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A revised taxonomy for *Uvaria* (Annonaceae) in continental Asia

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Abstract. This paper presents a revision of *Uvaria* L. (Annonaceae) in continental Asia and outlying islands, north of the Thailand–Malaysia border, on the basis of a combination of new morphological analyses and recent phylogenetic data. Two new taxonomic groupings are defined within the genus in Asia on the basis of detailed morphological character analysis in ~1800 specimens. Stamen and carpel structure are shown to be significantly more informative than calyx and corolla characters for subgeneric differentiation, and reliably discriminate basal and derived radiations when mapped onto recent molecular phylogenies for the genus in Asia. Thirty-three species and species varieties are recognised within *Uvaria* in continental Asia, incorporating taxa formerly assigned to *Anomianthus* Zoll., *Cyathostemma* Griff., *Ellipeia* Hook.f. & Thomson, *Ellipeiopsis* R.E.Fr. and *Dasoclema* J.Sinclair. Four new combinations are proposed, and outstanding taxonomic, nomenclatural and typification issues are resolved for included taxa. Keys for both flowering and fruiting material are included, and distribution data are provided for all taxa.

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Introduction

Uvaria L. is the second-largest palaeotropical genus in the Annonaceae (custard apple family) and includes ~150 species *sensu stricto* (Kessler 1993) and 210 species *sensu lato* (Zhou *et al.* 2010). *Uvaria* and associated genera have historically formed a well defined stellate-haired taxonomic group, the ‘*Uvaria*-group’ (Van Heusden 1992), comprising *Uvaria*, *Balonga* Le Thomas (Africa), *Anomianthus* Zoll. (Asia), *Cyathostemma* Griff. (Asia), *Ellipeia* Hook.f. & Thomson (Asia), *Ellipeiopsis* R.E.Fr. (Asia) and *Rauwenhoffia* Scheff. (Asia). However, many inconsistencies exist in nomenclature, taxonomy and typification (Meade 2001; Meade and Parnell 2002). Recent phylogenetic analysis of the *Uvaria* lineage within the wider Annonaceae has also raised questions regarding differentiation of genera within the *Uvaria* group, with the implication that a monophyletic *Uvaria* genus, encompassing all the above genera, is the most appropriate classification (Zhou *et al.* 2010, 2012; Chatrou *et al.* 2012).

To redress these issues, the current paper presents a revision of the *Uvaria* group in continental Asia, covering all taxa that occur from the western Ghats to the Thai–Malay border, just south of the Isthmus of Kra, and including Sri Lanka, the Andaman Islands and Hainan Island in the South China Sea. In support of this revision, key morphological traits are re-evaluated in terms of their taxonomic and phylogenetic utility across the lineage as a whole, with the objective of establishing a revised and more robust taxonomy.

Morphology of the *Uvaria* group

Uvaria species occur in the moist tropical regions of Africa, Madagascar, continental Asia, Malesia, northern Australia and the Bougainville–Solomon Island chain. Most species are climbers or scrambling shrubs, and grow by means of twining branchlets, although a small number are self-supporting shrubs. Lowland rainforest species can grow to heights of 30 m or more, often with a single 8–10-cm diameter main stem; however, the more usual habit is a many-branched climber in disturbed or marginal riverine vegetation, or less often in seasonally dry scrub and deciduous forest.

The general morphology of *Uvaria*, although consistent across key taxonomic traits such as the possession of stellate hairs, is, nonetheless, quite varied, attendant to the size of the genus and consistent within the broad parameters of the Annonaceae (Fig. 1, 2); the definitions presented in Van Heusden (1992), after Radford *et al.* (1974), are used here for morphological descriptions and terminology without significant alteration. Although *Uvaria* taxa in Africa and Asia share core homology across all diagnostic taxonomic traits for the genus (as per the generic description that follows), the analysis and discussion presented here focus on variation in Asian *Uvaria* taxa, with some additional reference to equivalent observed variation in African taxa, especially regarding inferred patterns of biogeographic radiation and floral character evolution across the genus.

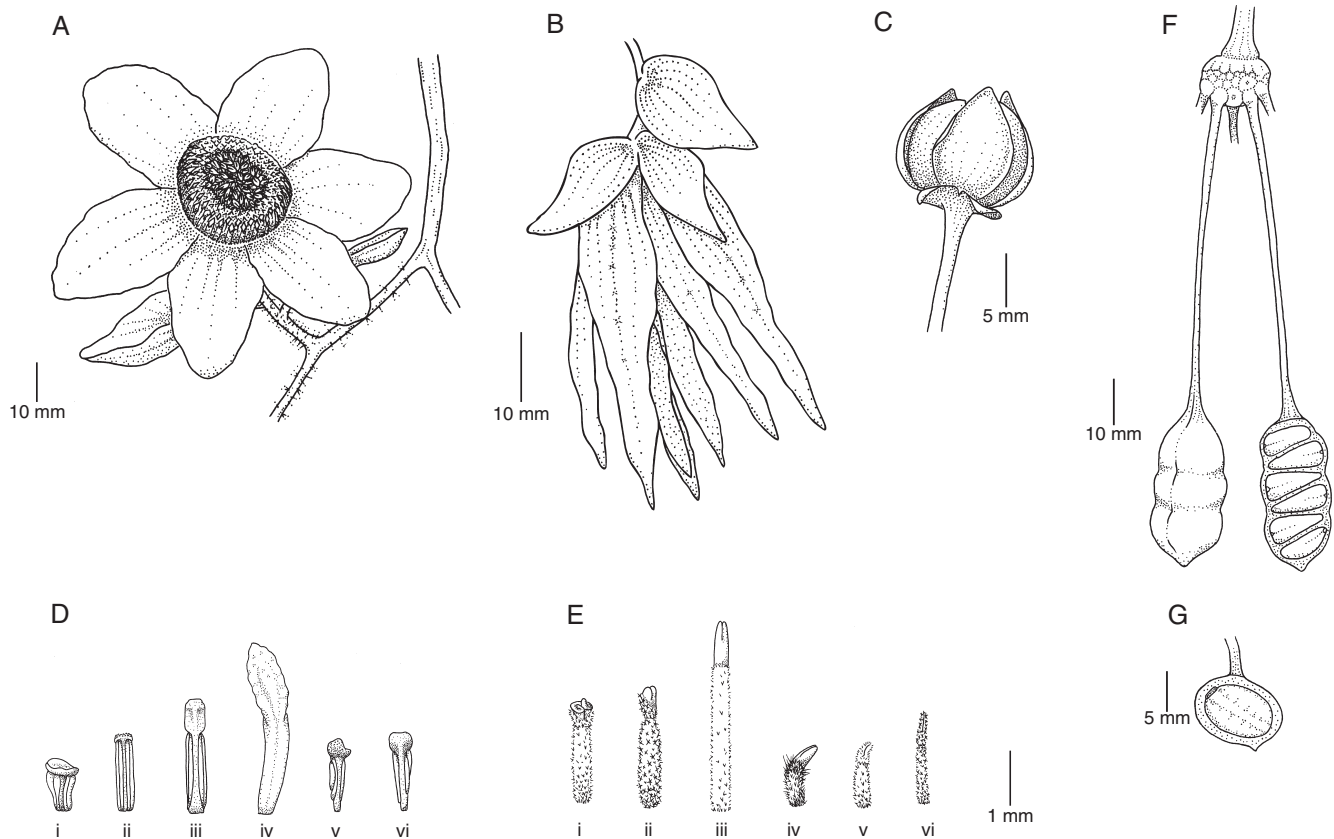


Fig. 1. Morphology of *Uvaria* group taxa. A. *U. grandiflora* flower, with spreading petals in two whorls of three. B. *U. hahnii* flower, with erect petals. C. *U. boniana* flower, with erect petals. D. Stamen structure: i. *U. zeylanica*, stamens cuneate in shape, locules subequal, extending full length of connective; ii. *U. semecarpifolia*, laminar in shape, locules subequal, extending full length of connective, connective apex elongate; iii. *U. rufa*, laminar in shape, locules subequal, extending full length of connective, connective apex elongate; iv. *U. microcarpa* staminode; v. *U. hahnii*, cuneate in shape, connective apex umbonate, locules unequal in length, raised on a short filament; vi. *U. pauciovulata*, cuneate in shape, connective apex obtuse, locules unequal in length, raised on a short filament. E. Carpel structure: i. *U. dac*, ii. *U. rufa*, iii. *U. utteridgei*, iv. *U. pierrei*, v. *U. siamensis*, vi. *U. pauciovulata*. F. *U. concava* mature monocarps, placentation lateral. G. *U. pauciovulata* mature monocarp, placentation subapical. F. Illustration C. V. Meade.

Inflorescence

The inflorescence can be leaf-opposed or axillary, and, in rare cases, is cauliflorous. Flowers range in number from one to five or six per inflorescence, with usually a maximum of two or three open at any one time. Among *Uvaria* taxa, calyx structure presents in three different states, namely, valvate, connate and calytrate (Fig. 2A), the latter sometimes splitting unevenly into 3+ sepals. The corolla comprises two whorls of three imbricate petals (Fig. 1A–C), except in the case of four taxa where the petals are basally connate in a single whorl (Fig. 3B). Inner and outer whorls are most often subequal, with the inner petals typically only marginally smaller than the outer ones; however, in a minority of taxa, the inner petals are distinctly smaller. Prior to opening of the floral bud, adjacent petals in each whorl are imbricate along their upper margins; at maturity, the petals form alternate whorls overlap, usually only at the base (Fig. 1A, 4D). In the majority of species, inner- and outer-whorl petals have the same shape and structure. Less often, inner-whorl petals differ from the outer-whorl ones, by carrying basal swellings on the margin, by having a different indument (for example, being basally glabrous on the inner

surface) or by having a different shape (for example, by being conspicuously narrower, or where the inner petal margins remain connivent). Petals are typically membranous (Fig. 1A, 5D) or coriaceous (Fig. 1B); however, some Asian and many African species have fleshy petals (Fig. 1C). In some species, the petals remain erect (Fig. 1B), but mostly they are spreading or reflexed at maturity (Fig. 5D). Petal colours range from white to yellow to purple to brown. Torus shape ranges from flat to globose to depressed ovoid.

Stamens

Stamen structure is highly variable. Stamens are typically laminar (Fig. 1Dii, iii) or cuneate (Fig. 1Dv, vi) and the apex of the stamen connective may be dorsally flattened (Fig. 1Di), blunt (Fig. 1Dii), elongate (Fig. 1Diii) or umbonate (convex) (Fig. 1Dv, vi). Many species have papillae on the stamen apex (Fig. 1Dii, v) and, although most species have glabrous stamens, a few have hairs on the locules (thecae) or on the connective. In the majority of taxa, the filament is rudimentary or absent and all locules extend the full length of the connective from below the apex to the base (Fig. 1Di–iii), less often the

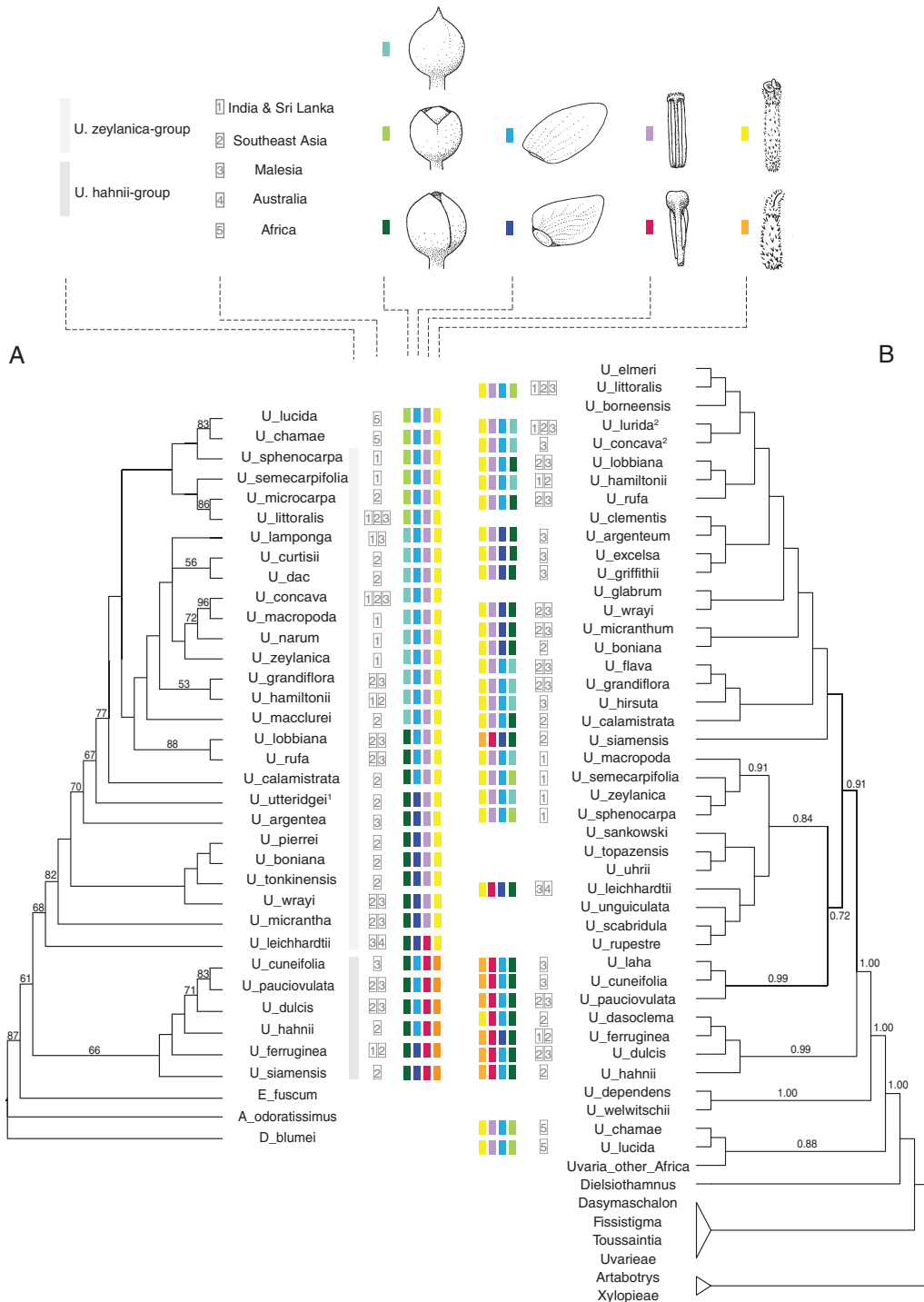


Fig. 2. A. Cladogram of morphometric association among sampled *Uvaria* group taxa inferred from maximum-parsimony analysis of 55 taxonomic traits (50% majority rule consensus tree of 3 most parsimonious trees). Tree length (with weights reset to 1) = 166, consistency index (CI) = 0.404, retention index (RI) = 0.708, and rescaled consistency index (RC) = 0.286. Bootstrap values above branches were calculated over 1000 repetitions using tree bisection reconnection (TBR). All dichotomous branches have 100% majority-rule consensus support. B. Maximum clade-credibility tree inferred in BEAST analysis of four plastid DNA regions in the sampled taxa. Branch support values indicate Bayesian posterior probability for each node (values less than 0.95 omitted, except where indicated; after Zhou *et al.* 2012). The four most informative character states used for the present taxonomic revision are indicated and colour-coded for the surveyed taxa in both trees (calyx in bud calyprate, connate or valvate; petals membraneous or thickened; stamen filament absent or present; stigma glabrous or hairy); taxa in B without coding were not sampled for the present analysis. Taxon names are listed according to the revised taxonomy proposed in the current paper, with all *Uvaria* group taxa subsumed into *Uvaria*. *Cyathostemma siamense* = *Uvaria utteridgei*. *Uvaria concava* and *U. lurida* are treated as the same taxon in the present revision.

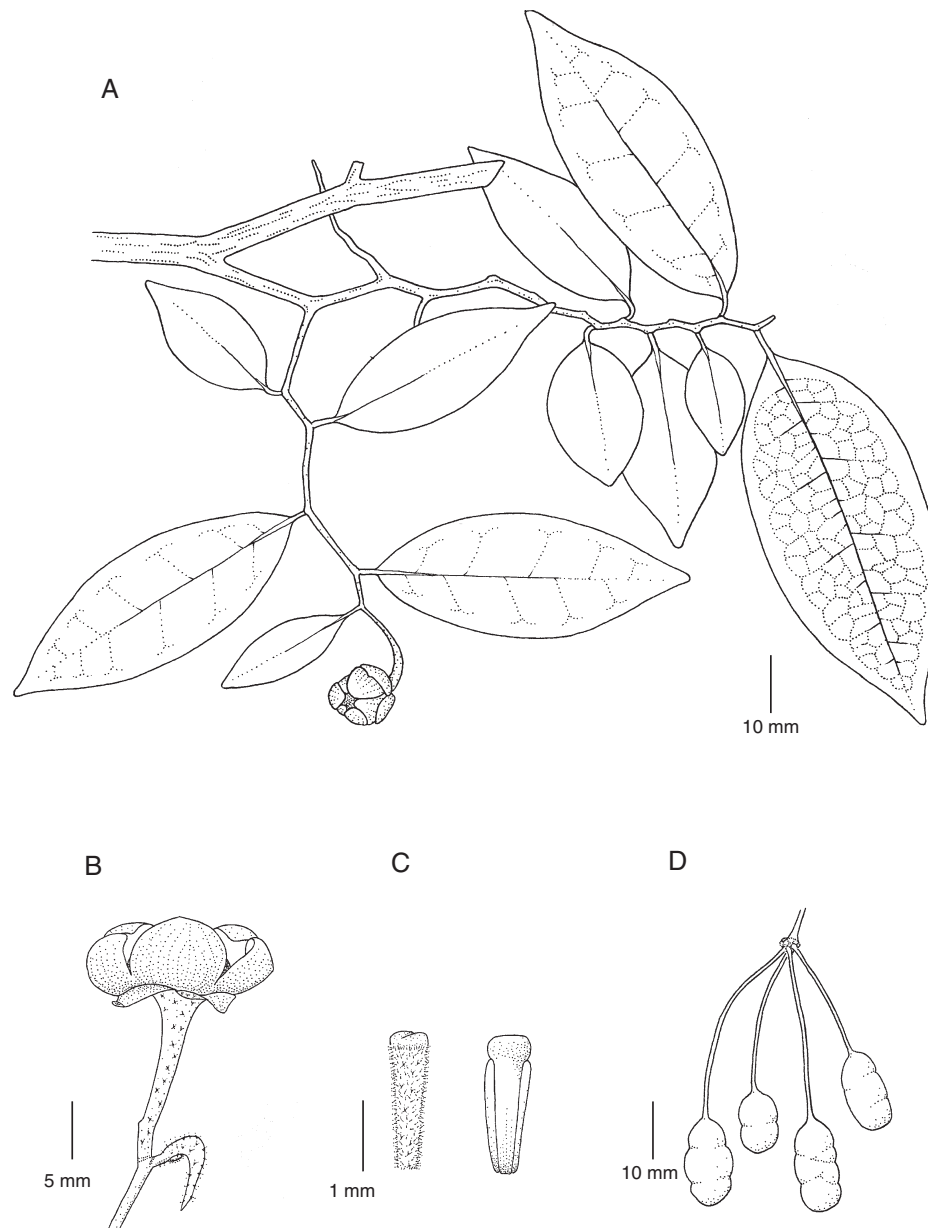


Fig. 3. *Uvaria narum*. A. Habit. B. Mature flower. C. Carpel and stamen. D. Mature monocarps. Illustration C. V. Meade.

locules are unequal in length and raised from the stamen base on a short filament (Fig. 1Dv, vi). In several species, an outer whorl of staminodes or substaminodes is present (Fig. 1Div, 4B, F).

Carpels and fruit

Ovaries are always hairy and the stigmas are U-shaped in cross-section and either glabrous (Fig. 1Ei–iv) or more rarely hairy (Fig. 1Ev, vi). In most taxa, there is a slight narrowing of the stigma base where it adjoins the carpel (Fig. 1Ei); however, in a minority of cases, this constriction is pronounced (Fig. 1Ev, vi). Ovule number ranges from 1 to

30, with most species having between 4 and 10 ovules, with lateral placentation (Fig. 1G); however, apical or subapical placentation is also observed. Mature seeds vary in shape according to number of fertilised ovules in the ovary, with lateral compression common in monocarps with multiple ovules (Fig. 1F, G, 4C, 6B); aril shape varies from triangular to bilaterally lobed. Monocarps are normally stipitate (Fig. 1F, 4C); however, in a few species, they are sessile or nearly so. The pericarp can be thin or thick and fleshy, although thinning via desiccation is common at maturity. The flesh is usually white in colour and bittersweet to taste. Monocarp surfaces are variable; the indument most often follows the mature vegetative parts, and can be hairy or

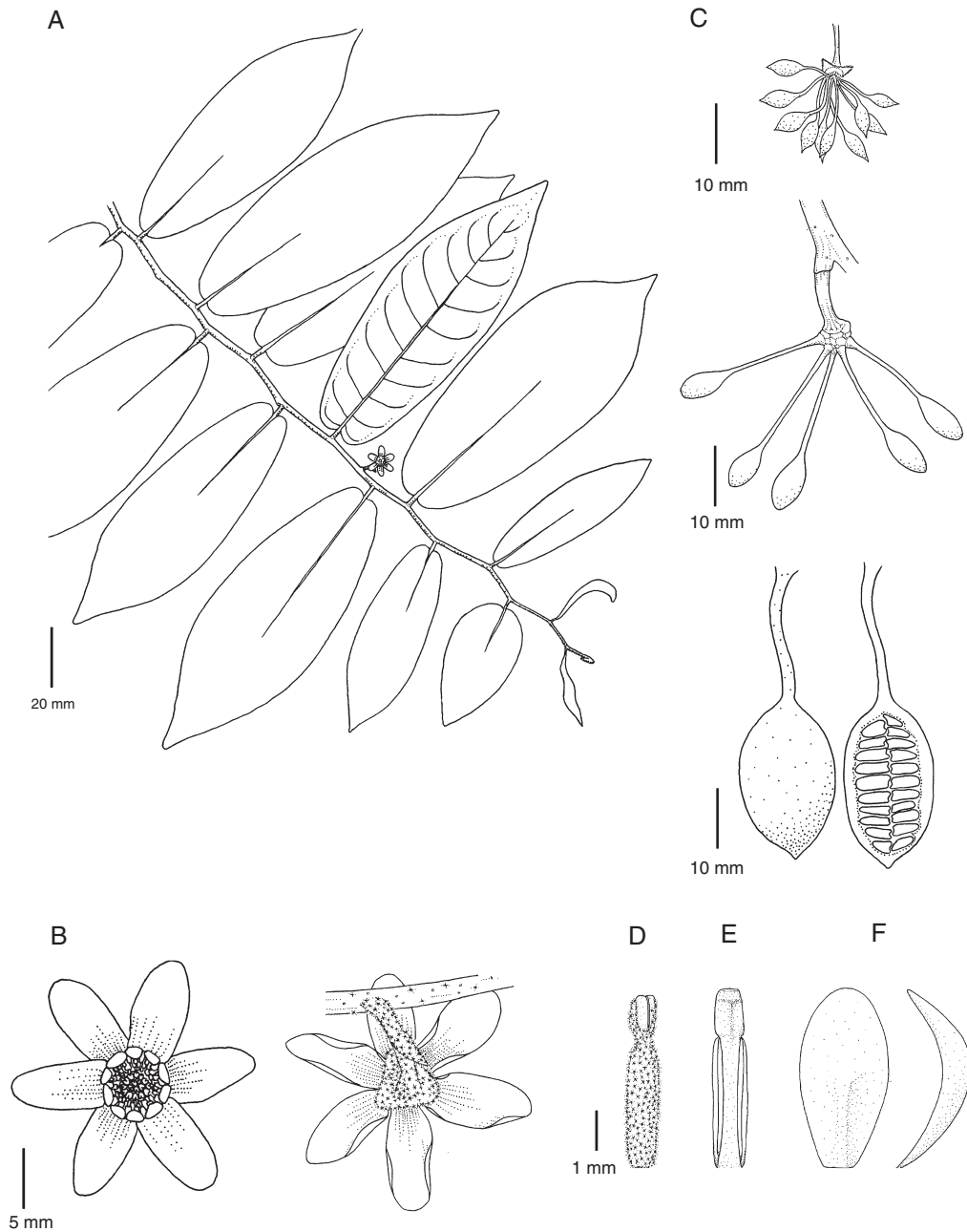


Fig. 4. *Uvaria rufa*. A. Habit. B. Mature flower. C. Ripening monocarp. D. Carpel. E. Stamen. F. staminode. Illustration C. V. Meade.

glabrous; rarely the fruit indument is long and branched (Meade 2005). Surface features are more independent, and vary from entirely smooth to being prominently tubercled, to having clear longitudinal striation which may be elongate, fine and shallow, or undulating, conspicuous and deep. In many species, a conspicuous dorsal keel and an apicule can persist to maturity (Fig. 1F).

Leaves and indument

The predominant leaf shape in *Uvaria* is obovate; however, elliptical and narrowly ovate leaves are also common (Meade

and Parnell 2003). The shape of the leaf base varies from cordate (most commonly, for example Fig. 6) to cuneate (Fig. 5, whereas the leaf apex varies from acute (most commonly, for example Fig. 6) to acuminate. Leaves show 6–25+ subparallel veins, depending on the taxon, and although this number can vary with leaf age, it is generally consistent within a narrow range for each taxon (Meade 2001). Most species have a tomentose indument with a characteristic ferruginous colour, especially in the juvenile stages. Many species lose this indument, sometimes very early in development (Fig. 7A), whereas others retain it into

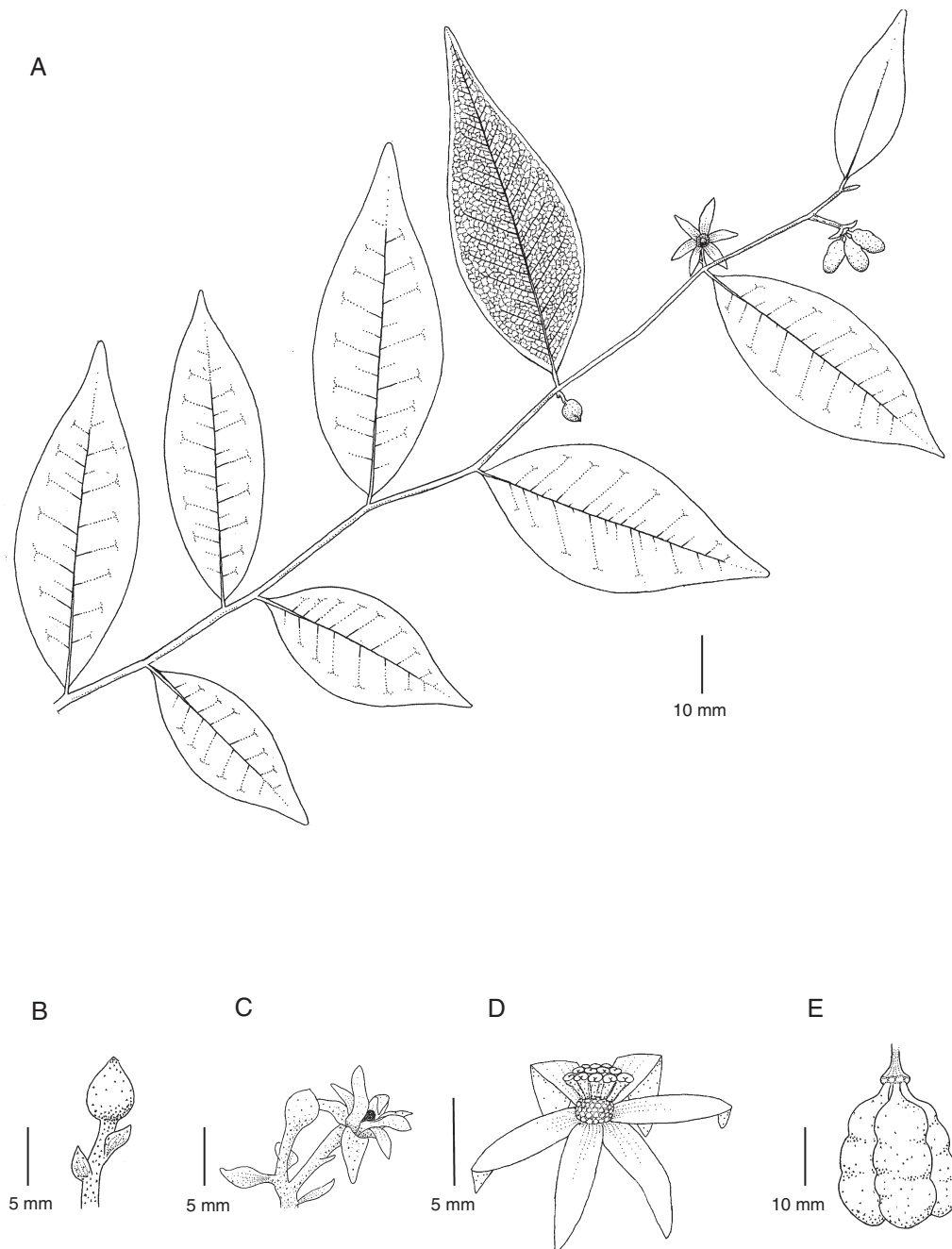


Fig. 5. *Uvaria zeylanica*. A. Habit. B. Flower bud. C. Flower early anthesis. D. Mature flower. E. Mature monocarp. Illustration C. V. Meade.

maturity, sometimes as a prominent hirsute tomentum (Fig. 6). In all species, the hairs are stellate, with 2–25+ branches.

Historical treatment of *Uvaria*

Delimitation of the *Uvaria* group within the Annonaceae has focused on the following four main characters: a scrambling or climbing growth habit, stellate hairs over all organs, valvate sepals and imbricate petals. There has been broad taxonomic agreement about the core composition of this grouping within

the family (Hooker and Thomson 1855; Finet and Gagnepain 1906; Sinclair 1955; Van Heusden 1992; Meade 2001); however, for example Fries (1959) included many additional genera of less obvious affinity. Disagreement has been greater regarding taxonomic differentiation of core genera within the group, primarily owing to varying emphasis on a variety of petal characters (Fries 1959; Nguyễn 1974, 2000 (often cited by his first name(s) as Bân or Tiễn Bân); Van Heusden 1992; Utteridge 2000). Meade and Parnell (1998), Meade (2001) and Meade *et al.* (2002) identified strong homoplasy in the

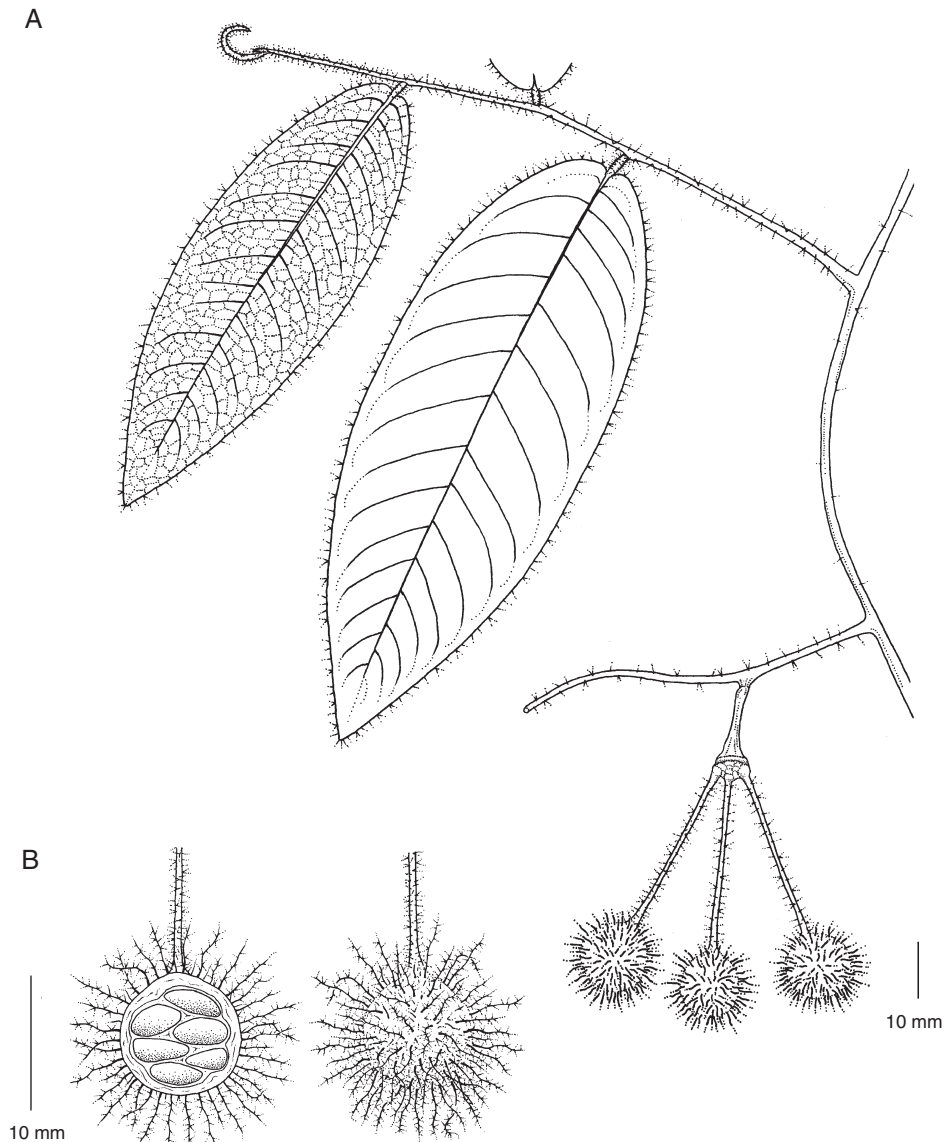


Fig. 6. *Uvaria vietnamensis*. A. Habit. B. Mature monocarps. Illustration C. V. Meade.

conspicuous floral traits most often used to discriminate among *Uvaria* group genera, whereas leaf shape and fruit structure appear to be reliable indicators only at species level (Meade 2001; Meade and Parnell 2003).

Early classifications of the Annonaceae, such as those of de Candolle (1824) and Hooker and Thomson (1855), described *Uvaria* with its multi-ovuled numerous free carpels and spreading petals as the most 'simple' floral arrangement in the family, akin to the Ranunculaceae and Magnoliaceae (Fig. 1A). The later phylogenetic interpretations of Sinclair (1955), on the Malaysian Annonaceae, and Fries (1959), on the entire family, also placed *Uvaria* in a primitive complex, with Sinclair (1955, p. 169) commenting as follows: 'There is a tendency to proceed from simplicity to complexity, e.g. from simple petals with no distinction between blade and claw, to the complex dome-shaped petals of the Mitrephoreae...'

Phylogenetic analysis

Molecular phylogenetic analysis of the Annonaceae has shown more complex floral evolution patterns than envisaged by these earlier workers, with both convergence and reversion of floral traits being displayed across the family, including the traits that delimit the *Uvaria* group (Saunders 2010, 2012; Couvreur *et al.* 2011; Chatrou *et al.* 2012; Thomas *et al.* 2015). In addition, *Uvaria* is not placed among the basal Annonaceae genera of origin *c.* 90 million years ago, but in the more derived lineage of the Annonoideae, or Long Branch Clade, which first arose in the late Cretaceous *c.* 65 million years ago (Couvreur *et al.* 2011; Chatrou *et al.* 2012). Plastid DNA evidence also suggests the *Uvaria* lineage first emerged in Africa during the mid-to-late Oligocene (*c.* 25–30 million years ago) and later dispersed to Asia from an East African *Uvaria* clade during the early Miocene (*c.* 20 million years ago; Couvreur *et al.* 2011; Zhou *et al.* 2012). Despite these recent origins within the Long

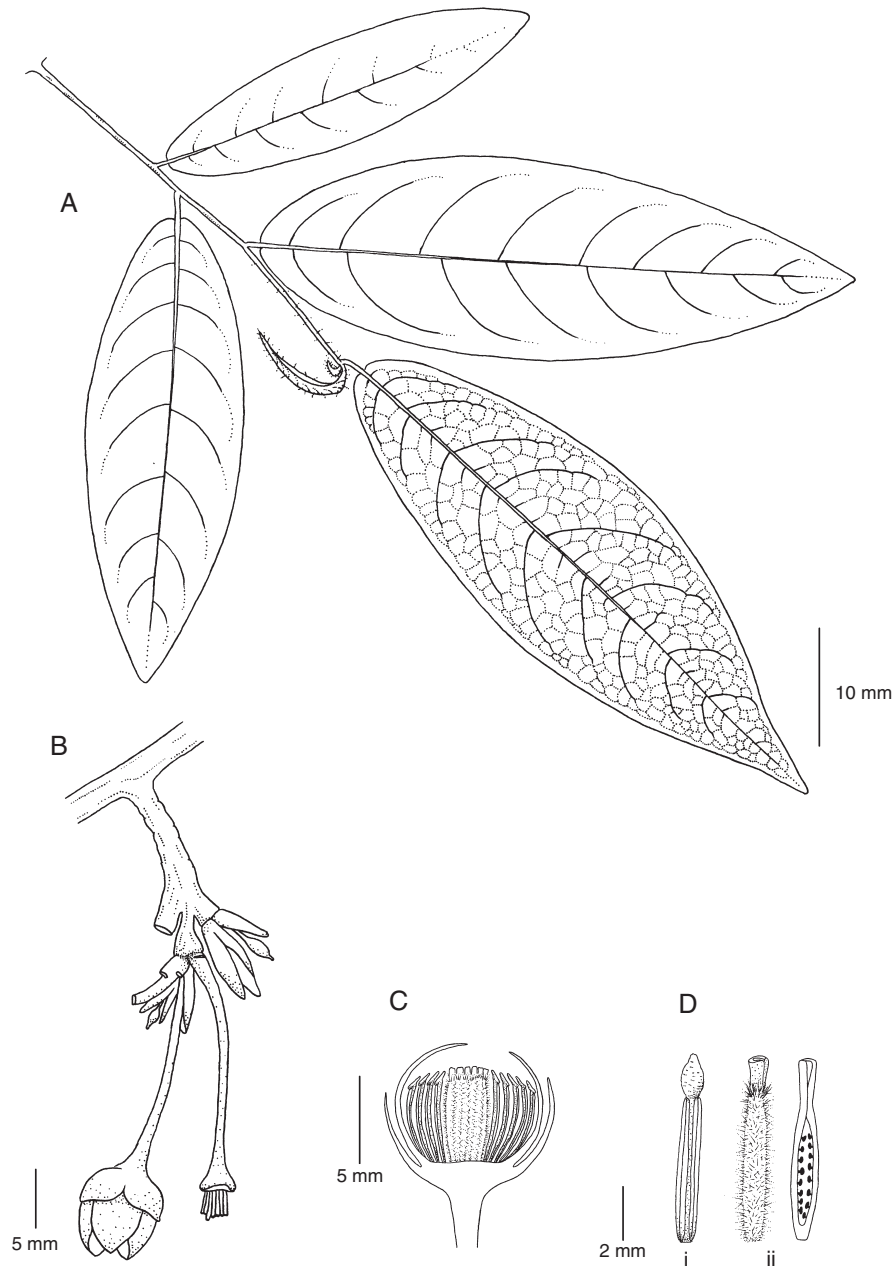


Fig. 7. *Uvaria utteridgei*. A. Habit. B. Inflorescence. C. Flower, section. D.i. Stamen. ii. Carpel. Illustration C. V. Meade.

Branch Clade (LBC), *Uvaria* is the third most species-rich genus in the Annonaceae, and on the basis of a *sensu lato* interpretation of Zhou *et al.* (2009), displays an elevated speciation rate compared with genera in the family as a whole (Couvreur *et al.* 2011). While this elevated speciation rate is partly attributable to the biogeographic radiation of *Uvaria* from Africa into Asia, it also reflects the *sensu lato* interpretation of Zhou *et al.* (2009), wherein all the *Uvaria* group genera of Van Heusden (1992) and Meade (2001) are subsumed into *Uvaria* on the principle of generic monophyly.

In many branches of the Annonaceae, discrete differences in taxonomy and morphology readily distinguish adjoining

monophyletic clades, and allow the maintenance of multiple smaller genera with much more recent origins than *Uvaria* (Couvreur *et al.* 2011; Chatrou *et al.* 2012). In the *Uvaria* lineage, by comparison, the conspicuous floral traits that have been used in taxonomic discrimination appear to map very poorly to the molecular phylogeny, especially among Asian taxa, and have encouraged strongly paraphyletic classifications for *Uvaria* group genera (Zhou *et al.* 2009). However, the resulting proposal that *Uvaria* group genera be incorporated into *Uvaria s.l.* has the dual effect not only of eliminating this paraphyly, but also greatly increasing the range of floral and fruit character diversity within the genus

(Fig. 1A–C). Monophyletic classifications based solely on molecular evidence have the potential to create taxonomic groupings that relate poorly to the (dis)continuity of morphology states within lineages (Kluge 1988), and the inclusion of associated genera into *Uvaria*, as above, raises this problem.

A revised taxonomy

Our objective here has been to prepare a taxonomic account of *Uvaria* in Asia that is congruent with inferred molecular phylogeny and of practical use to botanists in the field. First, to resolve existing confusion, we have re-evaluated the morphological utility of floral, fruit and vegetative traits that have traditionally been used for taxonomic discrimination across the *Uvaria* group, using a cladistic approach. Key character states that show robust informativeness are then mapped to the chloroplast phylogeny to determine which best mark out the inferred history of the *Uvaria* lineage. We then propose a revised taxonomy and key for *Uvaria*, incorporating new subdivisions demarcated by discriminating morphological traits that map to defined nodes on the chloroplast phylogeny, and, on this basis, we present a taxonomic revision for the genus in continental Asia.

Analysis of floral character evolution in *Uvaria*

Materials and methods

Data generation

A morphological-character binary-data matrix was generated from 55 characters scored from 37 taxa in the *Uvaria* group (Table 1, Table S1, available as Supplementary material to this paper), encompassing the measurable variation in morphology observed for the genus, as introduced above. Identification of variable traits was completed first in consultation with type material, and later validated across the observed variation in non-type collections. In the completed analysis, six characters were based on continuous count or size measurements, for which character states were determined using ratio comparisons (e.g. leaf length to width ratio), relational comparisons or statistical variance (e.g. in which a sample score is inside (0) or outside (1) one standard deviation of the sample mean). The remaining 49 characters were scored on the basis of discrete presence or absence traits. Traits 1–6 addressed variation in vegetative morphology (Table 1); Traits 7–10, inflorescence structure; Traits 11–27 and Traits 53–55, calyx and corolla structures; Traits 28–33, 46 and 51, carpel structure; Traits 34–39, stamen structure; and Traits 41–49 and 52, fruit and seed structure.

Thirty taxa from *Uvaria* and *Cyathostemma* were sampled, along with representatives from *Anomianthus*, *Ellipeia*, *Ellipeiopsis* and *Rauwenhoffia* (all putative members of the *Uvaria* group on the basis of morphology), plus the stellate-haired *Melodorum* Hook.f. & Thomson of Malesia and northern Australia. *Dasymaschalon* Dalla Torre & Harms (Annonoideae: Uvarieae), *Artabotrys* R.Br. (Annonoideae: Xylopieae) and *Enicosanthum* Becc. (Malmeoideae: Miliusiaceae) were sampled as outgroups, on the basis of their inferred floral dissimilarity or similarity with *Uvaria*, after Sinclair (1955) and Van

Heusden (1992). Approximately 1800 specimens (including most of the relevant types) were examined from the following herbaria: A, AAU, ABD, BK, BKF, BM, BR, C, CMU, E, G, HAM, PHH, HN, HNU, K, L, LIV, LISU, NY, P, PE, SING, TCD, U, US. In the main text accounts, barcodes are quoted for specimens studied, where available. The full list of examined material is included in the ‘Full list of material examined’ section in the Supplementary material.

Data analysis

Cladistic analysis of the morphological data matrix were performed using maximum-parsimony (MP) criteria (Edwards and Cavalli-Sforza, 1964; Camin and Sokal 1965) as implemented in PAUP (ver. 4.0b10. D. W. Swofford, Sinaur Associates, Sunderland, MA, USA; Swofford 2002). Maximum-parsimony analysis comprised an initial heuristic search using random stepwise addition and the tree bisection and reconnection (TBR) branch-swapping algorithm, followed by the same search with characters reweighted to their mean rescaled-consistency (RC) index score from the first analysis. Bootstrap values were calculated over 1000 iterations on these reweighted data by using TBR.

Results

Maximum-parsimony analysis of the entire sample dataset yielded three most parsimonious topologies, with a consistency index (CI) score of 0.404 (with character weights reset to 1 for the purpose of tree interpretation), a retention index (RI) score of 0.708 and an RC score of 0.286 (50% majority-rule consensus topology shown in Fig. 2A). A total of 11 characters had mean RC index scores of 1.0 and changed state just once on the topology (Table S2, available as Supplementary material to this paper). Five of these characters relate to petal structure (18, 22, 27, 53, 54), three to stamen structure (34, 35, 38), two to carpel structure (31, 33) and one to indument structure (50). One petal character (24) had an RC score of >0.5, whereas all the remaining characters (including all fruit, leaf and inflorescence characters) had scores of <0.5.

The inferred tree topologies show a basal morphometric division between a group containing *Anomianthus*, *Ellipeia*, *Ellipeiopsis*, *Rauwenhoffia*, *Uvaria hahnii* (Finet & Gagnep.) J.Sinclair and *U. pauciovulata* Hook.f. & Thomson (defined by a convex or umbonate connective apex in the stamen and a hairy stigma, termed here the ‘*U. hahnii*-group’, 66% bootstrap support, Fig. 2A) and a larger group containing all the remaining *Uvaria* and *Cyathostemma* taxa and *Melodorum leichhardtii* (F.Muell.) Benth. (connective apex not convex or umbonate, stigma glabrous, the ‘*U. zeylanica*-group’, 68% support). Bootstrap support for the ‘*U. zeylanica*-group’ above *M. leichhardtii* is 82%.

The following three major subgroupings within the ‘*U. zeylanica*-group’ can be delimited using calyx structure: the terminal group above and including *Uvaria macchurei* Diels (calyx calyprate, Character 13), the terminal group including *U. littoralis* Blume and *U. chamae* P.Beauv. (calyx connate, Character 11) and the remainder of the taxa on the tree (calyx valvate, Character 12). The only characters that robustly discriminate at the base of the topology are an umbonate

Table 1. Data scoring criteria for 55 morphological character states among *Uvaria* taxa, as applied in the presented cladistic analysis

Trait states have been demarcated on the basis of observed variation in type-specimen morphology and associated non-type collections. See text for discussion

Character	0	1	2	3
1	Shoot indument	≤1 mm	≥1 mm	
2	Leaf L : W ratio	≤2.07	2.08–2.44	≥3.07
3	Upper blade glabrous	No	Yes	2.45–3.07
4	Upper blade scabrous	No	Yes	
5	Secondary veins	Complete	Incomplete	
6	Leaves	Coriaceous	Membranous	
7	Inflorescence	Subterminal	Terminal	
8	Pedicle transverse section	Circular	Flattened	
9	Torus diameter	≤5 mm	>5 mm	
10	Torus	Raised	Flat	
11	Calyx connate	No	Yes	
12	Calyx valvate	No	Yes	
13	Calyx calyptrate	No	Yes	
14	Sepals	Flat	Concave	
15	Calyx	Smooth	Tuberculate	
16	Calyx apicule	No	Yes	
17	Calyx splitting	Evenly	Unevenly	
18	Petals variable in number	No	Yes	
19	Petals membranous	No	Yes	
20	Petals thickened	No	Yes	
21	Whorls	Equal	Outer > inner	
22	Inner whorl base	Hairy	Glabrous	
23	Inner whorl base	Obtuse	Narrowed	
24	Inner petals	Reflexed	Erect	Closed Connivent
25	Marginal glands	Absent	Present	
26	Petal colour	Red or purple	Yellow or white	
27	Petal base at maturity	Free	Connate	
28	Stigma	Short	Elongate	
29	Stigma	Conical	Not so	
30	Stigma lobes	Narrow	Broad	
31	Stigma	Glabrous	Hairy	
32	Neck at apex of ovary	No	Yes	
33	Neck at stigma base	No	Yes	
34	Stamens all fertile	No	Yes	
35	Substaminodes	Absent	Present	
36	Locules	Glabrous	Hairy	
37	Connective apex	Papillate	Smooth	
38	Connective apex	Not convex	Convex	
39	Locules raised	No	Yes	
40	Carpel length	<Stamen	=Stamen	>Stamen
41	Fruit stipe length	Sessile	1 ≤ x ≤ 30 mm	30 < x ≤ 55 mm >55 mm
42	Stipe thickened	No	Yes	
43	Fruit L : W ratio	x < 1	1 ≤ x < 2	2 ≤ x < 3 x = 3+
44	Monocarp keel or ridge	Absent	Present	
45	Monocarp apicule	Absent	Present	
46	Seed number	1	2–16	16+
47	Pericarp (dried)	Tight	Loose	Thick
48	Aril	Triangular	Lobed	
49	Seed orientation	Perpendicular	Angled	
50	Hairs	Stellate	Simple	
51	Ovaries	Basal	Lateral	Apical
52	Monocarps	Whole	Moniliform	
53	Petals	Imbricate	Valvate	
54	Petals	Not clawed	Clawed	
55	Sepals	Valvate	Imbricate	

connective apex and a hairy stigma (Characters 31 and 38; Fig. 1Dv, vi, Ev, vi, 2A).

Discussion

Maximum-parsimony analysis of morphometric trait variation in the Uvaria group

The goal of this analysis was to identify, from among the range of traits used traditionally by botanists, the characters with the most reliable discriminatory power for the purposes of taxonomic classification. These analyses returned a consensus topology (Fig. 2A) that shares close similarity with topologies inferred in molecular phylogenetic analyses of the *Uvaria* group (Fig. 2B, after Zhou *et al.* 2012; Zhou *et al.* 2009, 2010; Chatrou *et al.* 2012), a basal cluster of species associated with *U. hahnii* and *U. pauciovulata*, and the remainder of taxa placed above this group. As previously identified by Van Heusden (1992, for stamens and carpels) and Tsou and Johnson (2003, for stamens), androecium and gynoecium traits here emerge as characters of key discriminating importance.

While molecular data carries the determining phylogenetic signal for systematic analysis, and direct trait-mapping yields taxonomies that are entirely in keeping with the inferred DNA topology, the analyses presented here have independently identified morphological patterns that align well with the DNA topology, suggesting that robust morphometric evaluation can identify reliable discriminating apomorphies within this Annonaceae lineage. The CI score of 0.404 indicate that there is a large amount of character homoplasy in the data matrix, which is not uncommon for morphological data. However, a RI score of 0.708 indicates that although there is a large number of character changes in the topology, the number of changes observed is considerably smaller than the total number that are possible. Leaf characters emerge as having poor information value in the dichotomous topology, although, as already established by Meade and Parnell (2003), multivariate methods can more reliably exploit continuous leaf-shape characters for taxonomic discrimination.

In terms of using this morphological trait analysis to inform a new taxonomy and key, the following three principal morphological groupings are evident (Fig. 2A): (1) a large terminal group including Asian and African *Uvaria* species with coriaceous petals, (2) an intermediate group with mostly thickened petals, including *M. leichhardtii* and *U. boniana* Finet & Gagnep., and (3) a basal group that includes *Ellipeia*, *Rauwenhoffia*, *Ellipeiopsis* and *Anomianthus*, as well as *U. pauciovulata* and *U. hahnii*. Enforcing a stricter interpretation based only on the most reliable characters, namely stamen and carpel structure, shows only one major division in the cluster, namely, between the basal *U. hahnii* group and the remaining *U. zeylanica* group, including all taxa above *M. leichhardtii*, and the type species for the genus, *U. zeylanica* L. Notably, solely on the basis of the surveyed characters, the African *U. lucida* Bojer ex Sweet and *U. chamae* are clearly nested within the *U. zeylanica* group. The intermediate state of *M. leichhardtii* in terms of stamen structure between the two groups is not wholly reconciled in this (Asian) dataset; however, it seems likely, on the basis of this

anomaly, that the wider group of *Melodorum* taxa from Malesia–Australia also embody a distinct morphological identity within the *Uvaria* lineage.

Chloroplast phylogeny of the Uvaria group

The data of Zhou *et al.* (2009, 2010, 2012) and Chatrou *et al.* (2012) suggest that the entire '*Uvaria* group' in Asia appears to have radiated from a single dispersal event from Africa, implying (1) that *Uvaria sensu stricto* is paraphyletic, and (2) that the African and Asian lineages of *Uvaria* are not monophyletic sister groups (Fig. 2B).

The data also suggest that the following three monophyletic clades exist in the Asian *Uvaria* lineage: (1) a crown group comprising *Rauwenhoffia*, *Cyathostemma* and the majority of *Uvaria* species from South-east Asia and Malesia, (2) a basal group comprising *Anomianthus*, *Ellipeiopsis* and *U. hahnii*, along with the monotypic genus *Dasoclema* and (3) an intermediate clade comprising *U. pauciovulata* and all *Uvaria* species from Peninsular India and Sri Lanka, plus *Ellipeia*, and *Melodorum* from Malesia–Australia (Fig. 2B).

Although these inferred phylogenies differ from the established taxonomy for the *Uvaria* group, the plastid data contain a strong biogeographic signal, implying several region-specific radiation events in the Asian *Uvaria* lineage, including in India, in South-east Asia, in Malesia and in Australia. These events are consistent with a gradual colonisation of Asia by a *Uvaria* lineage that first emerged in East Africa, and later developed multiple region-specific morphological novelties as it dispersed across the heterogeneous landscape of southern and south-eastern Asia during the Miocene (24–5.5 million years ago) and Pliocene (5.5–2.5 million years ago). Implicit in this chloroplast data is that the calyx and corolla characters (principally sepal and petal thickness and reflexion, and the presence of marginal glands), which have traditionally been used to delineate genera in the *Uvaria* group, are homoplastic, and distinguish only apomorphic variants of an ancestral form, a pattern of character-trait distribution that also emerges in the morphometric analysis presented here.

Adhering to the principal of monophyly and assigning all the *Uvaria* group taxa to a larger *Uvaria s.l.* presents a basic problem for the taxonomist because this monophyletic group contains several morphological anomalies, notably the divergent floral types seen among the basal Asian clades, compared with the more derived type inherent in the original generic account (Linnaeus 1753).

Some underlying patterns provide a basis for a new taxonomy. Although branch support for terminal clades in the analyses of Zhou *et al.* (2009, 2010, 2012) is reduced, compared with more basal vicariance events in these phylogenies, in two cases, the basal member of the terminal clade displays raised stamen locules and a hairy stigma, whereas those in crown branches of the clade do not (Fig. 2B). This pattern implies that regional expansion events have given rise to multiple separate apomorphic changes to an ancestral Asian floral structure. It is likely that this ancestral floral type is the one retained by taxa in the basal *Uvaria hahnii* clade, because the alternative, namely that the

U. hahnii-group floral morphology is derived, would imply not two reversals (to the African type, in the clades containing *U. leichardtii* and *U. siamensis* (Scheff.) L.L.Zhou, Y.C.F.Su & R.M.K.Saunders, Fig. 2B), but four independent convergent apomorphies (to the *U. hahnii*-group type, including the *U. hahnii* and *U. pauciovulata* clades). Thus, the Asian ancestral type is likely to differ from its African equivalent, where the inferred ancestral morphology, as evident, for example, in *U. lucida*, matches the more derived Asian type, such as the genus type species, *U. zeylanica*, and the widespread *U. littoralis* and *U. grandiflora* Roxb. ex Hornem. The positioning of the sampled African *U. lucida* and *U. chamae* in the *Uvaria* group of the morphological analysis captures this similarity, adding weight to the molecular inference that the classic Asian *Uvaria* morphology is a reversion to an ancestral African form.

Although the various chloroplast lineages of *Uvaria* in Asia contain species that display both plesiomorphic and apomorphic structural traits (Fig. 2B), the stamen and carpel characters shared by basal members of the principal clades are also the characters that unite the basal clade in the morphometric topology inferred in Fig. 2A. Thus, although several taxa in the chloroplast phylogeny, notably *U. pauciovulata* and *U. siamensis*, emerge as basal to lineages that contain species with very different floral morphologies (Fig. 2B), they appear to retain plesiomorphic character traits associated with the earliest biogeographic expansion of *Uvaria* into Asia.

A revised taxonomy for *Uvaria* in Asia

The above chloroplast phylogeny analyses are unlikely to be final, and this is appropriate. Diagnostic and cladistically robust morphometric traits such as, in this analysis, stamen and carpel structure, may reflect more wide-ranging genomic affinities among *Uvaria* group taxa that are not captured in the chloroplast haplotype data of Zhou *et al.* (2009, 2010, 2012). Specifically, analysis of nuclear genomic affinities in *Uvaria s.l.* will provide a more holistic appraisal of species relations, allowing an inferred phylogeny with clearer links both to adaptive traits and to neutral morphological loci that have been subject to genetic drift (Hartl and Clark 2007; Knowles and Carstens 2007). For the present, these chloroplast data are the best available phylogenetic information for the *Uvaria* group, and it is reasonable to try and impose a primary monophyletic classification based on it, with additional detail that reflects diagnostic morphological differences among the major groups of taxa.

A monophyletic classification of *Uvaria* can be implemented by either splitting *Uvaria* into at least five separate genera (two in Africa, three in Asia), or subsuming all these associated genera into a broadened *Uvaria*. Although the data presented here suggest that the former would work for Asian taxa, there would be no taxonomic justification for separating *Uvaria* taxa in continental Africa from the more derived taxa in Asia, such as *U. zeylanica* and *U. hamiltonii*, and this approach would simply create a new paraphyletic classification. Thus, the latter option, creating a larger monophyletic genus, presents the fewest difficulties.

On the basis of this interpretation, and following Zhou *et al.* (2009), the defining morphological characteristic of the *Uvaria* lineage within the Annonaceae is the combined presence of stellate (star-shaped) hairs, a valvate calyx and an imbricate corolla. Within this monophyletic genus, and following the analysis presented here, the principal taxonomic division among the *Uvaria* of Asia rests on the presence or absence of raised stamen locules and an umbonate connective apex, and a hairy stigma. The following two taxonomic groupings are recognised on this basis: the *U. hahnii* group, which display the latter character traits; and the *U. zeylanica* group, the species in which display full-length locules, a flattened or elongate connective and a glabrous stigma. The dichotomy based on this division presents a conflict in terms of *Uvaria siamensis* and *U. pauciovulata* (and, although not included in this treatment, *U. cuneifolia* and affiliates of western Malesia) in that these taxa emerge as basal to the *Uvaria* lineage above the *U. hahnii* group in the chloroplast phylogeny. However, in terms of floral morphology, these species differ markedly from the remaining *Uvaria* species, although retaining the key traits of *U. hahnii* group that characterise the earliest colonial *Uvaria* lineages in Asia, as inferred by the molecular data. Considering this clear discontinuity in morphological identity, they are assigned for identification purposes to the *U. hahnii* taxonomic group.

The account presented here includes only a subset of *Uvaria* taxa that occur in Malesia and Australia (i.e. those species the distribution of which also extends into Peninsular Thailand, as detailed, where relevant, in the maps that follow). Importantly, because of the incomplete sampling of Malesian taxa, the two principal taxonomic groups described here are not proposed formally as sections; however, this may be appropriate with fuller evaluation of morphological diversity across Malesian taxa.

With this revised system, *Uvaria* is still unlikely to be confused with other Asian Annonaceae, because the only genera that also display stellate hairs are in other ways distinct. In *Cyathocalyx* Champion ex Hook.f. & Thomson, the petals are narrowly constricted and elongate above the base, whereas in *Anaxagorea* Saint Hilaire, *Neo-Uvaria* Airy-Shaw and the introduced *Annona squamosa* L. the ovules have basal placentation. *Anaxagorea* also displays an inner whorl of staminodes and there are two ovules only. In Africa, *Dielsothamnus* R.E.Fr. is distinct from *Uvaria*, in having valvate petals and a single carpel, *Annickia* van Setten & Maas has no outer whorl of petals and a single basal ovule, whereas *Tetrameranthus* R.E.Fr. has eight petals in two whorls and an elongate cylindrical torus. In the Americas, where *Uvaria* is absent, the stellate-haired *Duguetia* Saint Hilaire and *Pachypodanthium* Engler & Diels are both distinct in having a single basal ovule.

Uvaria L., *Sp. pl.* 1: 536 (1753)

Type: Uvaria zeylanica L.

Marenteria Noronha ex Thouars, *Gen. Nova Madagasc.* 18 (1806).

Type: not designated.

Cyathostemma Griff., *Not. Pl. Asiat.* 4: 707, t 650 (1854).

Type: Cyathostemma viridiflorum Griff. (as '*viridiflora*').

Ellipeia Hook.f. & Thomson, *Fl. Ind.* 1: 104 (1855).

Type: *Ellipeia cuneifolia* Hook.f. & Thomson.

Tetrapetalum Miq., *Ann. Mus. Bot. Lugduno-Batavi.* 2: 1 (1865).

Type: *Tetrapetalum volubile* Miq.

Armenteria Baill., *Bull. Mens. Soc. Linn. de Paris* 1: 338 (1882), *nom. inval.*, pro syn. *Rauwenhoffia* Scheff., *Ann. Jard. Bot. Buitenzorg* 2: 21 (1885).

Type: *Rauwenhoffia siamensis* Scheff.

Uvariella Ridl., *Fl. Malay. Penins.* 1: 35 (1922).

Type: *Uvariella leptopoda* (King) Ridl.

Dasoclema J.Sinclair, *Gard. Bull. Singapore* 14: 273 (1955).

Type: *Dasoclema siamensis* (Craib) J. Sinclair.

Ellipeiopsis R.E.Fr., *Ark. Bot. ser.* 2, 3: 41 (1955).

Type: *Ellipeiopsis ferruginea* (Ham. ex Hook.f. & Thomson) R.E.Fr.

Habit climbers or sarmentose shrubs, with often prominent ferruginous stellate indument. *Leaves* membranous or coriaceous, obovate or less often elliptic or ovate, base cordate, subcordate or cuneate, apex acute, acuminate or obtuse, *veins* 6–25+, subparallel or convergent, secondary veins complete and kinked or incomplete, *indument* (sub)tomentose and ferruginous on both surfaces of young leaves, in mature leaves abaxial surface sparse or glabrous, hairs erect when persistent, rarely scabrous, adaxial surface tomentose to subglabrous, hairs spreading. *Petiole* with abaxial groove, adaxial surface often transversely foliated, tomentose to subglabrous. *Inflorescence* a monochasial or rarely branched rhipidium of 1–5 flowers, typically on younger shoots, rarely cauliflorous, secondary buds arising from prophyll in axil of bract just below articulation of pedicel, bract also present midway along pedicel, bracts ovate or obovate, membranous or coriaceous, clasping or free, sometimes large and leaf-like, often wanting, peduncle, pedicel and calyx with identical indument, hairs tomentose or rarely sparse, fine or warted. *Calyx* valvate, basally connate or calyprate, sepals 3, rarely 2 or 4, membranous and spreading or fleshy and concave. *Corolla* petals in 2 imbricate whorls of 3 petals each, petals 6 in number or very rarely rarely 4–8, whorls subequal, less often inner petals conspicuously smaller than and distinct in shape compared with outer, mature petals erect, reflexed or partially reflexed at maturity, fleshy or membranous, ovate, oblong or obovate, red, purple, yellow, white or green, apex obtuse, acute or bluntly acute. *Stamens* laminar or rarely cuneate, locules equal or subequal and extending the full length of the stamen connective, or unequal in length and raised from the stamen base on a short filament, stamen apex papillate or smooth, globose, umbonate, flattened or concave, or elongate and flattened, stamens all fertile or with outer whorl of staminodes or substaminodes. *Carpels* 1 to ~50, hairy, stigmas glabrous or hairy, elongate or flattened, lobes conical or U-shaped, ovules 2–30 in 2 lateral rows, or rarely 1, inserted apically or subapically. *Fruit* monocarps globose, oblong or cylindrical, stipitate or rarely sessile, flesh soft at maturity, pericarp smooth, warted, bearded or with longitudinal ridges, green, red or yellow in colour; Seeds 1–30, lateral in 2 rows, or rarely apical or subapical, testa brown, smooth, ruminations visible, aril circular or triangular.

Key for flowering material

Note: flowers of *U. vietnamensis* are unknown; this taxon is identified only in the fruiting specimen key.

1. Inner petals without conspicuous marginal glands, stamen locules equal or subequal in length, extending full length from connective apex to stamen base, carpels 10–50+, stigma glabrous, ovules 2–30+, laterally inserted in 2 rows..... *Uvaria zeylanica*-group
- Inner petals often with conspicuous marginal glands at base, stamen locules unequal in length, raised on a short filament, extending 0.5–0.85 the length from connective apex to stamen base, carpels 10–30, or rarely 1, stigma hairy or rarely glabrous, ovules 1–3, apically or subapically inserted in 1 or 2 rows, or ovules 2–16, laterally inserted in 2 rows..... *Uvaria hahnii*-group

Key to continental Asian species of the *Uvaria zeylanica* group

1. Petals ovate, elliptical, oblong or obovate, acute or obtuse, spreading, often reflexed, membranous or fleshy, stigma short with broad U-shaped lobes.....2
- Petals broadly ovate, (bluntly) acute, erect, occasionally spreading but never reflexed, fleshy, never membranous, stigma elongate, conical or with broadened lobes18
2. Calyx calyprate in bud.....3
- Calyx valvate or, if fused, apex splitting early to leave connate (sometimes cup-shaped) ring around lower part of bud.....12
3. Pedicel and calyx warty with dense indument of many-branched thickly set hairs4
- Pedicel and calyx often hirsute, with uniform indument of ferruginous stellate hairs.....6
4. Leaf indument on lower surface ferruginous; compound peduncle–pedicel length <15 mm; stipe of mature monocarp <20 mm long1
- U. lamponga*
- Leaf indument on lower surface sparse to subglabrous; compound peduncle–pedicel length >15 mm; stipe of mature monocarp >20 mm long.....5
5. Petals ≤6, red throughout, obovate, apex obtuse, concave; apicule of mature monocarp rudimentary.....2
- U. concava*
- Petals ≥6, red with yellow base, elliptical, apex bluntly acute, flattened; apicule of mature monocarp thick and prominent 5–10 mm long.....3
- U. macropoda*
6. Mature petals 20–50 mm long, stamens and carpels ≥6 mm long.....4
- U. grandiflora*
- Mature petals <22 mm long, stamens and carpels <6 mm long7
7. Flowers 30–45 mm in diameter, buds 7.5–15 mm in diameter before opening.....8
- Flowers <30 mm in diameter, buds 5–7.5 mm in diameter before opening.....10
8. Young shoots, leaves, pedicel and outer surface of calyx with persistent ferruginous hairs >0.5 mm long and 1–3-branched hairs.....5
- U. curtisii*
- Young shoots, leaves, pedicel and outer surface of calyx with deciduous hairs ≤0.4 mm long and 1- to many-branched hairs, subtomentose, later sparsely hairy or subglabrous9
9. Leaf apex cuspidate or acuminate; bracts narrowly ovate-acute, ~2 mm wide, often lost at maturity; calyx splitting unevenly into 2–4 sepals; fruit oblong, stipe <15 mm long.....6
- U. dac*
- Leaf apex acute; bracts broadly obovate to circular–ovate, often wrapping around pedicel, ~10 mm wide, persistent; calyx splitting evenly into 3 sepals; fruit globose to oblong, stipe >15 mm long7
- U. hamiltonii*
10. Pedicel >20 mm long with prominent bracts8
- U. macclurei*
- Pedicel <20 mm long, bracts not prominent11

11. Petals yellow, oblong, apex obtuse, erect or partially recurved at maturity, never reflexed 9. *U. calamistrata*
 Petals red, elliptical, apex acute, fully reflexed at maturity 10. *U. zeylanica*
12. Calyx splitting apically in early bud to form 3-pointed connate ring around base of unopened corolla 13
 Sepals free in bud 14
13. Leaves 70–200 mm long, base retuse or shortly cordate, veins ≤ 12 ; inner petals opening with outer petals, never connivent 11. *U. sphenocarpa*
 Leaves 160–450 mm long, base cordate, veins ≥ 12 ; inner petals connivent, opening before senescence 12. *U. semecarpifolia*
14. Stamens all fertile 15
 Outer whorl of staminodes or substaminodes present 17
15. Corolla basally connate at maturity 13. *U. narum*
 Corolla free at maturity 16
16. Leaves $>150 \times 100$ mm, veins 5–25; inflorescence of 2–5 buds in tightly packed rhipidium, up to 3 open at any time, pedicels broad and flattened with abaxial groove, bracts broadly obovate, clasping 14. *U. littoralis*
 Leaves $<150 \times 80$ mm; veins 9–12; inflorescence of 1 or 2, rarely 3 buds, pedicel not flattened not grooved, bracts elliptic–oblong, free 15. *U. microcarpa*
17. Leaves distinctly scabrid on upper surface 16. *U. rufa*
 Leaves often smooth and waxy, subglabrous to glabrous on upper surface 17. *U. lobbiana*
18. Peduncle elongate, ~20–50 mm long 19. *U. griffithii*
 Peduncle <10 mm long, or pedicels sessile 19
19. Pedicel elongate, 30–90 mm long 20
 Pedicel ≤ 25 mm long 22
20. Pedicel >1.5 mm wide, flattened 20. *U. tonkinensis*
 Pedicel <1.5 mm wide, not flattened 21
21. Pedicel 35–40 mm long, 1 mm wide, outer petals >6 mm long $\times >5$ mm wide, inner petals >6 mm long $\times >4$ mm wide – north-eastern Vietnam and southern China 21. *U. boniana*
 Pedicel ~30 mm long, <1 mm wide, outer petals <6 mm long $\times <5$ mm wide, inner petals <6 mm long $\times <4$ mm wide – central Vietnam 22. *U. flexuosa*
22. Leaves distinctly oblong, base subcordate–obtuse 23. *U. pierrei*
 Leaves obovate, elliptical or lanceolate, base cuneate or retuse 23
23. Leaves elliptical, lanceolate or narrowly ovate, 70–150 \times 20–50 mm 24
 Leaves broadly obovate, 50–250 \times 30–95 mm 25
24. Leaf base cuneate, outer petals <6 mm long $\times <5$ mm wide, inner petals ~3.35 mm long $\times <3$ mm wide, stigma lobes broad – Myanmar, Indochina, Andamans, Malesia 24. *U. micrantha*
 Leaf base subcordate, outer petals up to >6 mm long $\times >5$ mm wide, inner petals 5–8.5 mm long $\times >3$ mm wide, stigma lobes narrow, elongate – south-western Thailand, Taninthari, Myanmar 25. *U. utteridgei*
25. Inflorescence from younger shoots, petals coriaceous, margin prominently tomentose, petals <7 mm long, not spreading at maturity – western Indochina, Assam 26. *U. argentea*
 Inflorescence from mature shoots or older wood, petals fleshy, margin not tomentose, petals >7 mm long, often spreading at maturity – Isthmus of Kra to Sumatra 27. *U. wrayi*

Key to continental Asian species of the *Uvaria hahnii* group

1. Carpels 1 28. *U. dasoclema*
 Carpels >1 2
2. Ovules 1–3, apically or subapically inserted 3
 Ovules >3 4
3. Habit an erect shrub, leaves broadly elliptic to oblong, base cordate, 120–150 \times 50–80 mm, inner petals basally glabrous with conspicuous marginal glands, ovules 1 29. *U. ferruginea*

- Habit a scandent shrub or woody climber, leaves ovate to elliptic to narrowly obovate, base shortly cordate or retuse, 95–140 \times 50–60 mm, inner petals basally glabrous but without marginal glands, ovules 1–3 30. *U. pauciovulata*
4. Sepals ovate-lanceolate, leaf-like with prominent central vein, up to ~10 \times 15 mm 31. *U. hahnii*
 Sepals ovate-acute, fleshy or coriaceous, prominent vein lacking, up to ~3 \times 6 mm 5
5. Inner petals with basal marginal glands, petals coriaceous to membranous, broadly elliptical-acute at first, expanding to obovate-acute at maturity, flattened, ~21.5 \times 11.5 mm, ovules ~14–16 32. *U. dulcis*
 Inner petals without marginal glands, petals fleshy, remaining ovate and concave, ~8 \times 8 mm, ovules ~4–8 33. *U. siamensis*

Key for fruiting material of all taxa in continental Asia

1. Shrub with shortened horizontal stems and erect branches; monocarps red, ellipsoidal, single seed with apical placentation 29. *U. ferruginea*
 Scandent shrub or climber with vertical stem, placentation lateral or sub-basal, seeds 1 to many 2
2. Monocarps 10–30+, 1–4-seeded, globose, ovoid or transversely ovoid; pericarp thin; stipes typically long and narrow, never wider than 2 mm 3
 Monocarps 2–10(–20), 4–30-seeded, globose, ovoid or oblong; pericarp thickened, fleshy; stipes typically short and thickened or long with deep striations 9
3. Fruit transversely ovoid with prominent apicule, densely tomentose; pericarp thin, seeds 1–2(–3) 30. *U. pauciovulata*
 Monocarps largely glabrous, apicule when present small and blunt, seeds 1–4 4
4. Leaves elliptic to broadly elliptic to shortly obovate, base retuse–shortly cordate, apex acute, veins 15–18, subparallel, frequently branching basally and medially; indument tomentose on younger shoots, later sparse becoming subglabrous, except over midrib with tomentose ~1 mm long erect hairs 32. *U. dulcis*
 Leaves narrowly ovate to elliptic to obovate, base cuneate to retuse, apex bluntly acute to acuminate, usually waxy; veins (6–)8–14(–16), rarely branching basally or medially; indument occasionally persistent over abaxial midrib, elsewhere hairs sparse, usually glabrous or subglabrous, hairs less than 0.5 mm long 5
5. Leaves 100–250 mm long, broadly elliptical to obovate, base broadly retuse to narrowly cordate, apex often with prominent acuminate 6
 Leaves 50–150 mm long, narrowly ovate–elliptical–obovate or narrowly oblong, base cuneate or narrowly retuse, apex acute 7
6. Leaves elliptical–narrowly obovate, base retuse, apex acuminate or rarely acute, ~130–170 \times 50–60 mm, thinly coriaceous, waxy above, veins 9–11 20. *U. tonkinensis*
 Leaves obovate, less often oblong, base retuse, apex acute–cuminate, up to 250 \times 95 mm, membranous, veins 12–15 27. *U. wrayi*
7. Leaves distinctively narrow-oblong, base retuse, apex obtuse or retuse, leaf margin turned downward 23. *U. pierrei*
 Leaves ovate-elliptical, base cuneate, apex acute to narrowly acute, leaf margin flattened 8
8. Monocarps 10–20, green turning yellow, globose to shortly oblong, ~9.5 \times 8 mm at maturity, no apicule present; smooth; stipe 14–20(–23) mm, smooth, seeds 1–2(–3) 24. *U. micrantha*
 Monocarps 25–45+, green turning red or purple at maturity, ovoid, to shortly cylindric, ~15–17(–20) \times 11–13 mm, surface often warty with short scattered stellate hairs; stipe ~35–45 mm long, striate with sparse hairs, seeds 4–6 21. *U. boniana*
9. Monocarps sessile, in pseudo syncarpous conglomerate 11. *U. sphenocarpa*
 Monocarps stipitate, sides not flattened against adjacent monocarps 10

10. Monocarp with dense covering of epidermal outgrowths.....11
 Monocarp smooth, striate or tubercled, but without epidermal outgrowths.....12
11. Monocarps 20+, with dense beard of 3–6 mm long hair-like outgrowths, each carrying a tomentum of rufous stellate hairs; stipe up to 45 mm long \times 2 mm in diameter..... 18. *U. vietnamensis*
 Monocarps 2–12, initially covered with prominent beard of 5–8 mm long membranous bluntly triangular outgrowths, later tuberculate with scattered remnants of outgrowths over surface; stipe short, 3–5 mm \times 2.5–3 mm.....9. *U. calamistrata*
12. Monocarp epidermis deeply grooved and warted; stipe 2–5 mm wide, 5–10 mm long, deeply striate.....13
 Monocarp smooth, glabrous, or where tubercled stipe much greater than 10 mm long.....14
13. Leaves narrowly elliptic–obovate, acute–distinctly acuminate, base retuse, \sim 180–190 \times 60–80 mm; veins 11–13; monocarps 1–8(–10), \sim 45 \times 25 mm in diameter, pericarp thickly striate; seeds 6–12.....
6. *U. dac*
 Leaves elliptical–narrowly obovate, apex acute, shortly acuminate or rarely obtuse, base cuneate–retuse, \sim 110–160 \times 40–60 mm, veins (9–) 10–12, monocarps 1–4, 40–45 \times 30–35 mm in diameter, pericarp tuberculate, seeds 6–10.....8. *U. macclurei*
14. Stipe short, \sim 2–4 mm \times 2 mm; monocarps oblong, pale yellow or cream in colour at maturity.....15
 Stipe \sim 5–50 \times 1.5–4 mm; monocarps green, red or purple at maturity, glabrous or hairy.....17
15. Leaves broadly elliptic to narrowly obovate..... 31. *U. hahnii*
 Leaves lanceolate or elliptical or ovate to elliptic to oblanceolate....16
16. Leaves lanceolate or elliptical, base retuse, apex acute, \sim 90–150 \times 30–40 mm.....33. *U. siamensis*
 Leaves ovate–elliptic–oblanceolate, base cuneate, apex acute–acuminate, \sim 55–70(–95) \times 20–28(–35) mm..... 10. *U. zeylanica*
17. Stipe elongate, \sim 50–150 \times 2–3 mm, striate.....19
 Stipe 5–50 mm long, smooth or shallowly striate.....18
18. Monocarp globose or ovoid, \sim 16–18 \times 20–25 mm, prominently tubercled; seeds 4–6..... 17. *U. lobbiana*
 Monocarp oblong or cylindrical, \sim 35–70 \times 20–30 mm, smooth or somewhat tubercled; seeds 2–16.....20
19. Monocarp narrowly cylindrical with prominent tapering apicule \sim 5–10 mm long; seeds 10–16.....3. *U. macropoda*
 Monocarp shortly oblong to oblong, apicule when present \sim 1–2 mm long; seeds 2–10.....2. *U. concava*
20. Monocarp oblong, glabrous to subglabrous.....21
 Monocarp broadly ellipsoidal to oblong, ferrugino-tomentose until maturity.....23
21. Stipe narrow, \sim 10–35 \times 1–2 mm in diameter; monocarps \sim 10–20 \times 6–10 mm.....22
 Stipe short, thickened, 2–10 \times 2–4 mm in diameter; monocarps up to \sim 30 \times 16.5 mm.....14. *U. littoralis*
22. Monocarps 4–8+, green turning yellow then dark purple at maturity, ovoid to shortly oblongoid \sim 20 \times 10 mm in diameter; stipe 10–15 \times 1–2 mm; seeds \sim 6–8..... 15. *U. microcarpa*
 Monocarps 5–20+, green turning orange then red, globose to oblong, 10–15 \times 6–8 mm in diameter; stipe 25–35 \times 1 mm in diameter; seeds 2–6.....13. *U. narum*
23. Monocarps oblong–cylindrical, 50–75 \times 10–20 mm in diameter; deeply striate; seeds 16–30.....4. *U. grandiflora*
 Monocarps globose–cylindrical, up to \sim 30 \times 20 mm in diameter; smooth or tubercled, seeds 5–20+.....24
24. Stipe 10–15 mm long; leaves broadly obovate 160–400 mm long, thickly coriaceous, glabrous above at maturity..... 12. *U. semecarpifolia*
 Stipe 25–35 mm long; leaves obovate, 100–200 mm long, coriaceous, upper surfaces scabrous to sparse at maturity.....25
25. Monocarps 10–14, globose–oblong, \sim 20 \times 15 mm in diameter, young? fruits green turning red; outer surface ferrugino-tomentose, indument tubercled; seeds 6–12..... 7. *U. hamiltonii*
 Monocarps 4–8(–20), cylindrical, 25–35 \times 14–21 mm in diameter, young fruits green with rufous tint, turning bright red, outer surface subglabrous, seeds 5–20+..... 16. *U. rufa*

Uvaria zeylanica group

1. *Uvaria lamponga* Scheff., *Natuurk. Tijdschr. Ned.-Indië* 31: 2 (1869)

Type citation: ‘in Sumatra, prov. Lampongs, speciem invenit TEYSMANN...’.

Type: BO?, n.v.

Uvaria andamanica King, *J. Asiat. Soc. Bengal Pt. 2, Nat. Hist.* 61(1): 21 (1892).

Type: INDIA. Andaman Islands, south Andaman, Port Blair, 1 Apr. 1884, *King’s Collector [H.H.Kunstler] 207* (lecto: CAL 000004186!, *fide* D.Mitra, *Fasc. Fl. India* 10: 14 (1982)).

[*Uvaria ferruginea* auct. non J.E.Teijsmann & S.Binnendijk, *Cat. Hort. Bot. Bogor.* 175 (1866)].

Climber. Young shoots stout, subtomentose or floccose, becoming subglabrous and striate, bark black, hairs many-branched, rufous. Leaves narrowly obovate to oblanceolate, base retuse, apex acuminate, 150–250 \times 60–80 mm, acumen up to 15 mm, veins 13–23; indument variable, upper blade glabrous, sparse erect ferruginous hairs over midrib and primary veins, hairs on lower surface many-branched, ferruginous, tuberculate, becoming subtomentose to subglabrous. Petiole 5–6 \times 2 mm, tomentose. Inflorescence leaf-opposed, flowers 2 or 3, or up to 5 in a branching rhipidium, peduncle 2–5 mm long, pedicel 4–10 mm long, basal and medial bracts ovate, 4–5 \times 4–5 mm, peduncle, pedicel and bracts tuberculate, hairs as for lower surface of leaves. Calyx calyptrate in bud, sepals 3, broadly ovate, 7–8 \times 4 mm, basally connate, outer surface as for pedicel, inner surface hairs fine, combed. Corolla 2 subequal whorls of 3 petals, red in colour, coriaceous, broadly ovate, \sim 10 \times 6 mm, apices incurved. Stamens numerous, 3–4 mm long, locules running full length of stamen, apex flattened. Carpels numerous, 3–4 mm long, ovary tomentose, stigma glabrous, U-shaped, ovules 4–6. Fruit monocarps 5–30, ovoid to oblongoid, \sim 18 \times 25 mm, pericarp thick, epidermis warted, hairs many-branched, spreading, deciduous, stipe \sim 10 \times 3–4 mm; seeds 1–6, compressed-ellipsoid, \sim 12 \times 10 \times 5 mm.

Distribution

Uvaria lamponga is a very rare species, with only isolated collections, all from mixed monsoon forest. The distribution is shown in Fig. 8.

Notes

Uvaria lamponga is similar to both *U. concava* Teijsm. & Binn. and *U. macropoda* Hook.f. & Thomson; however, the shorter stipe and floccose indument on the underside of the leaves should make it easily distinguishable. The indument is similar

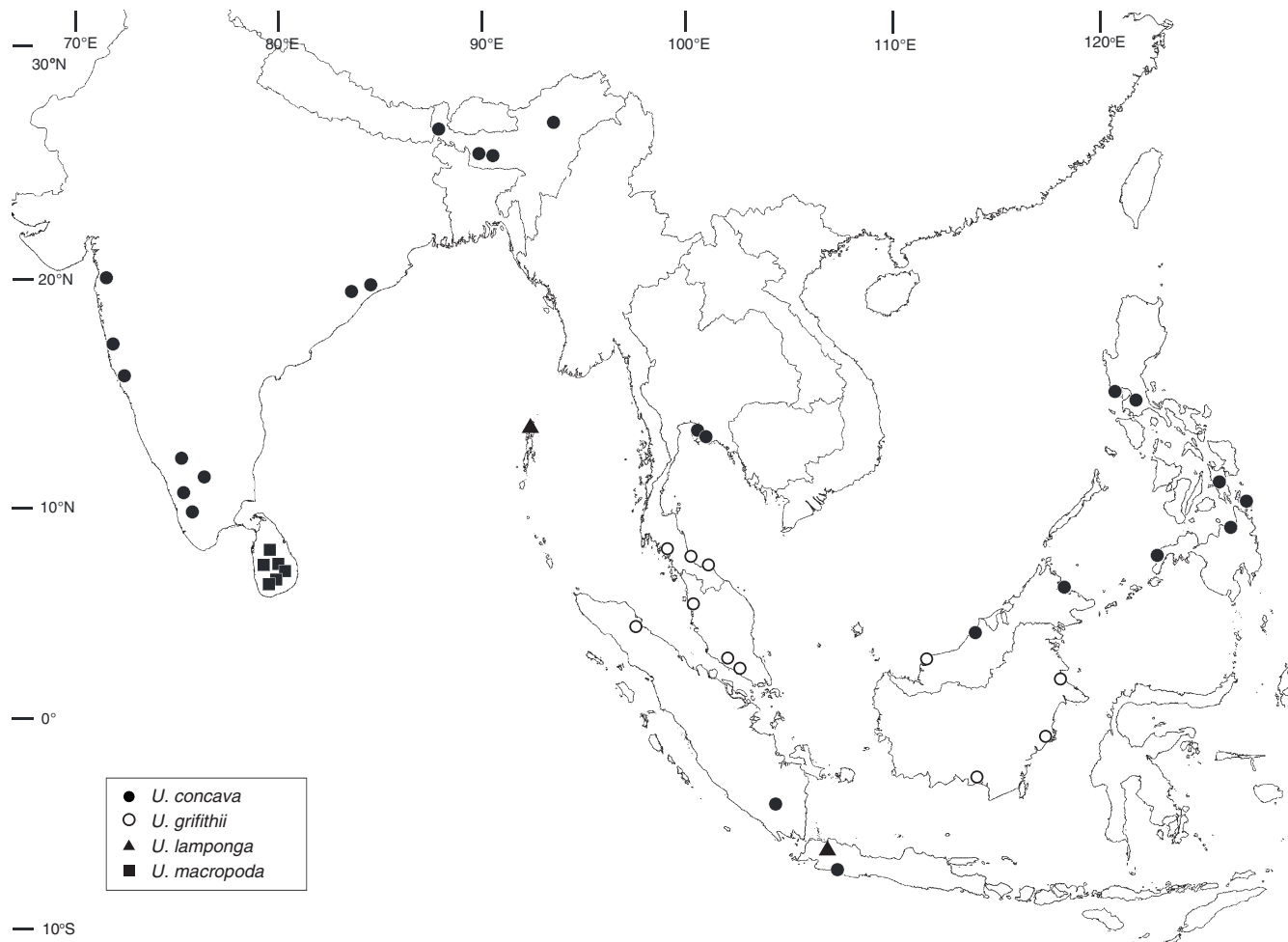


Fig. 8. Distribution of *Uvaria concava*, *U. griffithii*, *U. lamponga* and *U. macropoda* in southern and South-east Asia on the basis of herbarium specimens verified in this study.

to *U. lobbiana* Hook.f. & Thomson, but this latter species has valvate sepals, an outer whorl of staminodes and a 35–70-mm-long stipe.

2. *Uvaria concava* Teijsm. & Binn., *Natuurk. Tijdschr. Ned. Indië* 3: 331 (1852)

Type: INDONESIA. Java, cultivated in Hort. Bot. Bogor, *s. dat.*, *S.Binnendijk* HB 17623 (lecto: BO 1824857 (image!)), *fide* I.M.Turner, *Phytotaxa* 36: 97 (2011)).

Uvaria lurida Hook.f. & Thomson, *Fl. Ind.* 1: 101 (1855).

Type: INDIA, Assam, Khasia, 2000 ft [~609.6 m], 2 Oct. 1850, *J.D.Hooker & T.Thomson* 2468 (lecto: K 000380703!, *fide* I.M.Turner, *Phytotaxa* 36: 97 (2011)).

Uvaria narum var. *macrophylla* Hook.f. & Thomson, *Fl. Brit. India* 1: 50 (1872); *Uvaria hookeri* King, *Ann. Roy. Bot. Gard. (Calcutta)* 4: 28, t. 22 (1893).

Type: INDIA. Kerala, Travancore mountains, Oct. 1814, *Wall. Cat. no. 6473C* (lecto: K-W 000442824!, *fide* I.M. Turner, *Nordic J. Bot.* 33: 289 (2015)).

Unona leytenensis Elmer, *Leafl. Philipp. Bot.* 5: 1744 (1913); *Uvaria leytenensis* (Elmer) Merr., *Philipp. J. Sci., C* 10(4): 230 (1915).

Type: PHILIPPINES. Mindanao, Province of Agusan, Mt Urdaneta, *s. dat.*, *A.D.E.Elmer* 13880 (lecto: L 0190815!, *fide* I.M.Turner, *Phytotaxa* 36: 98 (2011)).

Uvaria eucineta Bedd. ex Dunn, *Bull. Misc. Inform. Kew* 1914: 182 (1914).

Type: INDIA. Madras, Russelondak Hills, *s. dat.*, *R.H. Beddome* 50 (lecto: CAL 000004182!; isolecto: BM 000527912!, *p.p.*, *fide* D.Mitra, *Fasc. Fl. India* 10: 15 (1982)).

Large woody climber up to 30 m tall. Young shoots tomentose, indument becoming sparse very quickly, hairs ferruginous, many-branched. Leaves elliptic-oblong to narrowly obovate, base retuse, apex acute or less often acuminate, ~130–150 × 40–50 mm, coriaceous; veins ~10–12; indument upper surface entirely glabrous, lower surface indument sparse, hairs many-branched, blunt. Petiole ~7–10 × 1.25 mm, hairs sparse, blunt, many-branched, abaxial groove deep, often overtopped by margins, transverse foliations distinct, warty. Inflorescence terminal or leaf-opposed by apposition, flowers

solitary or with dormant secondary bud, peduncle sometimes evident up to 5 mm; pedicel ~15–20(–50) × 2.5 mm, tuberculate, peduncle-pedicel often distinctly broader than supporting shoot, buds globose to conical with prominent apicule. Calyx calyptrate, sepals (2–)3(–4), basally connate, ~11 × 10 mm, ovate-acute, concave, outer surface with same indument as pedicel, inner surface with subtomentose indument of fine, few-branched straggling hairs, subglabrous basally. Corolla of 6 (rarely 4) petals, basally connate in a single whorl, petals dark pink or red in colour, very broadly obovate, apex obtuse, ~20 × 15 mm, outer surface densely tomentose with many-branched pale to rufous hairs, less tuberculate than calyx and pedicel, inner surface subtomentose as for inner surface of calyx, but denser, petals detaching from receptacle as connate ring. Stamens numerous, ~3.5 mm long, glabrous, locules extending to full length of stamen, connective apex flattened or shallowly truncate. Carpels numerous, ~3.5 mm long, ovary with flattened, many-branched spreading hairs, stigma short, U-shaped, not distinctly lobed, ovules 8–10 in two rows. Fruit monocarps ~5 to many, green turning orange or yellow at maturity, smooth, globular-oblongoidal, ~15–30 × 10–17 mm, often with 1 or more longitudinal ridges, small apicule often present, occasional constrictions between seeds, pericarp soft, fleshy at maturity, stipe long, ~50–100(–120) × 2–4 mm, typically flattened, often with prominent longitudinal ridges or striations, young stipe and monocarp with sparse indument, later subglabrous; seeds ~2–10 in two closely packed rows, ovoid-compressed ovoid, 8–11 × 6–9 × 3–5 mm, smooth, aril and raphe not prominent. (Fig. 1F.)

Distribution

This is the most widely distributed *Uvaria* species in Asia, covering almost the entire distribution of the genus. The distribution is shown in Fig. 8.

Notes

This taxon is widely distributed, with much continuous variation in floral and fruit characters. Even though Zhou *et al.* (2012) identified some variation at molecular level between Indian (identified as *U. lurida* Hook.f. & Thomson) and Indonesian (identified as *U. concava*) accessions, morphometric analysis by Meade (2001) demonstrated that *U. concava*, *U. eucineta* Bedd. ex Dunn and *U. lurida* differ only in continuous characters. King elevated *U. narum* var. *macrophylla* of Hooker and Thomson to *U. hookeri*. Both accounts distinguished this taxon by the co-occurrence of long, thick stipes and small, monocarps with seeds in two rows; however, the specimens in question are merely young fruiting specimens of *U. concava* (Meade 2001). The most variable characters in *U. concava* are fruit size and pedicel length. Plants from wetter habitats produce typically larger fruits than those from elsewhere, and some of the Philippine specimens exhibit much longer pedicels than normal. However, the tuberculate inflorescence, unevenly splitting calyx and connate corolla are distinctive characters throughout the range, and none of the variation is distinctive or consistent enough to warrant the formal designation of varieties. The thickened stipe and larger monocarps of *U. concava* should make it easy to distinguish this species from *U. narum* (Dunal) Blume.

3. *Uvaria macropoda* Hook.f. & Thomson, *Fl. Ind.* 1: 101 (1855)

Type: SRI LANKA. *s. loc. s. dat.*, 1600 ft [~487.7 m], *G.W. Walker 160* (lecto: K 000380706!, *fide* I.M. Turner, *Nordic J. Bot.* 33: 292 (2015)).

Climber up to 35 m tall. Young shoots subtomentose with blunt rufous hairs, quickly becoming deeply striate and grey in colour with prominent lenticels. Leaves elliptical–obovate, base narrowly retuse to cuneate, apex obtuse to shortly acute to acuminate, 80–130(–150) × 30–50(–60) mm, coriaceous, waxy; veins ~8–12(–14); indument upper blade completely glabrous, lower blade and midrib subglabrous with very rare rufous ~10+-branched hairs. Petiole ~5–6(–8) × 1 mm, indument sparse, hairs blunt. Inflorescence terminal or (sub)opposed by apposition, flowers solitary, pedicel ~15–20 × 1–1.5(–2) mm in diameter, peduncle-pedicel distinctly broader than young shoots, narrowing at base, bracts usually wanting, buds spherical or conical with a prominent apicule, pedicel and bud covered with thickened, many-branched hairs, giving coarsely tuberculate appearance. Calyx calyptrate, splitting irregularly into (2–)3(–4) unevenly sized sepals, up to ~10 × 9 mm, ovate, acute, often one larger sepal carrying apicule, outer surface indument as for pedicel, inner surface hairs smaller and finer, surface smooth, not tuberculate. Corolla of 6–8 petals, basally connate in a single whorl, petal bases fused for 1–4 mm, petals red with yellow base, elliptical to oblong, acute, ~18 × 8 mm, petal apices often concave but not distinctly obovate, indument on outer surface densely tomentose with pale, many-branched fine hairs, overlain by scattered large rufous hairs as found on calyx and pedicel, more dense along central axis and towards base, especially on outer whorl, inner surface densely and shortly tomentose with no large rufous hairs. Stamens numerous, ~2.25–3 mm long, glabrous, locules extending to full length of stamen, connective apex broad, convex or flattened or rarely shallowly truncate, shortly papillate. Carpels ~30, 3–3.75 mm long, ovaries tomentose with flattened spreading hairs, stigmas U-shaped with very large, broad lobes ~1–1.25 mm wide, raised distinctly above stamens, some occlusion of stigma on external side, ovules 12–16. Fruit monocarps, ~10–16, narrowly cylindrical and angular with 4 distinct longitudinal ridges, 50–70 × 10–15 mm, apicule usually thickened and prominent, ~5–10 mm long, pericarp thick but outline of seeds usually visible, indument sparse, stipes distinctly elongate, 65–150 mm+, thickened at base and apex, deeply striate; seeds 10–16, in two rows closely packed together to seem like one row, oval, ~7 × 5 × 4 mm, smooth, aril and raphe not well developed.

Distribution

Widely distributed in dry and moist areas of Sri Lanka, occasional in disturbed forest of the wetter south-western hills, absent from the southern and south-western lowlands. Distribution is shown in Fig. 8.

Notes

This taxon is intermediate in morphology between *U. concava* and *U. narum*, but easily distinguished from these two species by its few carpels with very large, broad stigmas and its

distinctive fruits with a large, tapering apicule. Huber (1985) reported that in Ceylon *U. narum* and *U. macropoda* are ecologically distinct, with *U. narum* being restricted to the wetter south and south-west of the island.

4. *Uvaria grandiflora* Roxb. ex Hornem., *Hort. Bot. Hafn.*, suppl. 140 (1819)

Type: INDIA. Bengal. Cultivated in the Calcutta Botanic Garden, Apr. 1818, *Anon. s.n.* (lecto: C 10005704!, *fide* I.M. Turner, *Phytotaxa* 36: 99 (2011)).

Uvaria grandiflora Roxb., *Hort. Bengal.* 43 (1814), *nom. inval.*, *nom. nud.* *Unona grandiflora* Lesch. ex DC., *Prodr.* 1: 90 (1824).

Type citation: '(Leschenault! in litt. ... in Bengalo.' *Type*: ?P, *n.v.*

Uvaria purpurea Blume, *Bijdr. Fl. Ned. Ind.* 1: 11 (1825).

Type: INDONESIA. Java, *s. dat.*, *Blume s.n.* (neo, here designated: NY 00059989!).

Uvaria grandiflora Roxb., *Fl. Ind. ed. 1832* 2: 665 (1832), *nom. illeg.*, *non* Roxb. ex Hornem. (1819).

Type: INDIA. India Orientalis, *s. dat.*, *Wallich s.n.* (neo, here designated: BM 000528031!).

Uvaria platypetala Champ. ex Benth., *Hooker's J. Bot. Kew Gard. Misc.* 3: 257 (1851).

Type: CHINA. Hong Kong, 1850, *Champion 38* (lecto, here designated: K 000380694!).

Uvaria rhodantha Hance ex Walp., *Ann. Bot. Syst.* 2: 19 (1851).

Type: CHINA. Hong Kong, Apr. 1852, *H.F. Hance 933* (neo: BM 000527943!, *fide* I.M. Turner, *Phytotaxa* 36: 99 (2011)).

Uvaria purpurea var. *tuberculata* King, *J. Asiat. Soc. Bengal Pt. 2, Nat. Hist.* 61: 18 (1892).

Type: MALAYSIA. Perak, Larut, Aug. 1883, *King's Collector [H.H. Kunstler] 4786* (lecto: K 000380129!; isolecto: G!, *fide* J. Sinclair, *Gard. Bull. Singapore* 14: 203 (1955)).

Uvaria rubra C.B. Rob., *Bull. Torrey Bot. Club* 35: 68 (1908).

Type: PHILLIPINES. Santa Cruz, Davao Province, Mindanao, 29 June 1905, *Williams 3042* (holo: NY 0005991!, iso: NY 0005992–3!).

Notes

The more commonly used name *U. purpurea* Blume (1825) postdates Horneman's publication of the original Roxburgh description (1819) of this taxon as *U. grandiflora*. In the case of both *U. purpurea*, and Roxburgh's later publication of the illegitimate later homonym *U. grandiflora* in 1832 (Roxburgh 1832), the original type material is lost, and the named neotypes (from the Blume and Wallich herbaria) are the only known material to have survived from the original collections, which Blume and Roxburgh reviewed in preparation of their taxonomic accounts. The fruit of *U. grandiflora* is variable. The monocarp can be wholly tubular or constricted between the seeds and the surface can be either smooth, striate or tuberculate. As the fruit matures, the pericarp softens, causing the outline of seeds within the monocarp to become more sharply defined. *Uvaria*

grandiflora produces the largest bracts, sepals, petals, stamens and carpels of any *Uvaria* species in Asia, and the fruit also produces the most seeds per carpel (up to 30). Where the inflorescence produces more than one flower, the dimensions of all organs are reduced, and this can lead to confusion with large-flowered specimens of *U. microcarpa* Champ. ex Benth. However, *U. microcarpa* has an outer whorl of staminodes. Infertile specimens are most likely to be confused with *U. littoralis*, *U. microcarpa* and *U. dac* Pierre ex Finet & Gagnep. The subcordate leaf base of *U. grandiflora* is usually enough to distinguish it from the two former species (which have cordate bases) and *U. grandiflora* also retains its leaf indument to a much greater extent than do these two species. The leaves of *U. dac* are smaller, have fewer veins and are much more acuminate than those of *U. grandiflora*. The only variety recognised in continental Asia is var. *flava*, which is restricted to the wetter habitats of south-eastern and peninsular Thailand and produces cauliflorous inflorescences. The fruits of *U. grandiflora* are edible, but not as highly regarded as those of *U. rufa* Blume. The year-round production of large, fragrant flowers makes it a popular feature of tropical Asian botanic gardens. In Hainan, the leaves are used in the making of cakes and rice whisky.

Key to the varieties in continental Asia

1. Petals red, coriaceous, elliptical or oblong, ~30–50 × 12–20 mm – Sri Lanka, Myanmar, Southern China, South-east Asia, Malasia.....
..... 4a. *U. grandiflora* var. *grandiflora*
Petals red or white, fleshy, broadly ovate–elliptical, ~20–40 × 15–25 mm – south-eastern Thailand, Malay Peninsula, West Malasia.....
..... 4b. *U. grandiflora* var. *flava*

4a. *Uvaria grandiflora* Roxb. ex Hornem var. *grandiflora*

Scrambling shrub up to 3 m or large woody climber up to 30 m. Young shoots densely tomentose, becoming striate and subglabrous, flexuous. Leaves elliptic–obovate, base subcordate or very shortly retuse, apex obtuse–acute, 130–190(–250) × 50–75(–100) mm, subcoriaceous to coriaceous; veins 11–14 (–16); indument upper surface sparse to subglabrous, hairs 1- to many-branched, lower blade tomentose to rarely sparse, hairs all stellate, ~10-branched, 0.3–0.5 mm in diameter. Petiole short, 5–6 × 2 mm, sparsely tomentose, warted and transversely foliated, black. Inflorescence leaf-opposed or subopposed, solitary or rarely with second dormant bud, or cauliflorous with elongate, often many-branched cyme of 3 to many pedicels, 1 or 2 bearing mature flowers, pedicel 10–15 × 2 mm, or up to 60 × 2 mm, ferruginous–tomentose, basally and medially bracteate, bracts large, ovate–elliptical, 10–33 × 5–20 mm, leafy, veins prominent, bud 15–25 mm in diameter before opening, indument densely tomentose to tomentose. Calyx calyptrate in bud, later forming (2–)3(–4) ovate–acute, 15–25 × 9–18 mm sepals, indument densely ferruginous, tomentose, short and paler on inside, longer on outside, sepals conspicuous, green, reflexing at maturity. Corolla 2 subequal whorls of 3 petals, petals deep red to purple, elliptical–oblong to rarely very narrowly obovate, 20–45 × 8–15 mm, apex obtuse or very bluntly acute, sparse stellate indument on inner surface of both whorls, more dense on outer surface. Stamens numerous, 6–8 × 1.25 mm, connective head shortly papillate,

flattened, dorsal ridge often prominent, with stellate indument running length of connective, locules extending to full length of stamen. Carpels numerous, $8.0\text{--}8.5 \times 1.5$ mm, ovary shortly and densely tomentose, stigma U-shaped, glabrous, somewhat lobed, $2 \times 1\text{--}2$ mm wide, producing copious secretions, ovules 24–36. Fruit monocarps 6–12(–20), receptacle up to ~25 mm in diameter, stamen abscission scars forming prominent ring at base, stipes up to 30×4 mm, thickened towards base and apex, smooth to (thickly) striate, shortly and densely tomentose; monocarps $50\text{--}75 \times 10\text{--}20$ mm, cylindrical, apex globose to conical, smooth or with longitudinal or lateral ridges and constrictions between seeds; seeds 16–30, hemi-ellipsoidal to ovoid, often dorso-ventrally flattened, up to $7 \times 5 \times 2$ mm, smooth, ruminations visible. (Fig. 1A.)

Distribution

Uvaria grandiflora var. *grandiflora* is found mostly in evergreen forest, but there are occasional records from semi-deciduous dipterocarp forest. Collected most frequently in Hongkong, Hainan and south-eastern Thailand and also in the middle and lower Malay Peninsula. Several early collections from

Tenasserim in Myanmar suggest that it is a common species there too; however, no recent material is available from this region. This species is most probably introduced in Sri Lanka. *Uvaria grandiflora* var. *grandiflora* also occurs in Malesia as far east as the Phillipines and New Guinea. Distribution is shown in Fig. 9.

4b. *Uvaria grandiflora* var. *flava* (Teijsm. & Binn.) J.Sinclair, *Gard. Bull. Str. Settlem.* 3: 44 (1953)

Uvaria flava Teijsm. & Binn., *Natuurk. Tijdschr. Ned.-Indië* 25: 419 (1863).

Type: INDONESIA. Bankga, cultivated Hort. Bog. XVI-E-6, *s. dat.*, *leg. ign.*, (lecto, here designated: L 1770656!).

Uvaria purpurea var. *alba* Scheff. *Natuurk. Tijdschr. Ned.-Indië* 31: 4 (1869).

Type: INDONESIA. Sumatra, Priaman, *s. dat.*, *Diepenhorst s.n.* (lecto, here designated: U 1074870!).

Differs from the typical form of the species in having thick, fleshy, usually broadly and bluntly ovate petals, which can be either red or yellowish white in colour.

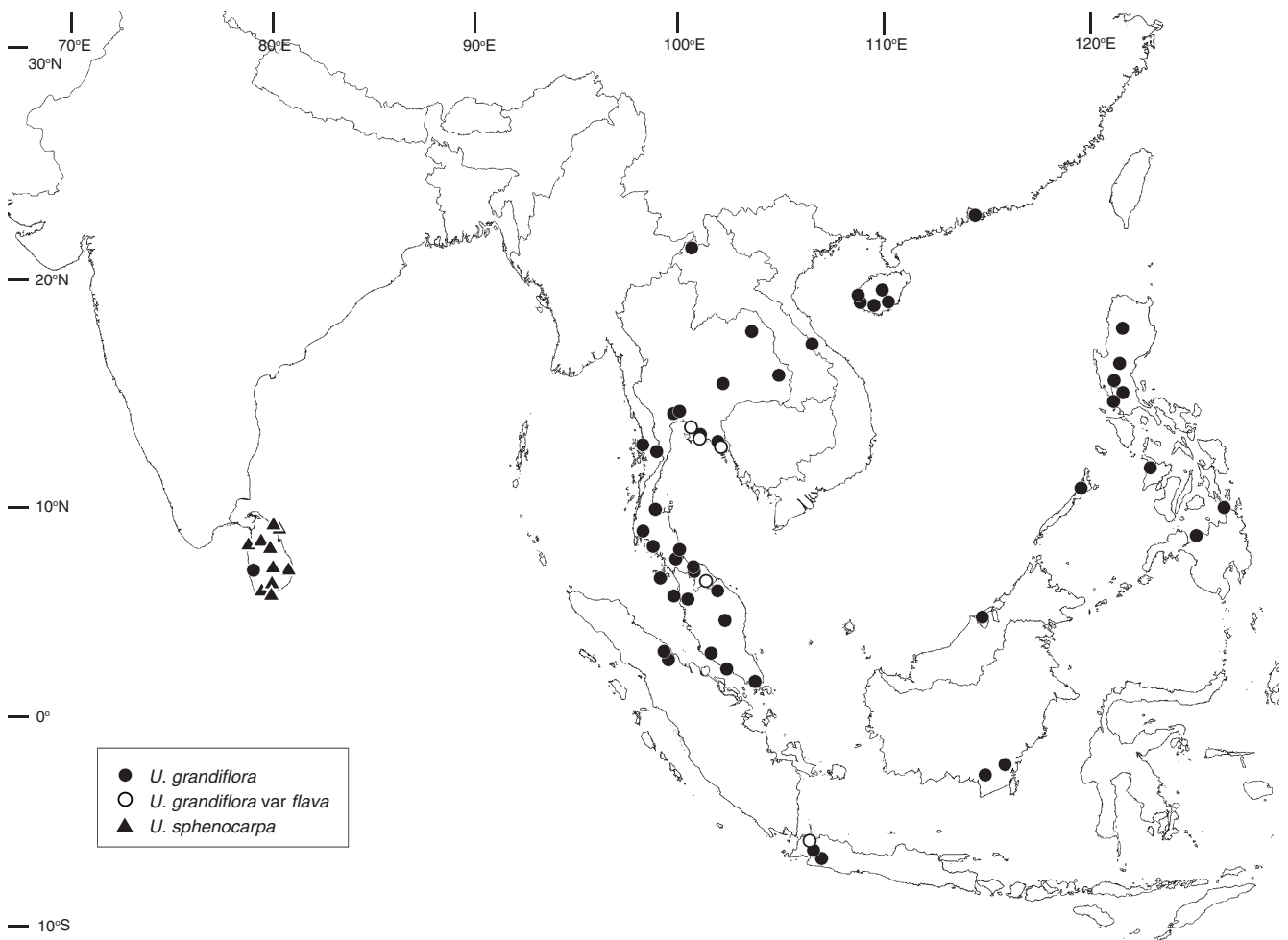


Fig. 9. Distribution of *Uvaria grandiflora*, *U. grandiflora* var. *flava* and *U. sphenocarpa* in southern and South-east Asia on the basis of herbarium specimens verified in this study.

Distribution

Uvaria grandiflora var. *flava* is recorded from evergreen forest sites in south-eastern Thailand, lower peninsular Thailand and western Java. Distribution is shown in Fig. 9.

5. *Uvaria curtisii* King, *J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist.* 61(1): 19 (1892)

Type: MALAYSIA. Penang, Government Hill, 2000 ft [~ 609.6 m], May 1893, *Curtis 1415* (lecto, here designated: S 0073636!; isolecto: BM 000527922!, G 00226139!, K 000380126–8!); MALAYSIA. Perak, Ulu Bubong, *s. dat.*, *King's Collector [H.H.Kunstler] 8543* (syn: C!).

Shrub or large climber up to 20 m tall, with distinctive hirsute indument. Young branchlets subtomentose, hairs ferruginous, hirsute, becoming sparse with age. Leaves subcoriaceous, elliptical to narrowly obovate, $\sim 210\text{--}250 \times 60\text{--}70$ mm, acute or shortly acuminate, base retuse; veins 10–12+; indument hairs ferruginous, hirsute, $\sim 0.5\text{--}1$ mm long, prominent at margin generating ferruginous tint. Petiole $\sim 8 \times 3$ m, ferrugino-tomentose, with long stellate hairs 0.6–1.0 mm long. Inflorescence leaf-opposed, flowers 2, secondary bud

normally dormant, peduncle 1.5–12 mm, pedicels long and thin, up to $\sim 20\text{--}30 \times 1$ mm, basal bract narrowly elliptical, $\sim 8 \times 2$ mm, often clasping, medial bract ovate to broadly elliptical, $\sim 4\text{--}5 \times 2.5\text{--}3$ mm., bud 8–15 mm in diameter before opening, indument ferrugino-hirsute on peduncle, pedicel, bracts and early bud. Calyx calyptrate in bud, sepals 3, $\sim 10 \times 6$ mm, ovate, acute to narrowly acute, apices sometimes reflexed at maturity, inner surface hairs fine, pale, subtomentose. Corolla 2 subequal whorls of 3 petals, petals white or greenish-yellow, elliptic–acute, $\sim 13 \times 6.5$ mm, membranous, spreading, hairs subtomentose, short, and pale on both surfaces, with scattered ferruginous hairs on outer surface, inner surface carrying prominent indents from stamen connectives. Stamens numerous, 3 mm long, glabrous, connectives papillate, truncate or somewhat flat and elongate in marginal stamens, ridge sometimes present on outer surface, locules extending to full length of stamen. Carpels numerous, 3 mm long, ovary with dense combed-tomentose indument, stigma U-shaped, lobes not broadened, ovules ~ 20 in 2 lateral rows. Fruit monocarps 10–30, cylindrical or oblongoidal, $\sim 65 \times 25$ mm, tomentose, stipe 10–40 $\times 2\text{--}3$ mm; seeds ~ 16 , flattened ellipsoidal.

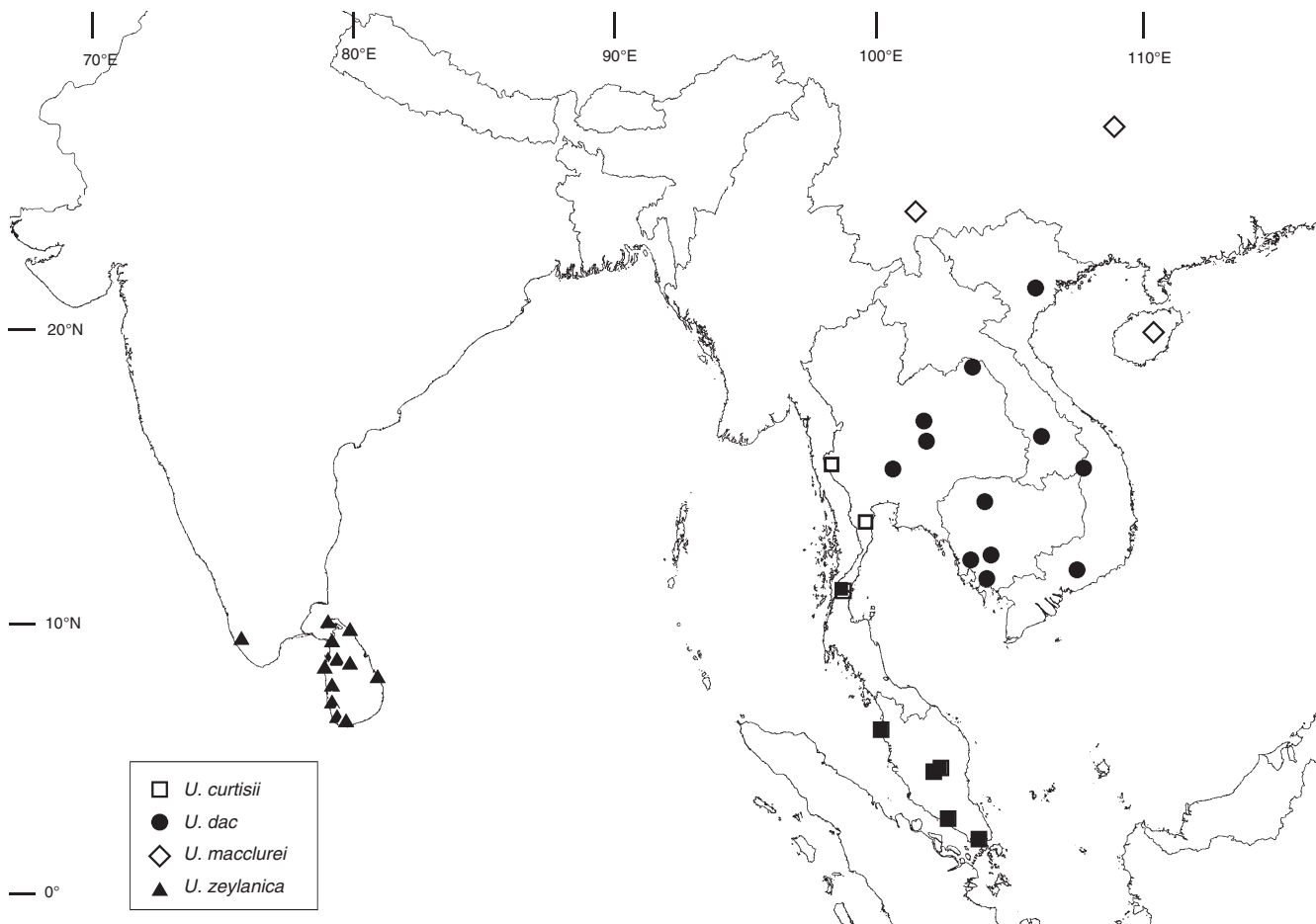


Fig. 10. Distribution of *Uvaria curtisii*, *U. dac*, *U. macclurei* and *U. zeylanica* in southern and South-east Asia on the basis of herbarium specimens verified in this study.

Distribution

Newly recorded for Thailand. Distribution is shown in Fig. 10.

Notes

Morphologically similar to *U. hirsuta* Jack (lower Malay Peninsula), but distinguished from that species by its smaller yellowish-white petals (v. the red petals of *U. hirsuta*), its shorter, less hirsute indument and its peculiar leaves, which have distinctly fewer, more narrowly angled veins than those of *U. hirsuta* (Meade and Parnell 2002). The lectotype selected presents the best-preserved material from the originally cited sheets.

6. *Uvaria dac* Pierre ex Finet & Gagnep., *Bull. Soc. Bot. France* (Mém. 4 (2)) 53: 65 (1906)

Type: CAMBODIA. Samrong-tong, Cherreo Mountains, Apr. 1870, *Pierre 748*, (lecto, here designated: K 000582098!; isolecto: P 00262204-5!); CAMBODIA. Tpong, Tamir Mountains, May 1870, *Pierre 748A* (syn: K 000582096!, P 00262203!, P 00432438!); Kampot, Kam-Chay Mountains, May 1874, *Pierre 1459* (syn: A!, PHH!, K 000582097!, P 00262206-8!).

Uvaria varaigneana Pierre ex Finet & Gagnep., *Bull. Soc. Bot. France* (Mém. 4 (2)) 53: 64 (1906).

Type: VIETNAM. Bien Hoa, near Chiao-shan, 1875-77, *Pierre 1785* (lecto, here designated: P 00262209!; isolecto: P 00262210-11!).

Climber or sarmentose shrub. Young branchlets ferruginotomentose, hairs quickly becoming blunt and sparse, bark striate. Leaves narrowly elliptic-ovate, acute-distinctly acuminate or cuspidate, base retuse, ~180-190 × 60-80 mm; veins 11-13; indument upper-surface hairs 1-4-branched, lower-surface hairs 10-branched. Petiole ~5-7 × 2 mm, tomentose becoming sparse. Inflorescence leaf-opposed, flowers solitary or rarely 2 or 3, pedicel 8-15(-25) mm, often flattened to ~2 mm broad, otherwise ~1.25 mm, bracts ovate-acute, ~4-7(-10) × 1.25-2 mm, often wanting, bud 8-15 mm in diameter before opening, pedicel and bract densely ferruginotomentose. Calyx calyptrate in bud, splitting into 2-4 often unevenly sized ovate-acute sepals, each (7-)10 × (8-)10 mm, at length spreading, outer indument tomentose to sparsely tomentose, ferruginous, inner surface subtomentose, hairs pale. Corolla 2 subequal whorls of 3 petals, petals yellow or rarely red, elliptic, obtuse-acute, spreading, ~15-20 × 8-10 mm, inner and outer surfaces sparsely tomentose, whorls subequal. Stamens numerous, ~4.5 mm long, glabrous, connective truncate, adaxial ridge often present, locules extending to full length of stamen, staminodes not present. Carpels ~10-15, ~3.5 mm long, ovary densely ferruginotomentose, stout in appearance, apex narrowed into neck, stigma glabrous with conspicuously broad U-shaped lobes, partly occluded by extension of ovary wall above neck, ovules ~16 in 2 lateral rows. Fruit monocarps 1-8(-10), sub-basally attached, ~45 × 25 mm in diameter, oblongoid, pericarp thickened, epidermis warted with fine tomentose indument, mature fruits green with brown tint, stipe 5-10 × 2.5-3 mm, thickly striate, tomentose; seeds 6-12 in 2 rows, ~10 × 6 × 4 mm, hemi-ellipsoidal.

Distribution

The distribution is shown in Fig. 10.

Notes

Uvaria varaigneana and *U. dac* were described by Finet and Gagnepain in the same work, based on Pierre's unpublished concepts. However, it and *U. dac* are merely flowering and fruiting specimens respectively of the same species. *Uvaria dac* is the name in more common usage, and is adopted here in preference to *U. varaigneana*. The species shows little phenotypic variation, save the occasional occurrence of red rather than yellow petals, and the presence of persistently tomentose leaves in some specimens from central Vietnam. The fruit is unusual in the genus, retaining a green colour up to maturity. The lectotype selected presents the best-preserved material from the originally cited sheets.

7. *Uvaria hamiltonii* Hook.f. & Thomson, *Fl. ind.* 1:96 (1855)

Type: INDIA. Bihar, Monghir or Goyalpara, Assam, 1808 or 1811, *F. Buchanan-Hamilton s.n.*, *Wallich Cat. no. 6485E* (lecto: CAL; isolecto: BM 000949957!, K-W 001124004-5!, *vide* D.Mitra, *Fasc. Fl. India* 10: 16 (1982)).

Notes

Although both varieties of *Uvaria hamiltonii* share characters with many *Uvaria* species, there are a few characters by which they can readily be identified, namely (1) the two or three thick, elongate pedicels, (2) the basally free, obovate, concave petals and (3) the partially verrucose ferruginous indument present on the pedicel and calyx and the stipe and monocarp of ripening fruits. The distinctive leaf venation shared by both varieties also helps their identification from sterile specimens. The petals of *U. hamiltonii* var. *kurzii* can be similar to those of *U. dac*, and, in specimens that lack fruits, the verrucose calyx and larger, more tomentose leaves of *U. hamiltonii* var. *kurzii* should make it possible to distinguish the two.

Key to the varieties in continental Asia

- 1a. Leaf veins ≥ 14 ; petals red, distinctly obovate and concave, apex obtuse, 15-20 × 9-11 mm - Assam, Myanmar, northern Indochina, Hong Kong 7a. *U. hamiltonii* var. *hamiltonii*
- Leaf veins < 14 ; petals white or yellow, elliptical to oblong, apex obtuse or rarely concave, 10-15 × 8-10 mm - Andaman Islands, Indochina, southern China 7b. *U. hamiltonii* var. *kurzii*

7a. *Uvaria hamiltonii* Hook.f. & Thomson var. *hamiltonii*

Large climber up to 30 m, or a scrambling, rarely upright, shrub. Young branchlets ferrugino-hirsute, becoming subglabrous and distinctly striate. Leaves (elliptic-)obovate, base subcordate to retuse, apex acute-acuminate, 115-175(-205) × 60-85 mm, membranous; veins 14-25, sometimes branching basally or medially; indument upper blade subtomentose with simple and stellate hairs, lower surface hairs stellate only. Petiole short, ~4 × 2 mm, not much thicker than midrib, warty, tomentose to subtomentose. Inflorescence flowers 1 or 2 or rarely 3, leaf-opposed or subopposed, peduncle ~5 mm, pedicel ~35 × 2 mm, bracts broadly obovate to circular-ovate, often wrapping around pedicel, ~10 × 10 mm, veins prominent, bud 8-15 mm in diameter before opening, hairs on peduncle, pedicel and bracts shortly ferruginous and tomentose, often verrucose. Calyx calyptrate in bud, sepals 3

or 4, spreading, partially recurved, connate at base, triangular to very broadly ovate, bluntly acute, 7×10 mm, tomentose or verrucose on outer surface. Corolla 2 subequal whorls of 3 petals, petals red, subequal, distinctly obovate, apex broadly concave-rounded, $\sim 10\text{--}22 \times 10\text{--}14$ mm, densely and shortly tomentose on both surfaces. Stamens numerous, 2.5–3 mm long, connective apex short, papillae often prominent, locules rarely marginally unequal in length. Carpels numerous, ~ 2 mm long, ovary densely tomentose, stigma glabrous, U-shaped, ovules 10–12. Fruits monocarps $\sim 10\text{--}14$, globose to oblong, $\sim 20 \times 15$ mm, green turning red, pericarp fleshy or thin, flesh pale white in colour, outer surface ferrugino-tomentose, often verrucose, stipe $\sim 25\text{--}35 \times 1.25\text{--}2.25$ mm, striate, especially when thick, tomentose, monocarp attachment basal or sub-basal; seeds 6–12, $\sim 11 \times 4 \times 2$ mm, ellipsoidal, laterally compressed, smooth, brown, ruminant.

Distribution

Uvaria hamiltonii var. *hamiltonii* has a northerly distribution relative to the remaining species in the genus. Plants originally from Assam have been cultivated since the early

1800s at Peradeniya Gardens in Sri Lanka (where it has become naturalised) and also at Bogor Gardens in Java. Like most *Uvaria* species in mountain or disturbed habitats, the species is often found in gullies and along watercourses where the soil is deep and damp. At the northernmost latitudes, *U. hamiltonii* var. *hamiltonii* has not been collected above 650 m, and so is essentially a lowland tropical species. Distribution is shown in Fig. 11.

7b. *Uvaria hamiltonii* var. *kurzii* King, *J. Asiat. Soc. Bengal*, Pt. 2, *Nat. Hist.* 61(1): 14 (1892)

Uvaria kurzii (King) P.T.Li, *Acta Phytotax. Sin.* 14(1): 106 (1976).

Type: INDIA. Andaman Islands, near Port Blair, 9 July 1884, *King's Collector* [H.H.Kunstler] 338 (lecto: CAL 000004190 (image!), *fide* D.Mitra, *Fasc. Fl. India* 10: 16 (1982)).

Differs from the typical form of the species in having smaller leaves with 10–13 subparallel veins and a white to yellow corolla with coriaceous, elliptical to oblong, obtuse, $10\text{--}15 \times 8\text{--}10$ mm petals.

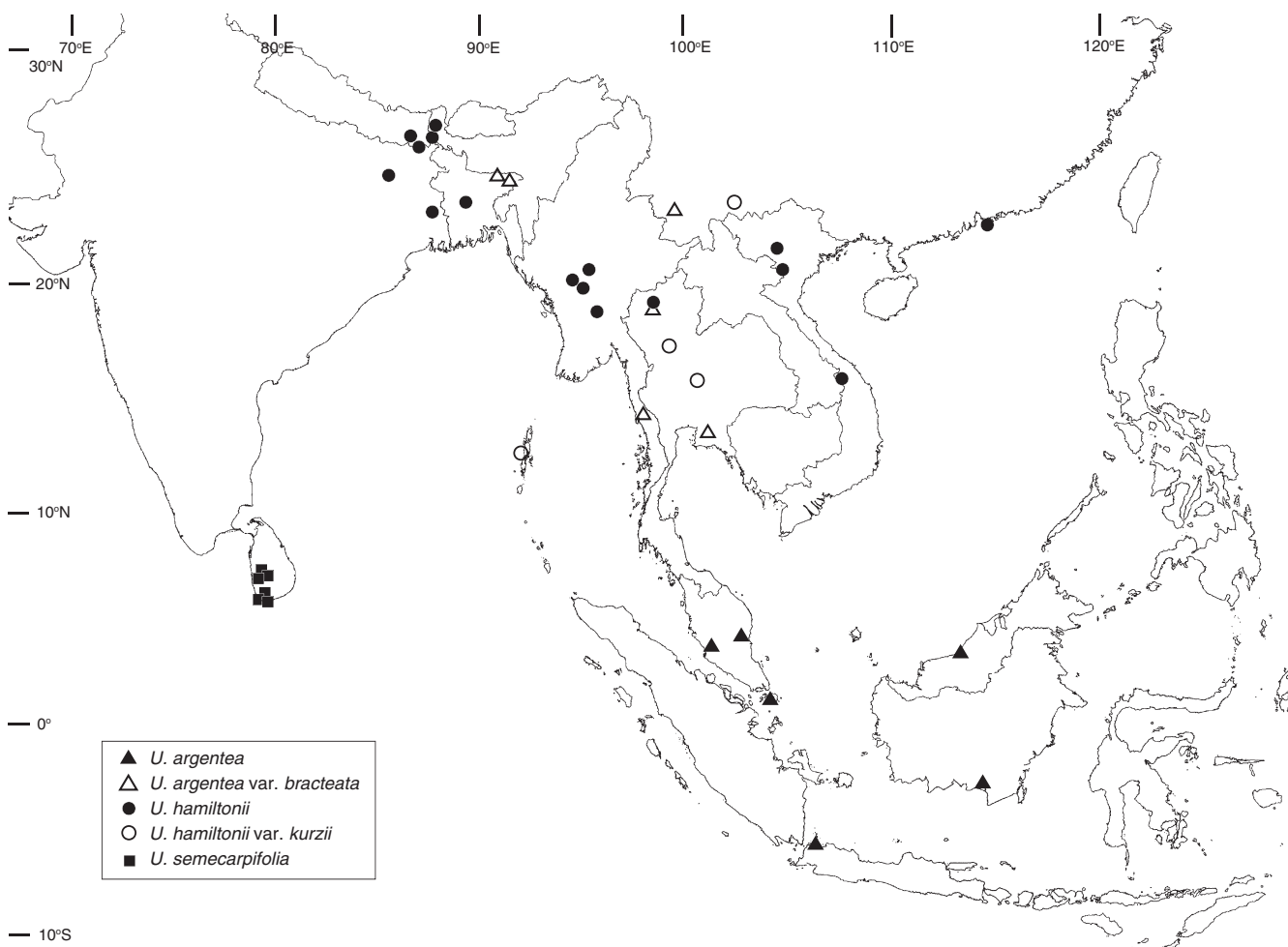


Fig. 11. Distribution of *Uvaria argentea*, *U. argentea* var. *bracteata*, *U. hamiltonii*, *U. hamiltonii* var. *kurzii* and *U. semecarpifolia* in southern and South-east Asia on the basis of herbarium specimens verified in this study.

Distribution

Andaman Islands, central Thailand and Yunnan province, China. Distribution is shown in Fig. 11.

8. *Uvaria macclurei* Diels, *Notizbl. Bot. Gart. Berlin-Dahlem*. (Append.) 11: 73 (1931)

Type: CHINA. Hainan. Tik Tsok Mau, 18 May 1922, McClure 9697 (lecto, here designated: E 00050326!; isolecto: A 00039699!, BM 000528083!, C 10005706!, G!, N!, P 00142625!).

Uvaria kweichowensis P.T.Li, *Acta Phytotax. Sin.* 14: 107 (1976).

Type: CHINA. Kweichow, 8 Aug. 1959, *leg. ign.* 739 (lecto, here designated: PE 00028383!; isolecto: PE 0028384!, PE 01843406!).

Climber or scandent shrub. Young shoots subtomentose, ferruginous. Leaves elliptical–narrowly obovate, apex acute, shortly acuminate or rarely obtuse, base cuneate–retuse, ~110–160 × 40–60 mm, coriaceous; veins (9–)10–12; indument upper surface completely glabrous, shiny, lower blade subglabrous, on midrib and lateral veins hairs ~4–6-branched, fine, becoming glabrous at maturity. Petiole 3.5–5.5 × 1.5–1.75 mm, subtomentose becoming sparse over warty black epidermis. Inflorescence flowers 1 or 2, peduncle subsessile, 1–2 mm, pedicel ~30–40 mm, basal and medial bracts ovate, ~5.5 × 4 mm with prominent veins, often persistent, peduncle, pedicel and bracts subtomentose as for young shoots. Calyx calyptrate in bud, sepals 3, ~5–5.25 × 4–4.5 mm, thin and leafy, hairs sparse on inner surface, sparse to subtomentose on outer surface, at length reflexed. Corolla 2 subequal whorls of 3 petals, petals purple, elliptical–acute, ~10–12 × 4–5.5 mm, tomentose on outer surface, at length spreading and reflexing, hairs 3–5-branched, sparse on inner surface. Stamens <50, ~3.5 mm, connective apex flattened, somewhat elongate, papillate, prominent dorsal ridge running to base, locules extending to full length of stamen. Carpels ~12–15, 3 mm long, ovary tomentose with flattened spreading hairs, stigma flat and glabrous, U-shaped, ovules 8–10. Fruit monocarps ovoid–ellipsoidal, 40–45 × 30–35 mm, tuberculate, pericarp thick; seeds 6–10, subsessile, stipe ~6 × 5 mm, striate.

Distribution

Rare. Distribution is shown in Fig. 10.

Notes

The stamens, carpels and petals of *U. macclurei* are similar to those of *U. rufa*; however, the calyx, pedicel and fruit are more similar to those in the *U. grandiflora* group. The species most likely to be confused with *U. macclurei* is *U. dac*, particularly in relation to the fruits; however, in *U. dac* the flowers are much larger, the stamens more numerous and the pedicels much shorter. The lectotypes selected here for *U. macclurei* and *U. kweichowensis* present the best-preserved material from the originally cited sheets.

9. *Uvaria calamistrata* Hance, *J. Bot.* 20: 77 (1882)

Type: CHINA. Hong Kong, Aug. 1861, Hance 7436 (lecto, here designated: K 000691193!; isolecto: BM 000528082!);

CHINA. Hong-Kong, 10 Aug. 1881, Ford s.n. (syn: K 000691192!).

Climber up to 20 m tall, or scandent shrub. Young shoots tomentose, becoming mostly glabrous, bark striate with pale lenticels. Leaves broadly elliptic, 70–120 mm × 35–45 mm, apex acute–acuminate–cuspidate, base retuse–cuneate; veins 8–11; indument upper surface of young leaves with sparse pale hairs, becoming glabrous and shiny with maturity, lower surface tomentose to subtomentose, later sparse, hairs stellate, pale, with occasional tufted rufous hairs, especially on veins and midrib. Petiole 5–8 mm long, tomentose. Inflorescence flowers solitary, 2 or rarely 3, subopposed, peduncle 2–3 mm, pedicel ~5–10 mm long, densely tomentose, basally and medially bracteate, one or both bracts often wanting, bracts ovate–obovate–oblanceolate, ~2 × 1 mm. Calyx calyptrate in bud with apicule, sepals 3, basally connate, triangular–ovate, apex acute to bluntly acute, up to 5–6 × 4 mm, membranous, concave, remaining incurved, tomentose on outer surface, sparse on inner surface, often persistent into fruiting stage. Corolla 2 subequal whorls of 3 petals, petals yellow in colour, ovate–oblong, 6–10 × 3–3.5 mm, apex rounded, whorls subequal, partially recurved at maturity, inner and outer surfaces of both whorls tomentose, hairs finer, shorter and more evenly distributed than on inner surface of sepals. Stamens numerous, 1.5–1.8 mm long, connective apex truncate, often obscuring locules completely, papillate, with prominent ridge on external surface, locules extending to full length of stamen, staminodes absent. Carpels ~20–40, 1.5 mm long, ovary tomentose apically and on sides exposed at margin of gynoecium, otherwise with scattered stellate hairs ~0.5 mm in diameter, stigma U-shaped with elongate lateral slit, 0.2–0.4 mm long × 0.4–0.65 mm wide, ovules 10–12. Fruit monocarps 2–12, spheroidal–oblongoid, ~30 × 20 mm, initially covered with prominent beard of 5–8 mm long membranous bluntly triangular outgrowths, later tuberculate with scattered remnants of outgrowths over surface, stipe short, 3–5 mm × 2.5–3 mm; seeds 1–12, ~12 × 6 × 4 mm, ellipsoid, to hemi-ellipsoidal, smooth, ruminations faint, hilum 5 × 4 mm, ovate.

Distribution

Uvaria calamistrata occupies a range of habitats similar that of to *Uvaria boniana*, particularly in Hainan, where many specimens have been collected scrambling over rocky scrub on steep hillsides. Distribution is shown in Fig. 12.

Notes

The bearded juvenile fruit of *U. calamistrata* is among the most distinctive in the genus. The beard is very different from that seen in *Uvaria vietnamensis* Meade, being not hair-like and not persistent. The lectotype selected presents the best-preserved material from the originally cited sheets.

10. *Uvaria zeylanica* L., *Sp. Pl.* 536 (1753)

Type: SRI LANKA. s. loc., *leg. ign.* (lecto: BM (Herb. Hermann) 5: 163, t. 224!). First step lecto *vide* H. Huber in M. D. Dassanayake & F. R. Fosberg (eds), *Rev. Handb. Fl. Ceylon* 5: 17 (1985); second step lecto *vide* P. J. A. Kessler in K. Kubitzki *et al.* (eds), *Fam. Genera Vasc. Pl.* 2: 97 (1993)). ‘Uvularia. Uva

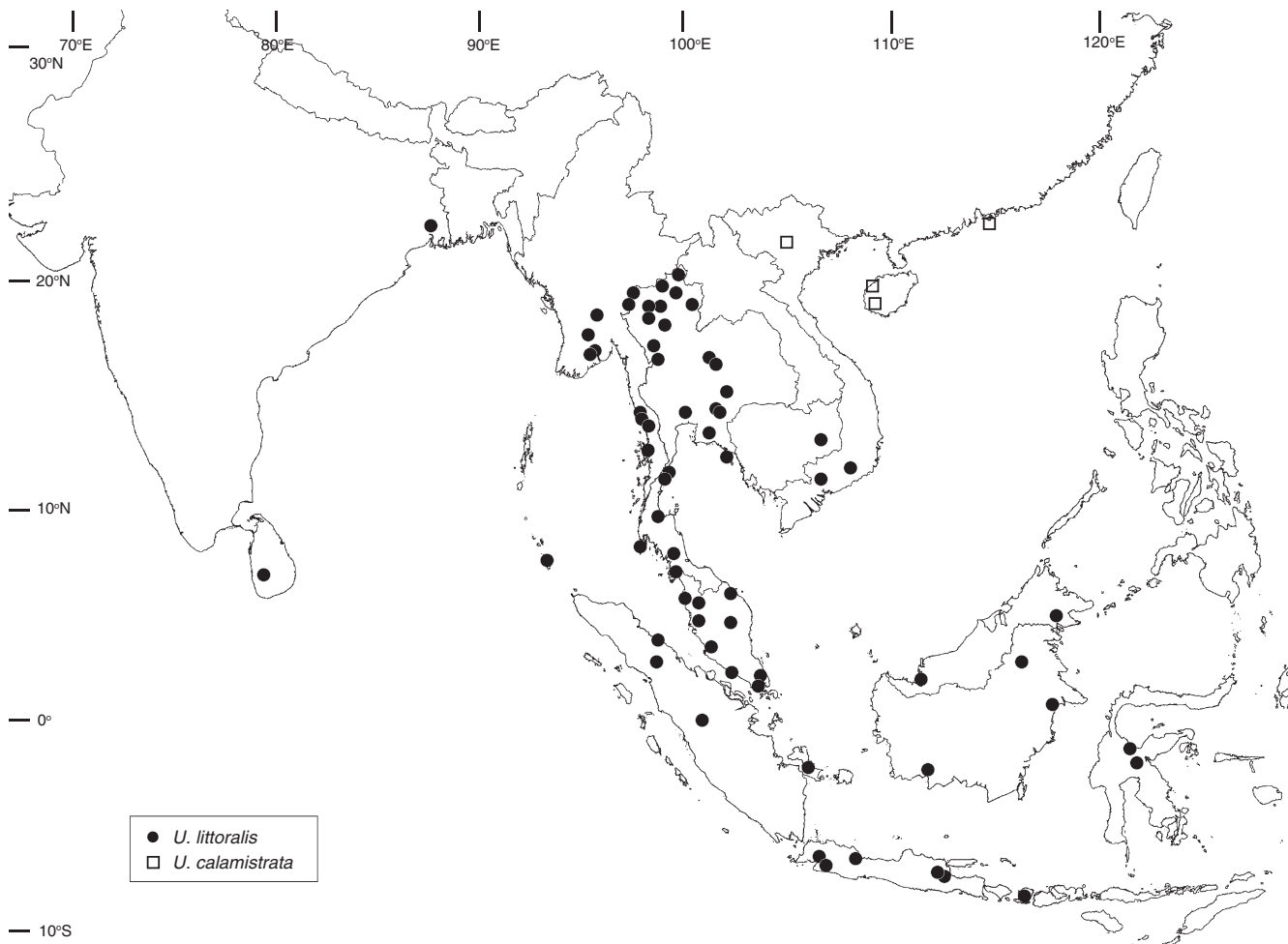


Fig. 12. Distribution of *Uvaria calamistrata* and *U. littoralis* in southern and South-east Asia on the basis of herbarium specimens verified in this study.

zeylanica. 224. (syn: BM 000621773 (Herb. Hermann!); 'Narum panel. Hort. Malab. tom. 2 p. 11. Balla paleti. Calo Apocaro. Uves de mato. 224' (syn: BM 000621836 (Herb. Hermann!)).

Uvaria coriacea Vahl, *Sym. Bot.* 3: 72 (1794).

Type: SRI LANKA. *s. loc.*, *s. dat.*, J.G.K.Konig *s.n.* (lecto: C 10005711, *fide* I.M.Turner, *Nordic J. Bot.* 33: 293 (2015)).

Guatteria malabarica Dunal, *Monogr. Anonac.* 134 (1817).

Type: 'Kaltsjerou-Panel' in Rheedee Tot Draakenstein, *Hort. Malab.* 5: t. 17 (1685) (lecto, *fide* I.M.Turner, *Nordic J. Bot.* 33: 293 (2015)); *Guatteria montana* DC., *Syst. Nat.* 1: 508 (1817), *nom. illeg.*

Uvaria lutea Wall., *Numer. List no.* 6462 (1832), *nom. inval.*, *nom. nud.*

Habit climber up to 30 m tall or sarmentose shrub 1–2 m high. Young shoots subtomentose, smooth, quickly becoming striate and subglabrous. Leaves ovate–elliptic–oblanceolate, base cuneate, apex acute–acuminate, ~55–70(–95) × 20–28(–35) mm, membranous, waxy; veins ~8–12; indument blades glabrous with occasional stellate hairs on midrib and vein bases. Petiole ~2–3 × 1 mm, tomentose when young,

sparse when mature, hairs ferruginous, surface black, waxy. Inflorescence terminal or leaf-opposed by apposition, flowers solitary or less often 2–3, peduncle 1.5–2 mm pedicel (4–)5(–7) mm, densely tomentose, hairs pale or ferruginous, bracts narrowly ovate–elliptical, membranous. Calyx calyptrate in bud, tearing into 3 subequal ovate–acute to broadly lanceolate membranous sepals, outer surface tomentose, later sparse, inner surface subglabrous, sepals persistent. Corolla 2 subequal whorls of 3 petals, petals dark red–purple in colour, narrowly elliptical–oblong, apex acute or less often narrowly obtuse, ~10 × 3 mm, membranous, somewhat warty, inner surface subglabrous, outer surface sparse to subtomentose with 1–5-branched straggling pale hairs, margins and apex tomentose, both surfaces. Stamens numerous, ~1 mm long, cuneate, locules extending full length of stamen, connective glabrous, broadly concave, undulating. Carpels ~20, 1 mm long, cuneate, ovary hairy, stigma glabrous, U-shaped, lobes broad, ~0.6 mm in diameter, ovules ~6. Fruit monocarps 6–12, shortly oblong, apex and base rounded, ~12 × 8.5 mm, densely and shortly tomentose, hairs ferruginous, blunt, pericarp thin in young fruits, later thickening, becoming fleshy, edible, stipe short, ~3 × 1.25 mm; seeds ~6 in 2 rows, hemispheroidal or

flattened hemi-ellipsoidal, $\sim 4 \times 3 \times 2$ mm, testa brown, smooth and shiny, ruminations visible. (Fig. 1D, 5.)

Distribution

In Sri Lanka, this species usually grows as a scrambling shrub in dry regions and as a medium to large climber in the wetter forested regions, usually in secondary vegetation. Huber (1985) noted that the species is most common near the coast, often on sand-dunes. In southern India *U. zeylanica* is confined to moist lower hill forests. Distribution is shown in Fig. 10.

Notes

Uvaria zeylanica is the type species for the genus. Linnaeus confused it with the 'narum-panel' of Rheede (later *Unona narum* Dunal) from the Malabar coast, although the specimens and plate that he described from Hermann's *Musaeum zeylanicum* (Hermann 1717) are of *U. zeylanica* only. Kessler (1993) lectotypified *U. zeylanica* on the basis of a plate from this collection; however, only the Hermann isolecotypes at BM actually illustrate floral structure.

11. *Uvaria sphenocarpa* Hook.f. & Thomson, *Fl. Ind.* 1: 99 (1855)

Type: SRI LANKA. *s. loc.*, *s. dat.*, *Thwaites 1045* (lecto: K 000691186!; isolecoto: BM 000528053!, G 00226154!, P 00142689-90!, P 00248403!, P 01989167!, TCD 0018020!, US 01049781!, *fide* I.M.Turner, *Nordic J. Bot.* 33: 293 (2015)).

Habit climber or sarmentose shrub. Young shoots ferruginotomentose, hairs becoming sparse, bark black, smooth at first, later grey-black and striate, hairs persistent in grooves. Leaves elliptic to narrowly obovate, base retuse to shortly cordate, apex acuminate, $70-140(-200) \times 25-40(-70)$ mm, acuminate up to 30 mm, subcoriaceous; veins $\sim 9-10$; indument upper-surface hairs 1-8-branched, sparse, becoming subglabrous, lower blade subtomentose to sparse, hairs larger, more rufous than above, 4-10-branched. Petiole $\sim 4-5 \times 1.5-2$ mm, subtomentose to sparse with large ferruginous hairs. Inflorescence leaf-opposed, flowers solitary or in short 2- or 3-flowered cymes, usually only 1 bud in flower at any one time, peduncle subsessile, pedicel $\sim 3-4$ mm, bracts clasping, ovate, $\sim 4 \times 2$ mm, pedicel and bracts with dense ferruginotomentose indument. Calyx sepals 3, basally connate, opening early, $\sim 4.5 \times 2.5$ mm, broadly ovate, indument ferruginotomentose on outer surface, sparse at margin, on inner surface glabrous at base, sparse elsewhere. Corolla 2 subequal whorls of 3 petals, petals pale yellow in colour, elliptical-obovate, obtuse or bluntly acute, $\sim 6-6.5 \times 4-4.5$ mm, spreading, tomentose on outer surface, subtomentose on inner surface. Stamens $\sim 50+$, 2 mm long, all fertile, connective head broad and flat, somewhat T-shaped, very shortly papillate, dorsal ridge prominent, locules full length. Carpels ~ 50 , 2 mm long, 0.5 mm wide, ovary tomentose, stigma U-shaped, lobes large, copious nectar often present, ovules ~ 4 . Fruit monocarps sessile, $\sim 10-16$, yellowish, gathered into pseudo syn-carpous conglomerate, individual monocarps cuneate-obovoid, $18-25 \times 15-20$ mm, sides flattened against adjacent monocarps, all

surfaces densely tomentose, apical surface coarsely warted; seeds ~ 4 , $10 \times 5 \times 3$ mm, smooth, brown.

Distribution

Endemic to Sri Lanka, occurring in wet and dry zones from sea level to ~ 700 m. Huber (1985) noted that it has become more common owing to disturbance of primary forest. Cultivated at Bogor. Distribution is shown in Fig. 9.

Notes

The flowers and leaves of *U. calamistrata* can be similar to those of *U. sphenocarpa* Hook.f. & Thomson.

12. *Uvaria semecarpifolia* Hook.f. & Thomson, *Fl. Ind.* 1: 97 (1855)

Type: SRI LANKA. *s. loc.*, *s. dat.*, *G.W. Walker s.n.* (lecto: K001096932!, *fide* I.M.Turner, *Nordic J. Bot.* 293 (2015)); SRI LANKA. *s. loc.*, *s. dat.*, *Thwaites 244* (syn: BM 000528050!, G 00226155!, K!, L 1768675!, P 00751048!, P 00142683!, P 00753701!, P 00248400-1!, TCD 0018019!); syn: *W. Griffith s.n.* (K!).

Large climber up to 30 m tall. Young shoots densely tomentose, shoots becoming woody and ridged quickly, indument retained in grooves, glabrous on ridges, lenticels large and numerous. Leaves elliptic to oblong, base cordate, apex obtuse to cuspidate, $160-230(-450) \times 90-110(-120)$ mm, coriaceous; veins $\sim 16-20(-25)$; indument upper blade completely glabrous and shiny, hairs on midrib erect, tomentose, 1-4-branched, up to 1 mm long, lower blade hairs sparse to subtomentose, 3-8-branched. Petiole thick, $7-10 \times 3-4$ mm, ferruginotomentose, epidermis warted below into transverse foliations. Inflorescence leaf-opposed, flowers 2 or 3, peduncle $\sim 6-7 \times 3$ mm, flattened in transverse section, pedicels ~ 10 mm, with basal 3 mm adnate to sympodial axis, densely tomentose, bracts broadly obovate, up to $\sim 4 \times 6.5$ mm, densely tomentose outside, glabrous within, often wanting. Calyx connate, splitting apically in early bud at $\sim 5-6$ mm in diameter, later forming connate ring, finally splitting into 3 sepals before opening of corolla, sepals ovate-acute, $\sim 8 \times 4$ mm, fleshy, shortly ferruginotomentose outside, glabrous within. Corolla 2 whorls of 3 petals, outer petals spreading, inner petals connivent, petals green in colour, maturing yellow-brown, outer whorl spreading, $\sim 9 \times 7$ mm, broadly ovate, outer surface shortly and densely tomentose, hairs finer than on calyx, inner petals connivent, obovate, basally constricted or shortly clawed, $\sim 8 \times 6$ mm, indument as for outer whorl. Stamens numerous, 1.5-2 mm, tubular, connective concave, prominently papillate, locules full length. Carpels $\sim 20-25$, 2.5 mm long, ovary tomentose, somewhat flattened apically, stigma U-shaped, glabrous, ovules ~ 8 . Fruit monocarps $\sim 10-20$, broadly ellipsoidal to obovoid, $\sim 30-40 \times 20-30$ mm, shortly and densely tomentose, surface tubercled or undulating, pericarp ~ 4 mm thick in unripe specimens, stipe $\sim 3 \times 10-15$ mm; seeds ~ 8 , up to $12 \times 10 \times 6$ mm.

Distribution

Endemic to lowland rainforest in the wetter parts of southwestern Sri Lanka. Distribution is shown in Fig. 11.

Notes

Uvaria semecarpifolia can be distinguished from the similar *U. littoralis* by its tomentose fruits, more oblong leaves with ~20 parallel veins and its juvenile flowers with a connivent inner whorl.

13. *Uvaria narum* (Dunal) Blume, *Fl. Javae* 21, 22: 5 (1830)

Unona narum Dunal, *Monogr. Anonac.* 99 (1817).

Type: 'Narum-panel' in Rheede Tot Draakenstein, *Hort. Malab.* 2, t. 10 (1679). SRI LANKA. *Uvaria zeylanica* enc. no. 3, Narum-panel Rheed. Mal. 2 t. 10, *s. dat., leg. ign., s.n.* (epi, here designated: P-JU!).

Uvaria narum Wall., *Numer. List no. 6473* (1832), *nom. inval., nom. nud.*

Uvaria flexuosa Wall., *Numer. List no. 6473b* (1832), *nom. inval., nom. nud.*

Uvaria malabarica Oken, *Allg. Naturgesch.* 3(2): 1254 (1841).

[*Uvaria zeylanica* auct. non L.: J.B.A.P.M. de Lamarck, *Encycl.* 1: 596 (1785); A.P.Candolle, *Syst. Nat.* 1: 481 (1817), *p.p.*].

Habit sarmentose shrub or climber. Young shoots black, very finely striate, (sub)glabrous, hairs ~0.2 mm in diameter.

Leaves oblong–elliptical–oblanceolate, base cuneate, apex acute–acuminate, ~145 × 45 mm, acumimum up to 15 mm, subcoriaceous, waxy; veins ~10–11; indument rare spreading hairs on very young leaves, quickly becoming glabrous above and below. Petiole ~4–5 × 1 mm, glabrous, transverse ridges prominent below, minutely tubercled. Inflorescence terminal or leaf opposed, flowers solitary, buds globose, peduncle ~4 mm long, pedicel ~20–30 mm, 0.75–0.85 mm in diameter, broadening at receptacle, indument sparse to subtomentose, hairs rufous, many-branched, bracts membranous, ovate–elliptical, ~3 × 1.5 mm, subglabrous to sparse. Calyx valvate, sepals 3, broadly ovate, ~6–8 × 3.5–4.5 mm, concave, reflexing at maturity, outer surface subglabrous and minutely tuberculate with ferrugino-tomentose margin and apex, inner surface densely and shortly tomentose with pale shaggy stellate hairs. Corolla petals 6, basally connate, usually in 2 whorls of 3, or rarely fused in a single whorl, petals blood-red in colour, membranous, outer whorl 10–12 × 9–11 mm, inner whorl 8–11 × 7–9 mm, all petals initially broadly ovate–acute, maturing obovate, obtuse–acute, concave, reflexed at maturity, shed as a ring, both surfaces of both whorls shortly tomentose with fine, straggling pale hairs, ~0.2 mm in diameter. Stamens

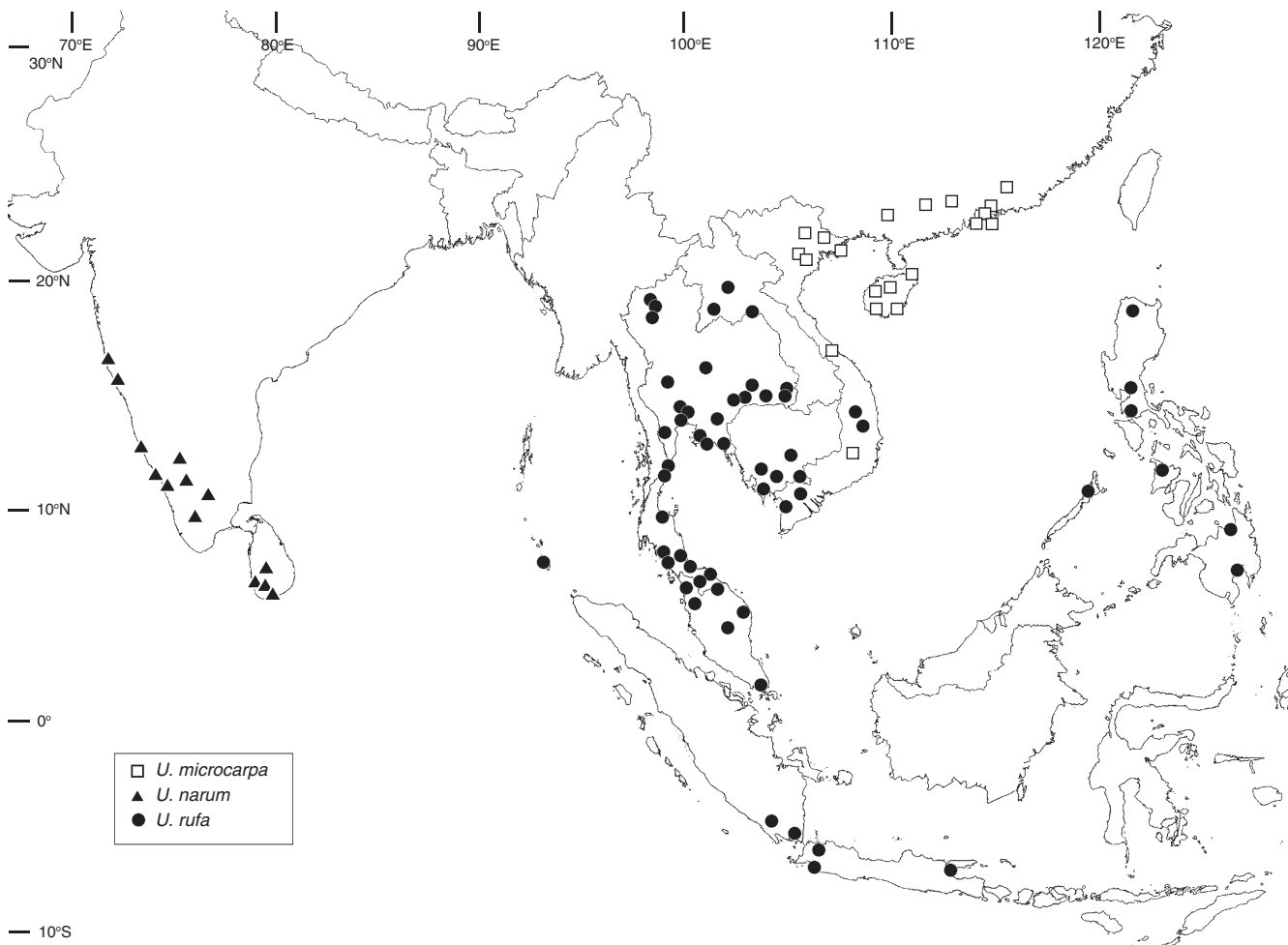


Fig. 13. Distribution of *Uvaria microcarpa*, *U. narum* and *U. rufa* in southern and South-east Asia on the basis of herbarium specimens verified in this study.

numerous, ~1.75 mm long, connective apex globose, very shortly papillate, locules extending to full length of stamen, staminodes absent. Carpels numerous, ~2 mm long, ovary hairy, stigma U-shaped, glabrous, black, often covered with exudate, ovules 6. Fruits 4–20+, green turning orange then red, monocarps globose to oblong, 10–15 × 6–8 mm, surface subglabrous to glabrous, granular or minutely tuberculate, pericarp fleshy at maturity, drying thin, stipe narrow, ~25–35 × 1 mm in diameter, subglabrous with scattered pale stellate hairs ~0.2 mm in diameter; seeds 2–6, ~5.5 × 4 × 3 mm, compressed ovoid, ruminations visible, raphe darker than remainder of testa, aril not prominent, 2 rows packed closely together. (Fig. 3.)

Distribution

A common species near watercourses on the wet coastal plains and hills of south-western Sri Lanka and the Malabar coast. Distribution is shown in Fig. 13.

Notes

Uvaria narum was the first taxon in the genus to receive attention from European botanists, most notably from van Rheede Tot Draakenstein (1679) who described and illustrated it as ‘Narum-panel’ in his *Hortus Malabaricus*. Linnaeus listed Rheede’s Narum-panel as a synonym of *U. zeylanica*. Later Dunal differentiated between Rheede’s Narum-panel and Linnaeus’ *U. zeylanica*, renaming the former *Unona narum*. He indicated that de Lamarck (1785) had misapplied the name *U. zeylanica* L. to *Unona narum* Dunal. The material on which de Lamarck based his description of *U. zeylanica* is held in the Jussieu family herbarium in Paris, and has been selected here as an epitype for *U. narum*.

This species is often confused with *U. concava*, and, to a lesser extent, *U. macropoda*. Both have a strongly tuberculate calyptate calyx with a prominent apicule, whereas the calyx of *U. narum* is valvate and covered with a short subtomentose indument of fine rufous hairs. The mature monocarps of *U. narum* are much smaller than those of *U. concava*, have a pericarp that becomes very thin on drying, and are mounted on a short, narrow stipe. The fruits of *U. concava* are variously thick-walled, usually large, carrying one or more longitudinal ridges on the monocarp surface, and are mounted on a long, thickened stipe. The monocarps of *U. macropoda* are narrowly cylindrical, tomentose, have a thick apicule and are mounted on stipes up to twice as long and broad as those of *U. concava*.

14. *Uvaria littoralis* (Blume) Blume, *Fl. Javae* 21, 22: 26 (1830)

Unona littoralis Blume, *Bijdr. fl. Ned. Ind.* 1: 16 (1825).

Type citation: ‘in Bataviae locis stagnosis.’

Type: INDONESIA. Java, *s. dat.*, *s.n.* ‘Unona littoralis Bl.’ Blume leg. (lecto, here designated: U-1074978!) (syn: BO *n.v.*).

Uvaria macrophylla Roxb., *Hort. Bengal.* 43 (1814), *nom. inval.*, *nom. nud.*

Guatteria cordata Dunal, *Monogr. Anonac.* 129 & pl. 30 (1817); *Uvaria cordata* (Dunal) Wall., *Numer. List no. 6486* (1832), *nom. illeg.*, *non* Schumach. & Thonn. (1827).

Type: ‘*Guatteria cordata*’ in M.F. Dunal, *Monogr. Anonac.* pl. 30 (1817). MALAYSIA. Penang, *s. dat.*, G. Porter in Wall. *Cat. no. 6486A* (epi, here designated: K-W 001124009!).

Uvaria macrophylla Roxb. ex Wall., *Pl. Asiat. Rar.* 2: 22, t. 122 (1830).

Type: INDIA. Cultivated in Calcutta Botanic Garden, *s. dat.*, Wall. *Cat. 6487A* (lecto: K 000442833!; isolecto: BM 000528071!, *fide* I.M. Turner, *Phytotaxa* 36: 102 (2011)).

Uvaria macrophylla Roxb., *Fl. Ind. Ed. 1832* 2: 663 (1832), *isonym.*

Habit large climber, reaching 30 m. Young shoots densely ferrugino-tomentose, becoming striate and glabrous. Leaves broadly ovate-oblong(–obovate), base cordate to subcordate, apex obtuse or shortly acuminate, rarely obcordate, ~200–300 × 150–180(–200) mm, coriaceous; veins 5–25+, often basally branched or merging; indument upper blade subglabrous, midrib and main vein traces densely tomentose, lower blade and veins tomentose to subtomentose. Petiole ~10 × 3.5 mm, ferrugino-tomentose, adaxial groove deep. Inflorescence 2–5+ buds in tightly packed rhipidium, up to 3 open at any time, compound peduncle 5–10(–15) mm long, 2–3 mm in diameter, flattened in transverse section, densely ferrugino-tomentose, pedicel 3–10 mm × 2–2.5 mm, flattened with shallow groove on inner surface, basally and medially bracteate, bracts broadly obovate, rarely ovate, fleshy, up to 5 × 7 mm in diameter, remaining concave and wrapping around pedicel, often enclosing younger buds, ferrugino-tomentose. Calyx connate in early bud then splitting apically to form a basally connate three-pointed ring around bud, ring later splitting into 3 ovate–acute sepals, 4–6 × 6–8 mm wide. Corolla petals 6, basally connate in a single whorl, petals red, fleshy, ovate–acute, usually distinctly concave, expanding to 15–18 × 10–12 mm, reflexing at maturity, outer surface shortly tomentose, inner surface hairs shorter, villose. Stamens numerous, 5–6 mm long, connective apex elongate, 5-sided in central whorls, flat in outer whorls, minutely papillate, locules full length, decreasing in size to staminodal outermost whorl. Carpels 20–25, 4–4.25 mm long, indument stellate, short and somewhat combed, stigma short, glabrous, U-shaped, base narrowed and subtomentose, ovules 12–14. Fruit monocarps 10–20, spherical–ovoid–oblong, younger fruits bright green, subglabrous, often with constrictions between seeds, mature fruits ~30 × 16.5 mm, usually glabrous, orange or yellow turning maroon red, ripening black with soft pericarp, stipe 2–5 × 2–3 mm; seeds 10–14, hemi-ellipsoidal, 10 × 7 × 3 mm.

Distribution

This is a morphologically variable species, particularly in the shape and indument of the leaves, found mainly in mixed and evergreen forests below 300 m, but also occurring in fire-prone or disturbed deciduous dipterocarp forest. Distribution is shown in Fig. 12.

Notes

The earliest legitimate epithet for this taxon at species rank is *cordata*, but this is pre-occupied in *Uvaria* by *Uvaria cordata* Schumach. & Thonn. (1827) (= *Uvaria ovata* DC.). Blume’s later name, *Unona littoralis*, therefore has priority. The type sheet at Bogor has not been seen; however, the Blume specimen

from Java at Utrecht (U 1074978, ex BO), also annotated by Blume, is a clear match for his type description, and is here designated as a lectotype.

The type material that Dunal mentioned in the original description for *Guatteria cordata* ('*Uvaria zeylanica* Herb. Deless.') appears to have been lost or destroyed. There are specimens of *Uvaria zeylanica* in Herb. Deless. in Geneva; however, because these are annotated by Dunal as types for *U. dulcis* Dunal and *U. javana* Dunal, they do not constitute original material of *G. cordata*. As a result, the plate accompanying the description is the sole original material remaining. The earliest surviving sheet identified on collection as *G. cordata* following Dunal's publication in 1817 is in Cat. 6486A at the Wallich herbarium, collected by G. Porter in Penang. Because it comprises material with both flowers and fruit, it is here designated as an epitype.

15. *Uvaria microcarpa* Champ. ex Benth. *Hooker's J. Bot. Kew Gard. Misc.* 3: 256 (1851)

Uvaria macrophylla var. *microcarpa* (Champ. ex Benth.) Finet & Gagnep., *Bull. Soc. Bot. France (Mém.* 4 (2)) 53: 67 (1906).

Type: CHINA. Hong Kong, 1850, *Champion* 39 (lecto, here designated: K 000691191!); CHINA. Hong Kong, *s. dat.*, *Champion s.n.* (syn: K 000691190!).

Uvaria badiiflora Hance, *Ann. Bot. Systemat.* 2: 19 (1851).

Type citation: 'Hab. in ins. Hongkong Sinarum.'

Type: *n.v.*, lost or destroyed?

Scandent shrub or climber. Young shoots ferrugino-tomentose, becoming striate and glabrous, sometimes flattened and broad. Leaves elliptic–broadly obovate, base cordate or broadly retuse, frequently oblique, apex acute–rounded, ~80–150 × 40–80 mm, thickly coriaceous, blade often undulate at margin, veins 9–11(–12); indument hairs stellate, tomentose and erect on upper surface of midrib, sparse to glabrous on veins and blade, hairs on lower surface fine, straggling, subtomentose–sparse. Petiole short and thickened, 5–6 × 2 mm, shortly and sparsely ferrugino-tomentose, black and warty underneath. Inflorescence leaf-opposed, flowers 1–2(–3), peduncle 1.5–3.5(–10) mm, pedicel ~10–15 × 1.4–1.8 mm, both sometimes flattened in transverse section, bracts elliptic–oblong, 3–5 × 2–3 mm, veins prominent, peduncle, pedicel and bracts all shortly ferrugino-tomentose. Calyx connate in early bud, then splitting apically to form a basally connate three-pointed ring around bud, ring later splitting into 3 triangular or broadly ovate ~5–7 × 5–10 mm sepals, remaining concave, sometimes reflexed, often persistent as connate ring, indument ferrugino-tomentose on outer surface, less dense on inner surface. Corolla 2 whorls of 3 petals, inner petals slightly smaller than outer, petals brown or red, fleshy, ovate–broadly elliptical, obtuse–bluntly acute, apex often incurved, inner whorl ~10–12 × 7–8 mm, outer whorl ~10–12 × 8–9 mm, inner and outer petals erect at first, later recurved, surface warty becoming smoother at maturity, densely and shortly tomentose on both surfaces. Stamens numerous, ~4.5–6 mm long, glabrous, connective apex papillate, flattened, becoming progressively longer and broader towards external whorl, on inner whorl locules extending full length of

stamens, outer whorl semi-staminodal with small basal locules ~0.5–1 mm long. Carpels numerous, ~4 mm long, in dense whorl, ovary ferrugino-tomentose, stigma ~1 × 0.5 mm, glabrous, U-shaped, lobes somewhat broadened, ovules ~6–8 in 2 rows. Fruit monocarps 4–8+, green turning yellow then dark purple at maturity, ovoid to shortly oblongoid, ~20 × 10 mm, pericarp thin, stipe ~10–15 × 1–2 mm, shortly tomentose; seeds ~6–8, flattened–ovoid, ~8 × 8 × 2 mm, dark brown, smooth, shiny, ruminations visible, aril ~4 × 2 mm, hilum circular–ellipsoid ~1 mm in diameter. (Fig. 1D.)

Distribution

Uvaria microcarpa shows a typical Indochina–southern China distribution and is often found as a scandent or erect shrub in open vegetation. However, it is most common growing as a climber in areas of (semi-)intact forest, usually near watercourses or on hillsides. In the Lianhua Shan Range (22.5 N), it is found at altitudes of up to 1500 m. Distribution is shown in Fig. 13.

Notes

This species and *U. littoralis* are often confused; however, their inflorescence structure differs, with *U. microcarpa* having one or two flowers mounted on a narrow elongate pedicel with small elliptical bracts, and the peduncle, where developed, is narrow and circular in transverse section. Furthermore, in *U. littoralis* the flowers are mounted on a closely packed cyme of 2–5+ pedicels and the peduncle is short and broad, usually having a prominent abaxial groove. The petals of *U. littoralis* are typically concave–acute and bright red in colour; those of *U. microcarpa* are flat or spreading, broadly elliptical and red to brown in colour. The fruits of *U. microcarpa* are considerably smaller and carry fewer seeds than those of *U. littoralis*. *Uvaria microcarpa* also tends to have smaller leaves, and the presence of any large leaves is usually a good indication that the specimen is *U. littoralis*. The two species occupy different geographic ranges, namely, *U. littoralis* west and south of the Mekong and *U. microcarpa* north and east of it. *Uvaria littoralis* is present in the Mekong Delta and probably also in Cambodia. The most southerly record for *U. microcarpa* is in Dac Lac Province, inland from Da Lat. McClure (collection number 638, Guandong Province, China, 5 January 1932, NY!; see the *Full list of material examined* section in the Supplementary material) reported that the leaves are used to make yeast cakes ('Tsau peng'). The lectotype selected presents the best-preserved material from the originally cited sheets.

16. *Uvaria rufa* Blume, *Fl. Javae* 21, 22: 19 t. 4, 13C (1830)

Type: INDONESIA. Java, *s. dat.*, *Blume s.n.* (lecto, here-designated: P 00248470!) (syn: BO *n.v.*, K 000380303!, L!, P 00248468–69!).

Guatteria rufa Dunal, *Monogr. Anonac.* 129, t. 29 (1817).

Type: INDONESIA. Annona (*Uvaria*) tomentosa, herbier de l'Inde de M. Poivre, Java, *Jussieu Cat no. 10 795 + B*, ab *Uvaria tomentosa* Roxb t.35, differ follis basi subcordati, *s. dat.*, *Poivre*

s.n. (lecto, here designated: P-JU 00662855!); INDIA. Cananga? tomentosa D.C., *Uvaria tomentosa* occurit in fallor antea sub numonae Annona tomentosa, indie, *Lahaye s.n.*, *Herb. Juss. Cat. 10 795 + A* (syn: P-JU 00662853!); INDONESIA. Guatteria rufa, isle de Timor, voyage Captain Boudin, *s. dat.*, *Riedlé s.n.* (syn: P 00142680!, G!).

Uvaria astrosticta Miq., *Fl. Ned. Ind., Eerste Bijv.* 370 (1860).

Type: INDONESIA. Sumatra, Lampang, Tarabangie, *s. dat.*, *Teijsmann s.n. 4261 H.B.* (lecto, here designated: U 0000436!); INDONESIA. Sumatra, Bepisang, Tigo Nemrin, *s. dat.*, *Teijsmann 4338 H.B.* (syn: U 0000435!).

Uvaria ridleyi King, *J. Asiat. Soc. Bengal Pt. 2, Nat. Hist.* 61(1): 19 (1892).

Type: MALAYSIA. Panang, *s. dat.*, *Ridley s.n.* (lecto, here designated: K!).

Uvaria hamiltonii var. *fauveliana* Pierre ex Finet & Gagnep., *Bull. Soc. Bot. France (Mém. 4 (2))* 53: 68 (1906); *Uvaria fauveliana* (Pierre ex Finet & Gagnep.) Pierre ex Jovet-Ast, *Not. Syst.* 9: 87 (1940), *p.p.*

Type: VIETNAM. Phu Quoc, hab in montibus, Raong Chiao, Mar. 1874, *Pierre 1787* (lecto, here designated: P 00248362!; isolecto: BM 000949957!, K 000380684!, P 00248363!).

Habit shrub or large woody climber up to 25 m high. Young shoots ferrugino-tomentose, hairs becoming blunt and sparse, bark smooth, becoming striate with prominent lenticels. Leaves elliptic–narrowly obovate, base retuse–subcordate, apex acute, 100–175 × 35–75 mm, blade rigid, subcoriaceous; veins 10–13; indument on upper blade sparse, hairs 2–5-branched, erect, scabrid, longer over midrib and veins forming prominent ferrugino-tomentose ridge, lower blade hairs 9–12-branched, subtomentose, blunt on midrib and veins. Petiole ~4–5 × 1.5 mm, ferrugino-tomentose. Inflorescence leaf-opposed, cymose with up to 4 pedicels, each bearing a single floral bud, with only the oldest 1 or 2 bearing mature flowers at any one time, peduncle ~3 × 1.5 mm, pedicels ~8–10 mm, bracts ~6 × 4.5 mm, ovate, apex acute–rounded, palmate veins visible on outer surface, peduncle and pedicel with ferrugino-tomentose hairs, hairs sparse and shorter on bracts. Calyx sepals 3, valvate at apex, connate basally, broadly triangular, ~6 × 3 mm, apex acute–obtuse, indument ferruginous on inner and outer surfaces, forming distinct ridge at margin, often persistent, forming detached ring at base of fruiting receptacle. Corolla 2 subequal whorls of 3 petals, petals red or dark purple in colour, broadly elliptic–oblong, apex rounded, ~12–14 × 5–6 mm, fully reflexed at maturity, indument sparse, fine and shaggy. Stamens ~30–40, 3–3.5(–4) long × 0.5 mm wide, flattened, connective cap up to 1 mm long, papillate, on inner whorl locules extending full length of stamen, submarginal whorl of stamens broad and flat and staminode-like with much reduced locules, outer whorl staminodes, ~14 in number, 3 mm long × 1.5–2 mm wide, broadly obovate and flattened. Carpels ~20 or fewer, 3.75 × 0.75 mm., ovary tomentose, hairs flattened, stigma U-shaped and glabrous but occluded on three sides by extension of ovary wall above a distinctly narrowed neck, ovules ~24 in two lateral rows. Fruit monocarps 4–8(–20), cylindrical, ~25–35 × 14–21 mm, young fruits green with rufous tint, pericarp thick and hard, mature fruits bright red in colour, flesh

white, juicy, pericarp wall subglabrous, thin and easily torn, stipe ridged, elongate, ~25–30 × 1–2 mm, indument sparse, hairs spreading; seeds 5–14(–20+), ~6 × 4 × 2 mm, compressed–ellipsoidal, ruminations visible, in 2 rows, occasionally compressed into what appears to be 1 row. (Fig. 1D, E, 4.)

Distribution

Probably the most common species of *Uvaria* in continental Asia. Although it is found in most forested habitats (although only occasionally in thickets in open dipterocarp forest), it is most common in dry evergreen and mixed deciduous types, and occurs in remnant forest vegetation. Distribution is shown in Fig. 13.

Notes

Uvaria rufa is most easily distinguished by the rough texture of the abaxial leaf surface and the outer whorl of broad and flat staminodes. The sweet tangy fruit is valued throughout much of Indochina and, although it is not actively cultivated, individual wild plants are often well known to local communities. The species is used in traditional medicine, particularly for the treatment of stomach cramp and period pain. Dunal (1817) first described this taxon as *Guatteria rufa*. Blume made reference to the latter in his description of *U. rufa*, but did not specifically mention it as a synonym, as he did with *U. javana*, for example. But Dunal's epithet 'rufa' cannot be transferred to *Uvaria* because of the presence of Blume's heterotypic taxon; therefore, Blume's name is affirmed here as the legitimate one for the taxon within the genus *Uvaria*. The lectotype (Blume *s.n.*, P 00248470) is selected as the best preserved sheet among Blume's original material, containing a full intact flower. Blume, correctly, noted that there are differences between this species and a related one from Timor with larger leaves and more obovate petals, which he called *U. timoriensis* Blume. Dunal included the two taxa under the same name, as the Paris and Geneva sheets that contain the type specimens for *Guatteria rufa* (Poivre and Lahaie collections from Java) also include the Timor taxon (Riedlé collections from Timor).

17. *Uvaria lobbiana* Hook.f. & Thomson, *Fl. Ind.* 1: 100 (1855)

Type: MALAYSIA. Peninsular Malaysia, Malacca, 1845, *W. Griffith s.n.* (lecto: K 000380689!, *vide* I.M. Turner, *Phytotaxa* 36: 102 (2011)); MALAYSIA. Malacca, *s. dat.*, *W. Griffith s.n.* (syn: BM!, K 000380688!, K 000380692!, P!, TCD 0017973!); *s. loc.*, *s. dat.*, *leg. ign.*, E.Ind.Comp. no. 434, 435 (K!); *s. loc.*, *s. dat.*, *T. Lobb s.n.* (syn: K 000691177!, SING!).

Uvaria subrepanda Wall., *Numer. List no.* 6483 (1832), *nom. inval.*, *nom. nud.* *Uvaria ptychocalyx* Miq., *Ann. Mus. Bot. Lugduno-Batavi* 2: 4 (1865).

Type: INDONESIA. Borneo, Poeloe Lampe, Sakoembang, *s. dat.*, *P.W. Korthals s.n.* (lecto: L 0195619!, *vide* I.M. Turner, *Phytotaxa* 36: 103 (2011)).

Large climber up to 30 m. Young-shoot hairs sparse, many-branched, becoming subglabrous, striate, with prominent lenticels.

Leaves elliptic–narrowly obovate, base shortly cordate, apex acute–cuspidate, $100\text{--}175\text{--}(200) \times 40\text{--}75\text{--}(85)$ mm, coriaceous; veins 8–14; indument upper blade subglabrous, hairs ~20-branched, midrib subtomentose, lower blade subglabrous, midrib subtomentose. Petiole $3\text{--}4 \times 1.25\text{--}2$ mm, appearing much broader than midrib base, sparse to subtomentose, transverse foliations prominent. Inflorescence supra-axillary or rarely leaf-opposed, flowers 1–2(–4), peduncle $\sim 2\text{--}5 \times 1.5$ mm, pedicel $5\text{--}10\text{--}(14) \times 1.5$ mm, both usually flattened in transverse section and densely tomentose with large rufous hairs, bracts broadly ovate, $\sim 6\text{--}10 \times 6\text{--}10$ mm, membranous, sparse–subtomentose with tomentose margin, veins prominent. Calyx sepals 3, undulate and imbricate in bud, ovate, 7×3.5 mm long, recurving at tips, outer- and inner-surface indument denser than on bracts. Corolla 2 subequal whorls of 3 petals, petals yellow but often turning pink or red, inner whorl $\sim 10 \times 8$ mm, outer whorl 11×8 mm, shortly and broadly ovate, less often

elliptical, apex obtuse or bluntly acute, inner surface undulate, tomentose, outer surface often with transverse ridges of large blunt stellate hairs. Stamens numerous, $2.25\text{--}2.5\text{--}(3)$ mm, connective flattened and shortly elongate with prominent papillae, locules extending full length of stamens, outer whorl of staminodes. Carpels numerous, $2.25\text{--}2.5\text{--}(3)$ mm, ovary densely tomentose with ring of elongate hairs ~ 0.25 mm long beneath stigma, stigma U-shaped, glabrous, ovules $\sim 6\text{--}8\text{--}(10)$. Fruit monocarps ovoid or globose, $\sim 16\text{--}18 \times 20\text{--}25$ mm, prominently tubercled, subtomentose, stipe $35\text{--}55\text{--}(70) \times 1.5\text{--}2$ mm, finely striate, indument sparse; seeds 4–6, $\sim 12 \times 10 \times 4.5$ mm, smooth, raphe prominent but not raised.

Distribution

A common species found in lowland rainforests recorded once from the Andaman Islands. Distribution is shown in Fig. 14.

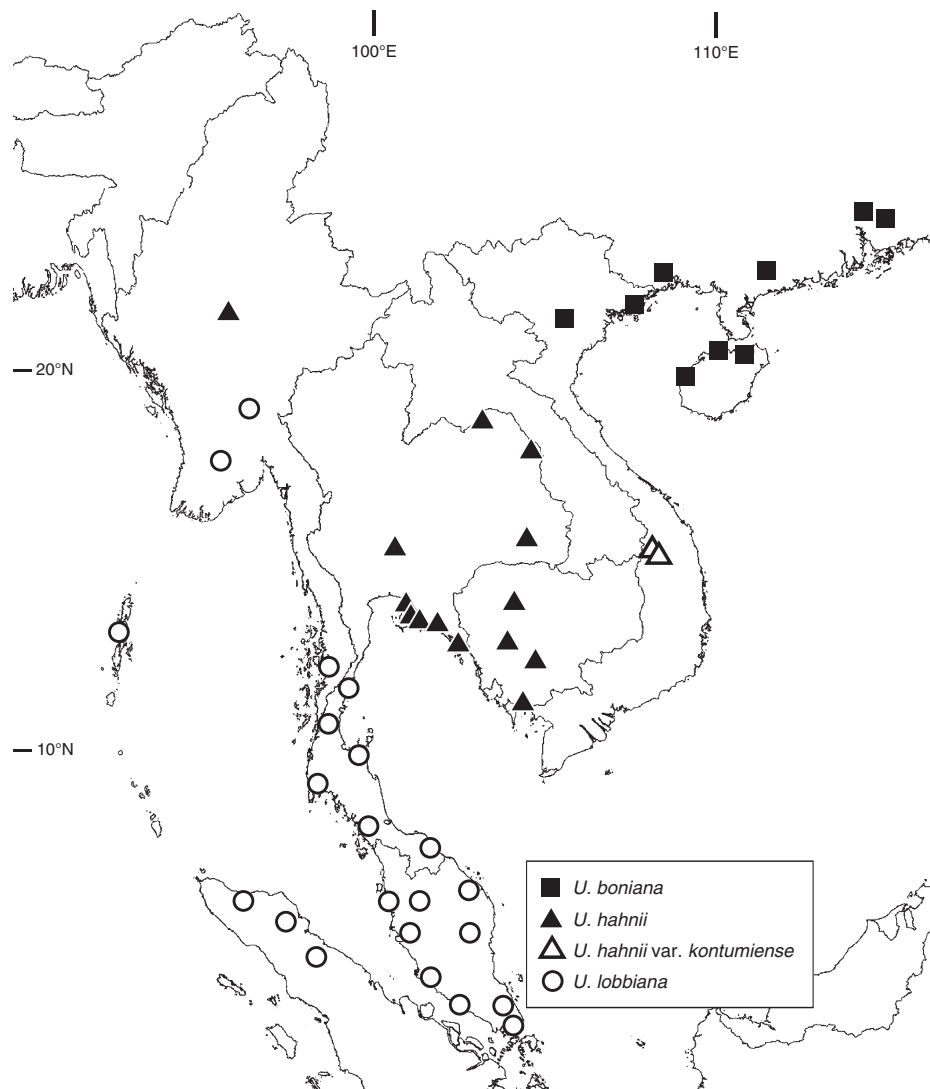


Fig. 14. Distribution of *Uvaria boniana*, *U. hahnii*, *U. hahnii* var. *kontumiense* and *U. lobbiana* in South-east Asia on the basis of herbarium specimens verified in this study.

Notes

Uvaria lobbiana is morphologically similar to *U. rufa* and *U. leptopoda* (King) R.E.Fr. (lower Malay peninsula). The densely tomentose broadly ovate petals and prominently tuberculate fruits of *U. lobbiana* distinguish it from both these species. The petals of *U. leptopoda* are glabrous on the inner surface, and the fruits, although mounted on a long stipe, are smooth and tomentose. The fruits of *U. rufa* have a short ~25–30-mm-long stipe and ~5–14(–20+) seeds, and the stamens are much reduced in number with an outer whorl of ~14–20 broadened staminodes. The staminodes of *U. lobbiana* are the same width as the outermost whorl of fertile stamens and 30–40 in number.

18. *Uvaria vietnamensis* Meade, *Adansonia* 27: 17 (2005)

Type: VIETNAM. Quang Nam, Ba Na, 25 km north-west of Đà Nẵng, 24 July 1923, *E. Poilane* 7326 (holo: P 00248413!; iso: E 00050316!).

[*Uvaria fauveliana* auct. non Pierre ex Finet & Gagnep.: S.Jovet-Ast, *Suppl. Fl. Indochine* 1: 64 (1938), p.p.; S.Jovet-Ast, *Not. Syst.* 9: 87 (1940), p.p.].

Habit climber or scrambling shrub. Young shoots subtomentose, hairs ferruginous with 2–5 ~1-mm-long multicellular branches, bark smooth becoming striate and sparse, with occasional persistent larger hairs. Leaves elliptic–narrowly obovate, (70–)90–225 × (35–) 40–75mm, apex acuminate to acute, base narrowly cordate, subcoriaceous; veins 14–16; indument upper blade sparse–subtomentose, hairs simple, occasionally 2-branched, ~1 mm long, midrib densely tomentose with erect 1 or 2+-branched hairs 0.75–1 mm long; lower midrib and blade subtomentose to sparse with 4–8-branched, ~0.6–0.85-mm-long stellate hairs. Petiole 3–5 × 1.5–2 mm, indument subtomentose, stellate, hairs fine and pale coloured or more thickly set and ferruginous. Inflorescence not known. Fruit monocarps ~20+, spheroidal, diameter ~20–30 mm, covered with distinctive 3+-branched

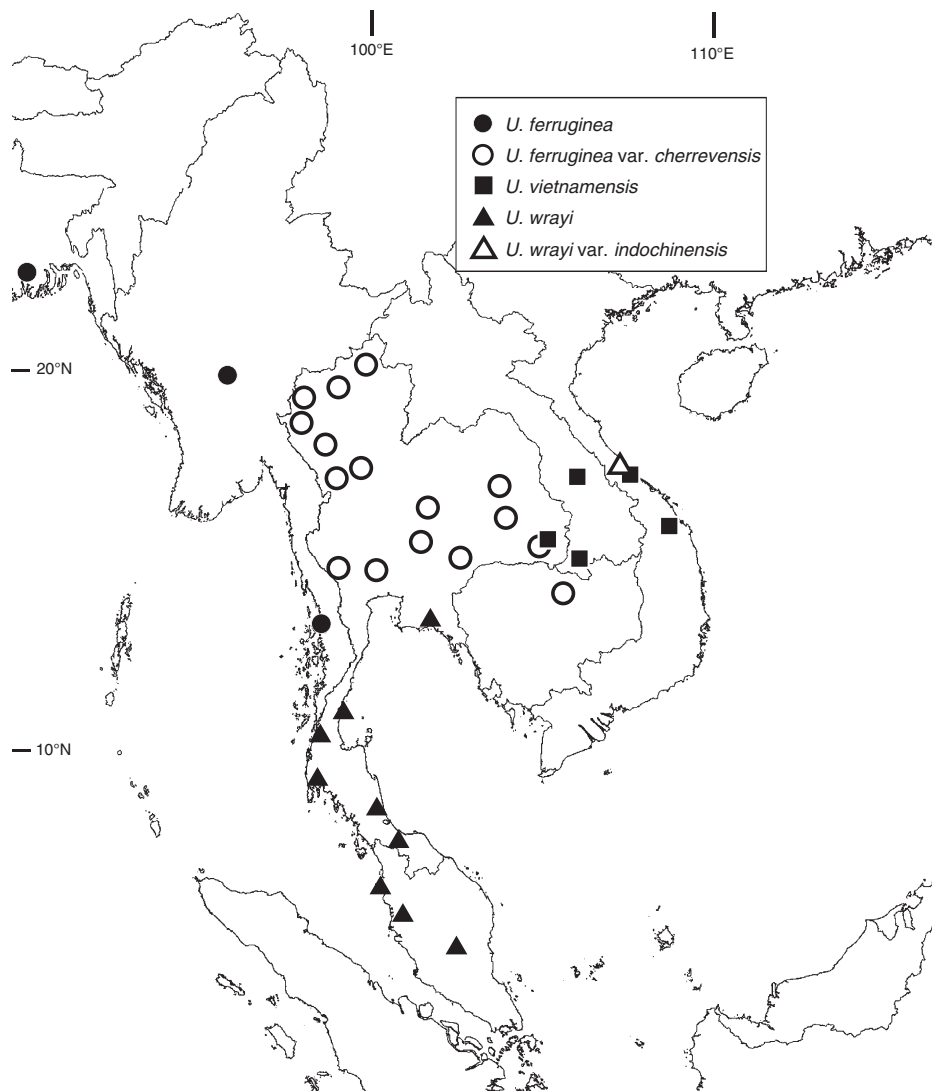


Fig. 15. Distribution of *Uvaria vietnamensis*, *U. wrayi* var. *wrayi*, *U. wrayi* var. *indochinensis*, *U. ferruginea* and *U. ferruginea* var. *cherrevensis* in South-east Asia on the basis of herbarium specimens verified in this study.

~5-mm-long outgrowths, each covered with ferruginotomentose branches, pericarp red at maturity, flesh pale white, bittersweet to taste, stipules up to 45×2 mm, striate with subtomentose indument; seeds 4–8, shortly hemi-ellipsoidal, $\sim 11 \times 5.25\text{--}7 \times 2\text{--}3$ mm, aril prominent, $4 \times 2.5\text{--}3 \times 3$ mm, surface leathery, brown, ruminations visible. (Fig. 6.)

Distribution

A rare species, occurring in mixed-deciduous or dry-evergreen forest habitats above 100-m altitude. Distribution is shown in Fig. 15.

Notes

Uvaria vietnamensis was described in part from fruiting material collected by Poilane (Poilane 7326) in Vietnam. This material was included by Jovet-Ast (1938, 1940) in her concept of *U. fauveliana* (syn. *U. hamiltonii* var. *fauveliana*), treated here as a synonym of *U. rufa*. The type material of *U. hamiltonii* var. *fauveliana* is a Pierre collection from Phu-quoc Island (Pierre 1787) that has flowers but no fruit, and was determined by Meade (2001) to represent *U. rufa*. The bearded epidermis on the fruit of the Poilane 7326 material is unique and clearly distinguishes it from *U. rufa* and all other species in the genus. The flower is unknown.

Uvaria hamiltonii and *U. hirsuta* resemble *U. vietnamensis* in fruit and vegetative morphology respectively. The fruit of *U. calamistrata* has epidermal outgrowths on the monocarp; however, in *U. vietnamensis* these outgrowths are covered with a dense, rufous indument, a feature that is absent in *U. calamistrata*. The stipe in *U. calamistrata* is short and broad, ~ 3.5 mm long, whereas it is ~ 45 mm long in *U. vietnamensis*. The narrowly obovate leaves of *U. vietnamensis* are also distinct from narrowly elliptic leaves of *U. calamistrata* (Meade and Parnell 2003).

19. *Uvaria griffithii* L.L.Zhou, Y.C.F.Su & R.M.K.Saunders, Syst. Biodivers. 7: 255 (2009)

Cyathostemma viridiflorum Griff., Notul. Pl. Asiat. 4: 707 (1854).

Type: MALAYSIA. Peninsular Malaysia, Malacca, s. dat., W. Griffith 432 (lecto: K 000582099!, fide T.M.A. Utteridge, Blumea 45(2): 390 (2000)).

Cyathostemma scortechinii King, J. Asiat. Soc. Bengal Part 2, Nat. Hist. 61(1): 9 (1892); *Cyathostemma viridiflorum* var. *scortechinii* (King) Ridl., Fl. Malay. Penins. 1: 27 (1922).

Type: MALAYSIA. Peninsular Malaysia, Selangor, Kepong, s. dat., King's collector [H.H.Kunstler] 5857 (lecto: K 000380130!; isolecto: BM 000020753!, SING 0073566!., fide T.M.A. Utteridge, Blumea 45(2): 390 (2000)).

Large climber up to 25 m. Young branchlets sparsely tomentose, quickly becoming subglabrous, bark black and striate. Leaves narrowly obovate, base retuse to cordate, apex acute–shortly acuminate, $100\text{--}150 \times 40\text{--}60$ mm, membranous or coriaceous; veins 9–15; indument hairs erect, subtomentose over upper midrib, quickly becoming sparse–glabrous, glabrous over upper blade, lower surface hairs sparse–subglabrous on midrib, subglabrous–glabrous on blade. Petiole 5–7 mm long \times

1.2–2.5 mm in diameter, lower side warted, indument sparse, later glabrous. Inflorescence leaf-opposed, sometimes cauliflorous, cymose, dichotomous, flowers 1–4, peduncle elongate, $\sim 20\text{--}50$ mm long $\times 1.5$ mm in diameter, pedicel 20–30 mm long, secondary buds arising in axil of medial bract, bracts ovate, $\sim 5 \times 5$ mm, hairs sparse, spreading, fine. Calyx sepals valvate, broadly ovate, 5 mm wide $\times 3$ mm long, often reflexed at maturity, apex acute, ferruginotomentose on inner and outer surfaces. Corolla 2 whorls of 3 petals, inner narrower than outer, petals green or yellow, outer whorl broadly ovate, $\sim 5 \times 5$ mm, inner whorl 5 mm long $\times 4$ mm wide, ovate, base constricted, both whorls concave, thickened basally and with prominent transverse foliations on outer surface, outer surfaces sparsely tomentose, hairs pale, fine, straggling, inner surface shortly and densely tomentose, base subglabrous, hairs pale. Stamens numerous, $\sim 2\text{--}2.5$ mm long, apex $\sim 0.5\text{--}0.7$ mm long, incurved, papillate, papillae often hair-like, locules extending full length of stamen. Carpels numerous, $\sim 3\text{--}4$ mm long, ovaries tomentose, stigma glabrous, elongate, conical, $\sim 1\text{--}1.25$ mm long, U-shaped in section, ovules 5 or 6 in 2 rows. Fruit monocarpous ovoid–oblong but irregular in shape because of compression of pericarp around seeds, 25–40 mm long $\times 10\text{--}20$ mm wide, pericarp thickened, glabrous, stipe ~ 20 mm long, 2.5 mm in diameter; seeds 4–6, in 2 rows but irregularly arranged in mature fruit.

Distribution

Restricted to wetter forests of the Malay Peninsula south of the Isthmus of Kra. Distribution is shown in Fig. 8.

Notes

The fruit of *U. griffithii* resembles that of *U. pierrei* Finet & Gagnep.; however, the oblong leaves of this latter species are highly distinctive. The inflorescence of *U. griffithii* is similar in structure to that of *U. wrayi* (King) L.L.Zhou, Y.C.F.Su & R.M.K.Saunders; however, the pedicel of *U. griffithii* is much longer. Owing to the previous description of *U. viridiflora* Ruiz & Pav. ex G. Don, Zhou *et al.* (2009) assigned the epithet *griffithii* in honour of William Griffith, who originally described the taxon.

20. *Uvaria tonkinensis* Finet & Gagnep., Bull. Soc. Bot. France (Mém. 4 (2)) 53: 74 (1906)

Melodorum vietnamense Bân, Bot. Zhurn. (Moscow & Leningrad) 59: 242 (1974), nom. nov. (non *Melodorum tonkinense* Finet & Gagnep. (1906)).

Type: VIETNAM. Tonkin, Ninh Binh, Thinh Chau Mountains, 28 Apr. 1884, H. F. Bon 2566 (first step lecto, fide N.T.Bân, Bot. Zhurn. (Moscow & Leningrad) 59: 242 (1974)); second step lecto, here designated: P 00142693!; isolecto: P 00142692!, P 00248405!).

Uvaria tonkinensis var. *subglabra* Finet & Gagnep., Bull. Soc. Bot. France (Mém. 4 (2)) 53: 74 (1906).

Type: VIETNAM. Tonkin, Mt But-Son, 7 Dec. 1883, H. F. Bon 2295A (lecto, here designated: P 00248048!).

Cyathostemma longipes Craib, *Bull. Misc. Inform. Kew* 1925: 8 (1925); *Uvaria longipes* (Craib) L.L.Zhou, Y.C.F.Su & R.M.K.Saunders, *Syst. Biodivers.* 7: 255 (2009).

Type: THAILAND. Ubon Ratchatani Province, Pu, 4 Mar. 1924, *Kerr 8607* (holo: K 000595343!; iso: BM 000020745!, P!).

Melodorum vietnamense var. *calcareum* Bân, *Bot. Zhurn.* (Moscow & Leningrad) 59: 242 (1974).

Type: VIETNAM. Tonkin. Cho Ganh, June 1923, *P. A. Petelot 906* (holo: P 00142619!; iso: A 00039447!, BM!, US 00098808!).

Climber or scrambling shrub. Young shoots sparsely tomentose, bark black, striate. Leaves elliptical–obovate, base retuse, apex acuminate or rarely acute, ~130–170 × 50–60 mm, thinly coriaceous, waxy; veins 9–11; indument upper surface glabrous in mature leaves, lower surface sparse to glabrous, hairs fine, 3–10-branched, rufous. Petiole 5–7 × 1.5 mm, black, lower surface with prominent transverse foliations, hairs subtomentose–sparse, rufous, fine, straggling. Inflorescence leaf-opposed or subopposed, flowers solitary or rarely 2 or 3 from young shoots, peduncle 3–5 × 1 mm, pedicel elongate, 35–90 × 1.5–2 mm, flattened medially, striate, subglabrous, basal bract up to 11 × 3 mm with prominent central vein, subtomentose–sparse above and below, medial bract very small, ~1 × 1 mm, ovate acute, tomentose, both bracts usually wanting. Calyx sepals 3, valvate, free, opening early, remaining small, ~4.5 mm wide × 2 mm long, surface warted, outer surface with sparse indument, tomentose at margins, inner surface glabrous. Corolla 2 whorls of 3 petals, inner smaller than outer, petals yellow to green in colour, erect, concave, outer petals ~8–15 mm wide × 9–15 mm long, broadly ovate, apex bluntly acute–obtuse, base narrowed, inner petals 4–8 mm wide × 6–10 mm long, narrowly ovate to acute, base of both whorls fleshy, apex and margins membranous, outer petals tomentose on inner- and outer-surface margins and apex, glabrous at base, inner petals tomentose on outer surface, inner surface basally glabrous, apex tomentose, hairs on all petals ferruginous, very short, almost papillate. Stamens numerous, ~2 × 0.4 mm, apex tomentose, locules extending full length of stamen. Carpels 3 mm long, stigma elongate, 1 mm long, glabrous, ovary tomentose, hairs ferruginous, 5-branched, 0.5 mm in diameter, ovules 2. Fruit monocarps numerous 15–30, green turning red, transversely ovate–glabrous, up to ~9 × 7 mm (1-seeded), 10 × 9 mm (2-seeded), pericarp thin, flaking easily after drying, stipe ~25–40 × 1.25 mm, finely striate with isolated spreading rufous hairs; seeds 1 or 2, to ~9 × 7 × 4.5 mm, hilum A-shaped, 1.5 × 1.5 mm.

Distribution

Distribution is shown in Fig. 16.

Notes

Leaf characters have been used to distinguish varietal taxa in *U. tonkinensis* and *Melodorum vietnamense*; however, in both cases, these characteristics are not sufficiently distinctive to warrant varietal status. There is considerable variation in pedicel length between specimens; however, this variation

does not appear to be correlated with any other character differences nor with any particular geographic distributions. The lectotypes selected present the best-preserved material from the originally cited sheets.

21. *Uvaria boniana* Finet & Gagnep., *Bull. Soc. Bot. France* (Mém. 4 (2)) 53: 71 (1906)

Type: VIETNAM. Nin-thai, Ha-Tay Province, 17 Sep. 1888, *H. Bon 3956* (lecto, here designated: P 00247945!; isolecto: G 00226477!, P 00247946!, P00557041!); VIETNAM. 21 May 1889, *H. Bon s.n.* (syn: P 00247944!); Quang-Yen, Quang Ninh Province, May 1886, *Balansa 4185* (syn: K 000691172!, P 00247943!, P 00142652!).

Sarmentose shrub up to 2.5 m or woody climber up to 20 m, crown a dense network of twining branchlets. Young shoots subglabrous to glabrous, with occasional ~1-mm-diameter pale, stellate hairs, bark black, striate, shiny. Leaves elliptic–obovate, apex narrowly acute–acuminate, base cuneate, (50–)80–110 × (20–)35–40 mm, membranous, both surfaces shiny; veins ~8–10, bifurcation often at mid-point between midrib and margin; indument leaf blade glabrous on both surfaces, upper midrib with sparse 2–5-branched hairs, lower midrib subglabrous. Petiole 4–5 × 1 mm, glabrous except for sparse hairs along abaxial groove. Inflorescence flowers 1(–2), leaf-opposed; peduncle 2–5 mm; pedicel ~40 mm long, diameter ~1 mm at base and apex, 0.5 mm or less medially, surface black, shiny and striate with scattered pale stellate hairs, bracts small and indistinct, up to ~2 × 1 mm, ovate, usually wanting. Calyx sepals 3, valvate, connate at base, broadly ovate–triangular, apex rounded, ~2.5 × 3.5 mm, reflexed basally, apex remaining incurved, inner and outer surfaces red to green drying black, glabrous centrally with ferrugino-tomentose margins especially prominent on inner surface, often persistent. Corolla 2 whorls of 3 petals, inner narrower than outer, petals red, drying black, thickened centrally and basally, thinner towards margins; outer whorl ~8 × 7 mm, 1.5–2 mm thick, ovate, rounded apically, concave, inner whorl ~8 × 5 mm, 1–1.5 mm thick, obovate, apex bluntly acute–rounded, concave, base constricted; both whorls ±glabrous and leathery on external surface, short stellate indument on margins and towards apex, inner surface with short ferrugino-tomentose indument most dense at apex and margins, glabrous at base, both whorls remaining erect and incurved. Stamens numerous, ~1.5–1.7 mm long, connective cap flat to discoid to convex, indument dense, blunt, sometimes present on external ridge of connective, locules subequal, basal filament evident, staminodes not present, outermost whorls of stamens reduced in size to ~1.2–1.5 mm, with connective cap extending as ridge on external side. Carpels numerous, ~3 mm long, ±erect at centre of gynoecium, incurved towards margin, ovary with dense indument of combed stellate hairs, stigma up to 0.75 mm long, glabrous, U-shaped in section, lobes narrow, ovules 6–8 in 2 rows. Fruit monocarps 25–45+, ovoid, ellipsoid or shortly cylindrical, ~15–17(–20) × 11(–13) mm, ±basally attached, occasionally with a prominent apicule, green turning red to purple at maturity, drying brown or black, surface somewhat warty with short, scattered, stellate hairs, pericarp ~2 mm thick, soft and juicy when ripe, stipe ~35–45 mm long,

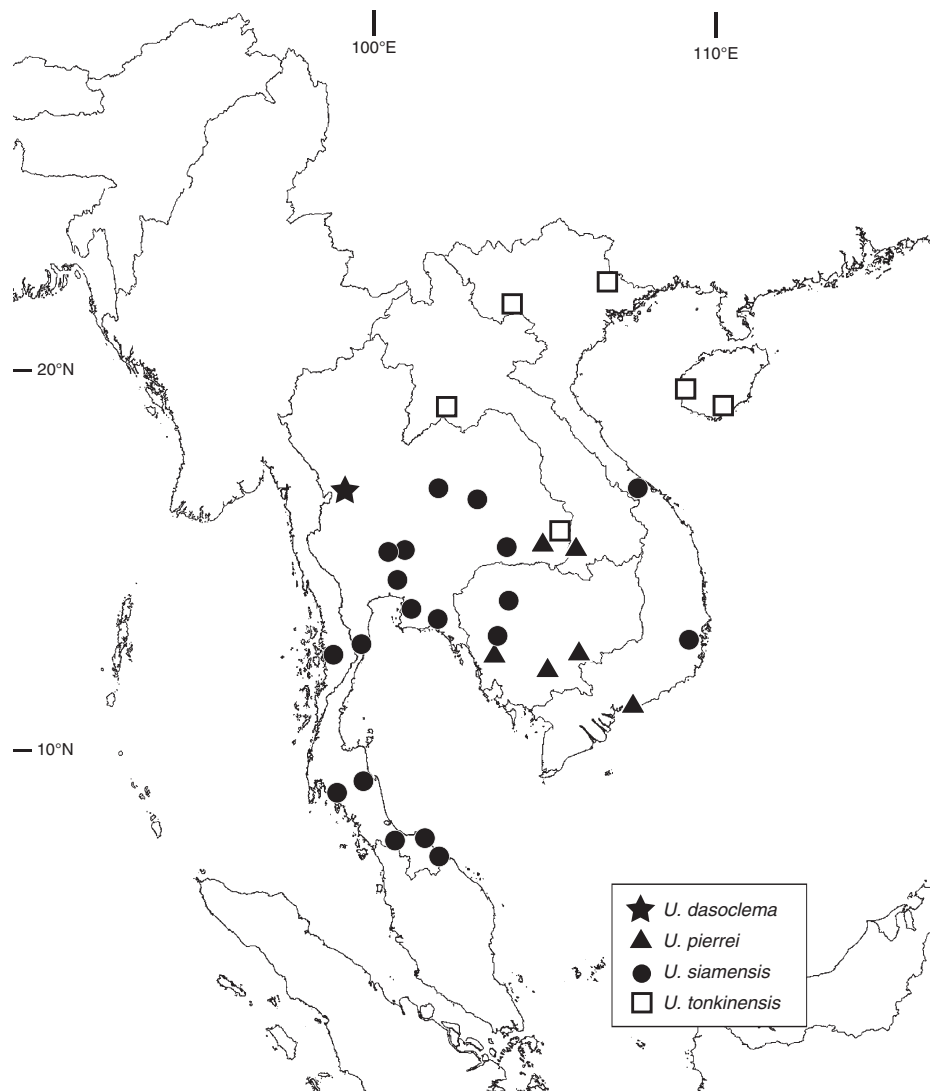


Fig. 16. Distribution of *Uvaria dasoclema*, *U. pierrei*, *U. siamensis* and *U. tonkinensis* in South-east Asia on the basis of herbarium specimens verified in this study.

1 mm in diameter, surface black to brown, striate, indument as for pedicel; seeds 4–6, $10 \times 7 \times 4$ mm, laterally attached in 2 rows, aril thickened above the raphe on one side, hilum V-shaped, testa brown, shining, ruminations visible. (Fig. 1E.)

Distribution

Uvaria boniana is typically found in evergreen and semi-deciduous forest and scrub from sea level to 850 m. In forest habitats, it can grow up to 20 m, and is frequent scrambling over rocks in scrub vegetation on steep open hillsides. Distribution is shown in Fig. 14.

Notes

The dense twining habit of crown branchlets is distinctive, as are the waxy and almost entirely glabrous leaves. This species is morphologically similar to *Uvaria tonkinensis*, but distinguished

by its much shorter, narrower pedicels, smaller, less broadly ovate petals and smaller, more delicate leaves. *Uvaria flexuosa* is very similar to *U. boniana*, exhibiting all the floral characters of the latter, but in miniature. The lectotype selected presents the best-preserved material from the originally cited sheets.

22. *Uvaria flexuosa* Jovet-Ast in F. Gagnepain (ed.), *Suppl. Fl. Indo-Chine* 1: 64 (1938)

Uvaria flexuosa Jovet-Ast, *Not. Syst.* 9: 73 (1940), isonym.

Type: VIETNAM. Annam, Massif de la Mere et L'Enfant, May 1923, *Poilane 6781* (holo: P 00248300!, iso: P 00248301!, PHH!).

Climber with small leaves, crown a dense network of twining branchlets. Young branchlets sparse indument of ~12+-branched rufous hairs, becoming glabrous, surface black, striate, smooth and shiny. Leaves narrowly elliptical–

lanceolate, base cuneate, apex narrow, tapering, acute-acuminate, $\sim 70\text{--}75 \times 20$ mm; veins $\sim 10\text{--}13$, branching early; indument upper surface glabrous except for tomentose hairs over midrib and sparse ring of hairs on margin, lower blade glabrous, hairs sparse on midrib. Petiole $2\text{--}6 \times 0.75$ mm, subtomentose-subglabrous, shiny, black, transversely foliated. Inflorescence flowers solitary, leaf-opposed or supra axillary, peduncle subsessile, $\sim 1\text{--}2$ mm long, pedicel ~ 30 mm long, very narrow, $\sim 0.35\text{--}0.45$ mm in diameter, smooth and shiny, black with sparse rufous hairs as for shoots pedicel with single basal obovate-round $\sim 3 \times 3$ -mm bract with hairs on margin and midrib. Calyx sepals 3, valvate, broadly ovate, $\sim 1 \times 1$ mm, tubercled, with sparse spreading rufous hairs, dense at margin. Corolla 2 whorls or 3 petals, inner whorl narrower than outer, outer whorl ovate, 4.5 mm long \times 3 mm wide, inner whorl obovate with narrowed base, 5 mm long \times 2.5 mm wide, inner and outer surface of both whorls basally subglabrous with tomentose margin and apex. Stamens numerous, ~ 1.2 mm long, connective apex enlarged, club-shaped, broad, papillate, locules

subequal, nearly full length, basal filament evident. Carpels numerous, ~ 2 mm long, ovaries hairy on ridges and apex, stigmas glabrous, U-shaped, elongate, ovules 6. Fruit not known.

Notes

This species is known only from the type collection. There is little discrete character difference between this specimen and *U. boniana*, other than the much smaller size of all organs in *U. flexuosa*. However, it is very unusual in the *Uvaria* group to see both young leaves and young flowers growing together on the same new shoots. It must be assumed, therefore, that the smaller leaves of *U. flexuosa* are not a juvenile form, but are distinctive for the species. For this reason, it seems wise to retain *U. flexuosa* until more material becomes available.

Distribution

Distribution is shown in Fig. 17.

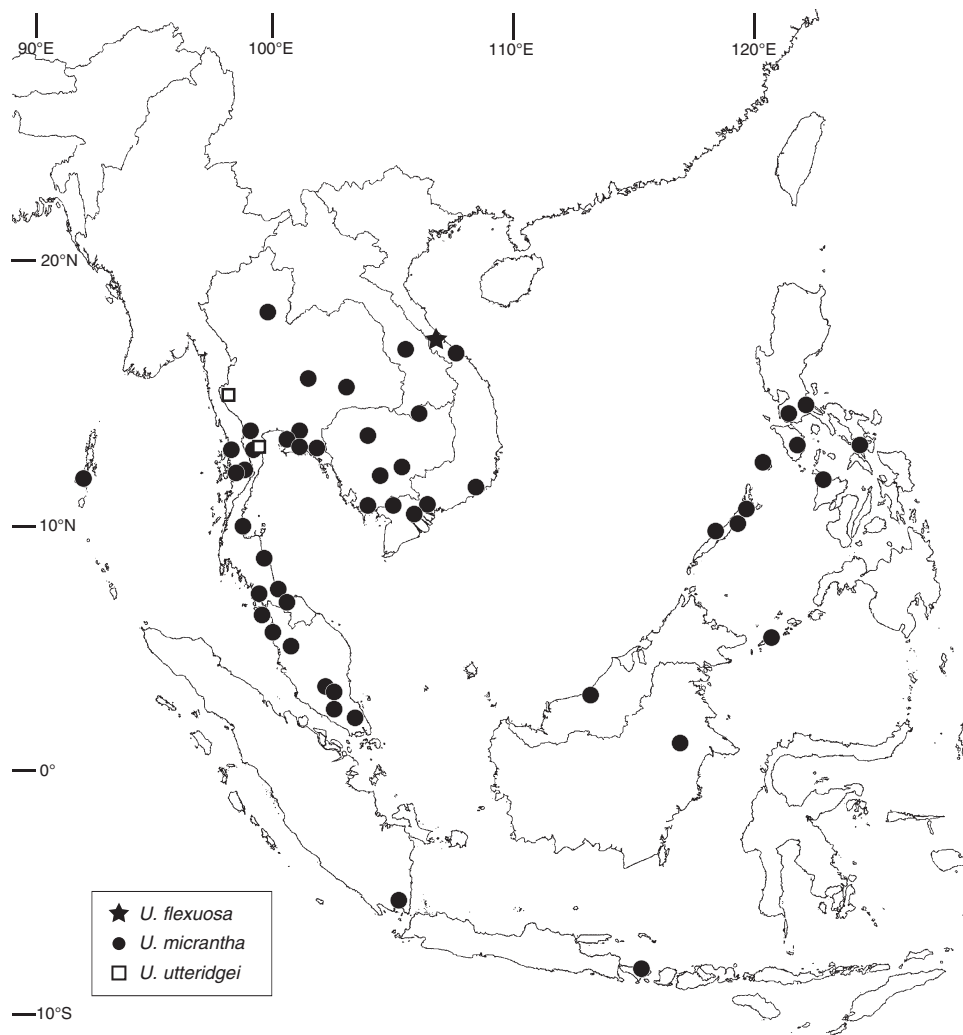


Fig. 17. Distribution of *Uvaria flexuosa*, *U. micrantha* and *U. utteridgei* in South-east Asia on the basis of herbarium specimens verified in this study.

23. *Uvaria pierrei* Finet & Gagnep., *Bull. Soc. Bot. France* (Mém. 4 (2)) 53: 64 (1906)

Type: CAMBODIA. Pnom-Penh, 29 May 1878, *M. Godefroy* 48 (lecto, here designated: P 00248308!; isolecto: VNM!, P00248305–7!); CAMBODIA. Pursat, June 1876, *Harmand s.n.* (syn: P 00248309!); VIETNAM. Baria, Dinh Mountains, June 1871, *Pierre 1789* (syn: A 00039701!, BM 000528084!, PHH!, K 000691170–1!, P 00248310–11!).

Scandent shrub or, more rarely, a climber. Young shoots subtomentose, becoming subglabrous and striate with distinct white lenticels. Leaves distinctively oblong, base retuse, apex obtuse or retuse, ~45–90 × 17–35 mm, coriaceous, often shiny, leaf margin turned downward; veins ~12–14; indument upper midrib with sparse erect stellate hairs near base, blade glabrous, lower midrib and veins sparse–subglabrous, blade glabrous. Petiole ~3–4.5 × 1.25 mm, distinctly broader than midrib, indument sparse. Inflorescence leaf-opposed or subopposed, flowers 2, often with 1 bud dormant, peduncle ~3–4 mm, tomentose–subtomentose, pedicels ~10 mm, often transversely flattened with a longitudinal groove, bracts broadly ovate–acute, ~2.5 × 4 mm in diameter, clasping, outer surface subtomentose, inner surface subglabrous. Calyx sepals 3, valvate, opening early, broadly ovate, acute, ~2.25 × 4.5 mm, sometimes reflexing at maturity, remaining concave, outer surface tomentose at base with thick ferruginous hairs, sparse towards apex, margin tomentose, hairs fine, paler-coloured, inner surface glabrous except for tomentose margin. Corolla 2 whorls of 3 petals, inner whorl marginally smaller than outer, petals purple, narrowly ovate–broadly elliptical, base constricted, apex obtuse or very bluntly acute, ~4.5–5.25 × 4–4.5 mm, fleshy, thickened basally, both whorls remaining erect, hardly expanding, indument sparse on both surfaces of both whorls, becoming tomentose at margin, hairs fine, spreading. Stamens numerous, ~1 mm long, connective apex flat, locules extending full length of stamen. Carpels ~40, 1.75 mm long, ridges and neck hairy, stigma large, ~0.6 × 0.4 mm, broad and elongate, U-shaped, glabrous, with a prominent longitudinal slit, ovules 4–6 in 2 rows. Fruit monocarp ~5–15, green maturing yellow then purple, globose or ovoid, ~17.5 × 12.5 mm, subglabrous, smooth or very finely tuberculate, pericarp fleshy, stipe ~7–12 mm, somewhat striate, sub-glabrous; seeds 2–4, up to ~12 × 9 × 4 mm at maturity, aligned longitudinally within monocarp. (Fig. 1E.)

Distribution

Distribution shown in Fig. 16.

Notes

The peculiar oblong leaves of this species make it instantly recognisable. The only uvarioid species in continental Asia the leaves of which resemble it, is *Rauwenhoffia siamensis* Scheff.; however, this species can be distinguished from *U. pierrei* by its large yellow flowers and sessile fruits. The longitudinal alignment of seeds in the mature monocarp appears to arise as a result of the non-expansion of tissue between seed attachments after fertilisation, causing the seeds to rotate within the monocarp as they grow. *Uvaria goloensis* Merr. from the

Philippines is a close relative, and the two are possibly varieties of the same taxon.

24. *Uvaria micrantha* (A.DC.) Hook.f. & Thomson, *Fl. Ind.* 1: 103 (1855)

Guatteria micrantha A.DC., *Mém. Anon.* 42 (1832); *Cyathostemma micranthum* (A.DC.) J.Sinclair, *Gard. Bull. Singapore* 14: 225 (1955).

Type: MYANMAR. Martaban, Amherst, 17 June 1827, *W. Gomez 15* [= *N. Wallich 1287*, *Wall. Cat. no. 6449*] (lecto: K-W 001123938!; isolecto: BM!, G 00237292!, *fide* T.M.A. Utteridge, *Blumea* 45(2): 388 (2000)).

Polyalthia fruticans A.DC., *Mém. Soc. Phys. Genève* 5: 216 (1832).

Type: MYANMAR. *Gomez s.n.* [*Wall. Cat. no. 6430*, Burma, Tavoy 1827, Myanmar] (syn: K-W 001123876–7!, BM!).

Anaxagorea sumatrana Miq., *Fl. Ned. Ind., Eerste Bijv.* 3: 382 (1861); *Uvaria sumatrana* (Miq.) Hook.f. & T.Thomson, *Fl. Br. Ind.* 1: 51 (1872).

Type: INDONESIA. Sumatra, Lampong. Sumatra austr. in Lampong prope Tega-nennin, *Teijsmann s.n.* (holo: L 0181487!).

Popowia nitida King, *J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist.* 61(1): 92 (1893).

Type: INDIA. Andaman Islands, Hobdaypur, 4 July 1891, *King s.n.* (lecto: K 000739196; isolecto: K 000739197, both *n.v.*, *fide* T.M.A. Utteridge, *Blumea* 45(2): 388 (2000)).

Climber or scrambling shrub with narrow tangling branches forming dense thicket. Young shoots subtomentose, striations appearing early. Leaves elliptical–shortly lanceolate–narrowly obovate, base cuneate, apex acuminate–acute, ~70–120 × 20–40 mm, thinly coriaceous, waxy, drying dark brown above and below; veins 9–12 (or up to 16 with long acuminum); indument blade glabrous above and below, hairs on upper midrib subtomentose–sparse, hairs erect, 2- or 3-branched, lower midrib with isolated ~1- or 2-branched hairs clinging to midrib, always aligned towards leaf apex. Petiole 2–3(–4) × 0.75 mm, hairs subtomentose, ferruginous. Inflorescence leaf-opposed, floral buds 1–3, often only the primary flower opened, the others enclosed by bracts, peduncle subsessile, ~1.5(–2) mm × 0.075 mm in diameter, pedicel ~2–4(–5) × 0.5 mm, basal bract ovate, 4–6 × 1–2(–4) mm, medial bract smaller, ovate–acute, up to 1.5 × 2 mm, peduncle and pedicel flattened, ferruginotomentose. Calyx sepals 3, valvate, broadly ovate–acute, ~2 × 2.75 mm, concave, outer surface and margins tomentose, becoming sparse centrally, hairs pale, inner surface glabrous and warty basally, tomentose towards margin. Corolla 2 whorls of 3 petals, outer petals broader than inner, petals green or yellow to maroon in colour, outer petals ovate–oblong, apex bluntly acute–narrowly obtuse, ~3.25 × 2.5 mm, inner petals broadly elliptical with distinctly constricted base, ~3.35 × 2 mm, apex as for outer petals, both whorls thick and fleshy, concave, spreading at maturity to clearly expose stamens and carpels. Stamens numerous, ~0.6–1 mm long, connective flat, cap-like, papillate, locules full length. Carpels ~20, 0.8–1.5 mm long, straight or bent inward at margin of gynoecium, hairy along ridges and just beneath stigma, hairs fine, many-branched, stigma U-shaped, glabrous, somewhat elongate, ovules 2(–4). Fruit

monocarps 10–20, green turning yellow, globose–shortly oblong, ~9.5 × 8 mm at maturity, pericarp fleshy, becoming thin and black after drying, stipe ~14–20(–23) mm, glabrous, smooth; seeds 1–2(–3), ~7 × 4 × 4 mm when in single-seeded monocarp, up to 7 × 4 × 2 mm when 2- or 3-seeded, aril 2.5 × 1.75 mm, triangular, hilum A-shaped.

Distribution

Although there are some records of *U. micrantha* from open dipterocarp forests in central Thailand, this species is usually found in wetter habitats near watercourses or in wet evergreen forests. Distribution is shown in Fig. 17.

Notes

Sinclair (1955) transferred *U. micrantha* to *Cyathostemma* on the basis of its petal aestivation. With the transfer of the type species of *Cyathostemma*, *C. viridiflorum*, to *Uvaria* (see above), this taxon reverts to the classification of Hooker and Thomson (1855).

25. *Uvaria utteridgei* L.L.Zhou, Y.C.F.Su & R.M.K.Saunders, *Syst. Biodivers.* 7: 255 (2009)

Cyathostemma siamense Utteridge, *Blumea* 45: 389 (2000).

Type: THAILAND. Kanchanaburi, Three Pagodas Pass, 14 May 1946, *Kostermans 428* (holo: L!; iso: K 000691368!).

Woody climber. Young shoots shortly tomentose, quickly becoming smooth and striate. Leaves elliptical, base subcordate–broadly cuneate, apex acute–acuminate, up to 150 × 50 mm, subcoriaceous; veins 8–10; indument upper surface glabrous at maturity, blunt hairs occasionally persistent along midrib depression, lower blade glabrous with isolated hairs alongside midrib, midrib with scattered 2–5-branched hairs oriented towards leaf apex. *Petiole* ~6 × 1 mm, smooth, indument sparse to subglabrous, more dense in abaxial groove. Inflorescence cauliflorous, dichasial, peduncles short and closely packed, ~1 mm long × 2 mm wide, pedicel up to 22 × 1 mm, basal bract triangular, clasping pedicel, ~4 × 3 mm, medial bract wanting, pedicel flattened with 2 or 3 shallow longitudinal grooves, indument tomentose on bracts, tomentose–subtomentose on peduncle and pedicel, up to 5 mature flowers at a time. Calyx sepals 3, valvate, basally connate, ovate, up to ~7 mm wide × 5 mm long, subtomentose on both surfaces. Corolla 2 whorls of 3 petals, inner smaller than outer, petals adjoining petals imbricate along entire margin, outer petals ovate, bluntly acute, concave, coriaceous, up to 9 mm long × 7 mm wide, inner whorl narrowly ovate, bluntly acute, concave, coriaceous, up to 8.5 mm long × 6.5 mm wide, bases of both whorls somewhat thickened, inner and outer indument shortly tomentose. Stamens numerous but reduced to 3 or 4 whorls, ~5 × 1 mm, glabrous, connective with prominent extrorse ridge, apex flattened, bluntly acute, papillate, locules extending full length of stamen. Carpels ~50, ~5 × 1 mm, ovary tomentose, stigma narrow, 1 mm long, U-shaped, glabrous, ovules ~16. Fruit unknown. (Fig. 7.)

Distribution

Uvaria utteridgei is restricted to the dry evergreen forests of south-western Thailand. Distribution is shown in Fig. 17.

Notes

The petals are similar to those of *U. littoralis* and *U. microcarpa*, and are distinctly imbricate in bud, and the ~16 ovules reminiscent of *Uvaria grandiflora* or *U. rufa*.

26. *Uvaria argentea* Blume, *Fl. Javae* 21, 22: 24 & t. 6 & t. 13d (1830)

Cyathostemma argenteum J.Sinclair, *Sarawak Mus. J.* 5(3): 599 (1951). *Cyathostemma nitidum* Bakh.f., *Blumea* 12: 61 (1963), *nom. illeg.*

Type: INDONESIA. Java, at Menes, Bantam, June 1823, *van Hasselt s.n.* (holo: L 1770530!).

Key to the varieties in continental Asia

1. Petals red, leaves elliptic or oblong..... **26a. *U. argentea* var. *argentea***
 Petals white or yellow to green, leaves usually obovate.....
 **26b. *U. argentea* var. *bracteata***

26a. *Uvaria argentea* Blume var. *argentea*

Much-branched climber with distinctive wrapping branchlets. Leaves elliptic or oblong, less often obovate, 50–100(–180) × 30–50(–65) mm, obtuse, acute or shortly acuminate, narrowly retuse, membranous; veins (9)–10–12(–13), fine, gradually inarching, trailing traces fine, not forming distinct submarginal vein, secondary veins kinked or incomplete, tertiary venation very fine, dense, reticulate, midrib shallowly depressed above, emergent below, primary veins marginally raised above, distinct below, microvenation visible above and below; indument upper blade glabrous, sparse stellate erect hairs over midrib, sparse spreading hairs over primary veins, lower surface sparse hairs on midrib and veins, blade glabrous. *Petiole* 4–7 × 1.5 mm, tomentose becoming subglabrous, adaxial surface prominently warted and transversely foliated. Young shoots tomentose becoming subglabrous and prominently striate early. Inflorescence flowers solitary or occasionally 2–4, peduncle 2 mm long, pedicel up to 7 mm, basal bract 7–9 mm long × 5–6 mm wide, membranous, medial bract ~5 × 3.5 mm, obovate, often wrapping over floral bud, indument dense over peduncle, pedicel and bracts, becoming less dense as bracts expand. Calyx sepals 3, free, valvate, broadly ovate, apex obtuse–cuspidate, up to 4.5 mm wide × 3 mm long, often reflexed at maturity, indument tomentose on both surfaces, outer surface hairs somewhat rufous, on inner surface hairs straggling, fine, often subglabrous basally. Corolla 2 whorls of 3 petals, inner petals smaller than outer, petals red in colour, drying dark green–black, outer petals ovate–oblong, acute, concave, 5–6 mm long × 4.5–5.5 mm wide, inner whorl narrowly ovate, acute, strongly concave, 4–5 mm long × 3.5–4 mm wide, outer surface of both whorls warty, indument sparse, tomentose at margin, hairs straggling, straw-coloured, inner surface hairs fine, straggling, glabrous medially on outer petals, glabrous basally on inner petals, with prominent stamen indents in both whorls, both whorls remaining erect. Stamens numerous, 2 mm long, connective with short, blunt tomentum, apex 0.75 mm long, oblongoid or globose, locules extending full length of stamen. Carpels ~30, 3.5 mm long, S-shaped, ovaries hairy, stigma U-shaped, elongate, 1–1.25 mm long, glabrous,

ovules 4–10. Fruit monocarps numerous, red or purple, ovoid, ~10–18 × 10–12 mm, glabrous, stipe ~10–15 mm long, glabrous; seeds 1–2, ~9 × 7 × 4 mm.

Distribution

In continental Asia restricted to peninsular Malaysia. Distribution is shown in Fig. 11.

Notes

Uvaria argentea var. *argentea* is recognised from herbarium specimens by its membranous leaves and grey–green to black petals with a pale tomentose indument on the margins.

26b. *Uvaria argentea* var. *bracteata* (Roxb.) Meade & J. Parn., *comb. et. stat. nov.*

Uvaria bracteata Roxb., *Fl. Ind. Ed.* 1832 2: 660 (1832).

Type: ‘*Uvaria bracteata*’, Roxb. *Icon.* 2290 (lecto: K!, *fide* T.M.A. Utteridge, *Blumea* 45(2): 383 (2000)).

Uvaria bracteata Roxb., *Hort. Bengal.* 43 (1814), *nom. inval.*, *nom. nud.*

Uvaria bracteata Wall., *Numer. List no.* 6468 (1832), *nom. inval.*, *nom. nud.*

Uvaria gomeziana A.DC., *Mém. Soc. Phys. Genève* 5: 203 (1832).

Type: MYANMAR. Tavoy, 8 Sep. 1827, *W. Gomez 197* [*Wall. Cat. no.* 6459] (lecto: K-W 001123956!, *fide* I.M. Turner, *Phytotaxa* 36: 47 (2011)).

Cyathostemma yunnanense Hu, *Bull. Fan Mem. Inst. Biol.* 10: 121 (1940).

Type: CHINA. Yunnan, Fo Hai, *Wang 74547* (holo: PE 00028347!; iso: PE 00028346!, A 00039271!).

Differs from the type variety in having white or yellow to green petals, and the leaves are usually larger and almost exclusively obovate.

Distribution

Uvaria argentea var. *bracteata* occurs in mountain foothills up to ~1100 m. Distribution is shown in Fig. 11.

Notes

Sinclair (1951) treated *U. argentea* var. *bracteata* as synonymous with *Cyathostemma argenteum* (= *Uvaria argentea*). However, the petals of *U. argentea* var. *bracteata* are always green or yellow or grey or white, as opposed to deep red or purple for *U. argentea* var. *argentea*, and there also is a marked disjunction in the distributions of the two taxa. For these reasons, it seems wise to retain the two as varieties. The type of *C. yunnanense* matches the Roxburgh lectotype of *U. bracteata*. Roxburgh (1832, p. 661) described the fruits of this species as ‘...few, pendulous, of the size of a small pullet’s egg, from oval to oblong, obtuse at both ends, smooth, when ripe of a rich yellow. Seeds a few, oval, compressed, smooth...’. On the basis of the accounts of Sealy (1956) and Forman (1997), a Roxburgh specimen at BM(!) labelled as ‘*U. bracteata*’ is probably the only surviving material on which he based his *Icones* illustration;

however, this material is not listed in the lectotypification of Utteridge (2000).

27. *Uvaria wrayi* (King) L.L. Zhou, Y.C.F. Su & R.M.K. Saunders, *Syst. Biodivers.* 7: 255 (2009)

Cyathostemma wrayi King, *J. Asiat. Soc. Bengal Pt. 2, Nat. Hist.* 61(1): 9 (1892).

Type: MALAYSIA. Perak, *s. dat.*, *Scortechini 131b* (lecto: K 000691375!, *fide* T.M.A. Utteridge, *Blumea* 45(2): 391 (2000)).

Notes

The large obovate membranous leaves of this species make it easily recognised from sterile specimens. Utteridge (2000) cited the collection number of the lectotype specimen as ‘1316’, in error for ‘131b’, as corrected above.

Key to the varieties in continental Asia

1. Leaves obovate or rarely oblong, veins 12–15.....
..... 27a. *U. wrayi* var. *wrayi*
- Leaves oblong or rarely narrowly obovate, veins 15–17.....
..... 27b. *U. wrayi* var. *indochinensis*

27a. *Uvaria wrayi* (King) L.L. Zhou, Y.C.F. Su & R.M.K. Saunders var. *wrayi*

Small shrub or climber. Young shoots sparsely tomentose, distinctive light-ferruginous hue of fine hairs over black bark, hairs persistent, becoming short. Leaves obovate, less often oblong, base retuse, apex acute–acuminate, up to 250 × 95 mm, membranous, veins 12–15; indument upper-surface hairs erect and shortly tomentose over midrib, spreading, sparse–glabrous over veins, blade subglabrous–glabrous; lower blade subglabrous with occasional hairs on tertiary venation, midrib hairs sparse, spreading. Petiole indument ferruginous–tomentose, later sparse, hairs fine, straggling. Inflorescence axillary or supra-axillary, often cauliflorous, flowers 2–5, peduncle up to 3 mm, pedicels 2–8 mm long, bracts laminar, acute, enlarging up to 4 × 2 mm, narrowly ovate–acute, ferruginous–tomentose, later sparse. Calyx sepals 3, free, opening early and reflexing, remaining small, concave, broadly ovate–acute, coriaceous, up to 4 mm wide × 3 mm long, indument subtomentose, hairs fine, ferruginous. Corolla 2 subequal whorls of 3 petals, petals green to yellow in colour, free, imbricate at tips, broadly ovate in bud, becoming narrowly ovate, bluntly acute–obtuse, thickly coriaceous–fleshy, up to ~9 mm long × 6 mm wide, often opening but not reflexing, indument subtomentose–sparse, hairs becoming short, blunt, almost papillate, glabrous basally on inner side. Stamens numerous, ~1.4 mm long, glabrous, connective flattened, distinctly papillate, locules extending full length of stamen. Carpels numerous, ~2 mm long, neck of longer hairs at apex of ovary, below glabrous except on ridges, arched inwards at outer whorls, stigma glabrous, elongate, ovules 2 or 3, lateral. Fruit monocarps numerous, ovoid, ~9–13 × 6–9 mm, stipe 15–20 mm, narrow, pericarp thin, flaking off easily when dry, thickened apicule often present, seeds 1 or 2, ~9 × 8 × 4 mm, single seeds ellipsoidal or pronouncedly hemi-ellipsoidal when 2 seeds present, hilum A-shaped, ~1.5 × 1.5 mm.

Distribution

Uvaria wrayi var. *wrayi* is common across its range, occurring in evergreen forests up to ~400 m. Distribution is shown in Fig. 15.

27b. *Uvaria wrayi* var. *indochinensis* (Jovet-Ast) Meade & J.Parn., *comb. nov.*

Cyathostemma wrayi var. *indochinensis* Jovet-Ast., *Notul. Syst.* 9: 86 (1940).

Type: VIETNAM. Annam, Blao, Haut Donai Province, 13 Feb. 1933, *Poilane 21930* (lecto, here designated: P 00411099!; isolecto: P 00411100!, P 00411101!); VIETNAM. Annam, Blao, Haut Donai Province, 26 May 1933, *Poilane 22517* (Syn: P 00234100!, P 00411102–3!)

Jovet-Ast described this variety on the basis of the greater number of leaf veins, plus the distinctly oblong as opposed to obovate leaves, compared with typical *Cyathostemma* (*Uvaria*) *wrayi*, a difference that is evident in the composite leaf shape for *U. wrayi* var. *wrayi* as presented in Meade and Parnell (2002, p. 242). *Poilane 15387* from north-western Cambodia, cited as type material by Jovet-Ast, is in fact *U. wrayi* var. *wrayi*. The lectotype selected presents the best-preserved material from the originally cited sheets.

Distribution

Uvaria wrayi var. *indochinensis* is known from one locality, in Vietnam. Distribution is shown in Fig. 15.

***Uvaria hahnii* group**

28. *Uvaria dasoclema* L.L.Zhou, Y.C.F.Su & R.M.K. Saunders, *Bot. J. Linn. Soc.* 163: 37 (2010)

Monocarpia siamensis Craib, *Bull. Misc. Inform. Kew* 1924: 81 (1924); *Dasoclema siamensis* (Craib) J.Sinclair, *Gard. Bull. Singapore* 14: 273 (1955).

Type: THAILAND. Kampeng Pet, Me Lamung, 8 June 1932, *Kerr 6087* (lecto, here designated: K00691507!; isolecto: K 00691506!).

Scrambling shrub or climber. Young shoots sparsely tomentose. Leaves elliptical-oblong, apex acute-shortly acuminate, base retuse or rarely cuneate in younger leaves, up to 125 × 60 mm, membranous, veins 6–13, indument upper surface sparse becoming glabrous, midrib hairs erect, subtomentose becoming sparse, lower surface hairs sparse on midrib and veins, blade sparse-subglabrous. Petiole 5–8 mm, sparsely tomentose. Inflorescence solitary, leaf-opposed, pedicel up to 60 mm, diameter 1–3 mm, widest at base of receptacle, sparsely tomentose, bracts wanting. Calyx sepals 3, valvate, ovate-acute, up to 5 × 6 mm, outer surface tomentose, inner surface basally glabrous. Corolla, 2 whorls of 3 petals, inner petals smaller than outer, petals white to green in colour, outer whorl 25–30 mm long, 8–10 mm wide, free, inner whorl 23–28 mm long, 5–8 mm wide, lower margins often connivent, outer surface sparsely tomentose, inner surface mostly glabrous, margins and apex sparsely tomentose. Stamens numerous, 2.5 mm, cuneate, locules raised on short filament, connective apex convex or flattened, smooth. Carpels solitary, ovules 6–12, laterally inserted in 2 rows, stigma

disc-shaped, 3 mm in diameter, glabrous. Fruit monocarp solitary, subsessile, ovoid-oblong, 15–35 × 10–15 mm; stipe subsessile, 3–4 × 3–4 mm, tomentose; seeds 6–12.

Distribution

A rare species, restricted to limestone areas in central Thailand. Distribution shown in Fig. 16.

Notes

The unusual single carpel and broad flat stigma of this taxon are understood now to be derived characteristics that have caused much taxonomic confusion (Zhou *et al.* 2010). All other morphological traits are characteristic of *Uvaria*; the raised stamen locules and subequal petal whorls reflect its phylogenetic affinity with *Hahnii*-group taxa. The lectotype selected presents the best-preserved material from the originally cited sheets.

29. *Uvaria ferruginea* Buch.-Ham. ex Hook.f. & Thomson, *Fl. Ind.* 1: 96 (1855)

Ellipeia ferruginea (Buch.-Ham. ex Hook.f. & Thomson) Hook.f. & Thomson, *Fl. Brit. Ind.* 1: 52 (1872); *Ellipeiopsis ferruginea* (Buch.-Ham. ex Hook.f. & Thomson) R.E.Fr., *Ark. Bot. ser.* 2, 3: 41 (1955).

Type: MYANMAR. Ava (Tenasserim), Meaday, *s. dat.*, *Buchanan-Hamilton s.n.* (lecto: BM 000547032!, *fide* I.M. Turner, *Nordic J. Bot.* 33 : 290 (2015)).

Notes

Uvaria ferruginea is of unusual growth habit and morphology. The climbing stem has become modified so that plants may creep directly over the soil, with successive branchlets growing upward. Fries (1955) established the genus *Ellipeiopsis* and maintained the distinction between var. *ferruginea* and var. *cherrevensis* at species level. The key morphological difference between the two is in leaf shape, with var. *ferruginea* having ovate-oblong leaves and var. *cherrevensis* having obovate leaves (Meade and Parnell 2003). The two varieties have distinct distributions, with var. *cherrevensis* occurring in Thailand and Indochina, and var. *ferruginea* occurring only to the east of the Thai-Myanmar mountain border. The Paris type material of var. *cherrevensis* is the most complete of the duplicate set and is here designated as the lectotype.

Key to the varieties in continental Asia

1. Leaves ovate-oblong – Myanmar 29a. *U. ferruginea* var. *ferruginea*
 Leaves obovate – Thailand-Indochina 29b. *U. ferruginea* var. *cherrevensis*

29a. *Uvaria ferruginea* Buch.-Ham. ex Hook.f. & Thomson var. *ferruginea*

A small shrub with a single or branched horizontal stem producing erect ~1-m high branchlets. Young shoots densely ferruginous-tomentose, later striate, sparse-subglabrous. Leaves coriaceous, broadly elliptical-oblong, base cordate, apex obtuse, cuspidate or acute, 120–150 × 50–80 mm, veins 11–12(–14); indument upper blade subtomentose, hairs erect, 1–3-branched,

pale, becoming sparse-subglabrous with age, midrib and primary vein bases tomentose, hairs erect, ~2–5-branched; lower blade hairs subtomentose, ~6–10+-branched, spreading, rufous, tomentose over midrib and vein traces. Petiole ~8–10 × 2 mm, ferrugino-tomentose. Inflorescence leaf-opposed, flowers solitary, peduncle much reduced, pedicel ~8–12(–20) × 1 mm, tomentose, medial bract narrowly elliptical, 8–15 × 2–3 mm, tomentose on both surfaces, venation not prominent. Calyx sepals 3, basally connate, tips valvate, ovate–acute, ~5–6 × 8 mm, concave, recurving basally at maturity, outer surface densely tomentose, inner surface warty and sparse basally, tomentose elsewhere. Corolla 2 whorls of 3 petals, inner narrower than outer, petals yellow to white in colour, outer petals broadly ovate, ~12–14 × 10–12 mm, apex bluntly acute, base constricted to ~3.25 mm wide, outer surface tomentose, inner surface tomentose along margins and at apex, glabrous at base, inner petals narrowly ovate, ~12–14 × 7–8 mm, outer surface tomentose, inner surface basally glabrous, base ~2.25–2.5 mm wide, with 2 conspicuous marginal glands contiguous to glabrous base of inner surface. Stamens numerous, ~1.8–2 mm, cuneate, connective apex glabrous, rusty in colour, shiny, often extending as ridge down external side, locules raised on short filament. Carpels ~25–30, 2.5–3 mm long, ovary tomentose, hairs fine, many-branched, forming even surface, stigma elongate, ~0.8–1 mm long, hairy, U-shaped with lateral groove, ovule 1, placentation apical or subapical. Fruit monocarps 5–20, ~10 × 4.5 mm, red in colour with conspicuous black apicule, pericarp fleshy, smooth, sparse-subglabrous, becoming black, thin and undulate on drying, 1 seed, basally attached, ellipsoidal.

Distribution

Bangladesh and Myanmar. Distribution is shown in Fig. 15.

29b. *Uvaria ferruginea* var. *cherrevensis* (Pierre ex Finet & Gagnep.) Meade & J.Parn., *comb. et stat. nov.*

Ellipeia cherrevensis Pierre ex Finet & Gagnep., *Bull. Soc. Bot. France (Mém. 4 (2))* 53: 76 (1906); *Ellipeiopsis cherrevensis* (Pierre ex Finet & Gagnep.) R.E.Fr., *Ark. Bot. ser. 2, 3*: 41 (1955); *Uvaria cherrevensis* (Pierre ex Finet & Gagnep.) L.L.Zhou, Y.C.F.Su & R.M.K.Saunders, *Syst. Biodivers.* 9: 255 (2009).

Type: THAILAND. Petchaburi, Aug. 1868, *Pierre 1790* (lecto, here designated: P 00432161!; isolecto: P 00432162!); CAMBODIA. Samrong-Tong, Chereer Mountains, Apr. 1870, *Pierre 1790A* (syn: A!, C!, L!, NY!, P 00432162–4!); CAMBODIA. Samrong-Tong. Chereer Mountains, Apr. 1870, *Pierre 745* (syn: P 00432165–6!).

Leaves broadly obovate.

Distribution

Thailand and Cambodia. Although widespread, this taxon is much less common in the evergreen vegetation favoured by *Uvaria* species, and is unrecorded from most of the evergreen forests in southern Indochina and peninsular and south-eastern Thailand and from the driest regions of north-eastern Thailand. Distribution is shown in Fig. 15.

30. *Uvaria pauciovulata* Hook.f. & Thomson, *Fl. Brit. Ind.* 1: 51 (1872)

Type: MALAYSIA. Malacca, 14 June 1865, *Maingay 104/1023* (lecto, here designated: K000380686!); MALAYSIA. Malacca, 27 May 1868, *Maingay 104/3392* (syn: K000380687!, SING!).

Notes

The inflorescence structure, petals, stamens, carpels and fruits of *U. pauciovulata* are most similar to those of *U. cuneifolia* (Malesia south of the Isthmus of Kra). The major difference between it and *U. cuneifolia* is that the inner petals remain closed and imbricate over the gynoecium in *U. cuneifolia*, whereas they open in *U. pauciovulata*. The shape, indument and venation of the leaves in the two species are also different. The type material for var. *scortechinii* shows a variant leaf form compared with the type for *U. pauciovulata*, but otherwise there are no discrete character differences that warrant a species-level distinction.

Key to the varieties in continental Asia

1. Leaves ovate to elliptic to narrowly obovate with ferruginous leaf venation on abaxial surface **30a. *U. pauciovulata* var. *pauciovulata***
Leaves broadly ovate–elliptical with prominent thickened ferruginous leaf venation on abaxial surface **30b. *U. pauciovulata* var. *scortechinii***

30a. *Uvaria pauciovulata* Hook.f. & Thomson var. *pauciovulata*

A scandent shrub or woody climber. Young shoots tomentose, hairs ferruginous, stout, ~20+-branched, quickly becoming sparse, bark black, striate. Leaves (ovate–)jellyptical–narrowly obovate, base shortly cordate or retuse, apex acute, 95–140 × 50–60 mm, coriaceous; veins 9–12(–14), almost perpendicular to midrib at base, then arching gradually; indument hairs many-branched, ferruginous, young leaves with sparse hairs on both surfaces, at maturity upper surface glabrous, lower blade subglabrous, hairs tomentose–sparse on vein bases and midrib. Petiole ~4–5 × 1.5 mm, hairs subtomentose–sparse, verrucose. Inflorescence terminal, cymulose, flowers 1 or 2, rarely 3, peduncle 2–7 mm long, pedicel ~8–10 × 2.5 mm, broad and flattened, tomentose–subtomentose, hairs stocky, ~20+-branched, ferruginous, bracts ovate, clasping, often enclosing floral buds, persistent, ~9 × 5 mm, prominent central vein often visible, indument as for pedicel. Calyx sepals 3, basally connate, ovate–triangular, acute, ~7–8 × 6–7 mm, somewhat thickened, often persistent, outer surface ferrugino-tomentose as for pedicel and bracts, inner surface glabrous basally, surface black, shiny, warted, elsewhere subtomentose, hairs 1–5-branched, downy, combed. Corolla 2 whorls of 3 petals, inner narrower than outer, petals white, yellow or cream in colour, large and showy, incurved, coriaceous, outer whorl broadly obovate, obtuse, ~15–20 × 12–14 mm, base 3.5 mm, coriaceous, undulating, inner whorl narrowly obovate, obtuse, ~15–20 × 11–13 mm, base ~2.5 mm, indument on outer surface of both whorls as for pedicel and bracts, central vein trace often covered with ferruginous hairs, inner surface of outer whorl subtomentose, hairs downy, straggling, 3–8-branched, petal base glabrous, black, inner surface of inner whorl

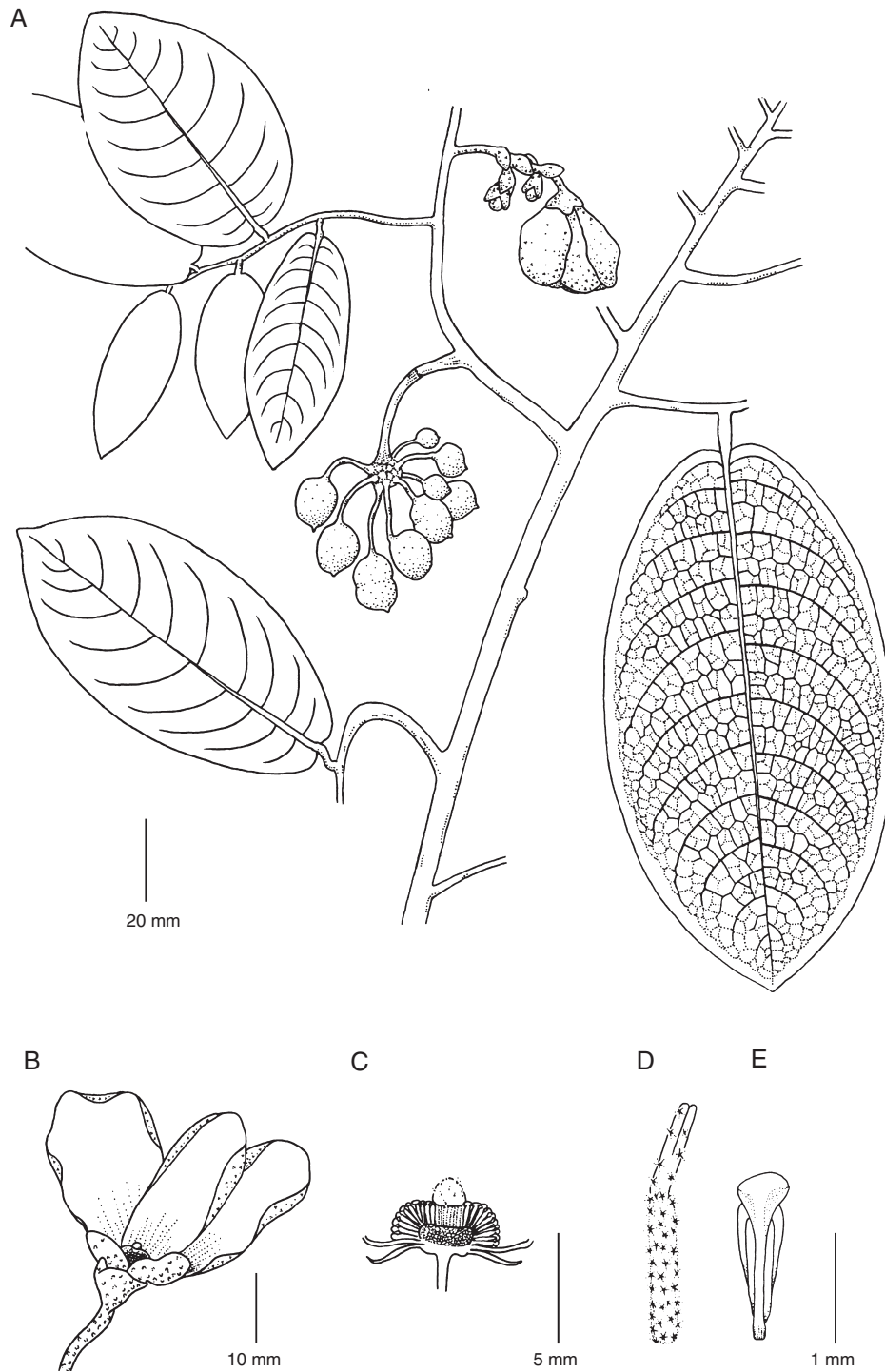


Fig. 18. *Uvaria pauciovulata* var. *pauciovulata*. A. Habit. B. Flower, section. C. Flower, section. D. Carpel. E. Stamen. Illustration C. V. Meade.

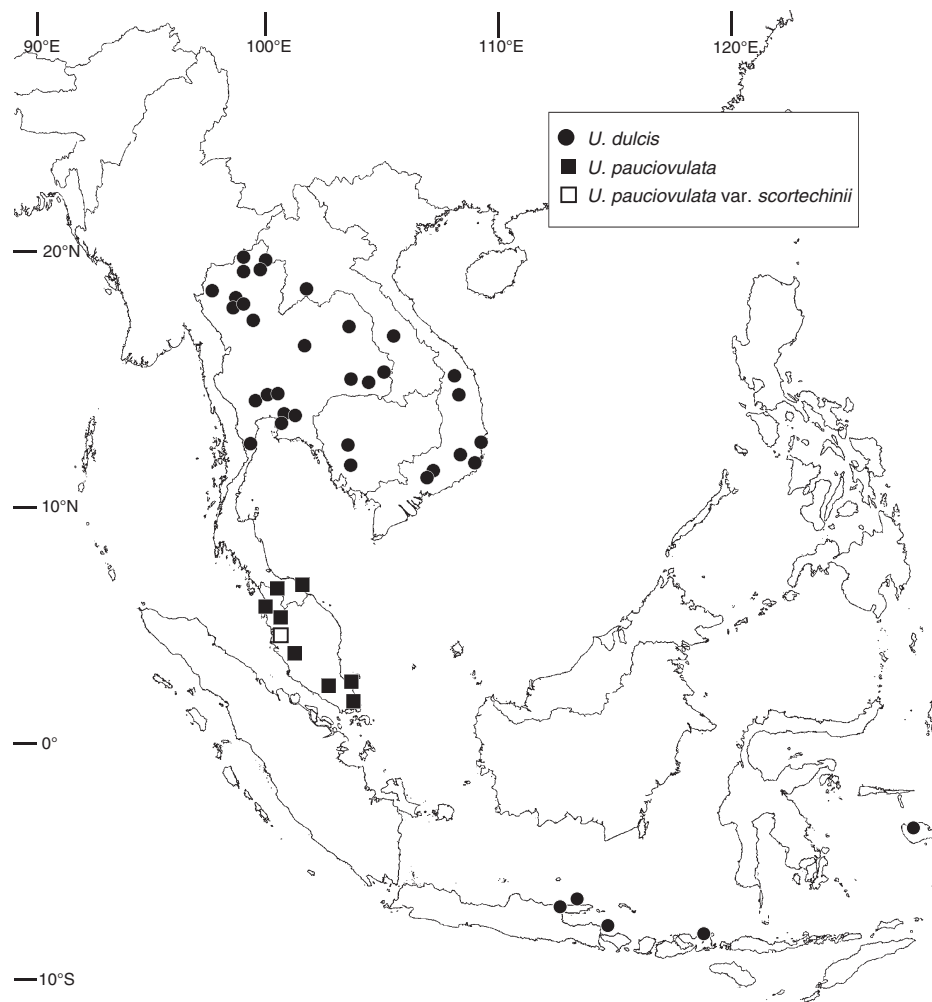


Fig. 19. Distribution of *Uvaria dulcis*, *U. pauciovulata* and *U. pauciovulata* var. *scortechinii* in South-east Asia on the basis of herbarium specimens verified in this study.

glabrous, except for downy indument at apex and around margins, both whorls remaining incurved. Stamens numerous, 1.25–1.5 mm, cuneate, locules uneven in length, raised on short filament, connective apex convex or flattened, smooth. Carpels numerous, ~2.5–2.75 mm, ovaries tomentose, hairs flattened and spreading, stigmas elongate with sparse stellate hairs over surface, ~1 mm long, U-shaped with prominent longitudinal slit, ovules 1–2(–3), gynoecium dome-shaped, raised. Fruit monocarps numerous, spheroidal or shortly oblongoidal, ~8–23 × 9 mm in diameter, pericarp thin with prominent apicule, monocarps basally or sub-basally attached, stipe ~10–15 mm × 1 mm, striate, monocarp and stipe densely and shortly tomentose; seeds 1 or 2 or very rarely 3, smooth, wrapped tightly by monocarp tissue, ruminations not visible beneath surface, raphe dark, prominent. (Fig. 1D, E, 18.)

Distribution

Lower peninsular Thailand and peninsular Malaysia. Distribution is shown in Fig. 19.

30b. *Uvaria pauciovulata* var. *scortechinii* (King) Meade & J.Parn., *comb. et stat. nov.*

Uvaria scortechinii King, *J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist.* 61(1): 20 (1892).

Type: MALAYSIA. Perak, *s. dat.*, *Scortechini s.n.* (holo: K 000380695!, iso: A 00039706!).

Leaves broadly ovate–elliptical with prominent, thickened venation.

Distribution

Lower peninsular Thailand and northern peninsular Malaysia. Distribution is shown in Fig. 19.

31. *Uvaria hahnii* (Finet & Gagnep.) J.Sinclair, *Gard. Bull. Singapore* 14: 44 (1955)

Unona hahnii Finet & Gagnep., *Bull. Soc. Bot. France (Mém. 4 (2))* 53: 78 (1906); *Desmos hahnii* (Finet & Gagnep.) Merr., *Philipp. J. Sci.* 10: 235 (1915); *Melodorum hahnii* (Finet & Gagnep.) Bân, *J. Biol. (Vietnam)* 16(4): 8 (1994).

Type: CAMBODIA. Kamchay Mountains, north-west of Kampot, 2 Feb. 1896, *Hahn s.n.* (lecto: P 00261139, isolecto: P 00261140–1, *fide* N.T.Bân, *Fl. Vietnam* 1: 41 (2000)); CAMBODIA. Kampot, 13 May 1904, *Geoffray 385* (syn: P 00261138!); Kampot, Mar. 1874, *Pierre 1786* (syn: P 00261144!).

Notes

The narrow elongate petals and large wavy sepals and bracts of *U. hahnii* make it easy to distinguish from *U. dulcis* (peninsular Malaysia), its most similar-looking relative.

Key to the varieties in continental Asia

1. Petals ≥ 35 mm long – Indochina and Myanmar
 **31a. *U. hahnii* var. *hahnii***
 Petals ≤ 30 mm long – Kontum Province, Vietnam
 **31b. *U. hahnii* var. *kontumense***

31a. *Uvaria hahnii* (Finet & Gagnep.) J.Sinclair var. *hahnii*

Scandent shrub or woody climber. Young shoots subtomentose, becoming glabrous, bark black with deep striations. Leaves elliptic–narrowly obovate, subcoriaceous, apex acute–acuminate, base retuse, $\sim 100\text{--}160 \times 40\text{--}65$ mm, veins 9–12(–14); indument upper blade sparse becoming glabrous, hairs 3–5-branched, fine, spreading, midrib hairs erect, $\sim 5+$ -branched, subtomentose becoming sparse, lower blade hairs mixed, smaller fine hairs 4–6-branched, sparse at first, becoming glabrous, larger ferruginous hairs erect, rare on blade, subtomentose on veins and midrib. Petiole $\sim 7 \times 1$ mm, black and warty, tomentose, later sparse or subglabrous. Inflorescence flowers solitary, leaf-opposed, peduncle 1–3.5 mm long, pedicel $\sim 9\text{--}10$ mm long, prominently striate, broadening up to ~ 2 -mm-diameter near receptacle, hairs tomentose, many-branched, ferruginous, bracts ovate–acute, $\sim 15\text{--}20 \times 10\text{--}15$ mm, leaf-like with prominent palmate venation, outer-surface indument sparse, hairs $\sim 5+$ -branched, stocky, subtomentose along central vein, hairs on inner surface finer, evenly spread over surface. Calyx sepals 3, valvate, ovate–lanceolate, $\sim 15 \times 10$ mm, large and leaf-like with prominent central vein, flat or convex, reflexed at maturity, inner and outer indument as for bracts. Corolla 2 whorls of 3 petals, inner petals narrower than outer, petals creamy-white or yellow in colour, lanceolate–acute with prominent longitudinal veins, whorls unequal, outer petals $\sim 35\text{--}45 \times 10$ mm, base narrowed to ~ 2 mm, inner petals $\sim 35\text{--}45 \times 6\text{--}7$ mm, base narrowed to ~ 1.5 mm with two ~ 3 -mm-long marginal glands present, indument on outer surface of both whorls mixed, underlying tomentum of fine pale hairs overlain basally and along central axis by scattered $5+$ -branched erect ferruginous hairs, inner surface of both whorls tomentose, hairs fine, base somewhat glabrous on outer whorl, distinctly glabrous on inner whorl. Stamens numerous, ~ 2.5 mm long, cuneate, connective apex convex, umbonate, bright orange in colour and distinctly papillate, locules raised on short filament, varying in length. Carpels ~ 20 , ~ 3.5 mm long, ovary tomentose, narrowed into distinct neck below stigma, stigma ~ 1 mm long, U-shaped, hairy, ovaries ~ 14 in 2 rows. Fruits monocarps $\sim 4\text{--}8$, ovoid–oblong, $\sim 16\text{--}10 \times$

$9\text{--}10.5$ mm, minutely striate, tomentose, pericarp thick and soft at maturity, stipe short, ~ 8 mm long; seeds 10–14 in 2 rows, $\sim 7 \times 4 \times 2$ mm, compressed ovoid, smooth, aril 3×2 mm, often transversely compressed. (Fig. 1B.)

Distribution

Myanmar, Thailand, Cambodia and Laos. Distribution is shown in Fig. 14.

31b. *Uvaria hahnii* var. *kontumensis* (Bân) C.Meade & J.Parn., *comb. et stat. nov.*

Melodorum kontumense Bân, *Fl. Vietnam* 1: 39 (2000).

Type: VIETNAM, Kontum Province, Moray Dak To, 3 Apr. 1978, *Ly 430* (holo: VNMI!).

Melodorum kontumense T.B.Nguyen in Pham–hoàng Hô (ed.), *Ill. Fl. Vietnam* 1: 334 (1991), *nom. inval.*

Differs from the typical variety of the species in having subequal whorls with slightly shorter petals, and narrowly obovate and acuminate leaves with a subtomentose indument on both surfaces.

Distribution

Kontum Province, central Vietnam. Distribution is shown in Fig. 14.

32. *Uvaria dulcis* Dunal, *Monogr. Anonac.* 90, t. 13 (1817)

Anomianthus dulcis (Dunal) J.Sinclair, *Gard. Bull. Straits Settle.* 3: 40 (1953).

Type: INDONESIA. Java, Ventenat hb., *La Haye s.n.* (lecto, here designated: G 00237861! (Herb. Delessert)).

Uvaria javana Dunal, *Monogr. Anonac.* 91, t. 14 (1817).

Type: INDONESIA. *Uvaria javana*, [*Uvaria tomentosa*? Roxb. t. 35 perquam affinis], Java, Ventenat hb., *La Haye s.n.* (lecto, here designated: G 00237862! (Herb. Delessert)).

Uvaria aurita Blume, *Fl. Javae* 21, 22: 15, pl. 2 (1830). *Anomianthus auritus* (Blume) Backer, *Schooffl. Java* 23 (1911).

Type citation: ‘...in montosis *Javae occidentalis*...’.

Type: ?BO n.v. ‘*Uvaria aurita*’, C.L.Blume, *Fl. Javae* 21, 22: pl. 2 (1830) (lecto, here designated).

Uvaria heterocarpa Blume, *Fl. Javae* 21, 22: 41, pl. 17 (1830). *Anomianthus heterocarpus* (Blume) Zoll., *Linnaea* 29: 324 (1858).

Type citation: ‘...in interioribus provinciae *Bantam*, ... VAN HASSELT...’.

Type: ?BO n.v.

Type: ?BO n.v. ‘*Uvaria heterocarpa*’, C.L.Blume, *Fl. Javae* 21, 22: pl. 2 (1830) (lecto, here designated).

Uvaria pachychila Jovet–Ast, *Suppl. Fl. Indochine* 1: 62 (1938), *nom. inval. pro syn.*

Uvaria pachychila T.B.Nguyen in Pham–hoàng Hô (ed.), *Ill. Fl. Vietnam* 1: 307 (1991), *nom. inval.*

Sarmentose shrub or climber, reaching lengths of 30 m or more. Young shoots tomentose–subtomentose, becoming glabrous and striate with distinctive pale lenticels. Leaves

elliptic–broadly elliptic–shortly obovate, apex acute, base subcordate–shortly cordate, ~100–140 × 45–60 mm, membranous; veins 15–18, frequently branching basally and medially; indument upper blade hairs 1–4+-branched, sparse becoming subglabrous, over midrib hairs erect, tomentose, ~1 mm long, lower blade hairs 5+-branched, subtomentose, on veins and midrib hairs ~10-branched, ferruginous, stocky, tomentose towards petiole. Petiole tomentose, ~3.5–5 × 1 mm. Inflorescence terminal, pendulous, flowers 1 to many, usually 2 or 3, peduncle ~5–10 mm, pedicel ~12–25 mm, both ferruginotomentose, bracts broadly ovate, subtomentose, ~2–3 × 3.5–4.5 mm, often wanting. Calyx sepals 3, valvate, connate at base, ~3.25 × 4.5 mm, ovate–acute, outer surface ferruginotomentose, inner surface subtomentose, hairs finer. Corolla 2 whorls of 3 petals, inner petals smaller than outer, petals white or yellow to pink in colour, broadly elliptical–acute at first, expanding to obovate–acute at maturity, outer petals ~21.5 × 11.5 mm, indument on outer surface mixed, underlying tomentum of fine pale hairs overlain by scattered larger rufous hairs usually gathered into distinct trace along central axis, inner surface basally glabrous, at apex hairs as for underlying tomentum on outer surface, inner petals ~20.5 × 10.5 mm, outer surface tomentose, rufous hairs present but less numerous than on outer whorl, inner surface basally glabrous with two lateral orange–coloured glands inserted above the base. Stamens numerous, ~1.5 mm long, connective broad and flattened, often forming lip on inner side, papillate, glabrous, locules raised on short filament. Carpels ~25, 2.5 mm long, hairy usually below stigma neck and along lateral ridges, stigma long and hairy with distinct neck, U-shaped, gynoecium forming distinct dome above stamens, ovules ~14–16. Fruit monocarps ~10+, oblong or shortly cylindrical, ~10 × 6.5 mm, glabrous, green turning orange, then red, pericarp hard at first, juicy when ripe, becoming thin and flaky on drying, particularly in mature fruits, stipe ~5–10 mm; seeds 1–8, ~5 × 4 × 4 mm, compressed–ovoid, raphe distinct, aril transversely compressed.

Distribution

Uvaria dulcis is often found in scrub vegetation; however, it is most common in disturbed moist forest where it can form large localised populations. It is common in the low-rainfall zones of north-eastern Thailand and central Java. Distribution is shown in Fig. 19.

Notes

The membranous obovate petals with conspicuous lateral glands on the inner whorl should be enough to distinguish this species from its closest relatives. Examination of the type material of *U. dulcis* and *U. javana* at Geneva showed that they are in fact the same species, explaining why Dunal's original descriptions of the two are almost identical. The name *U. javana* Dunal was misapplied to a different unnamed taxon from Java by Blume (1830). The type material for both *U. aurita* and *U. heterocarpa* is missing; thus, Blume's full-colour illustrations from the original accounts are designated here as lectotypes.

33. *Uvaria siamensis* (Scheff.) L.L.Zhou, Y.C.F.Su & R.M.K. Saunders, *Syst. Biodiv.* 7: 255 (2009)

Rauwenhoffia siamensis Scheff., *Ann. Jard. Bot. Buitenzorg.* 2: 23 (1885); *Melodorum siamensis* (Scheff.) Bân, *Bot. Zhurn.* (Moscow & Leningrad) 39: 241 (1974).

Type: INDONESIA. ‘...cultivée dans notre jardin, dans lequel elle a été introduite par M. TEYSMANN, qui la trouva en Siam (Herb. Bog. no. 17785).’ (?BO, n.v.).

Uvaria godefroyana Finet & Gagnep., *Bull. Soc. Bot. France* (Mém. 4 (2)) 53: 71 (1906).

Type: CAMBODIA. Pursat, 11 June 1875, *Godefroy/Harmand 298* (lecto, here designated: P 00520753; isolecto: P 00520752!, P 00142663!); CAMBODIA. Angkor, 1875, *Godefroy/Harmand 612* (syn: P 00252671!); CAMBODIA. Angkor, 1875, *Godefroy/Harmand 621* (syn: P 00142664!).

Melodorum schefferi Pierre ex Finet & Gagnep., *Bull. Soc. Bot. France* (Mém. 4 (2)) 53: 134, pl. 19a (1906).

Type: CAMBODIA. Bien Hoa Province, North, Chiao Xhay, Mar. 1877, *Pierre 1772* (lecto, here designated: P 00373696!).

Shrub or small tree up to 2 m, or climber up to 20 m. Young shoots tomentose with large many-branched ferruginous hairs scattered over smaller, finer, less pigmented hairs, not quite obscuring bark, but nearly so, older wood becoming striate with prominent lenticels, subglabrous. Leaves (bluntly) lanceolate to elliptical, base retuse, apex narrowly–bluntly acute, ~90–150 × 30–40 mm, thinly coriaceous, waxy texture above; veins 8–11(–14); indument glabrous above, except for sparse spreading stellate hairs on upper midrib, subtomentose below with underlying layer of fine, ~6–8-branched hairs overlain with scattered, thickened, many-branched hairs, especially on midrib and midrib base. Petiole tomentose, ~3.5 × 1.25 mm. Inflorescence leaf-opposed or subopposed, flowers solitary or rarely 2 or 3, peduncle subsessile, ~1.5 × 1.25 mm, pedicel ~8 × 1.25 mm, shortly and densely tomentose, hairs pale, overlain by scattered larger rufous hairs, deeply grooved or striate, basal and medial bracts ovate–acute, ~2–5 × 1–2 mm, subtomentose, usually wanting. Calyx sepals 3, valvate, opening early, very broadly ovate–acute, ~3 × 6 mm, thickened and remaining incurved, base concave, outer surface indument as for pedicel, inner surface glabrous. Corolla 2 whorls of 3 petals, inner petals narrower than outer, petals yellow to white in colour, outer petals broadly ovate, ~8 × 8 mm, inner petals broadly elliptical with constricted base, ~8 × 5.5 mm, outer surface of both whorls densely tomentose, hairs fine, pale, inner surface of outer whorl tomentose at apex and on all margins, base glabrous, inner whorl glabrous at base, apex and apical margins tomentose. Stamens numerous, ~1.5 mm long, cuneate, apex flat or shallowly convex, obscuring locules, rusty brown or orange in colour with waxy texture, covered with minute blunt papillae, locules raised on short filament. Carpels ~10, 3 mm long, ovaries covered with blunt stellate hair-scales, giving very finely warted appearance, neck between ovary and stigma covered with long stellate hairs, stigmas prominent, lobed, U-shaped, hairy, ~1 mm long, forming distinct dome above stamens, often with copious exudate, ovules ~4–8. Fruit monocarps 2–10 (usually 3–6), globose or shortly oblong, ~10–12 × 8–9 mm, very minutely

tubercled with subtomentose indument of blunt stellate scales, outline of seeds often clear within pericarp, stipe subsessile, $\sim 3 \times 1$ mm, striate; seeds $\sim 2-4(-6)$, compressed hemi-ellipsoidal, $\sim 7 \times 4 \times 3$ mm. (Fig. 1E.)

Distribution

Although there are no records, it is probable that the species also occurs in the northern Malay States of Kelantan, Perlis and Kedah. Approximately 50% of collections record *U. siamensis* as a shrub or small tree, most often occurring in disturbed or marginal forest vegetation, particularly bamboo scrub and forest. Distribution is shown in Fig. 16.

Notes

Uvaria siamensis and *U. ferruginea* have similar flowers, but the fruit, leaf and growth habits are very different. *Uvaria siamensis* is morphologically similar to *U. hahnii*, with the two species sharing fruit and leaf characters. The lectotypes selected present the best-preserved material from the originally cited sheets.

Conflict of interest

The authors declare that they have no conflict of interest.

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