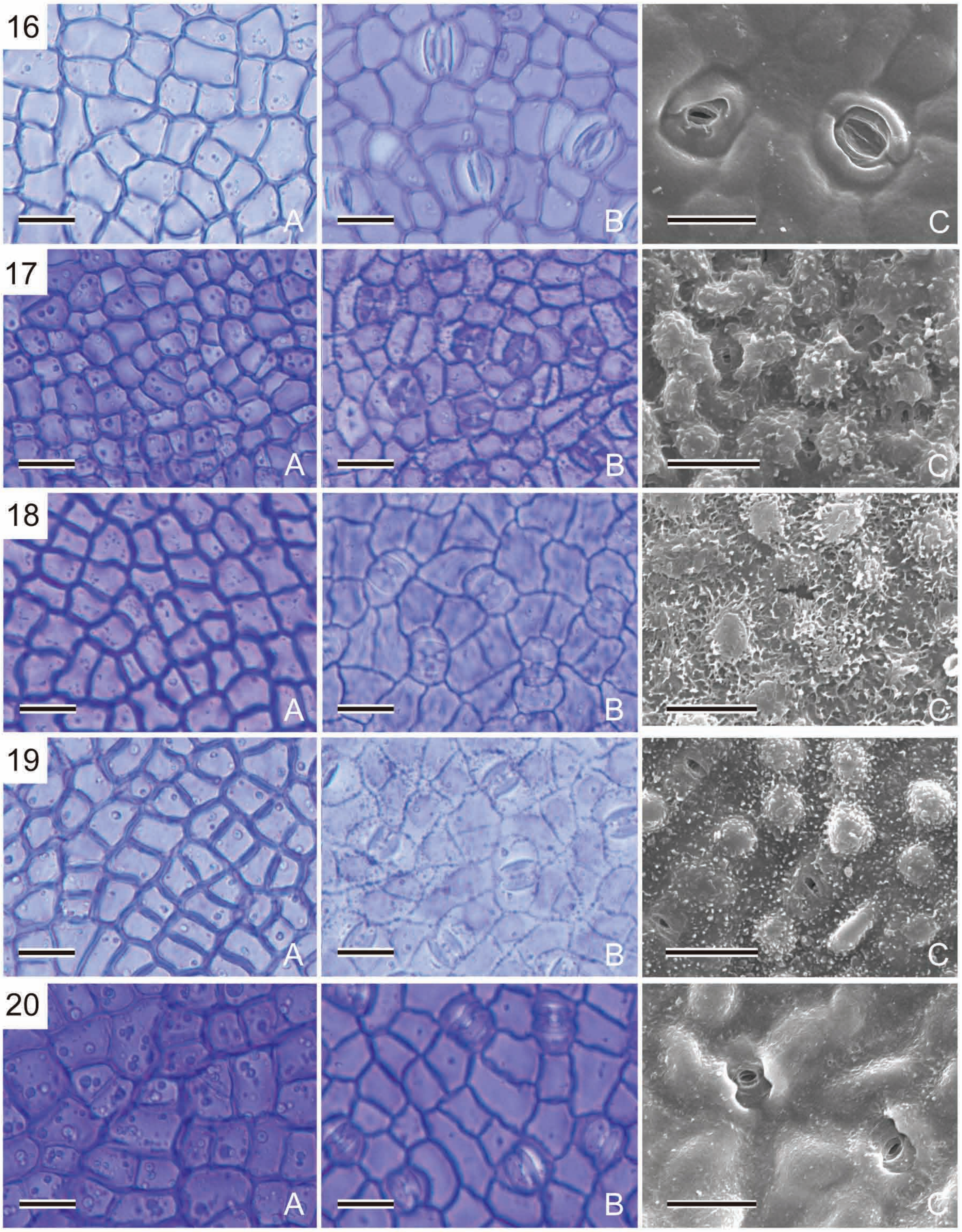
FIGURES 6–10. Optical micrographs of the adaxial cuticles (A), abaxial cuticles (B) and SEMs of the stomatal complex (C) of the *Cryptocarya* species.—6. *C. densiflora*.—7. *C. diversifolia*.—8. *C. enervis*.—9. *C. ferrea*.—10. *C. griffithiana*. Scale bars = 20 µm.

The epidermis of the abaxial leaf surface, on the other hand, showed several features that varied amongst the species. The periclinal cell walls were smooth in *C. bracteolata* (Fig. 2C), *C. costata* (Fig. 5C), *C. enervis* (Fig. 8C), *C. hainanensis* (Fig. 11C), *C. impressa* (Fig. 12C), *C. laevigata* (Fig. 14C), and *C. nitens* (Fig. 16C); somewhat rough or slightly granular in *C. densiflora* (Fig. 6C), *C. nana* (Fig. 15C), *C. sublanuginosa* (Fig. 20C), and *C. wrayi* (Fig. 23C); conspicuously granular in *C. amygdalina* (Fig. 1C), *C. chanthaburiensis* (Fig. 3C), *C. concinna* (Fig. 4C), *C. diversifolia* (Fig. 7C), *C. ferrea* (Figs. 9C), *C. griffithiana* (Fig. 10C), *C. kurzii* (Fig. 13C), *C. pallens* (Fig. 17C), *C. pustulata* (Fig. 18C), *C. rugulosa* (Fig. 19C), and *C. teysmanniana* (Fig. 21C). Those of *C. tuanku-bujangii* were covered with dense pubescence (Fig. 22B, C). Each sample of *C. ferrea* (Fig. 9C), *C. pallens* (Fig. 17C), *C. pustulata*



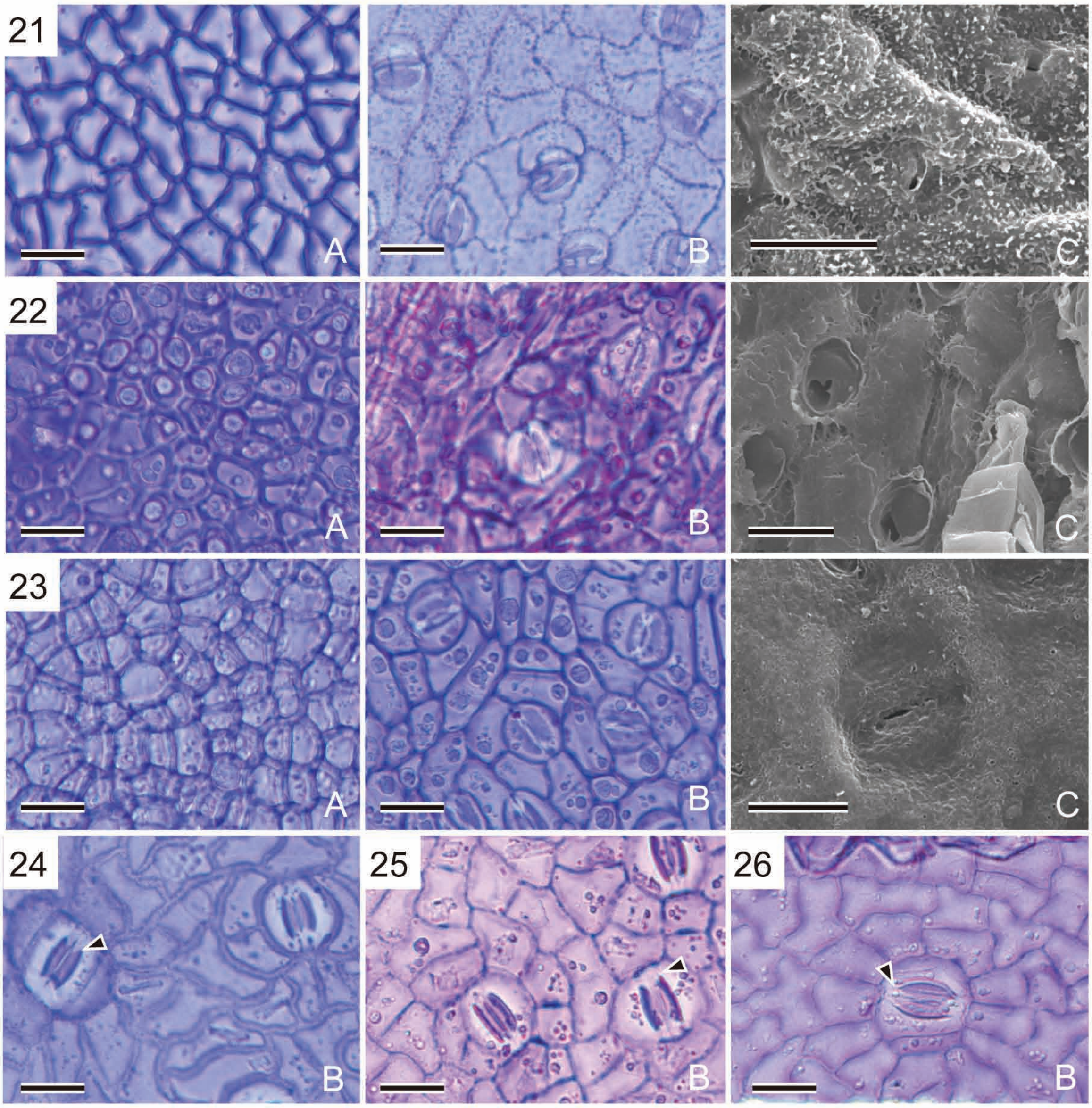
FIGURES 11–15. Optical micrographs of the adaxial cuticles (A), abaxial cuticles (B) and SEMs of the stomatal complex (C) of the *Cryptocarya* species.—11. *C. hainanensis*.—12. *C. impressa*.—13. *C. kurzii*.—14. *C. laevigata*.—15. *C. nana*. Arrows in Figs. 14B and 15B indicate unstained and darkly stained subsidiary cells, respectively. Scale bars = 20 µm.

(Fig. 18B, C), *C. rugulosa* (Fig. 19B, C), and both samples of *C. impressa* (Fig. 12B, C) had some abaxial epidermal cells with their periclinal walls protruding or papillose (only central part of the cell protruding), but one sample of *C. kurzii* (*Lesmy FRI 35940)* had the cells not protruding (Fig. 13B, C), while another sample (*Corner 25972*) had several cells (not all the cells, though) protruding. The anticlinal cell walls were usually straight to moderately curved, but sometimes undulate in *C. costata* (Fig. 5B), *C. hainanensis* (Fig. 11B), and *C. laevigata* (Fig. 14B). As for the ornamentation, the anticlinal walls were similar to one another among the various species and were more or less beaded (regularly uneven; sensu Christophel *et al*. 1996) to quite smooth.



FIGURES 16–20. Optical micrographs of the adaxial cuticles (A), abaxial cuticles (B) and SEMs of the stomatal complex (C) of the *Cryptocarya* species.—16. *C. nitens.*—17. *C. pallens.*—18. *C. pustulata.*—19. *C. rugulosa.*—20. *C. sublanuginosa.* Scale bars = 20 µm.

The stomatal complex, which consists of a stoma and a pair of subsidiary cells, was found only on the abaxial epidermis and showed some variation amongst the species when viewed under a light microscope. For instance, although the pairs of subsidiary cells usually stained as darkly as the surrounding epidermal cells, those of *C. nana* were conspicuously darker than the surroundings (Fig. 15B), and those of *C. laevigata*, were scarcely stained (Fig. 14B). The lower stomatal ledges were usually butterfly-shaped, darkly stained, with roundish edges, although in *C. laevigata* the ledges were lip-shaped (Fig. 14B). The lip-shaped ledges in *C. laevigata* appeared to have angular edges



FIGURES 21–26. Optical micrographs of the adaxial cuticles (A), abaxial cuticles (B) and SEMs of the stomatal complex (C) of the *Cryptocarya* species.—21. *C. teysmanniana*—22. *C. tuanku-bujangii*.—23. *C. wrayi*.—24. *C. laevigata* (*#Corner 28958* from Malaysia).—25. *C. laevigata* (*#Chua et al. FRI 38578* from Malaysia).—26. *C. laevigata* (*#Forester* from Australia). Arrows in Figs. 24, 25, and 26 indicate angular edges of the stomatal ledges. Scale bars = 20 μm.

when the edges were focused on (see arrows in Figs. 24, 25, 26). Under SEM, the surface appearance of the stomatal complex showed wider variation: it usually had a protruding dome-shape, in which the wall of the subsidiary cell facing the slit is convex in the center (Fig. 27A), in *C. amygdalina* (Fig. 1C), *C. chanthaburiensis* (Fig. 3C), *C. concinna* (Fig. 4C), *C. diversifolia* (Fig. 7C), *C. ferrea* (Fig. 9C), *C. griffithiana* (Fig. 10C), *C. kurzii* (Fig. 13C), *C. pallens* (Fig. 17C), *C. pustulata* (Fig. 18C), *C. rugulosa* (Fig. 19C), *C. sublanuginosa* (Fig. 20C), and *C. teysmanniana* (Fig. 21C); protruding as a circular rim with the circle broken at both ends of the stomatal slit (Fig. 27B) in *C. bracteolata* (Fig. 2C), *C. costata* (Fig. 5C), *C. enervis* (Fig. 8C), *C. hainanensis* (Fig. 11C), *C. impressa* (Fig. 12C), and *C. nitens* (Fig. 16C); slightly depressed (Fig. 27C) in *C. densiflora* (Fig. 6C), *C. nana* (Fig. 15C), *C. tuanku-bujangii* (Fig. 22C), and *C. wrayi* (Fig. 23C); and scarcely protruding except for the rim of the complex (Fig. 27D) in *C. laevigata* (Fig.14C). Species in which the surface protrudes in a dome-shape sometimes have the surface protruding in reniform rims (sensu Nishida & van der Werff 2007), as shown in Fig. 4C (the right stoma in the figure).

TABLE 2. Cuticular features of the *Cryptocarya* species in Peninsular Malaysia, Thailand and Indo-China

Species	Adaxial epidermal cell walls			Abaxial epidermal cell walls			Stomatal complex			Figure no.
	Periclinal	Anticlinal		Periclinal	Anticlinal		Stainability	Lower ledge shape	Surface appearance	
	Ornamentation	Ornamentation	Straightness	Ornamentation	Ornamentation	Straightness				
C. amygdalina	smooth	beaded	straight to curved	granular	smooth-beaded	straight to curved	ST	BU	PD	1
C. bracteolata	smooth	smooth-beaded	straight to curved	smooth	smooth-beaded	straight to curved	ST	BU	PC	2
C. chanthaburiensis	smooth	beaded	straight to curved	granular	beaded	straight to curved	ST	BU	PD	3
C. concinna	smooth	smooth-beaded	straight to curved	granular	beaded	straight to curved	ST	BU	PD	4
C. costata	smooth	beaded	straight to curved	smooth	smooth-beaded	undulate	ST	BU	PC	5
C. densiflora	smooth	smooth-beaded	straight to curved	slightly granular	smooth	straight to curved	ST	BU	DE	6
C. diversifolia	smooth	smooth-beaded	straight to curved	granular	smooth-beaded	straight to curved	ST	BU	PD	7
C. enervis	smooth	smooth-beaded	straight to curved	smooth	smooth-beaded	straight to curved	ST	BU	PC	8
C. ferrea	smooth	smooth-beaded	straight to curved	granular and papillose	smooth-beaded	straight to curved	ST	BU	PD	9

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TABLE 2. (continued)

Species	Adaxial epidermal cell walls			Abaxial epidermal cell walls			Stomatal complex			Figure no.
	Periclinal	Anticlinal		Periclinal	Anticlinal		Stainability	Lower ledge shape	Surface appearance	
	Ornamentation	Ornamentation	Straightness	Ornamentation	Ornamentation	Straightness				
C. griffithiana	smooth	smooth-beaded	straight to curved	granular	smooth-beaded	curved	ST	BU	PD	10
C. hainanensis	smooth	smooth-beaded	straight to curved	smooth	beaded	undulate	ST	BU	PC	11
C. impressa	smooth	smooth-beaded	straight to curved	smooth and protruding	smooth-beaded	straight to curved	ST	BU	PC	12
C. kurzii	smooth	beaded	undulate	granular (partly protruding)	beaded	straight to curved	ST	BU	PD	13
C. laevigata	slightly granular	smooth-beaded	curved	smooth-beaded	smooth-beaded	undulate	UN	LI	NP	14
C. nana	smooth	smooth-beaded	straight to curved	slightly granular	smooth	straight to curved	DA	BU	DE	15
C. nitens	smooth	smooth-beaded	straight to curved	smooth	smooth	straight to curved	ST	BU	PC	16
C. pallens	smooth	smooth-beaded	straight to curved	granular and papillose	smooth-beaded	straight to curved	ST	BU	PD	17
C. pustulata	smooth	smooth-beaded	straight to curved	granular and papillose	smooth-beaded	straight to curved	ST	BU	PD	18

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TABLE 2. (continued)

Species	Adaxial epidermal cell walls			Abaxial epidermal cell walls			Stomatal complex			Figure no.
	Periclinal	Anticlinal		Periclinal	Anticlinal					
	Ornamentation	Ornamentation	Straightness	Ornamentation	Ornamentation	Straightness	Stainability	Lower ledge shape	Surface appearance	
C. rugulosa	smooth	smooth-beaded	straight to curved	granular and papillose	smooth-beaded	straight to curved	ST	BU	PD	19
C. sublanuginosa	smooth	smooth-beaded	straight to curved	slightly granular	smooth-beaded	straight to curved	ST	BU	PD	20
C. teysmanniana	smooth	smooth-beaded	straight to curved	granular	beaded	straight to curved	ST	BU	PD	21
C. tuanku-bujangii	smooth	smooth-beaded	straight to curved	densely pubescent	smooth-beaded	straight to curved	ST	BU	DE	22
C. wrayi	smooth	smooth-beaded	straight to curved	slightly granular	smooth-beaded	straight to curved	ST	BU	DE	23

Abbreviations: DA = darkly stained, ST = stained as epidermis, UN = unstained (in stainability); BU = butterfly-shaped, LI = Lip-shaped (in stomatal ledge shape); DE = depressed, NP = not protruding except for the rim of the complex, PC = protruding in a circular rim with the circle broken at both ends of the stomatal slit, PD = protruding in a dome-shape with the slit line on the top being convex toward the center (in stomatal surface appearance).

Discussion

The grouping value of epidermal features in *Cryptocarya*.—We considered the epidermal features of the stomatal complex, i.e., the shape of the lower stomatal ledges observed under light microscope and the appearance of the surface of the stomatal complex observed under SEM, as the most important ones for grouping the species, since these features have been used previously to identify or classify other species of Lauraceae, e.g., *Beilschmiedia scintillans* (Nishida & van der Werff 2007), *Yasunia* van der Werff (van der Werff & Nishida 2010: 494), and *Syndiclis* (Yang *et al.* 2012). These features also have been shown to be correlated with the molecular phylogeny in a study on a complex of *Ocotea* Aublet (1775b: 780, t. 310) (Nishida & van der Werff 2011), although the comparison of the features and the molecular phylogeny is still preliminary and more verification is needed to clarify the correlations.

We additionally used one of the ornamentation features of the periclinal epidermal cell wall surface, i.e., smooth or granular, as a discriminating feature. In a previous study, by Nishida & van der Werff (2011), the value of this character could not be evaluated in relation to the molecular phylogeny because there was no variation among the species examined then. However, it has been found useful in distinguishing some laurel species (Christophel *et al.* 1996), it was used to discriminate between some neotropical species of *Beilschmiedia* by Nishida & Christophel (1996), and was also used to recognize the close relationship between *Yasunia* and some species of *Beilschmiedia*, i.e., *B. angustifolia* Kostermans (1938: 875), *B. curviramea* Kostermans (1938: 853), *B. linharensis* Sach.Nishida & van der Werff (Nishida 1999: 681), and *B. rigida* (Mez) Kostermans (1938: 856) (van der Werff & Nishida 2010). However, we deflate the value of another feature of the ornamentation, i.e., differences in the cell protrusion (almost flat and not protruding, protruding, or papillose), because the feature was inconsistent within one of the species we examined, and a certain gradation in the feature was seen among the species, between slightly and strongly protruding surfaces.

The other features listed in the Table 2 showed some variation among the species, but we consider them also less important. For the straightness and ornamentation of the anticlinal cell walls, some extreme character states, such as undulate, sinuous or branched walls, could be used to recognize groups, if we considered their congruence with molecular phylogeny (Nishida & van der Werff 2011) or with the groupings recognized by the other epidermal characteristics (Nishida & Christophel 1996, van der Werff & Nishida 2010). However, the usage of the features in the anticlinal cell walls still needs more evaluation, since the comparison with molecular phylogeny (Nishida & van der Werff 2011) is preliminary, and a certain variation in the features has been reported (Wilkinson 1979). Among the species of *Cryptocarya* studied here, some variation in the straightness of the anticlinal walls was observed (e.g., Figs. 5B, 11B, 14B). Less unusual character states, such as beaded walls, were ignored for grouping purposes by us because intermixed states within a species are known to exist (e.g., Nishida & van der Werff 2011, 2014). We have also listed stainability of the subsidiary cells of the stoma (see arrows in Figs. 14B, 15B) in Table 2, although this feature has not been evaluated for its consistency or usefulness.

Groupings of the species of *Cryptocarya* from Peninsular Malaysia, Thailand and Indo-China based on features of the epidermis.—Based on our results, we recognized four groups among the *Cryptocarya* species studied, and further divided Group 2 into two subgroups (Table 3).

Among the four groups recognized by the cuticular features, the most distinctive is Group 4, which consists of only one species, *C. laevigata*. The appearance of the surface of its stomatal complex is distinctive, since it is flat or slightly depressed with the outer rim of the complex slightly protruding (Fig.14C, Fig. 27D). This species is also unique in having lip-shaped lower stomatal ledges (Fig. 14B), whereas all the other species we examined have butterfly-shaped ledges. Scarcely stained subsidiary cells are also distinctive under the light microscope (see arrows in Fig. 14B), although the significance of this character state has not been evaluated.

Groups 1, 2 and 3 share similar butterfly-shaped stomatal ledges, but are discriminated by the appearance of the surface of their stomatal complexes as observed under SEM. In Group 1 it is slightly protruding in a dome-shape with the slit line on the top convex toward the center (Figs. 1C, 3C, 4C, 7C, 9C, 10C, 13C, 17C, 18C, 19C, 20C, and 21C). In Group 2, it is protruding in a circular rim with the circle broken at both ends of the stomatal slit (Figs. 2C, 5C, 8C, 11C, 12C, and 16C), and in Group 3 it is slightly depressed (Figs. 6C, 15C, 22C, and 23C). These three groups differ from one another also in the ornamentation of the periclinal walls of the abaxial epidermis, which is conspicuously granular in Group 1, smooth in Group 2, and slightly granular in Group 3. The granular ornamentation in Groups 1 and 3 can be attributed not to the cutinized epidermal cell walls but to epicuticular wax on the epidermis. However, we used this feature for grouping purposes because it usually remains constant throughout the observational procedure, and it has been shown to be useful in recognizing some laurel taxa in previous studies (e.g., Christophel *et al.* 1996, Nishida & van der Werff 2014).

Group 2 was divided into two subgroups based on the straightness of the anticlinal epidermal cell walls. *Cryptocarya costata* and *C. hainanensis* in Group 2b share most of the cuticular features with the species in Group 2a, but their abaxial epidermis has the anticlinal cell walls often undulate (Figs. 5B and 11B), which is an exceptional character state among the species studied here.

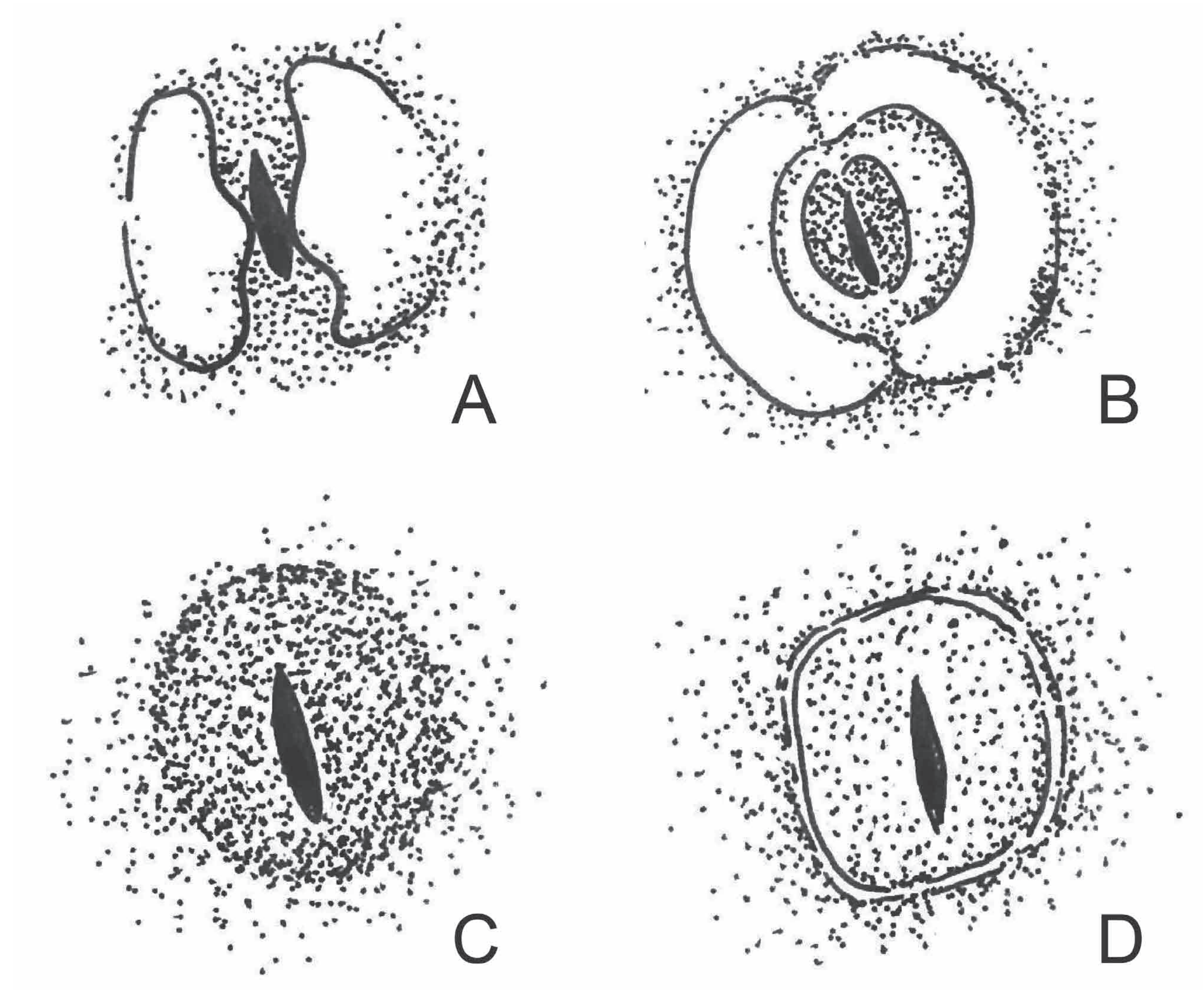
TABLE 3. Groups of the *Cryptocarya* species in Peninsular Malaysia, Thailand and Indo-China based on cuticular features.

Group	Subgroup	Abaxial epidermis			Stomatal complex		Species
		Periclinal wall ornamentation	Anticlinal wall straightness	Stainability	Lower ledge shape	Surface appearance	
1		granular, or granular and protruding to papillose	straight to curved	stained as epidermis	butterfly-shaped	protruding in a dome-shape with the slit line on the top being convex toward the center	*C. amygdalina*, *C. chanthaburiensis*, *C. concinna*, *C. diversifolia*, *C. ferrea*, *C. griffithiana*, *C. kurzii*, *C. pallens*, *C. pustulata*, *C. rugulosa*, *C. sublanuginosa*, *C. teysmanniana*
2	2a	smooth	straight to curved	stained as epidermis	butterfly-shaped	protruding in a circular rim with the circle broken at both ends of the stomatal slit	*C. bracteolata*, *C. enervis*, *C. impressa*, *C. nitens*
	2b	smooth	undulate	stained as epidermis	butterfly-shaped	protruding in a circular rim with the circle broken at both ends of the stomatal slit	*C. costata*, *C. hainanensis*
3		slightly granular or pubescent	straight to curved	stained as epidermis or darkly stained	butterfly-shaped	slightly depressed	*C. densiflora, C. nana, C. tuanku-bujangii, C. wrayi*
4		smooth	undulate	unstained	lip shaped, fusiform slit	scarcely protruding except for the rim of the complex	*C. laevigata*

Comparison of cuticular and the other morphological characters among the species of *Cryptocarya* from Peninsular Malaysia, Thailand and Indo-China.—Although no other morphological characters divide the *Cryptocarya* species studied here in the same way as the cuticular features do, some macro-morphological characters are concordant with the groups based on cuticles. Group 3 is easily defined by leaf morphology, because all its members have triplinerved leaf venation with the veins becoming faint halfway up the blades. *Cryptocarya laevigata*, the only member of Group 4, also has triplinerved leaves, but the veins are prominent all the way to the leaf apex. Members of Groups 1 and 2 share similar pinninerved leaves, with no macro-morphological characters discriminating between these groups, although the subgroup Group 2a can be defined as having globose fruits, which is a rare character among *Cryptocarya* species from this region. None of the other groups, however, is supported by macro-morphological, ecological or biogeographical characters. Given the lack of macro-morphological characters to group species of *Cryptocarya* in general, this is not surprising. The informal groups for Peninsular Malaysia and Thailand (de Kok 2015; de Kok, in press) are based on two morphological characters and their geographical distribution, which is a weak basis for a classification. Our grouping using cuticular features should be further evaluated by using other characters or molecular phylogenetic results before being applied to the taxonomy of *Cryptocarya*.

Comparison of cuticular features between the species of *Cryptocarya* from Peninsular Malaysia, Thailand and Indo-China and congeners from other countries.—When we compared the cuticular features of the *Cryptocarya* species from South-east Asia to those of congeners from elsewhere, we recognized some characters were shared between some of the species studied here and some from earlier studies.

Firstly we compared cuticles of the same species from different regions. Although most of the *Cryptocarya* species studied here are restricted to Thailand, Indo-China and the Sunda Plateau, *C. densiflora* and *C. laevigata* occur also in Australia. The cuticles of Australian Lauraceae are, however, known only by the text descriptions and black and white photos taken under a light microscope by Christophel & Rowett (1996). This restricts the comparisons we can make, because one of the most important characters, the appearance of the stomatal complex under SEM, cannot



FIGURES 27. Appearance of the stomatal surface for the *Cryptocarya* species.—A. Protruding in a dome-shape with the slit line on the top being convex toward the center (PD).—B. Protruding in a circular rim with the circle broken at both ends of the stomatal slit (PC).—C. Depressed (DE).—D. Not protruding except for the rim of the complex (NP).

be used. As far as possible, we compared the texts and pictures available from this study with the Australian samples, and found some congruence and discrepancies. The Malaysian sample of *C. densiflora* shared several similar cuticular features with the Australian one, including curved anticlinal walls on the abaxial epidermis, narrowly elliptic pairs of subsidiary cells, and wide butterfly-shaped stomatal ledges that covered most of the subsidiary cells. However, the anticlinal walls on the adaxial surface in the Malaysian sample were almost straight (angular) walls whereas in the Australian one they were undulate. For *C. laevigata*, both our Malaysian samples and the Australian one in Christophel & & Rowett (1996) had similar anticlinal walls that are almost straight on the adaxial surface but undulate on the abaxial surface. The shapes of the stomatal ledges were, however, differently described between ours and theirs: ours were categorized as lip-shaped, whereas theirs were described as "butterfly-shaped". We are aware that the straightness of anticlinal walls, which differed between Malaysian and Australian *C. densiflora*, can vary to some degree within a single species (Nishida & van der Werff 2007); however, we have not previously been aware that the shape of the stomatal ledge can vary within a species, as it apparently does in *C. laevigata*. We therefore compared cuticles of two Malaysian specimens and one Australian specimen of *C. laevigata* by ourselves, and found that the stomatal ledges appeared to have angular edges when we focused the camera on the edge of the lower ledges (Figs. 24, 25, 26), which have some resemblance with those in the picture of Christophel & Rowett (1996). The width of the stained ledges was, however, larger in the Australian samples (both of ours and theirs) compared to the Malaysian samples. We assume that cuticles of Malaysian samples and Australian samples actually share more or less common features, but the widths of the ledges have some variation, and the range of the terminology we used (whether the ledge shape of *C. laeviata* is included in "butterfly-shaped" or not) may be different from the one Christophel & Rowett (1996) used. We need to conduct further studies to determine whether this discrepancy in the description of stomatal ledge shape is really attributable to infraspecific variation in this cuticular character, or in fact reflects some other cause, such as a difference in taxonomic concepts or in usages of terminology. Especially, terminology should be revised, now that the number of examined species has increased and more diversity has been recognized in the morphology since Christophel & Rowett (1996) started to study the cuticles of Lauraceae.

As for the remaining species, we found certain similarities between our samples and the Australian cuticles. We tried to compare our groups with those for the Australian species recognized by Christophel & Rowett (1996), but failed to match them because the latter groupings were determined mainly by the straightness of anticlinal walls, which we do not consider the most important character. We therefore compared our groups with each Australian species in turn.

Firstly, Groups 1, 2a, 2b, and 3 share similar butterfly-shaped stomatal ledges with many of the Australian species. Our Group 1 is similar to *C. brassii* Allen (1942: 137), *C. leucophylla* B. Hyland (1989: 192), *C. mackinnoniana* von Mueller (1866: 169), *C. melanocarpa* B. Hyland (1989: 196), *C. putida* B. Hyland (1989: 203) and *C. vulgaris* B. Hyland (1989: 212) in having granular periclinal walls on the abaxial epidermis. Although their similarity is not exclusive, species of our Group 2b are similar to *C. meisneriana* Frodin (1976: 223) by having somewhat undulate anticlinal walls on the abaxial epidermis.

As for the surface of the stomatal complex, we recognized some similarities between our groups and a few Australian taxa, e.g., stomatal surface sometimes protruding in reniform shape seen in our Group 1 is similar to that of *C. mackinnoniana*, and the protruding in a circular rim of our Group 2a is similar to that of *C. hypospodia* von Mueller (1866: 170). Summarizing these comparisons suggests that our Group 1 shares certain common features with *C. mackinnoniana* (and maybe *C. brassii*), and our Group 2b with *C. hypospodia*.

In his account of the Australian species of *Cryptocarya*, Hyland (1989) placed *C. mackinnoniana, C. brassii* and *C. putida* together in his Group 5 on the basis of the adult leaves sharing strongly reticulate venation and fetid flowers. While he placed *C. meisneriana* with *C. laevigata* in his Group 2 on the basis of sharing a ribbed endocarp, *C. hypospodia* and *C. melanocarpa* were placed in his Group 1 on the basis of having ruminate cotyledons and fetid flowers. *Cryptocarya leucophylla* and *C. vulgaris* comprise his Group 7 because they have fetid flowers and leaves that are white or glaucous on the underside. It is difficult to make sense of these groupings and this is probably mainly due to the way that Hyland has put them together, based partly on characters and partly on intuition (Hyland 1989). However, some patterns are clear: our Groups 1 and 2a, b have pinninerved leaves, and *C. brassii, C. hypospodia*, *C. leucophylla*, *C. mackinnoniana, C. melanocarpa, C. meisneriana, C. putida* and *C. vulgaris* also have pinninerved leaves. Our Group 2a is distinct by having globose fruits, and *C. hypospodia* also has globular fruits. Further comparison between the species we have studied and these Australian species, by observing the Australian cuticles under SEM, would be helpful to clarify if any groupings by cuticular features cut across the regions.

For Malagasy *Cryptocarya*, the cuticles of three species, *C. crassifolia* Baker (1883: 241), *C. dealbata* Baker (1883: 241), and *C. thouvenotii* (Danguy 1920: 550) Kostermans (1939: 114) were examined by Nishida & van der Werff (2007). Our Malaysian and Thai Group 1 has the surface of the stomatal complex sometimes protruding in a reniform shape, which was also recognized in the three Malagasy species. Besides this, our Groups 1, (as well as 2a, 2b and 3, though) share butterfly-shaped stomatal ledges with the three Malagasy taxa. However, our Group 1 differs from the Malagasy species in the degree of protrusion in the stomatal complex, which is much lower than that of the Malagasy material; and in the ornamentation of the periclinal walls of abaxial epidermis, which is granular in our groups but smooth in the Malagasy species. In summary, there is no species of *Cryptocarya* sharing overall similarities in the cuticular features between Malaysia and Madagascar.

Cuticular features of the Neotropical *Cryptocarya* have been studied by a few researchers including Petzold (1907) and Moraes (2007). Petzold (1907) reported that the abaxial epidermis of several species had undulated cell walls, which might resemble those of our Group 2b and Group 4. However, the stomatal complex of Brazilian *Cryptocarya* appeared depressed according to him, which should differ from the protruding complex of our Group 2b or almost flat complex of our Group 4. As for the stomatal features, the description about strongly thickened subsidiary cells by Petzold (1907) might suggest several Brazilian *Cryptocarya* species have butterfly-shaped stomatal ledges, as many of the species that we examined. Recently, Moraes (2007) provided clear views of the leaf surfaces of *C. mandioccana* Meissner (1864: 75), which indicates that the species have several cuticular features (undulate anticlinal cell walls on the adaxial epidermis, somewhat granular periclinal cell walls on the abaxial epidermis, and butterfly-shaped stomatal ledges) in common with our species *C. kurzii*. Further studies of the Neotropical *Cryptocarya* species would be promising to improve our understanding of cuticular features of the genus.

Comparison of the cuticular features of *Cryptocarya* species from Peninsular Malaysia, Thailand and Indo-China with those of other genera.—When we compared the cuticular features we found for the *Cryptocarya* species studied here to those of other laurel genera, we confirmed that no features occurred exclusively in our species or in *Cryptocarya* in general, but many of them are in fact seen sporadically in several genera of the family. For example, butterfly-shaped stomatal ledges are common in *Cryptocarya* but have been reported also for *Beilschmiedia* (Nishida & Christophel 1999), *Ocotea*, *Aniba* Aublet (1775a: 327), *Dicypellium* Nees & Mart. in Nees (1833: 14), *Kubitzkia* van der Werff (1986: 165), *Paraia* Rohwer, H.G. Richter & van der Werff (1991: 392), and *Licaria* Aublet (1775a: 313) (Nishida & van der Werff 2011). Reniform protrusions of the surface of the stomatal complex have rarely been seen outside *Cryptocarya*, but have been reported for *Alseodaphne insignis* Gamble (1910b: 221) and *A. oblanceolata* (Merril 1929: 84) Kostermans (1968: 292) (Nishida & van der Werff 2014). Although a combination of cuticular features, including the ornamentation of the periclinal walls of the epidermal cells, the type of stomatal ledges, and the appearance of the surface of the stomatal complex, could narrow down the number of species that share resemblances in cuticle across the genera, it still cannot discriminate one genus from another. Our Group 2b, for instance, has almost the same combination of characters as *Ocotea rhynchophylla* (Meissner 1864: 155) Mez (1889: 241) (Nishida & van der Werff 2011).

Conclusion

Based on cuticular features, especially the ornamentation of the periclinal walls of the abaxial epidermal cells, the shape of the stomatal ledges, and the appearance of the stomatal complex surface, we recognized four groups and two subgroups in the *Cryptocarya* species studied. Groups 3 and 4 coincided very well with the triplinerved species of *Cryptocarya*, while the species of Groups 1 and 2 have pinnate leaf venation. Some of the species studied share certain cuticular similarities with a few Australian congeners, and observations of the Australian cuticles under SEM would be helpful for further comparison. No cuticular feature, however, is exclusive in the genus across the regions discussed here, and even combinations of features can be found in other Lauraceae genera. Cuticular features, therefore, are more likely to be useful in the taxonomy of the Lauraceae for the recognition of groups within a genus, recognizing the possibility that they might have evolved in parallel in different genera.

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