



Taxonomic placement of four confusable *Crepidium* species (Orchidaceae, Malaxidinae) based on macro-and micro-morphological analyses, including a note on two new records to Peninsular Malaysia

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Abstract

Crepidium amplexens and *Crepidium lowii* are reported as two newly recorded *Crepidium* species belong to sect. *Commelinodes* from Peninsular Malaysia. The taxonomic affinity is discussed and validated involving another two of their complexes, *Crepidium micranthum* and *Crepidium rheedei* subsp. *rheedei*, to which they share some similar characteristics of the leaves and flowers. The comparative study was conducted based on a comprehensive description and clear photographic evidence of the macro-morphology and surface micro-morphology of the labellar and gynostemium parts. This paper emphasizes the usefulness of diversity and distribution of ultrastructures and epicuticular sculpturing of the reproductive parts in delimiting the confusable and sympatric *Crepidium* species, and a brief note on the nectar or reward secretion in the genus with inference on the ecological adaptation and pollination strategies. Macro-morphologically, *C. amplexens* differs from *C. lowii* in having the leaves smaller, greenish and widely ovate. Individually, both species can be differentiated from *C. micranthum* based on the smaller flower and shorter labellum auricles, and inconspicuous gynostemium stelia. Micro-morphologically, *C. amplexens* is also distinguishable from *C. lowii* by having different diversity and distribution of the epicuticular ornamentation and papillae on the labellum and gynostemium. Also, amongst the four studied species, only *C. lowii* has nectarostomata, occurring on the fovea or nectary.

Keywords: Physio-ecology, gross morphology, new record, SEM, taxonomy, Terengganu, ultrastructure

Introduction

Crepidium Blume (1825) is a genus of orchids encompassing over 250 species occurring in Southeast Asia, Australasia and the Pacific Islands (Margońska, 2005a, 2005b, 2018). In Malaysia, *Crepidium* mostly occurs as terrestrial or lithophyte, but rarely epiphyte, distributed from lowland to montane forests of 1500 m elev. (Go *et al.*, 2009; Go *et al.* 2015; Besi *et al.*, 2019). Diagnostic features of these orchids are leaves in a whorl of 4–5 or 11, greenish purple or bronzed or dark purple, thin, more or less elongate, plicate, at least slightly oblique basally; inflorescence always terminal, erect, bear many small flowers with floral bracts always deflexed when flowers are mature (Seidenfaden & Wood, 1992; Comber, 2001; Go *et al.*, 2015; Margońska, 2018). Flowers are non-resupinate whose colour usually changes with age. The labellum 3-lobed and roughly hippocrepiform or horseshoe-shaped, which the side lobes are separated from the mid lobe with prominent and free triangular auricles that usually extending beyond the gynostemium (or column) base, and basally with chambered fovea or nectary (Comber, 2001). The gynostemium at least twice as long as the anther with stelia erect, exceeding the tip of the cordate anther, rostellum erect and thin, and stigma always opening apically in a deep cavity (Margońska *et al.*, 2012). Eleven species are known from Peninsular Malaysia (Go *et al.*, 2009; Ong *et al.*, 2017), whereas a total of 38 species are recorded for Borneo (Govaerts *et al.*, 2020). Three sections are recognised within genus *Crepidium*: sect. *Crepidium* Blume, sect. *Commelinodes* (Schltr.) Szlach. and sect. *Hololobus* (Schltr.) Marg. (Margońska, 2018).

While working on the diversity and conservation of Orchidaceae inhabiting the disturbed forests in Terengganu, Malaysia, we encountered several confusable and sympatric *Crepidium* species displaying complex structure of the leaves and flowers (Besi *et al.*, 2019). As this genus diversity is considerably low in Peninsular Malaysia, these species complexes were at first grouped as ‘*Crepidium micranthum* species complexes’ based on the floral characters alone. After almost two years of a comparative botanical investigation based on the adequate available taxonomic materials, we concluded these confusable species to be referred as *Crepidium amplexens* (J.J.Sm.) Szlach., *Crepidium lowii* (É.Morren) Szlach., *Crepidium micranthum* (Hook.f.) Szlach., and *C. rheedei* Blume subsp. *rheedei*. *C. amplexens* and *C. lowii* are new records for Peninsular Malaysia. Both species are belonging to sect. *Commelinodes* subsect. *Lowiae* Marg. (Margońska & Szlachetko, 2010). The typical representative of the subsection is *C. lowii*, having stems decumbent even without inflorescence; leaves middle to small-sized, arranged only along the whole raising part of the stems, and often showily coloured red, purple, brown to nearly black, frequently with stripes or spots (Margońska & Szlachetko, 2010). *C. micranthum* is belonging to sect. *Commelinodes* subsect. *Commelinodes*, with *Crepidium commelinifolium* (Zoll. & Moritzi) Szlach. as the type species, recognised with stems strongly elongated and creeping, ascending only at the apex, especially while forming an inflorescence; leaves numerous, relatively small (Margońska & Szlachetko, 2010). *C. rheedei* subsp. *rheedei* is placed in sect. *Crepidium*, considering its habit and dentate flowers, and also known as the type species for genus *Crepidium*. Morphologically, this section has rhizome either very short or elongated, distinctly demarcated from the usually basally swollen stems that bearing leaves clustered together; labellum apical margin denticulate or with 4 or more teeth or filaments.

Previously, *C. amplexens* was recorded in Borneo, Java and Bali; and *C. lowii* was endemic to Borneo (Go *et al.* 2009; Go & Pungga, 2018; Govaerts *et al.*, 2020), and occurred mainly from lowland to lower montane forest (Wood & Cribb, 1994). Considering its occurrence at a wide range of elevation and on various substrates, predictably that these species show variation (Margońska, 2015). The newly recorded orchid species reported in this paper were collected from lowland and hill dipterocarp forests in Terengganu that fall within the Riau Pocket *sensu stricto*, beginning from the southeast of Peninsular Malaysia and extending as a belt up to 32–48 km wide as far north as the Kelantan-Terengganu border (Tam, 1999; Kiew & Saw, 2019; Besi *et al.*, 2019). The flora is strongly influenced by elements from Borneo and the Riau province on the central-eastern coast of Sumatra (Tam, 1999; Kiew & Saw, 2019). Meanwhile, the former forest area falls within the Terengganu Hills area which is rich in endemic species and is also interesting phyto-geographically because their flora is known to show similarities to the flora of Borneo rather than to that of the Main Range on the west coast (Ashton, 1992). This dispersal event leads to a strong possibility of Bornean taxa occurring within the Terengganu forest area.

To advance our taxonomic evaluation, we employed Scanning Electron Microscope (SEM) observations to understand the role of floral-surface microstructures in taxonomic delimitation and to gain valuable insights on the physio-ecological functions. Visual and olfactory cues offer by the flowers combined with perceptive abilities of pollinators are associated with specialisation for particular pollinators, and even specific sex of them (van der Pijil & Dodson, 1969). The knowledge of physio-ecology of many orchid species, related to pollination in particular, especially those species with inconspicuous or small and very rarely scented flowers, as *Crepidium*, is very poor, other than based on often accidental observations or few notes of specimen’s collectors taken during field and *ex-situ* studies. According to the above, our current study by means of SEM may provide insight in bridging the knowledge gaps. There are not many publications on floral-surface micro-morphology, which perhaps is due to difficulties with flowers availability, fragility and special procedure of sample preparation (Davis & Winters, 1999).

Materials and methods

Specimens collection and processing:—Plants were collected from lowland and hill dipterocarp forests area in Terengganu, Malaysia. Living specimens were transplanted into an *ex-situ* conservatory, and then further nurtured into identifiable samples within six months. Complete specimens were processed using standard herbarium technique after Bridson & Forman (2000), for taxonomic evaluation. Detailed locality data are withheld to prevent potential exploitation of wild populations for commercial purposes.

Macro-morphology examination:—Both spirit-preserved and fresh flower specimens were dissected, described and photographed under AM4113ZT Dino-Lite Digital Microscope. The classic method of taxonomy with reference to the type specimens and protologues was employed. Botanical literatures and protologues including Ridley (1888), Smith (1906, 1908), and Comber (2001) were used in the identification process and evaluation of the species’ distribution

status. Digitised images of herbarium collections, botanical drawing and records deposited in National Herbarium of the Netherlands (NHN) accessed through Browse Dutch Natural History Collections: BioPortal (Naturalis), Herbarium of Singapore Botanic Gardens (SING) accessed through BRAHMS Online managed by University of Oxford (March 2020), Swiss Orchid Foundation (March 2020), Kew Herbarium Catalogue (March 2020), and Natural History Museum Specimen Collection (2020, April) were studied in detail. The accepted names were validated via KEW World Checklist of Selected Plant Families (WCSP) (Govaerts *et al.*, 2020).

Micro-morphology examination via SEM:—To view the flower's labellum and gynostemium using SEM, sample processing steps were carried out as following a modified protocol by Institute of Bioscience (IBS), Universiti Putra Malaysia, Malaysia: First, the samples were put into separate vials and soaked in fixative (4% Glutaraldehyde) for two days at 4°C. After two days, samples were washed with 0.1 M Sodium Cacodylate Buffer for three changes of 30 minutes each and post-fixed in 1% Osmium Tetraoxide for two hours at 4°C. Next, samples were rewashed again with 0.1 M Sodium Cacodylate Buffer for three changes of 30 minutes each prior to a dehydration step with a series of Acetone: 35% (30–45 minutes), 50% (30–45 minutes), 75% (30–45 minutes), 95% (30–45 minutes), and 100% (one hour for three changes). After following critical point drying in a critical dryer Leica EM CPD 030 for about 30 minutes, the samples were mounted on stubs that have been covered with double-sided carbon adhesive tabs and then sputter-coated with gold in auto fine coater Baltec SCD 005 Sputter Coater. The coated samples were examined and imaged under the Jeol JSM 6400 SEM for photo-micrographic examination. The surface structures of each floral part were observed under various magnifications. All the stubs prepared are housed in the Electron Microscopy (EM) unit in IBS, UPM, Malaysia. In SEM study, we used the papillae terminologies and other surface characters provided in Theobald *et al.* (1979) and Wilkinson (1979). The parameter measurements were done using a ruler under a clear magnification and the values obtained were multiplied with the magnification scales. For interpretation of the epicuticular ornamentation, the terminologies and characters after Piwowarczyk (2015), Ghimire *et al.* (2018), and Kong & Hong (2018) were used, and the description on epicuticular waxes was based on Wilkinson (1979). Enumeration of the examined species and the comparative study were following Ghazalli *et al.* (2019) based on the following combined characters: (1) epicuticular waxes, (2) epicuticular ornamentation, (3) stomata frequency and distribution, (4) trichomes frequency and distribution, (5) papillae frequency and distribution, and (6) papillae type. The micro-morphological descriptions of epicuticular ornamentation and papillae were described as in Table 1 and Table 2.

TABLE 1. Type and morphology of papillae on labellar and columnar parts of *C. amplexens*, *C. lowii*, *C. micranthum* and *C. rheedei* subsp. *rheedei*.

Type	Morphology
I	short (ca. 30 µm), triangular, rounded basal cells, striated
II	tall (ca. 90 µm), triangular, rounded and elongated basal cells, striated
III	subsessile (ca. 15 µm), triangular, widely rounded basal cells, striated

TABLE 2. Type and morphology of epicuticular ornamentation on the labellar and columnar parts of *C. amplexens*, *C. lowii*, *C. micranthum* and *C. rheedei* subsp. *rheedei*.

Type	Morphology
I	polygonal-striated outer periclinal wall; furrowed, striated, straight and rounded anticlinal wall
II	rectangular-striated outer periclinal wall; furrowed, striated, straight and rounded anticlinal wall
III	polyhedral-striated outer periclinal wall; furrowed, straight and rounded anticlinal wall
IV	rectangular outer periclinal wall; furrowed, straight and rounded anticlinal wall
V	flat, polygonal outer periclinal wall; furrowed, striated, straight and rounded anticlinal wall
VI	covered with dense papillae, rounded outer periclinal wall; furrowed, rounded and striated anticlinal wall

Taxonomic treatments based on macro-morphology and micro-morphology

Crepidium amplexens (J.J.Sm.) Szlach., Fragm. Florist. Geobot., Suppl. 3: 124 (1995) [Figure 1(A–G)]

Homotypic synonyms:—*Malaxis amplexens* (J.J.Sm.) Ames & C.Schweinf. in O.Ames, Orchidaceae 6: 73 (1920); *Microstylis amplexens* J.J.Sm., Icon. Bogor.: t. 108 E (1903).

Heterotypic synonyms:—*Microstylis amplexans* var. *viridis* J.J.Sm., Bull. Dépt. Agric. Indes Néerl. 53: 35 (1910); *Crepidium amplexans* var. *viride* (J.J.Sm.) Marg., Taxon. Red. Subtribe Malaxidinae: 202 (2012).

Specimen examined:—**MALAYSIA**. Terengganu: Setiu. ca. 300 m elev., 23 February 2019, Besi *et al.* EEB 010 (UPM!); Setiu. ca. 300 m elev., 23 February 2019, Besi *et al.* EEB 002 (UPM!); Setiu. ca. 300 m elev., 23 February 2019, Besi *et al.* EEB 011 (UPM!); Hulu Terengganu, ca. 330 m elev., 23 February 2019, Besi *et al.* EDW002 (UPM!).

Macro-morphology:—Terrestrial or lithophytic, sympodial herb with a creeping rhizome, greenish-white; flowering shoot erect from a decumbent base, plant size ca. 30 cm tall (ca. 9 cm tall without inflorescence). **Rhizome** green-brown, terete, 9–27 cm long, 5–6 mm in diameter, internodes ca. 1 cm long. **Roots** 1–3 arising from each node of the rhizome and from the lower nodes of the stems. **Stem** greenish-white, semi-terete, erect, 4–8 cm long, ca. 5 mm in diameter, bearing up to 6 matured leaves (about 10 leaves if including the newly developed leaves on the lower part of the stems), often branched; internodes 5–8 mm long. **Leaves** 5–12, petiolate, widely ovate, apex acuminate, plicate, upper surface greenish-yellow, lower surface greenish-white, margins copiously undulate; lamina 3.5–5.5 cm × 1.5–2.5 cm, apical and basal ones smallest, few small young leaves on lower part of the stems, 6 parallel veins extending from base to apex with 3 veins sunken above (observed on matured leaves), base decurrent forming clasping sheaths, 1.0–1.5 cm long; base oblique, greenish-white. **Inflorescence** racemose, erect, ca. 13 cm long; peduncle green with purplish-brown stripes, ca. 6 cm long, with several longitudinal ridges, bearing a few lanceolate sterile bracts; rachis laxly flowered extending to about 24 cm long; floral bracts purplish-green, lanceolate with apex acuminate, ca. 4 mm × 1 mm, more or less the same length as the pedicels. **Flowers** purplish-yellow, ca. 4.5 mm × 4.2 mm, perianth margins revolute; **pedicel-with-ovary** purplish-green, cylindrical, curved apically at ovary, ca. 4.0 mm long, ca. 0.8 mm in diameter, with several longitudinal ridges. **Dorsal sepal** ovate, apex obtuse, convex, ca. 2.6 mm × 1.6 mm. **Lateral sepals** ovate, apex obtuse, convex, ca. 3 mm × 1.7 mm. **Petals** oblong, apex rounded, convex, ca. 2.3 mm × 0.6 mm. **Labellum** 3-lobed, hippocrepiform in outline with a strongly sagittate-auriculate base, ca. 3.2 mm × 2.7 mm; apically rounded with unevenly 2- or 3-dentate margin at each side including the acute base of the side lobes, tooth 0.5–0.6 mm long; a widely triangular, bifid, incurved apiculum, ca. 0.7 mm long; side lobes triangular, clearly separated from the midlobe, basal triangular with margins obtuse, auricles obliquely ovate, apex obtuse, ca. 2 mm long; fovea narrowly triangular to rectangular in outline, ca. 1.3 mm × 0.7 mm. **Gynostemium** greenish-yellow, erect, stout, ca. 1.3 mm long including steldia, ca. 0.8 mm wide at apex; anther cap ca. 0.6 mm wide; steldia widely triangular, apex obtuse, ca. 0.2 mm long; pollinia 4, triangular, ca. 0.5 mm × 0.1 mm.

Micro-morphology of labellar and gynostemium surfaces:—*Waxes*: scattered, warty-granulated. *Epicuticular ornamentation*: Type I, II and VI. *Stomata*: Absent. *Trichomes*: Absent. *Papillae*: Present and aggregated on the side lobes and teeth (or the dentate margin). *Papillae type*: Type I and II.

Previous distribution and ecology:—Borneo and Jawa to Lesser Sunda Islands (Bali) (Govaerts *et al.*, 2020). It grows in humus-rich soil in evergreen lowland dipterocarp forest.

Additional specimens examined:—**INDONESIA**. Cultivated in Hortus Botanicus Bogoriense, Java, s. coll., AMES-15197 (isotype: AMES-photo!); Java, s. coll., L1517104 (NHN-photo!); **PAPUA NEW GUINEA**. Inapa, ca. 150 m elev., 7 April 1936, Carr L0571153 (NHN-photo!); Isaurava, ca. 1370 m elev., 31 Januari 1936, Carr L0571154 (NHN-photo!).

Crepidium lowii (É.Morren) Szlach., Fragm. Florist. Geobot., Suppl. 3: 128 (1995) [Figure 1(H–M)]

Homotypic synonyms:—*Malaxis lowii* (É.Morren) Ames, J. Straits Branch Roy. Asiat. Soc. 84(Spec. No.): 151 (1921); *Microstylis lowii* É.Morren, Ann. Hort. Belge Étrangère 34: 281 (1884).

Specimen examined:—**MALAYSIA**. Terengganu: Setiu. ca. 150 m elev., 24 January 2019, Besi *et al.* EEB 001 (UPM!); Gawi, ca. 244 m elev., 30 April 2018, Besi *et al.* EDW 037 (UPM!).

Macro-morphology:—Terrestrial or lithophytic, sympodial herb with a creeping rhizome, purplish-green; flowering shoot erect from a decumbent base, plant size ca. 35–39 cm tall (ca. 11 cm tall without inflorescence). **Rhizome** green-brown, terete, ca. 12 cm long, 3–5 mm in diameter, internodes ca. 1 cm long. **Roots** ca. 1–3 arising from each node of the rhizome and from the lower nodes of the stems. **Stem** purplish-green, semi-terete, erect, ca. 7 cm long, ca. 5 mm in diameter; internodes ca. 1 cm long. **Leaves** ca. 10, petiolate, ovate-lanceolate, apex acuminate, plicate, upper surface dark copper or copper-green coloured, lower surface green, margins undulate; lamina ca. 5.5–8.5 cm × 1.5–2.6 cm, apical ones smaller, 6 parallel veins extending from base to apex with 3 veins sunken above (observed on matured leaves), base decurrent forming clasping sheaths about 2 cm long; base oblique, purplish-green. **Inflorescence**

racemose, erect, ca. 30 cm long; peduncle green to purplish-brown, ca. 8 cm long, with several longitudinal ridges, bearing a few lanceolate sterile bracts; rachis laxly flowered extending to ca. 20 cm long; floral bracts purplish-green, ovate-lanceolate with apex acute, ca. 5.5 mm × 1.5 mm. **Flowers** purplish-yellow, ca. 4.2 mm × 4 mm, perianth margins revolute; **pedicel-with-ovary** purplish-green, cylindrical, curved apically, ca. 3 mm long, ca. 0.5 mm in diameter, with several longitudinal ridges. **Dorsal sepal** ovate-oblong, apex subobtuse, convex, ca. 2.7 mm × 1.3 mm. **Lateral sepals** ovate, apex obtuse, convex, ca. 2.6 mm × 2 mm. **Petals** oblong, apex rounded, convex, ca. 2.5 mm × 0.5 mm. **Labellum** 3-lobed, hippocrepiform in outline with a strongly sagittate-auriculate base, ca. 3.3 mm × 3 mm when flattened; apically rounded with 1-or 2-dentate margin at each sides including the acute base of the side lobes, ca. 0.3 mm long; a widely triangular, bifid, incurved apiculum, ca. 0.5 mm long; side lobes clearly separated from the midlobe, basal widely triangular with margins obtuse, auricles obliquely ovate, apex obtuse, ca. 2.3 mm long; fovea narrowly triangular to rectangular in outline, ca. 1.5 mm × 0.6 mm. **Gynostemium** greenish-yellow, erect, stout, ca. 1.5 mm long including stelia, ca. 0.8 mm wide at apex; anther cap ca. 0.6 mm wide; stelia triangular, apex obtuse, ca. 0.2 mm long; pollinia 4, triangular, ca. 0.4 mm × 0.1 mm.

Micro-morphology of labellar and gynostemium surfaces:—*Waxes*: scattered, warty-granulated. *Epicuticular ornamentation*: Type I and VI. *Stomata*: Nectarostomata (nectaries) on the fovea. *Trichomes*: Absent. *Papillae*: Present and aggregated on the side lobes and teeth (or the dentate margin). *Papillae type*: Type I.

Previous distribution and ecology:—Endemic to Borneo (Sabah and Sarawak) (Govaerts *et al.*, 2020). It grows in mixed lowland and lower montane forests, occurring in leaf-litter amid rocks or boulders or humus-covered ground.

Additional specimens examined:—**INDONESIA**. West-Borneo. Bukit Raja, ca. 1100 m elev., 15 December 1924, *Winkler HBG500506* (holotype: HBG-photo!); **MALAYSIA**. Sabah. Sungai Lohan, ca. 1100 m elev., 3 November 1936, *Vogel L1506133* (NHN-photo!).

Crepidium micranthum (Hook.f.) Szlach., *Fragm. Florist. Geobot., Suppl. 3*: 129 (1995) [Figure 1(N–S)]

Homotypic synonyms:—*Malaxis micrantha* (Hook.f.) Kuntze, *Revis. Gen. Pl.* 2: 673 (1891); *Microstylis micrantha* Hook.f., *Hooker's Icon. Pl.* 19: t. 1834 (1889).

Heterotypic synonyms:—*Microstylis retusa* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 19: 29 (1908); *Microstylis flavoviridis* Ridl., *J. Straits Branch Roy. Asiat. Soc.* 61: 37 (1912); *Microstylis trinervia* Ridl., *Bull. Misc. Inform. Kew* 1926: 84 (1926); *Microstylis retusa* var. *brevis* J.J.Sm., *Nova Guinea* 14: 360 (1929); *Malaxis retusa* (J.J.Sm.) P.F.Hunt, *Kew Bull.* 24: 84 (1970); *Malaxis retusa* var. *brevis* (J.J.Sm.) P.F.Hunt, *Kew Bull.* 24: 84 (1970); *Crepidium trinervium* (Ridl.) Szlach., *Fragm. Florist. Geobot., Suppl. 3*: 133 (1995); *Crepidium retusum* (J.J.Sm.) Szlach. & Marg., *Adansonia, sér. 3*, 20: 342 (1998).

Specimen examined:—**MALAYSIA**. Terengganu: Setiu, ca. 150 m elev., 23 February 2019, *Besi et al. EEB 009, EEB 016* (UPM!); Gawi, ca. 220 m elev., 30 April 2018, *Besi et al. EDW 038* (UPM!).

Macro-morphology:—Terrestrial or lithophytic, sympodial herb with a creeping rhizome; flowering shoot erect from a decumbent base, 15–37 cm tall. **Rhizome** green to green-brown, terete, ca. 16 m long, ca. 0.5 cm in diameter, internodes ca. 1 cm long. **Roots** appearing from nodes of rhizome and lower part of the stems. **Stems** purplish-brown, semi-terete, erect. **Leaves** ca. 8, petiolate, green to purplish-brown, pale green in the middle, dull purple at lower surface, lanceolate to ovate-lanceolate with oblique base, plicate, sheathed at base, apex acuminate, margins undulate; lamina ca. 4–8 cm × 0.7–2 cm, 3-to 5-veined. **Inflorescence** racemose, erect, ca. 15 cm long; peduncle greenish-yellow, ca. 6 cm long, ca. 0.2 cm in diameter, with several longitudinal ridges, bearing a few lanceolate sterile bracts; rachis laxly many-flowered; floral bracts greenish-yellow, reflexed, triangular, acuminate, ca. 4.8 mm × 1.8 mm. **Flowers** greenish-yellow, more or less flushed with purple, ca. 5.3 mm × 6 mm; perianth with margin revolute; **pedicel-with-ovary** purplish-brown, cylindrical, with 6 longitudinal ridges, ca. 2 mm long. **Dorsal sepal** ovate-oblong, apex rounded, ca. 3 mm × 1.2 mm. **Lateral sepals** broadly ovate, apex obtuse, margins revolute, ca. 2.5 mm × 1.5 mm. **Petals** spreading, oblong, apex rounded, ca. 2.6 mm × 0.6 mm. **Labellum** 3-lobed, hippocrepiform in outline with a strongly sagittate-auriculate base, ca. 4 mm × 5.1 mm; apically rounded with coarsely and unevenly 3-dentate margin at each side including the acute base of the side lobes; a widely triangular, bifid, incurved apiculum, ca. 0.9 mm long; fovea oblong-ovate in outline, ca. 2 mm long, ca. 1.3 mm wide; side lobes triangular, basal triangular with margin rounded, ca. 2 mm long, ca. 1.6 mm wide at base, auricles obliquely ovate, apex obtuse, ca. 3.3 mm long; fovea narrowly triangular in outline, ca. 1.5 mm × 0.5 mm. **Gynostemium** greenish-yellow, erect, stout, ca. 1.5 mm long, ca. 0.9 mm wide at apex; anther-cap yellow, ca. 0.7 mm wide; stelia conspicuously erect, narrowly triangular, ca. 0.4 mm long, triangular, apex acuminate, ca. 0.3 mm long; pollinia 4, triangular, ca. 0.5 mm × 0.1 mm.

Micro-morphology of labellar and gynostemium surfaces:—*Waxes*: scattered, warty-granulated, flake-like.

Epicuticular ornamentation: Type I, II, III, IV, V and VI. *Stomata*: Absent. *Trichomes*: Absent. *Papillae*: Present and aggregated on the side lobes and teeth (or the dentate margin). *Papillae type*: Type III.

Previous distribution and ecology:—Peninsular Thailand to West Malesia, Borneo and New Guinea (Govaerts *et al.*, 2020). It grows in mixed lowland, lower montane and limestone hill forests, growing amongst leaf-litter.

Additional specimens examined:—**PAPUA NEW GUINEA**. Irian Jaya, Idenburg, ca. 130 m elev., 2 September 1914, *Feuilletau de Bruyn L0063831* (holotype: NHN-photo!); **MALAYSIA**. Sarawak, Gunung Batu, 8 October 1977, *Martin L1506146* (NHN-photo!); **INDONESIA**. Sumatra, *Korthals L1506145* (NHN-photo!).

Crepidium rheedei* Blume subsp. *rheedei, Bijdr. Fl. Ned. Ind.: 387 (1825) [Figure 1(T–Y)]

Homotypic synonyms:—*Microstylis rheedei* (Blume) Wight, Icon. Pl. Ind. Orient. 3: t. 902 (1844), nom. Illeg; *Microstylis blumei* Boerl. & J.J.Sm., Icon. Bogor.: t. 108 B (1903), nom. Illeg; *Malaxis blumei* Bakh.f., Blumea 12: 68 (1963); *Crepidium blumei* (Bakh.f.) Szlach., Fragm. Florist. Geobot., Suppl. 3: 124 (1995).

Heterotypic synonyms:—*Microstylis acutangula* Hook.f., Hooker's Icon. Pl. 19: t. 1835 (1889); *Malaxis acutangula* (Hook.f.) Kuntze, Revis. Gen. Pl. 2: 673 (1891); *Crepidium acutangulum* (Hook.f.) Szlach., Fragm. Florist. Geobot., Suppl. 3: 123 (1995).

Specimen examined:—**MALAYSIA**. Terengganu: Kuala Berang, ca. 200 m elev., 19 August 2019, Besi *et al.* HS 036 (UPM!); Kuala Berang, ca. 460 m elev., 27 February 2019, Besi *et al.* EEB 046, EEB 015 (UPM!).

Macro-morphology:—Terrestrial or lithophytic, sympodial herb, caulescent, flowering shoot erect from an erect base, ca. 20 cm tall. **Rhizome** erect. **Stems** conical or cylindrical, greenish-white, sheaths covered with leaves. **Leaves** 7–10, clustered with base clasping on stems, oblong-lanceolate, apex acuminate, plicate, spreading, away from stems, narrowed at the base, bright green, 3-veined, lamina 5.5–11 cm × 1.7–3 cm; erect in loose clusters. **Inflorescence** racemose, erect, ca. 20 cm long; peduncle greenish-yellow, ca. 6 cm long, ca. 0.2 cm in diameter; rachis laxly many-flowered; floral bracts greenish-yellow, reflexed, triangular, apex acuminate, ca. 4.2 mm × 1.1 mm. **Flowers** purplish-white, tinged purple along the perianth margin, ca. 5.2 mm × 6.2 mm; perianth with margin revolute; **pedicel-with-ovary** greenish, cylindrical with 6 longitudinal ridges, ca. 6 mm long. **Dorsal sepal** oblong, apex rounded, ca. 4.2 mm × 0.8 mm. **Lateral sepals** broadly ovate, apex obtuse, ca. 4.3 mm × 1.8 mm. **Petals** spreading, oblong, apex obtuse, ca. 4 mm × 0.6 mm. **Labellum** 3-lobed, hippocrepiform in outline with a strongly sagittate-auriculate base, ca. 4.5 mm × 4.3 mm; apically rounded with coarsely and unevenly 3-dentate margin at each side including the acute base of the side lobes, longer than apiculus; a widely triangular, bifid, incurved apiculus, ca. 0.6 mm long; fovea deep and rounded in outline, ca. 0.9 mm long, ca. 0.6 mm wide; side lobes triangular, ca. 3.1 mm long, ca. 1.3 mm wide at base; auricles obliquely oblong, apex rounded, ca. 3.1 mm long; fovea rectangular, deeply furrowed, ca. 1.3 mm × 0.5 mm. **Gynostemium** greenish-yellow, erect, stout, ca. 1.5 mm long, ca. 1 mm wide at apex; anther-cap yellow, ca. 0.7 mm wide; stelia conspicuously erect, long, triangular, apex rounded, ca. 0.6 mm long; pollinia 4, triangular, ca. 0.5 mm × 0.1 mm.

Micro-morphology of labellar and gynostemium surfaces:—*Waxes*: scattered, warty-granulated, flake-like. *Epicuticular ornamentation*: Type I and II. *Stomata*: Absent. *Trichomes*: Absent. *Papillae*: Absent.

Previous distribution and ecology:—Peninsular Malaysia, Borneo, Java and Philippines (Govaerts *et al.*, 2020). It grows in lowland and hill forests with soil covered with leaf-litter.

Additional specimens examined:—**INDONESIA**. Java, s. coll., *Blume L0063669* (holotype: NHN-photo!).

Tentative key to *Crepidium* species from Peninsular Malaysia, with stems creeping or decumbent and the labellum apical margin denticulate, including *Crepidium oculatum* (Rchb.f.) Szlach. from Sumatra (Ridley 1888: 338)

1. Rhizome long (>10 cm), creeping, leafless, gradually passing in the laxly leaved shoot.....2
Rhizome either very short or elongated (<10 cm), distinctly demarcated from the basally swollen stems with clustered leaves
..... *C. rheedei* subsp. *rheedei*
2. Stem erect; leaves large, oblong with apex acute, ca. 10 cm long by 3.5 cm broad *C. oculatum*
Stems decumbent or creeping; leaves literally small, ovate to ovate-lanceolate, 3–8 cm long by 1–3 cm broad3
3. Flowers greenish-yellow, sometimes flushed with purple, larger, ca. 6 mm long by 6 mm broad *C. micranthum*
Flowers purplish-yellow, smaller, ca. 4 mm long by 4 mm broad4
4. Leaves widely ovate, greenish, lamina 3.5–5.5 cm long by 1.5–2.5 cm broad; labellum apical margin 2-to 3-dentate, prominent ...
..... *C. amplexens*
Leaves ovate-lanceolate, copper, lamina 5.5–8.5 cm long by 1.5–2.6 cm broad; labellum apical margin 1-to 2-dentate, stout and inconspicuous *C. lowii*

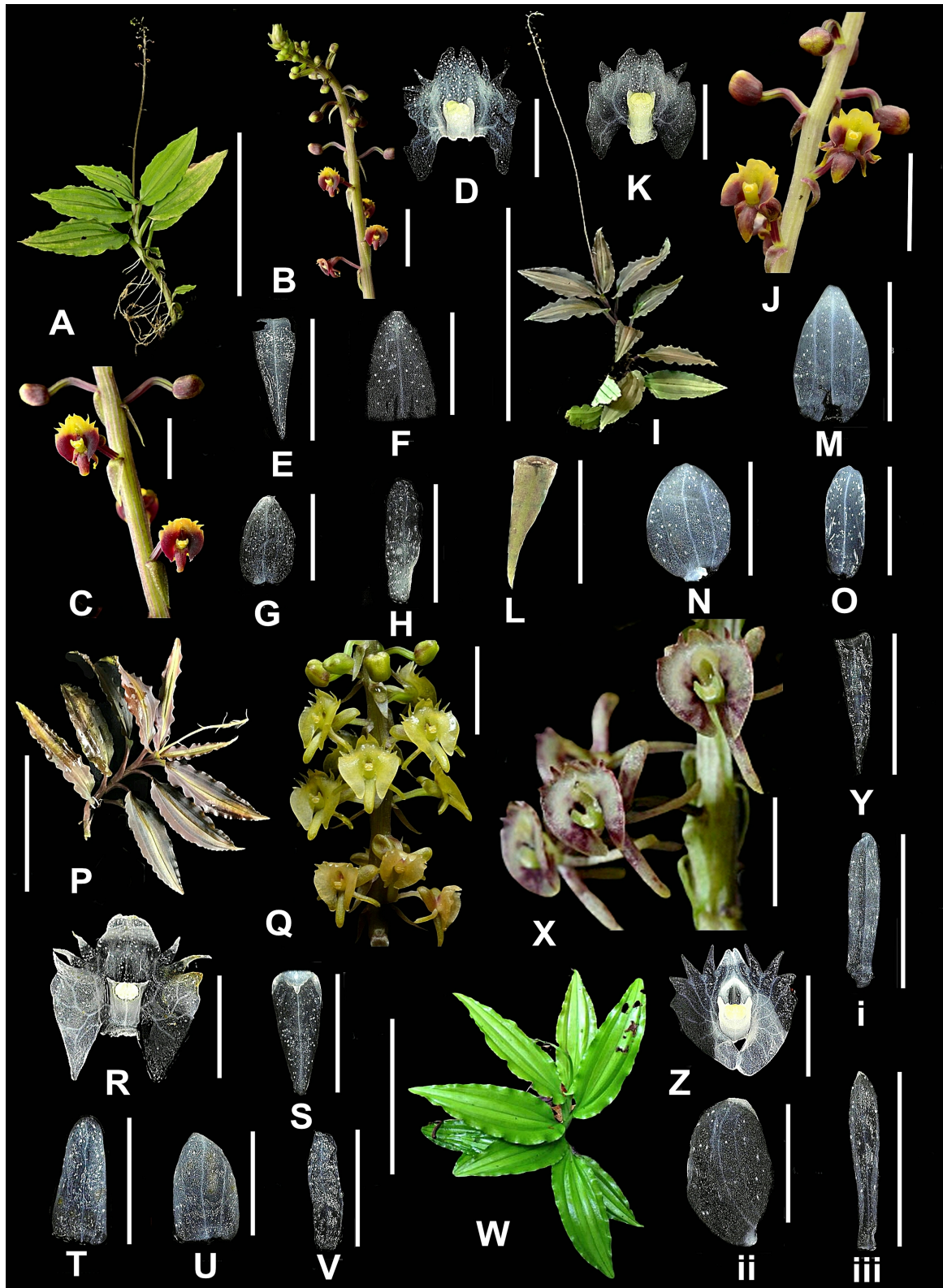


FIGURE 1. Floral and vegetative parts of *C. amplexens* (A–H), *C. lowi* (I–O), *C. micranthum* (P–V), and *C. rheedei* subsp. *rheedei* (W–ii). **A.** Plant. **B.** Inflorescence. **C.** Flowers. **D.** Labellum and column (flattened). **E.** Bract. **F.** Dorsal sepal. **G.** Lateral sepal. **H.** Petal. **I.** Plant. **J.** Flowers. **K.** Labellum and column (flattened). **L.** Bract. **M.** Dorsal sepal. **N.** Lateral sepal. **O.** Petal. **P.** Plant. **Q.** Inflorescence. **R.** Labellum and column (flattened). **S.** Bract. **T.** Lateral sepal. **U.** Dorsal sepal. **V.** Petal. **W.** Plant. **X.** Inflorescence. **Y.** Bract. **Z.** Labellum and column (flattened). **i.** Dorsal sepal. **ii.** Lateral sepal. **iii.** Petal. **Scale bars:** A = 10 cm. B, W = 10 mm. C, E, L, Q, X = 5 mm. F, N, Y = 2.6 mm. G, M, U, V = 3 mm. D, H, O = 2 mm. I = 17 cm. J, Z, i, ii, iii = 4 mm. K = 2.5 mm. P = 8 cm. R = 2.8 mm. S = 3.3 cm. T = 2.5 mm. Images by Edward and Dome.

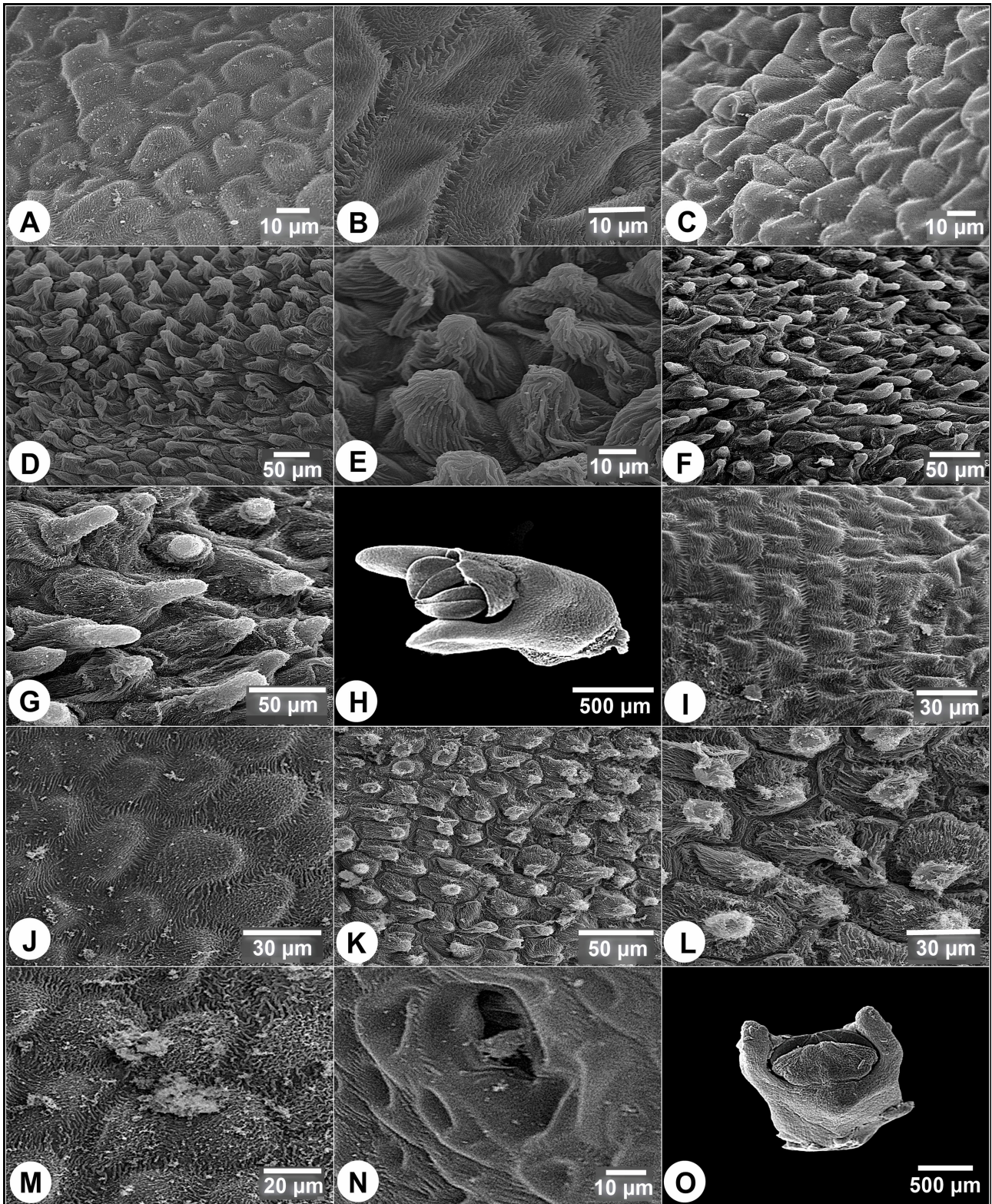


FIGURE 2. SEM observations of epicuticular ornamentation and papillae on surface of labellar and gymnostemium of *C. amplexens* (A–H) and *C. lowii* (I–O). **A, B, C.** Type I epicuticular ornamentation on the side lobes, fovea and column. **D, E.** Type I papillae on the side lobes. **F, G.** Type II papillae on the side lobes and teeth of the apical margin. **H.** Column showing exposed four triangular pollinia. **I, J, K, L.** Type I epicuticular ornamentation of the side lobes and column. **K, L.** Type I papillae on the side lobes and teeth of the apical margin. **M.** Warty-granulated waxes on the labellum surface. **N.** Nectarostomata on the fovea functioned as nectary. **O.** Column showing cordate anther.

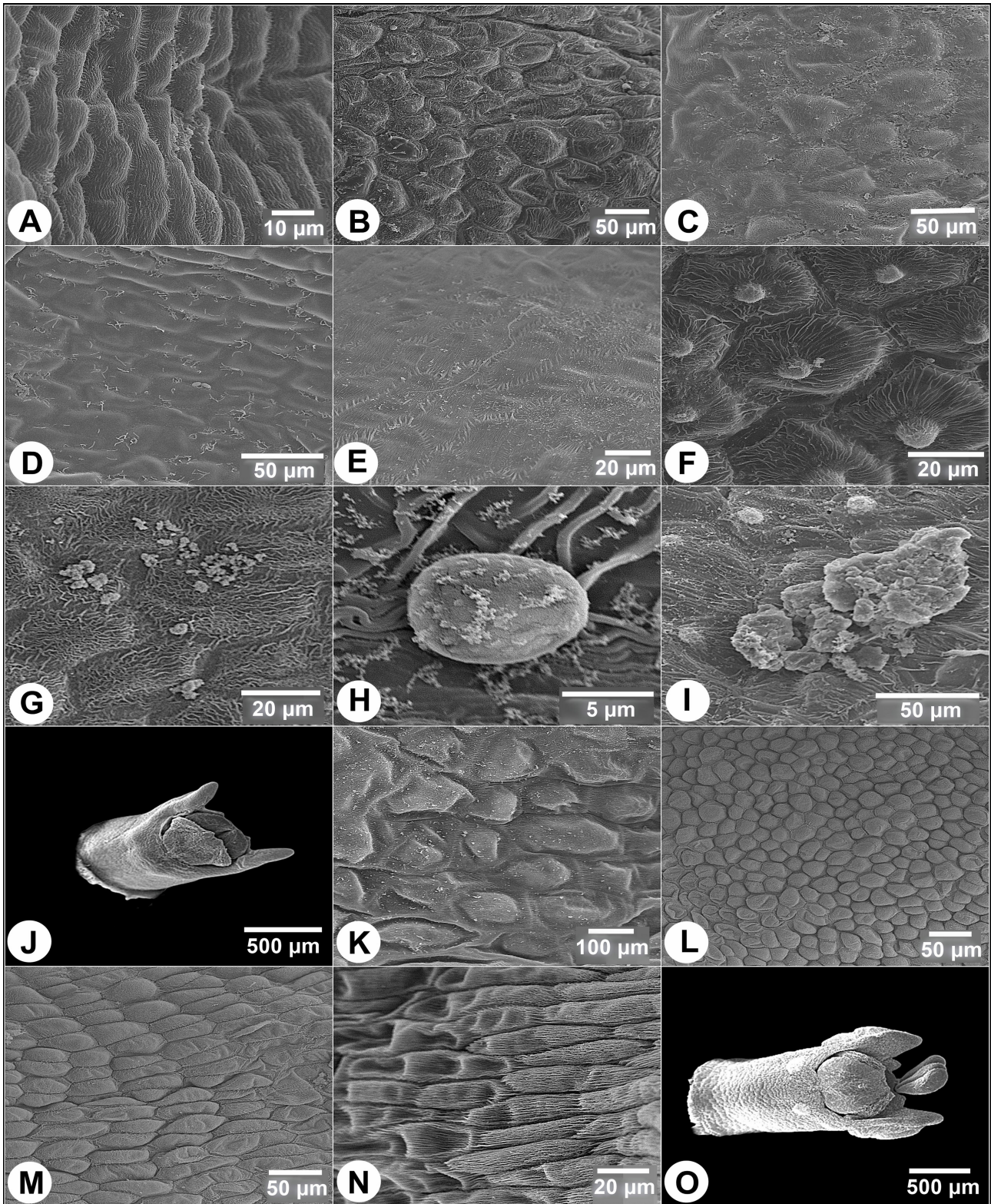


FIGURE 3. SEM observations of epicuticular ornamentation and papillae on surface of labellar and gymnostemium of *C. micranthum* (A–J) and *C. rheedei* subsp. *rheedei* (K–O). **A, B.** Type I epicuticular ornamentation on the side lobes and column. **C.** Type III epicuticular ornamentation on the fovea. **D.** Type IV epicuticular ornamentation on fovea. **E.** Type V epicuticular ornamentation on fovea. **F.** Type III papillae on teeth of the apical margin. **G.** Warty-granulated waxes on the labellum surface. **H, I.** A solid clump of warty-granulated waxes. **J.** Column showing anther. **K, L.** Type I epicuticular ornamentation on side lobes and teeth of the apical margin. **M, N.** Type II epicuticular ornamentation on fovea and column. **O.** Column showing exposed pollinia.

TABLE 3. Comparative macro-morphology of *C. amplexens*, *C. lowii*, *C. micranthum* and *C. rheedei* subsp. *rheedei*

Characters	<i>C. amplexens</i>	<i>C. lowii</i>	<i>C. micranthum</i>	<i>C. rheedei</i> subsp. <i>rheedei</i>
Leaves shape	Widely ovate, apex acuminate	Ovate-lanceolate, apex acuminate	Lanceolate to ovate-lanceolate, apex acuminate	Oblong-lanceolate, apex acuminate
Leaves lamina size	ca. 3.5–5.5 cm × 1.5–2.5 cm	ca. 5.5–8.5 cm × 1.5–2.6 cm	ca. 4–8 cm × 0.7–2 cm	ca. 5.5–11 cm × 1.7–3 cm
Leaves colour and pattern	Greenish-yellow (upper), greenish-white (lower)	Dark copper or copper-green (upper), green (lower)	Green to purplish-brown (upper), pale green in the middle (upper), dull purple (lower)	Bright green
Flowers colour	Purplish-yellow	Purplish-yellow	Greenish-yellow, more or less flushed with purple	Purplish-white, tinged purple along the perianth margin
Flowers size	ca. 4.5 mm × 4.2 mm	ca. 4.2 mm × 4 mm	ca. 5.3 mm × 6 mm	ca. 5.2 mm × 6.2 mm
Dorsal sepal	ca. 2.6 mm × 1.6 mm, ovate, apex obtuse	ca. 2.7 mm × 1.3 mm, ovate-oblong, apex subobtuse	ca. 3 mm × 1.2 mm, ovate-oblong, apex rounded	ca. 4.2 mm × 0.8 mm, oblong, apex rounded
Lateral sepals	ca. 3 mm × 1.7 mm, ovate, apex obtuse	ca. 2.6 mm × 2 mm, ovate, apex obtuse	ca. 2.5 mm × 1.5 mm, broadly ovate, apex obtuse	ca. 4.3 mm × 1.8 mm, broadly ovate, apex obtuse
Petals	ca. 2.3 mm × 0.6 mm, oblong, apex rounded	ca. 2.5 mm × 0.5 mm, oblong, apex rounded	ca. 2.6 mm × 0.6 mm, oblong, apex rounded	ca. 4 mm × 0.6 mm, oblong, apex obtuse
Labellum size	ca. 3.2 mm × 2.7 mm	ca. 3.3 mm × 3 mm	ca. 4 mm × 5.1 mm	ca. 4.5 mm × 4.3 mm
Labellum teeth (excluding apiculum)	2–3 on each side, shorter than apiculum	1–2 on each side, shorter than apiculum	3 on each side, shorter than apiculum	3 on each side, longer than apiculum
Labellum auricles	ca. 2 mm long, obliquely ovate, apex obtuse	ca. 2.3 mm long, obliquely ovate, apex obtuse	ca. 3.3 mm long, ovate, apex obtuse	ca. 3.1 mm long, oblong, apex rounded
Labellum fovea	ca. 1.3 mm × 0.7 mm	ca. 1.5 mm × 0.6 mm	ca. 1.5 mm × 0.5 mm	ca. 1.3 mm × 0.5 mm
Gymnostemium stielidia	ca. 0.2 mm long, widely triangular, apex obtuse	ca. 0.2 mm long, triangular, apex obtuse	ca. 0.4 mm long, narrowly triangular, apex acuminate	ca. 0.6 mm long, conspicuously erect, long, triangular, apex rounded
Anther-cap	ca. 0.6 mm wide	ca. 0.6 mm wide	ca. 0.7 mm wide	ca. 0.7 mm wide
Pollinarium	ca. 0.5 mm × 0.1 mm.	ca. 0.4 mm × 0.1 mm	ca. 0.5 mm × 0.1 mm	ca. 0.5 mm × 0.1 mm

TABLE 4. Features and distribution of floral-surface micro-morphology characteristics on the labellar and gynostemium parts of *C. amplexens*, *C. lowii*, *C. micranthum* and *C. rheedei* subsp. *rheedei*

Species	Floral Parts	Epicuticular ornamentation	Anticlinal wall features	Epicuticular striation	Occurrence of stomata	Papillae	Papillae type
<i>C. amplexens</i>	Side lobes	I, VI	Furrowed, striated	Striated	Absent	Present	I, II
	Fovea	I	Furrowed, striated	Striated	Absent	Absent	Absent
	Teeth	I	Furrowed, striated	Striated	Absent	Present	II
	Column	I	Furrowed, striated	Striated	Absent	Absent	Absent
	Side lobes	I, VI	Furrowed, striated	Striated	Absent	Present	I
	Fovea	I	Furrowed, striated	Striated	Present	Absent	Absent
<i>C. lowii</i>	Teeth	VI	Furrowed, striated	Striated	Absent	Present	Absent
	Column	I	Furrowed, striated	Striated	Absent	Absent	I
	Side lobes	I, III	Furrowed, smooth	Striated	Absent	Present	III
	Fovea	III, IV, V	Furrowed, smooth	Smooth	Absent	Absent	Absent
	Teeth	VI	Furrowed, smooth	Striated	Absent	Present	III
	Column	I, II	Furrowed, striated	Striated	Absent	Absent	Absent
<i>C. micranthum</i>	Side lobes	I, II	Furrowed, striated	Striated	Absent	Absent	Absent
	Fovea	II	Furrowed, striated	Striated	Absent	Absent	Absent
	Teeth	I	Furrowed, striated	Striated	Absent	Absent	Absent
	Column	II	Furrowed, striated	Striated	Absent	Absent	Absent
	Side lobes	I, II	Furrowed, striated	Striated	Absent	Absent	Absent
	Fovea	II	Furrowed, striated	Striated	Absent	Absent	Absent
<i>C. rheedei</i> subsp. <i>rheedei</i>	Teeth	I	Furrowed, striated	Striated	Absent	Absent	Absent
	Column	II	Furrowed, striated	Striated	Absent	Absent	Absent

Comparative study on the macro-morphology and floral-surface micro-morphology of *C. amplexans*, *C. lowii*, *C. micranthum* and *C. rheedei* subsp. *rheedei*

Here we established and elucidated diagnostic taxonomic features, as well as an array of macro-morphological and micro-morphological variations demonstrated by the examined confusable *Crepidium* species. Herbarium collections deposited in the international herbaria display a great geographical variation and morphological differentiation of the leaves, in particular, that may be influenced by natural selection exerted by geographically patterned ecological factors and genetic drift (Slatkin, 1983; Grant, 1991). It is difficult to verify the legitimacy of each specimen's credentials, especially in regard to the old ones. The leaf morphology alone is unreliable and insufficient for identifications of the *Crepidium* species that grow along a wide range of geographical elevation and habitat. *Crepidium lowii* resembles *C. amplexans*, by having the flowers horse-shaped and purplish-green in colour, except the later species has the labellum apical margin usually 3-dentate on both sides with prominent tooth, and the leaves widely ovate and green above (Table 3). Based on the gross morphology, both species are very close to *C. micranthum* with the labellum 2-to 3-dentate at both sides of the apical margins and variegated leaves, except it shows differences in the size and colour pattern of the flowers and length of the labellum auricles (Table 3). Macro-morphology of the anther-cap and pollinarium offer no help to justify the intrageneric separation as the size and shape are more or less similar for the studied *Crepidium* species. Also, in Margońska & Szlachetko (2010), sect. *Commelinodes* is re-circumscribed and delineated into two subsections, earlier is subsect. *Commelinodes*, to which *C. micranthum* is now placed, and the newly proposed subsect. *Lowiae*, comprises of *C. amplexans* and *C. lowii*, based on the habit of stem that is decumbent above their creeping base, rather than creeping and ascending only at the apex. Our observations on the stems habit are approving of this newest infrageneric classification. SEM observation on the surface micro-morphology of the labellar and gymnostemium help here by displaying that *C. amplexans* is comparable with *C. lowii* by having different diversity and distribution of the epicuticular ornamentation and papillae on the labellum and gymnostemium (Table 4). The combination of these features is here expressed as taxonomically important in discriminating these morphologically complex group owing to their wide ecological and geographical distribution. The concavity presents in all studied *Crepidium* species has a small canal starting at the base of the apiculum leads to the fovea area where the nectary could be located. However, our SEM observations revealed that nectarostomata only occurred on the fovea of *C. lowii*, which is also a diagnostic character differentiating it from *C. amplexans*.

Physio-ecological aspects of the labellar and gymnostemium micro-morphology

Congregations of waxes in the absence of trichomes and normal stomata indicate an active function of the nectarostomata and epicuticular cells as secretory structures. The absence of both secretory structures infers that the waxes are secreted through either papillae presence on the teeth of the apical margin or exuded through the epidermal cells. One clear role of waxes is to protect the plant from desiccation and herbivorous insects (Davies & Turner, 2004), which offers a great adaptation strategy for such inconspicuous flowers. Dense waxes on the labellum surface may attract potential pollinators by stimulating their probing and licking behaviour (Dressler, 1993). The papillate cells at the teeth of the labellum may function as an osmophore that produce the wax-like substances glistening the labellum surface. Though, in contrast, there were no raphides formed on the labellum surface of the examined species as observed in several *Crepidium* mentioned in Kowalkowska & Margońska (2009), that may enhance the pollinators visit. However, without inclusive studies of the ultrastructures, there is no possibility of any reliable claims of these viscid substances as food rewards or protection against desiccation and insects. Probably, apart from using SEM, cyto-chemistry may reveal answers for these demands.

Conclusion

The plants are of threatened taxa that are confined to the evergreen and undisturbed forest fragments, considering the rapid forest destruction by logging activities in the Terengganu area. The reports of its presence in these at-risk forest areas should not be easily dismissed without making detailed and critical studies. This study provides several characters of the species that would help in its morphological and floral anatomical authentication, supported by photographic illustrations. Our current gross morphology and SEM studies provide additional and concrete features for the identification of the almost indistinguishable *Crepidium* species. These key characters would help in correct

identification of the plant materials including those preserved specimens deposited in the herbaria and would help to prevent taxonomic confusion, which is very likely due to limited knowledge on distribution, taxonomy and microstructures of subtribe Malaxidinae.

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