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Taxonomic novelties and pollen morphological study in the genus *Neo-uvaria* (Annonaceae)

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Abstract

Two new species of *Neo-uvaria* are described from southern Thailand: *Neo-uvaria sparsistellata* and *N. telopea*. In addition, new combinations are made for two *Mitrephora* species from the Philippines: *N. merrillii* and *N. viridifolia*. The pollen morphology of eight *Neo-uvaria* species and three species of the closely related genus *Enicosanthum* is studied, using light, scanning electron and transmission electron microscopy. The systematic affinity of *Neo-uvaria* is discussed on the basis of macromorphology, pollen morphology and molecular phylogenetics. The genus *Enicosanthum* appears to be the closest relative of *Neo-uvaria.*

Key words: miliusoid clade, palynology, short branch clade, systematics, taxonomy, the Philippines, Thailand

Introduction

Neo-uvaria Airy Shaw is one of the poorly known genera of Asian Annonaceae. It was erected by Airy Shaw (1939) based on *Popowia foetida* Maingay ex Hooker & Thomson (1872: 69) and *Uvaria acuminatissima* Miquel (1865: 6). The main reasons for establishing *Neo-uvaria*, which he thought to be allied to *Uvaria* Linnaeus (1753: 536), were the tree habit and the stellate hairs. *Uvaria* species, in contrast, are usually woody climbers. In a revision of the Malayan Annonaceae, Sinclair (1955) stated that *Neo-uvaria* is likely to be related to *Popowia* Endlicher (1839: 831). The only resemblance between *Uvaria* and *Neo-uvaria* he observed was the stellate indumentum.

Van Heusden (1992) studied the floral morphology of all Annonaceae. She noticed that the petals of *Neo-uvaria* are unusually thick and fleshy. Additionally, the presence of stellate indumentum is also peculiar for *Neo-uvaria* because most annonaceous genera do not possess stellate hairs. Therefore, a genus of tall trees having stellate indumentum and unusually thick and fleshy petals was, according to her, somewhat difficult to place in any group she recognized.

Recent phylogenetic studies using molecular data (Mols *et al*. 2004a, b, Richardson *et al*. 2004) have confirmed that *Neo-uvaria* is unrelated to *Uvaria*, since *Neo-uvaria* was resolved in the 'miliusoid clade', which also includes *Popowia*. All members of the 'short branch clade' (SBC), to which the miliusoid clade belongs, are shrubs or small to large trees, while the occurrence of climbers is restricted to the 'long branch clade' (LBC), which includes *Uvaria* and allied genera (Richardson *et al*. 2004).

Recent collections from southern Thailand show the aforementioned features of *Neo-uvaria*: tall trees, stellate indumentum and remarkably thick/fleshy petals (Fig. 1A, B, E). Comparisons with the known *Neo-*

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uvaria species necessitate the description of two new species: *N. sparsistellata* Chaowasku and *N. telopea* Chaowasku, which represent the first records of *Neo-uvaria* for Thailand.

During the study it became evident that two Philippine species of *Mitrephora* Hooker & Thomson (1855: 112): *M. merrillii* Robinson (1908: 67) and *M. viridifolia* Elmer (1913: 1716), considered by Airy Shaw (1939) and Sinclair (1955) as synonyms of *N. acuminatissima* (Miq.) Airy Shaw (1939: 279), differ considerably from this species. Therefore, two new combinations, *N. merrillii* (C.B.Rob.) Chaowasku and *N. viridifolia* (Elmer) Chaowasku, are proposed here. Further, the lectotypes of *N. foetida* (Maingay ex Hook.f. & Thomson) Airy Shaw, *N. merrillii* and *N. viridifolia* are designated herein.

The total number of *Neo-uvaria* species is still doubtful. Prior to this article, three species were recognized: *N. acuminatissima*, *N. foetida* and *N. parallelivenia* (Boerlage 1899: 32) Okada & Ueda (1984: 173). Personal observations by the first author suggest that 9–15 species occur. Further taxonomic study is needed to reveal the actual diversity found in this genus.

In the present article, the pollen morphology of eight *Neo-uvaria* species including two unidentifiable (because of the incomplete material, but the first author's impression is that they are likely to be also new to science) collections from the Philippines (*Neo-uvaria* sp. 1) and Thailand (*Neo-uvaria* sp. 2) and three species of the related genus *Enicosanthum* Beccari (1871: 183) (on the basis of macromorphology and molecular phylogenetics hitherto known) was investigated, using light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM) in order to provide additional evidence for elucidating and evaluating the infra- and inter-generic relationships of *Neo-uvaria*.

In addition, the branching architecture of *Neo-uvaria* and some other Annonaceae is discussed as it appears to be one of the good characters for recognizing major clades in Annonaceae.

Material and Methods

Dried herbarium specimens (and associated spirit material) from BKF, BM, E, G, K, KEP, L, NY, P and U herbaria were used for observations and measurements (= types of all seven recognized species + *N. acuminatissima*: *Elmer 21112*, *Sinclair et al. 9250*; *N. foetida*: *Rogstad 950, Soepadmo & Mahmud 1032*; *N. parallelivenia*: *Keßler sub IV-H-73*, *Okada 3391*; *N. sparsistellata*: *Chaowasku 99*; *N. telopea*: *Gardner & Sidisunthorn ST 1992*; *Neo-uvaria* sp. 1: *PNH 91908*; *Neo-uvaria* sp. 2: *Binhasun 1*). The indumentum terminology follows Hewson (1988). Material for the pollen morphological study was sampled from dried herbarium specimens (*Enicosanthum* spp., *N. acuminatissima*, *N. foetida*, *N. parallelivenia*, *N. viridifolia*, *Neo-uvaria* sp. 1) or spirit collections (*N. sparsistellata*, *N. telopea*, *Neo-uvaria* sp. 2) (Table 1). The pollen was not acetolysed, following Chaowasku *et al.* (2008) and Couvreur *et al.* (2009). The material for TEM was prepared after the techniques described by Van der Ham (1990). The subdivision of the exine into tectum, infratectum and basal layer (Le Thomas 1980) is used. Further pollen terminology follows Punt *et al.* (2007).

Taxonomy

Neo-uvaria Airy Shaw (1939: 278). TYPE:—*Neo-uvaria foetida* (Maingay ex Hook.f. & Thomson) Airy Shaw (1939: 278). Basionym: *Popowia foetida* Maingay ex Hook.f. & Thomson (1872: 69). Lectotype (here designated):—PENINSULAR MALAYSIA. Malacca, 1867, *Maingay 1349A* (K-000190013!), in fruit.

Observations:—The inner petals of *Neo-uvaria foetida*, *N. sparsistellata* (Fig. 1E), *N. telopea* (Fig. 1A, B), *N. viridifolia* and *N.* sp. 1 are markedly apically thickened while they are not or less so in *N. acuminatissima*, *N. parallelivenia* (see Fig. 20 in Okada & Ueda 1984) and *N.* sp. 2. Furthermore, the inner petals of *N. foetida*, *N. sparsistellata*, *N. telopea*, and *N. viridifolia* in submature stage (i.e. not yet expanded) bear three small

openings at the base of two adjacent ones, which can be seen when the outer petals are removed. This feature is also observable in *Goniothalamus* Hooker & Thomson (1855: 105), some species of *Friesodielsia* Steenis (1948: 458), *Stelechocarpus cauliflorus* (Scheffer 1885: 5) Sinclair (1953: 43) and certain species of *Trivalvaria* Miquel (1865: 19) (pers. obs. TC; see also Sinclair 1955). Unfortunately, it cannot be verified in the other species of *Neo-uvaria* due to insufficient material.

Key to *Neo-uvaria* species in Thailand

1. Lower leaf surface sparsely covered with stellate indumentum. Flowers pedicellate, pedicels (in flower and in fruit) (3–)5–6(–8) mm long, sepals ca. 2.1 × 2.5 mm, outer petals 5.2 × 2.8–3.0 mm, inner petals 4.0–5.0 × 2.5 mm, stamens 12–15 per flower. Monocarps 3.1–3.3 × 2–2.5 cm..... ***N. sparsistellata***
- Lower leaf surface densely covered with stellate indumentum. Flowers (almost) sessile, sepals ca. 7.5 × 6.5 mm, outer petals 11.5–13.5 × 6.5–8.0 mm, inner petals 8.5–10.0 × 7.5–8.5 mm, stamens 16–20(–22) per flower. Monocarps 6.5–7.0 × 5.2–5.5 cm..... ***N. telopea***

Neo-uvaria sparsistellata* Chaowasku, *sp. nov. (Figs. 1E, F; 2; 3)

Neo-uvaria viridifolia proxima, praecipue petalis minoribus, staminibus carpellisque paucioribus differt.

TYPE:—THAILAND. Phatthalung Province: Si Ban Phot District, Khao Pu/Khao Ya National Park, headquarters, August 2005, *Gardner et al. ST 1894* (holotype L!, isotypes BKF, K), in flower and fruit (quite young).

Medium-sized trees, ca. 15 m tall, ca. 24 cm in dbh, all parts generally covered with stellate hairs intermixed with simple hairs. Young twigs tomentose. Petioles 2.0–4.5 mm long, densely tomentose. Leaves elliptic, 10.2–32.3 × 3.3–10.1 cm, base (broadly) wedge-shaped, apex generally (narrowly) acuminate, lamina (very) sparsely (appressed-)puberulous above, indumentum mostly on the lower half near the midrib, sparsely puberulous below, upper surface of midrib slightly sunken, (sparsely) (appressed-)tomentose, lower surface of midrib raised, (sparsely) tomentose, secondary veins 15–21 pairs per leaf, angle with midrib 35°–43°. Flowers solitary, axillary, pedicels (in flower and in fruit) (3–)5–6(–8) mm long, densely (appressed-)tomentose, bracts ca. 2 per flower, rather inconspicuous, at the base of the pedicels. Sepals broadly triangular, ca. 2.1 × 2.5 mm, persistent in fruit, outside and margin densely tomentose, inside glabrous. Outer petals elliptic-ovate, 5.2 × 2.8–3.0 mm, outside and margin tomentose, inside glabrous at the base, indumentum of the rest same as outside. Inner petals ovate, 4.0–5.0 × 2.5 mm, apically thickened, indumentum same as outer petals. Stamens 12–15 per flower, ca. 1.4 mm long, connective tissue flat-topped. Carpels 4–6 per flower, stigmas subglobose-ellipsoid, ovaries appressed-tomentose, ovules 1 per ovary, basal. Torus more or less flat, sparsely puberulous, slightly enlarged in fruit. Monocarps 1–3 per fruit, sessile, ellipsoid, 3.1–3.3 × 2.0–2.5 cm, surface (sparsely) tomentose-villous. Seeds 1 per monocarp, ellipsoid, 2.6–2.8 × 1.6–2.1 cm.

Distribution:—Peninsular Thailand [Phatthalung Province (Fig. 3)] [only known from two collections (*Chaowasku 99* and *Gardner et al. ST 1894*) collected from the same individual].

Habitats and Phenology:—Occurring in aggrading evergreen/deciduous forests amongst limestone outcrops. Elevation ca. 120 m. Flowering August, December. Fruiting August, December.

Field notes:—Bark grey; inner bark brownish-yellow. Petals white maturing yellow. Monocarps pale green with white and pale brown hairs.

Etymology:—The epithet refers to the sparse stellate indumentum on the lower leaf surface.

Vernacular names:—Ma-Khiew (Thai).

Observations:—This new species seems very close to *Neo-uvaria viridifolia* from the Philippines. They both possess a (very) sparse stellate indumentum on the lower leaf surface whereas it is (much) denser in the other species. In addition, a single stellate hair on the lower leaf surface of both species is relatively (much)

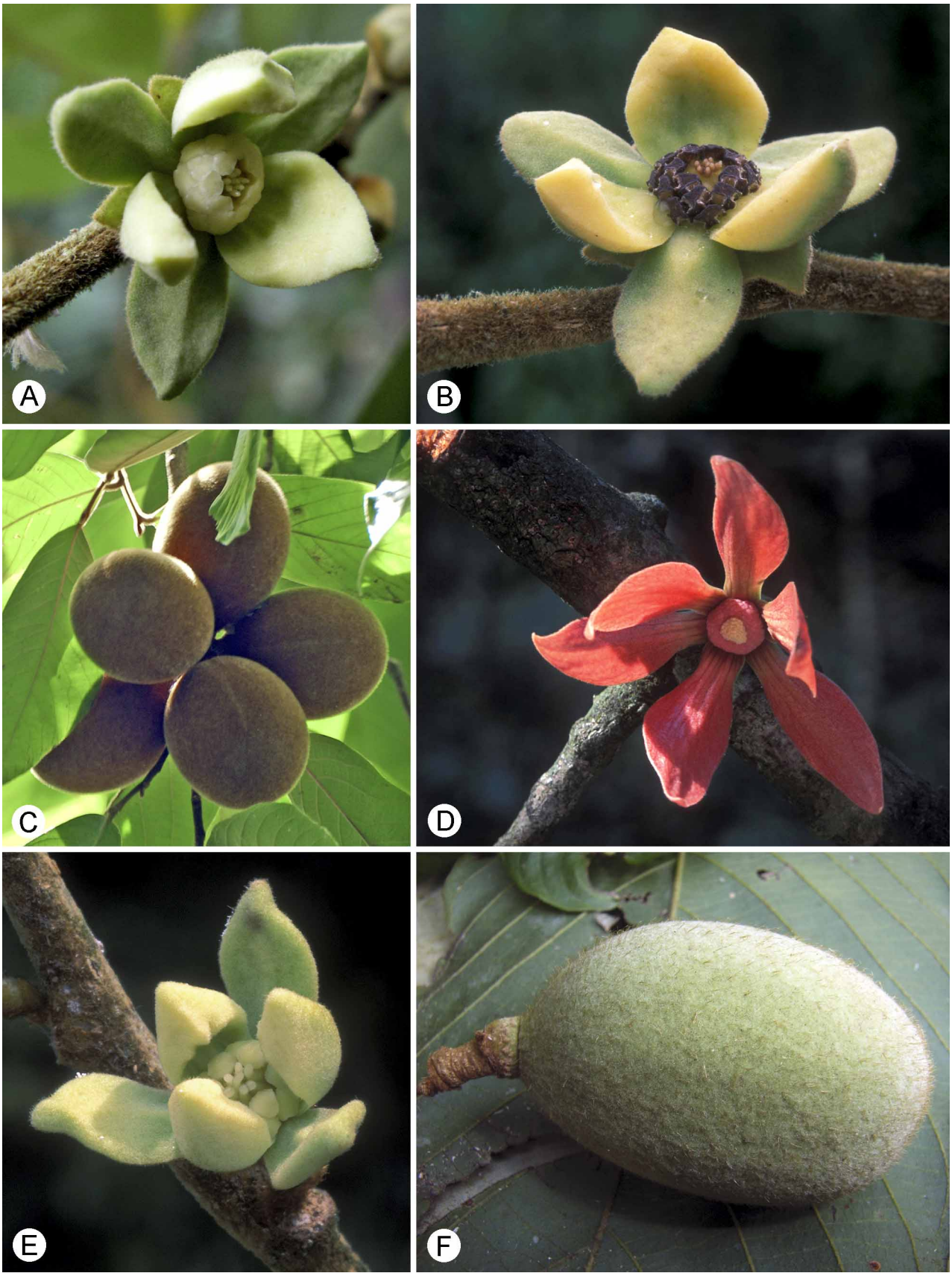


FIGURE 1. Flowers and fruits of *Neo-uvaria* and a flower of *Enicosanthum*. A–C. *Neo-uvaria telopea*: (A) Flower at female anthesis; (B) Flower at male anthesis, showing the blackened stamens; (C) Fruit with five monocarps. D. *Enicosanthum* sp.: (D) Flower at female anthesis. E, F. *N. sparsistellata*: (E) Flower at female anthesis; (F) Fruit with a single monocarp. Photographs: B, D, E, S. Gardner; A, C, S. Punnadee; F, T. Chaowasku.

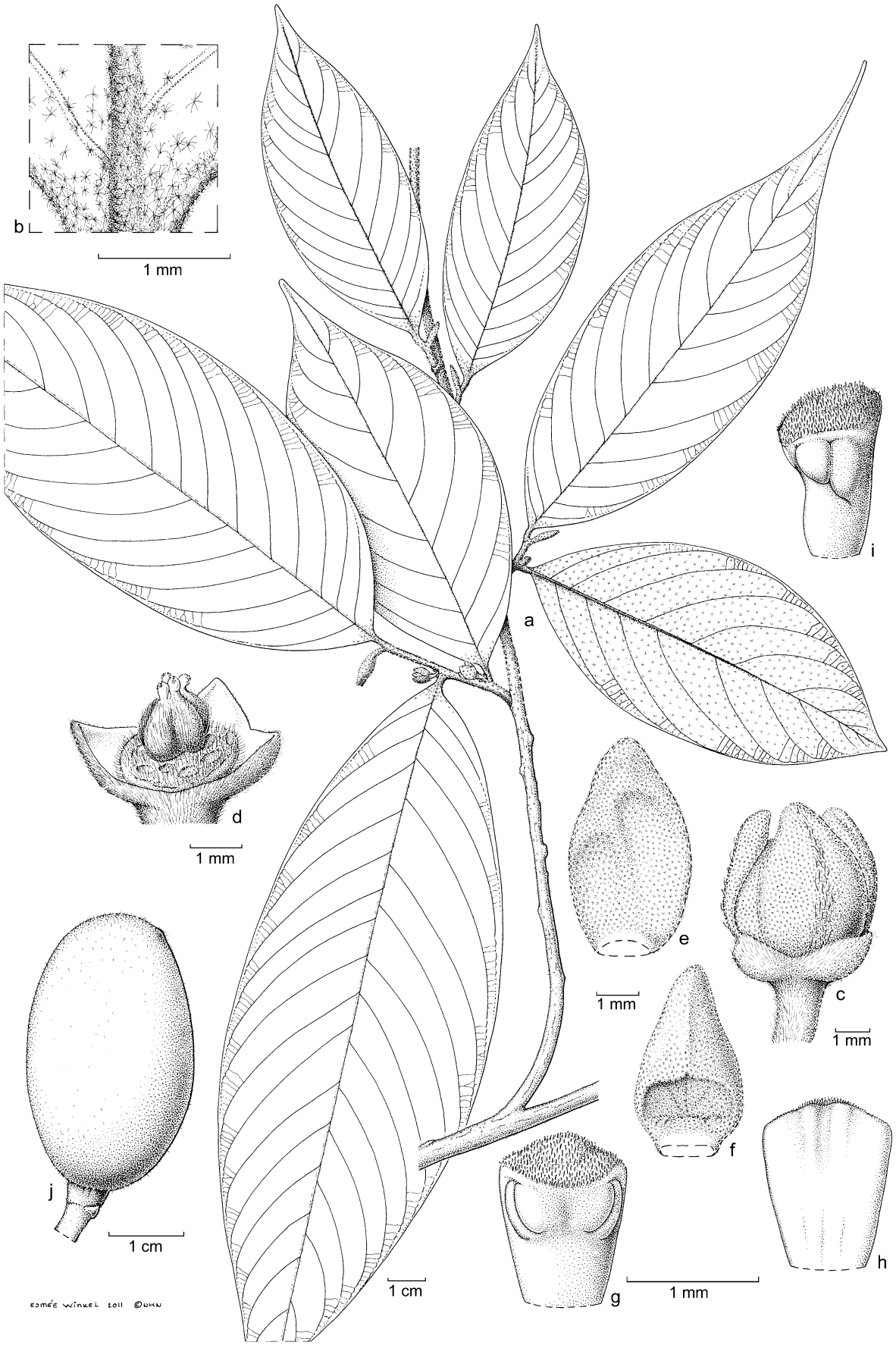


FIGURE 2. *Neo-uvaria sparsistellata*. a. Habit. b. Lower leaf surface. c. Nearly open flower. d. Flower with petals and stamens removed. e. Inside of an outer petal. f. Inside of an inner petal. g. Stamen, abaxial side. h. Stamen, adaxial side. i. Stamen, lateral view. j. Monocarp. (a–c, *Gardner et al. ST 1894*; d–j, *Chaowasku 99*).

smaller than that of the other species. *N. sparsistellata*, however, principally differs from *N. viridifolia* in having smaller petals (outer petals 5.2 × 2.8–3.0 mm, inner petals 4.0–5.0 × 2.5 mm in *N. sparsistellata* vs. outer petals (7.0–)10.2 × (3.6–)4.1 mm, inner petals (6.7–)9.5 × 3.4–3.7 mm in *N. viridifolia*), fewer stamens per flower (12–15 in *N. sparsistellata* vs. ca. 31 in *N. viridifolia*) and carpels per flower (4–6 in *N. sparsistellata* vs. ca. 12 in *N. viridifolia*). Besides, *N. sparsistellata* always has solitary flowers while *N. viridifolia* often have two (or three) flowers per inflorescence.

FIGURE 3. Distribution of *Neo-uvaria sparsistellata* (▼) and *N. telopea* (▲).

Neo-uvaria telopea* Chaowasku, *sp. nov. (Figs. 1A–C; 3; 4)

Neo-uvaria foetida e Malaysia peninsulari proxima, precipue foliis plerumque maioribus, venis tertiariis adiacentibus plus distantibus, pilis (plus) densibus, floribus maioribus, staminum numero minore differt.

TYPE:—THAILAND. Ranong Province: Klong Nakha Wildlife Sanctuary, September 2008, *Chaowasku 77* (holotype L!, isotype BKF!), in fruit.

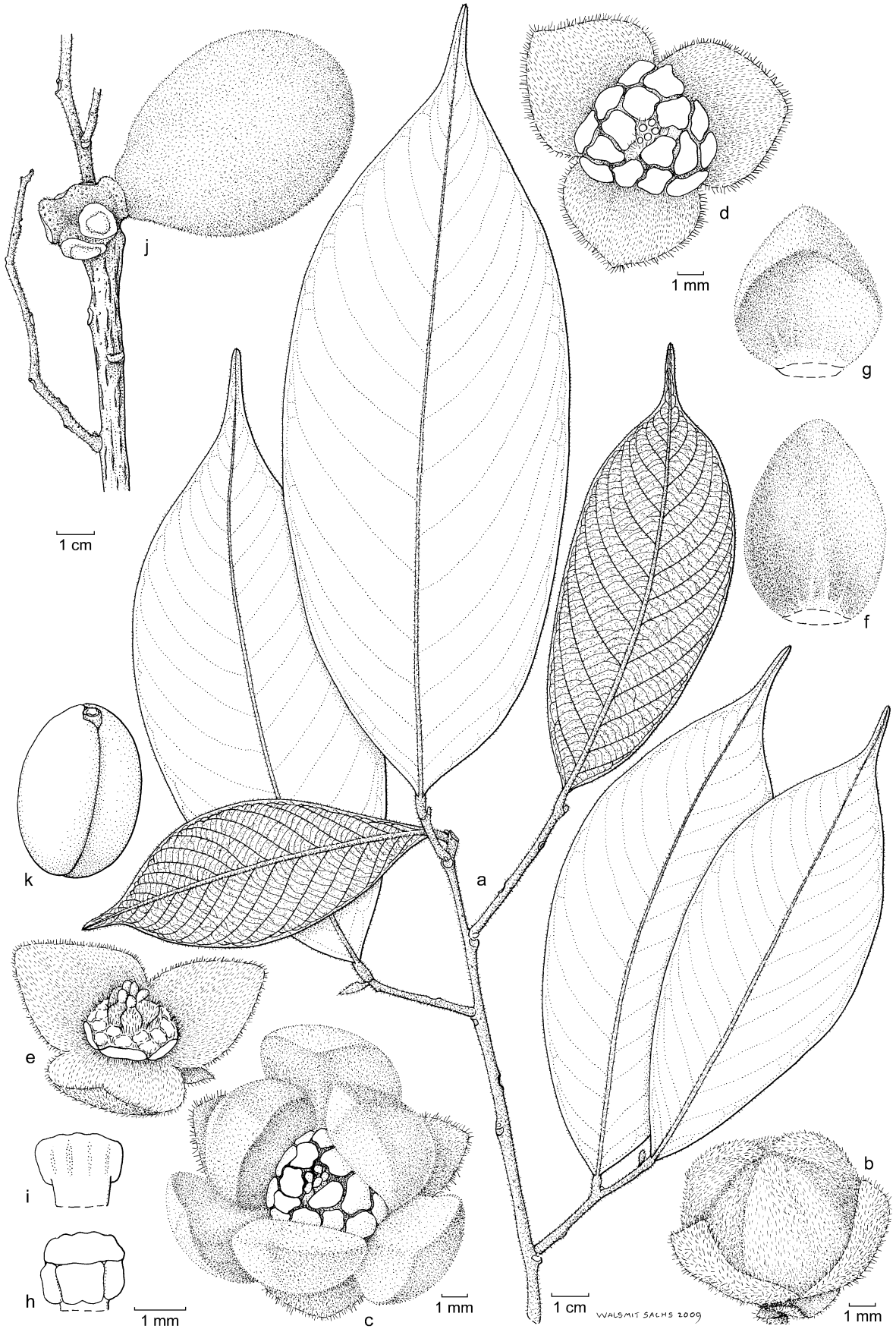


FIGURE 4. *Neo-uvaria telopea*. a. Habit. b. Flower bud. c. Flower. d. Flower with petals removed. e. Flower with petals and stamens removed. f. Inside of an outer petal. g. Inside of an inner petal. h. Stamen, abaxial view. i. Stamen, adaxial view. j. Fruiting branch with four monocarps detached. k. Seed. (a, j, k, *Chaowasku 77*; b–i, *Gardner and Sidisunthorn ST 1992*).

Medium-sized trees, ca. 11 m tall, ca. 12 cm in dbh, all parts generally covered with stellate hairs intermixed with simple hairs. Young twigs densely velvety-villous. Petioles 5–7 mm long, densely velvety-villous. Leaves elliptic, (9.5–)13.0–21.5 × (4.0–)4.7–9.1 cm, base broadly wedge-shaped to obtuse, apex caudate-acuminate, lamina almost glabrous above, (densely) villous below, upper surface of midrib slightly sunken, velvety, lower surface of midrib raised, densely (appressed-)velvety-villous, secondary veins 17–18 pairs per leaf, angle with midrib 45º–50º. Flowers solitary, axillary, (almost) sessile, bracts usually 2 per flower, ovate. Sepals broadly ovate to slightly triangular, ca. 7.5 × 6.5 mm, outside and margin (appressed-)velvety-tomentose, inside (appressed-)tomentose. Outer petals elliptic, 11.5–13.5 × 6.5–8.0 mm, indumentum on outer side and margin similar to sepals, inside shortly cobwebbed with sparser hairs, base (almost) glabrous. Inner petals slightly ovate to broadly elliptic, 8.5–10.0 × 7.5–8.5 mm, apically thickened, outside (appressed-) velvety-tomentose in the middle, sparser towards the margin which is shortly cobwebbed, inside shortly cobwebbed, sparser towards the base which is (almost) glabrous. Stamens 16–20(–22) per flower, 1.6–1.7 mm long, connective tissue flat-topped. Carpels 5–8 per flower, stigmas ellipsoid-cylindrical, ovaries densely villous, ovules 1(–2) per ovary, basal. Torus more or less flat, villous, enlarged in fruit. Monocarps 1–5 per fruit, sessile, ellipsoid-ovoid, 6.5–7.0 × 5.2–5.5 cm, surface (appressed-)velvety-tomentose. Seeds 1 per monocarp, ellipsoid(-ovoid), 5.0 × 3.4–3.5 cm.

Distribution:—Peninsular Thailand [Ranong Province (Fig. 3)] [only known from two collections (*Chaowasku 77* and *Gardner & Sidisunthorn ST 1992*) collected from the same individual].

Habitats and Phenology:—Occurring in understory of semi-disturbed lowland evergreen forests. Elevation ca. 120 m. Flowering December (collection *Gardner & Sidisunthorn ST 1992*). Fruiting September (collection *Chaowasku 77*).

Field notes:—Crown monopodial with horizontal branching. Bark dark brown, smooth with very shallow horizontal cracks with raised edges; middle bark indistinct; inner bark cream, fibrous. Petals pale green aging greenish-yellow, thick and fleshy; staminal mass pale yellow, blackened at male anthesis (Fig. 1B). Monocarps brown with velvety hairs.

Etymology:—The epithet refers to the huge size of the monocarps (Fig. 1C), which therefore can be easily seen from afar.

Vernacular names:—Ma-Neng (Thai).

Observations:—Odour of rotten fish was emitted from (nearly) dried monocarps. This smell was also detected in those of *N. foetida* (pers. obs. TC). This new species seems to be closely related to *N. foetida* occurring in Peninsular Malaysia. It chiefly differs in having generally larger leaves [(9.5–)13.0–21.5 × (4.0–)4.7–9.1 cm in *N. telopea* vs. 7.7–15.7(–18.0) × 2.5–5.0(–6.0) cm in *N. foetida*] with wider distance of the adjacent tertiary veins, denser indumentum on nearly all parts, larger flowers [sepals ca. 7.5 × 6.5 mm, outer petals 11.5–13.5 × 6.5–8.0 mm, inner petals 8.5–10.0 × 7.5–8.5 mm in *N. telopea* vs. sepals ca. 4.0 × 3.6 mm, outer petals ca. 9.2 × 5.4 mm, inner petals, ca. 6.7 × 5.4 mm in *N. foetida*], fewer stamens per flower [16–20(–22) in *N. telopea* vs. (26–)27 in *N. foetida*], and generally fewer carpels per flower [5–8 in *N. telopea* vs. 7–11 in *N. foetida*]. Vegetatively, *N. telopea* resembles *N. acuminatissima* in the density of the indumentum, but the latter species has much smaller monocarps and flowers. The fruits of *N. parallelivenia* are unknown but its flowers are noticeably different from those of *N. telopea*, especially the much smaller sepals and the non-thickened apex of the inner petals of the former.

New combinations

Neo-uvaria merrillii* (C.B.Rob.) Chaowasku, *comb. nov.

Basionym:—*Mitrephora merrillii* C.B.Rob. (1908: 67). *Griffithianthus merrillii* (C.B.Rob.) W.H.Brown ex Merrill (1915: 231). *Mitrephora ferruginea* Merrill (1904: 16), *nom. illeg.* TYPE:—THE PHILIPPINES. Luzon, Bataan Province: Mt. Mariveles, January 1904, *Merrill 3728* (PNH (destroyed), lectotype (here designated) NY!, isotypes BM!, P!), in fruit.

Observations:—Originally, the syntypes of this species consist of disparate elements as stated by Merrill (1915) and Weerasooriya & Saunders (2010). Nevertheless, no one has designated a lectotype, therefore it is done here. *Neo-uvaria merrillii* primarily differs from *N. acuminatissima* in having usually (broadly) wedge-shaped leaf base (whilst usually obtuse to rounded in *N. acuminatissima*), larger sepals (4.5–5.0 × 4.0–4.5 mm in *N. merrillii* vs. ca. 2.6 × 2.9 mm in *N. acuminatissima*) and wider monocarps (ca. 2.2 cm wide in *N. merrillii* vs. ca. 1.7 cm wide in *N. acuminatissima*).

Neo-uvaria viridifolia* (Elmer) Chaowasku, *comb. nov.

Basionym:—*Mitrephora viridifolia* Elmer (1913: 1716).

TYPE:—THE PHILIPPINES. Mindanao, Agusan Province: Cabadbaran (Mt. Urdaneta), October 1912, *Elmer 14184* (PNH (destroyed), lectotype (here designated) NY!, isotypes BM!, BP, DS, E!, G!, GH, L!, NA, P!, U!), in flower.

Observations:—*N. viridifolia* is considerably different from *N. acuminatissima*, especially in the much sparser stellate indumentum on the lower leaf surface. Moreover, its pedicels are longer than those of *N. acuminatissima* [(4–)5–6 mm long in *N. viridifolia* vs. nearly absent in *N. acuminatissima*]. The leaf base of *N. viridifolia* is usually (broadly) wedge-shaped in contrast to *N. acuminatissima* which usually has obtuse to rounded leaf base. *N. acuminatissima* was very rarely collected concerning the flowers. Of all specimens investigated, only the collection *Sinclair et al. 9250* [this collection seems to have generally smaller leaves with more obtuse base and wider distance of the adjacent tertiary veins compared to those of *Elmer 21112* and the type of *N. acuminatissima*, however, all other morphology of the three collections is similar] has flowers which are smaller than those of *N. viridifolia* [outer petals ca. 3.6 × 2.5 mm, inner petals ca. 3.8 × 3.0 mm in *N. acuminatissima* vs. outer petals (7.0–)10.2 × (3.6–)4.1 mm, inner petals (6.7–)9.5 × 3.4–3.7 mm in *N. viridifolia*].

Provisional key to seven recognized species of *Neo-uvaria*

(monocarps and petals are unknown in *N. parallelivenia* and *N. merrillii*, respectively)

1 Lower leaf surface (very) sparsely covered with stellate indumentum 2
- Lower leaf surface (moderately to) densely covered with stellate indumentum ..... 3 or 6
2. Flowers solitary. Outer petals 5.2 × 2.8–3.0 mm, inner petals 4.0–5.0 × 2.5 mm, stamens 12–15 per flower, carpels 4–6 per flower ..... *N. sparsistellata*
- Flowers solitary or in an inflorescence with 2 (or 3) flowers. Outer petals (7.0–)10.2 × (3.6–)4.1 mm, inner petals (6.7–)9.5 × 3.4–3.7 mm, stamens ca. 31 per flower, carpels ca. 12 per flower ..... *N. viridifolia*
3. Monocarps > 4 cm long 4
- Monocarps < 4 cm long 5
4. Leaves (9.5–)13.0–21.5 × (4.0–)4.7–9.1 cm. Sepals ca. 7.5 × 6.5 mm, outer petals 11.5–13.5 × 6.5–8.0 mm, inner petals 8.5–10.0 × 7.5–8.5 mm, stamens 16–20(–22) per flower, carpels 5–8 per flower ..... *N. telopea*
- Leaves 7.7–15.7(–18.0) × 2.5–5.0(–6.0) cm. Sepals ca. 4.0 × 3.6 mm, outer petals ca. 9.2 × 5.4 mm, inner petals ca. 6.7 × 5.4 mm, stamens (26–)27 per flower, carpels 7–11 per flower ..... *N. foetida*
5. Leaf base usually (broadly) wedge-shaped. Sepals 4.5–5.0 × 4.0–4.5 mm. Monocarps ca. 2.2 cm wide ... *N. merrillii*
- Leaf base usually obtuse to rounded. Sepals ca. 2.6 × 2.9 mm. Monocarps ca. 1.7 cm wide. ..... *N. acuminatissima*
6. Outer petals ca. 3.6 × 2.5 mm, inner petals ca. 3.8 × 3.0 mm ..... *N. acuminatissima*
- Outer and inner petals ≥ 5.4 mm long and wide 7
7. Apex of the inner petals not thickened ..... *N. parallelivenia*
- Apex of the inner petals conspicuously thickened 4

Pollen morphology

Walker (1971) described the pollen of one *Neo-uvaria* species (identified as *N. acuminatissima*), using LM, as: solitary, apolar, radiosymmetric, inaperturate, globose, medium-sized (longest axis 32 μm), tectate (columellae indistinct) and microbaculate. We studied several more species (Table 1), using LM/SEM/TEM.

In general, their pollen is similar to that of *Neo-uvaria* sp. described by Walker (1971). The following description of *Neo-uvaria* pollen summarises our observations (Tables 2, 3).

TABLE 1. Origin of *Enicosanthum* and *Neo-uvaria* pollen samples, and applied techniques.

	voucher	LM	SEM	TEM
Enicosanthum fuscum	*Kostermans 774*, Thailand (L)	X	X	X
E. membranifolium	*KEP/FRI 98720*, Peninsular Malaysia (L)	X	-	-
E. paradoxum	*Ambriansyah & Arifin B 1520*, Borneo (L)	X	X	X
Neo-uvaria acuminatissima	*Sinclair et al. 9250*, Borneo (L)	-	-	X
N. foetida	*Rogstad 950*, Peninsular Malaysia (KEP)	-	X	X
N. merrillii	not available	-	-	-
N. parallelivenia	*Keßler sub IV-H-73*, Bogor, Java (L)	X	X	X
N. sparsistellata	*Chaowasku 99*, Thailand (L)	-	X	X
N. telopea	*Gardner & Sidisunthorn ST 1992*, Thailand (L)	X	X	X
N. viridifolia	*Elmer 14184*, Philippines (L)	X	X	-
N. sp. 1	*PNH 91908*, Philippines (L)	X	X	X
N. sp. 2	*Binhasun 1*, Thailand (L)	-	X	X

TABLE 2. LM and SEM observations of pollen grain size and ornamentation in *Enicosanthum* and *Neo-uvaria*. L (long axis) and B (short axis) in μm.

	L	B	L/B	ornamentation
Enicosanthum fuscum	39	35	1.11	scabrate
E. membranifolium	26	22	1.18	(micro)echinate
E. paradoxum	39	37	1.05	scabrate
Neo-uvaria foetida	16	16	1.00	(micro)echinate
N. parallelivenia	26	24	1.08	microechinate
N. sparsistellata	17	15	1.13	(micro)echinate
N. telopea	24	22	1.06	microechinate
N. viridifolia	29	25	1.16	(micro)echinate
N. sp. 1	25	22	1.14	(micro)echinate
N. sp. 2	21	19	1.10	microechinate

TABLE 3. TEM observations of thickness of pollen wall sublayers in *Enicosanthum* and *Neo-uvaria*. Exine, supratectal elements (height), exintine and endintine in μm; tectum, infratectum and basal layer as proportions of exine thickness.

	exine	supratectal elem.	tectum	infra-tectum	basal layer	exintine	endintine
Enicosanthum fuscum	1.1	-	1/3	1/2	thin	c. 1.1	0.5
E. paradoxum	1.0	-	1/3	1/2	thin	c. 1.0	0.5
Neo-uvaria acuminatissima	0.35	≤ 1.4	1/2	1/4	1/4	c. 1.1	0.5
N. foetida	0.25	≤ 1.05	1/5	3/5	1/5	c. 0.3	c. 0.3
N. parallelivenia	0.2	≤ 0.3	1/3	1/3	1/3	c. 0.7	0.3
N. sparsistellata	0.2	≤ 0.4	1/2	1/2	thin	c. 0.8	thin
N. telopea	0.2	≤ 0.6	1/3	1/3	1/3	c. 0.6	0.2
N. sp. 1	0.3	≤ 0.5	1/3	1/3	1/3	c. 0.7	0.5
N. sp. 2	0.4	≤ 0.65	1/4	1/2	1/4	c. 0.8	?

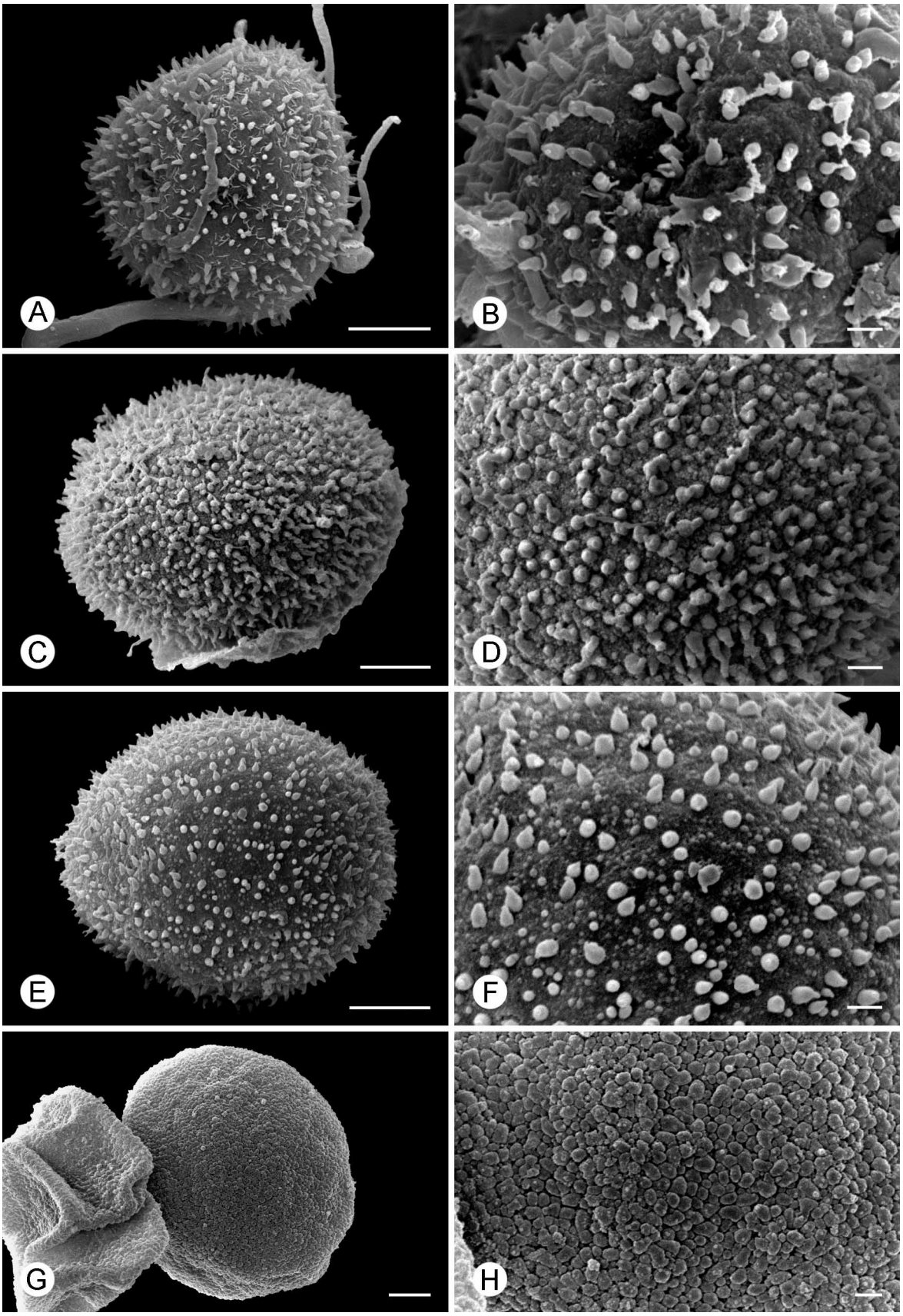


FIGURE 5. Pollen of *Neo-uvaria* and *Enicosanthum*, SEM. **A, B**. *Neo-uvaria foetida*: (A) Pollen grain, showing (micro)echinate exine; (B) Detail of exine. **C, D**. *N. sparsistellata*: (C) Pollen grain, showing (micro)echinate exine; (D) Detail of exine. **E, F**. *N. telopea*: (E) Pollen grain, showing microechinate exine; (F) Detail of E, showing ornamentation. **G, H**. *Enicosanthum paradoxum*: (G) Pollen grain, showing scabrate exine; (H) Detail of G, showing ornamentation. Scale bars —5 μm (A, C, E, G), 1 μm (B, D, F, H).

LM: Pollen grains apolar, (spheroidal to) subspheroidal, inaperturate monads, L (long axis) 16–29 μm, B (short axis) 15–25 μm, L/B 1.00–1.16.
SEM (Fig. 5A–F): Exine ornamentation microechinate to echinate.
TEM (Fig. 6A–F): Exine inaperturate, tectate, 0.2–0.4 μm thick. Supratectal elements: (micro)echinae up to 1.4 μm. Tectum usually distinct, 1/5–1/2 of exine thickness. Infratectum usually distinct, 1/4–3/5 of exine thickness, consisting of ± distinct granules. Basal layer usually distinct, very thin to 1/3 of exine thickness, sometimes distinctly lamellate. Intine continuous, without recognizable germination zone(s), consisting of a 0.3–1.1 μm thick tubular exintine and a 0.2–0.5 μm thick homogeneous endintine.

Discussion

Growth architecture consideration

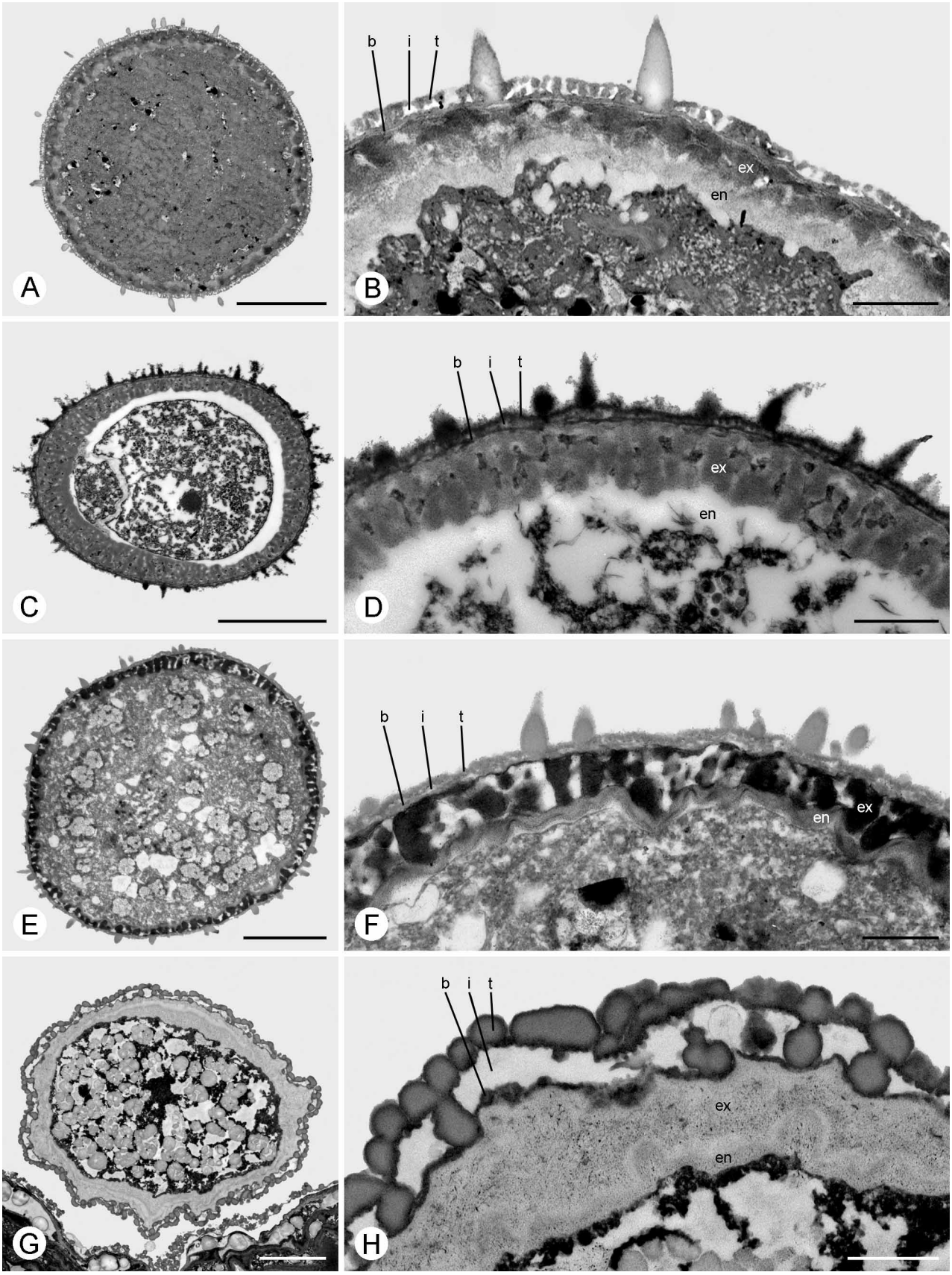
Johnson (2003) demonstrated the importance of growth architecture in Annonaceae. He distinguished two types: 1. spiral and 2. distichous branching patterns. These types are considered as a diagnostic/ synapomorphic character of particular clades. For example, an Afro-Asian subclade (uvarioid clade + African long branch clade) of the LBC (Couvreur *et al*. 2008), consisting of woody climbers, shrubs and trees, is easily recognizable by its distichous architecture. Similarly, as observed so far, members of the SBC exhibit spiral branching. It is likely that this trait had evolved in the common ancestor of the SBC and hence is expected to occur also in the other SBC genera where the growth architecture has not been observed. This correlation can greatly help to identify major Annonaceae clades in the field. *Neo-uvaria* shows spiral branching, and therefore is unlikely to be allied with *Uvaria* (a member of the uvarioid clade). The branching architecture, in combination with pollen morphology (discussed below), corroborates the systematic position of *Neo-uvaria* as belonging to the miliusoid clade, which is a subclade of the SBC.

Intergeneric relationships

The genus *Enicosanthum sensu lato* [Fig. 1D; including certain species assigned to *Polyalthia* Blume (1830: 68), these species will be eventually transferred to *Enicosanthum* elsewhere] appeared to be sister to *Neo-uvaria* (Mols *et al*. 2004a, b, Richardson *et al*. 2004, Chaowasku *et al*., unpublished study). *Enicosanthum* and *Neo-uvaria* share the following synapomorphic characters:

— Percurrent tertiary venation of the leaves (though some species of *Enicosanthum* have reversed to possess less percurrent/more reticulate tertiary venation)
— Axillary flowers/inflorescences
— An ovary bearing a single basal ovule (though sometimes two ovules were observed in *N. telopea*; Hooker & Thomson (1872), Airy Shaw (1939) and Sinclair (1955) stated that *N. foetida* usually has two ovules per ovary, but only one ovule per ovary was observed in the present study)
— Relatively large (much larger in *N. telopea* and *N. foetida*) single seed per monocarp with obvious raphe seen as a longitudinal groove
— Four-part-lamellate ruminations of the endosperm (in cross section)

FIGURE 6. Pollen of *Neo-uvaria* and *Enicosanthum*, TEM. **A, B**. *Neo-uvaria foetida*: (A) Cross-section of pollen grain, showing continuous exine and intine without recognizable germination zone(s); (B) Detail of cross-section, showing exine and intine sublayers. **C, D**. *N. sparsistellata*: (C) Cross-section of pollen grain, showing continuous exine and intine without recognizable germination zone(s); (D) Detail of cross-section, showing exine and intine sublayers. **E, F**. *N. telopea*: (E) Cross-section of pollen grain, showing continuous exine and intine without recognizable germination zone(s); (F) Detail of cross-section, showing exine and intine sublayers. **G, H**. *Enicosanthum paradoxum*: (G) Cross-section of pollen grain, showing continuous exine and intine without recognizable germination zone(s); (H) Detail of cross-section, showing exine and intine sublayers. Scale bars —5 μm (A, C, E, G), 1 μm (B, D, F, H); b = basal layer, en = endintine, ex = exintine, i = infratectum, t = tectum.


A
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Neo-uvaria differs from *Enicosanthum* in having much thicker petals, relatively larger stamens [which look more or less like those of *Sageraea* Dalzell (1851: 207) and *Stelechocarpus* Hooker & Thomson (1855: 94), according to Van Heusden 1995, 1997], a reduced number of stamens and carpels, and importantly the stellate indumentum. The last character is peculiar and has so far not been (consistently) observed in any other genera in the miliusoid clade, or even the SBC. Additionally, *Neo-uvaria* usually possesses sessile monocarps whilst they are usually markedly stipitate in *Enicosanthum*.

The sister genera *Sageraea* and *Stelechocarpus* are possibly allied to *Neo-uvaria* and *Enicosanthum* because they all share the axillary flowers/inflorescences and seeds with a grooved raphe and four-part-lamellate ruminations of the endosperm (pers. obs. TC; Mols *et al*. 2004b; see also Van Setten & Koek-Noorman 1992). Nevertheless, *Sageraea* and *Stelechocarpus* possess an ovary with many ovules arranged in two rows and lack the percurrent tertiary venation of the leaves (pers. obs. TC; Mols *et al*. 2004b). The most recent and comprehensive phylogenetic analyses of the SBC (= the Malmeoideae, Chaowasku *et al*., unpublished study) also reveal this relation, but only with moderate support in Bayesian analysis while no support in the analysis under maximum parsimony criterion. The genus *Phaeanthus* Hooker & Thomson (1855: 146) appears to become part of a clade comprising the mentioned four genera. It shares all characters with *Neo-uvaria* and *Enicosanthum* except the axillary flowers/inflorescences (terminal in *Phaeanthus*) and the similarly-sized outer petals and inner petals (similarly-sized sepals and outer petals in *Phaeanthus*). Further study is required to unravel the relationships of *Neo-uvaria*/*Enicosanthum*, *Sageraea*/*Stelechocarpus* and *Phaeanthus*.

Pollen morphology

Pollen morphologically the genus *Neo-uvaria* is rather homogeneous. Pollen of the transferred species *N. viridifolia* and the newly described *N. sparsistellata* and *N. telopea* agree well with those of *N. acuminatissima*, *N. foetida* and *N. parallelivenia*. Also pollen of *Neo-uvaria* sp. 1 and *N.* sp. 2 fit well in the generic description. *Enicosanthum*, the closest relative of *Neo-uvaria*, has more or less similar pollen, showing inaperturate monads with scabrate [*E. fuscum* (King 1893: 10) Airy Shaw (1939: 277), *E. paradoxum* Beccari (1871: 184); Fig. 5G, H, Fig. 6G, H] or (micro)echinate [*E. membranifolium* Sinclair (1955: 191)] ornamentation and a continuous intine without recognizable germination zone(s) (see also Mols *et al*. 2004b). However, in comparison to the *Neo-uvaria* species, the scabrate *Enicosanthum* species have larger pollen grains (39 μm vs. 16–29 μm) with a much thicker exine (1.0–1.1 μm vs. 0.2–0.4 μm). Unfortunately, no TEM data of the echinate *E. membranifolium* are available.

Conclusion

Neo-uvaria is a small genus in the miliusoid clade of the SBC. It consists of 9–15 species, seven of which are now formally recognized, including the two newly described species, *N. sparsistellata* and *N. telopea*, and the transferred *N. merrillii* and *N. viridifolia*. The genus *Enicosanthum* is the closest relative of *Neo-uvaria* based on macromorphology, pollen morphology, and molecular phylogenetics. *Neo-uvaria* is presently circumscribed by having the following characters: 1) leaves with percurrent tertiary veins, 2) stellate hairs generally covering all parts, 3) thick and fleshy petals, 4) reduced number of stamens and carpels, 5) usually single ovule per ovary and thus one seed per monocarp, 7) usually sessile monocarps, 8) relatively large seeds with distinct longitudinal groove, 8) lamelliform ruminations of the endosperm, divided into four equal parts (in cross section), and 9) inaperturate (micro)echinate pollen grains dispersed as monads. Taxonomic study covering the entire distribution area of *Neo-uvaria* is still needed. Up to now, *Neo-uvaria* is known from southern Thailand, Peninsular Malaysia, Sumatra, Borneo and the Philippines.

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References

Airy Shaw, H.K. (1939) Additions to the Flora of Borneo and other Malay Islands: 12. The Annonaceae of the Oxford University expedition to Sarawak, 1932. *Bulletin of Miscellaneous Information, Royal Botanic Gardens, Kew* 1939: 275–290.

Beccari, O. (1871) Illustrazione di nuove o rare specie di piante Bornensi – Anonaceae. *Nuovo Giornale Botanico Italiano* 3: 177–193.

Blume, C.L. (1830) *Flora Javae. [Anonaceae]*. J. Frank, Brussels.

Boerlage, J.G. (1899) *Catalogus plantarum phanerogamarum quae in horto botanico Bogoriensi coluntur herbaceis exceptis*. Fascicle 1. Lands Drukkerij, Batavia [Jakarta].

Chaowasku, T., Mols, J.B. & Van der Ham, R.W.J.M. (2008) Pollen morphology of *Miliusa* and relatives (Annonaceae). *Grana* 47: 175–184.

Couvreur, T.L.P., Richardson, J.E., Sosef, M.S.M., Erkens, R.H.J. & Chatrou, L.W. (2008) Evolution of syncarpy and other morphological characters in African Annonaceae: A posterior mapping approach. *Molecular Phylogenetics and Evolution* 47: 302–318.

Couvreur, T.L.P., Van der Ham, R.W.J.M., Mbele, Y.M., Mbago, F.M. & Johnson, D.M. (2009) Molecular and morphological characterization of a new monotypic genus of Annonaceae, *Mwasumbia* from Tanzania. *Systematic Botany* 34: 266–276.

Dalzell, N.A. (1851) Contributions to the Botany of Western India [Anonaceae]. *Hooker's Journal of Botany and Kew Garden Miscellany* 3: 206–208.

Elmer, A.D.E. (1913) New Anonaceae. *Leaflets of Philippine Botany* 5: 1705–1750.

Endlicher, S. (1839) *Genera plantarum secundum ordines naturales disposita*. Vienna.

Hewson, H.J. (1988) Plant indumentum. A handbook of terminology. *Australian Flora and Fauna Series* 9.

Hooker, J.D. & Thomson, T. (1855) *Flora Indica* 1. Pamplin, London.

Hooker, J.D. & Thomson, T. (1872) Anonaceae. *In*: Hooker, J.D. (ed.), *Flora of British India*, 1. L. Reeve & Co., London.

Johnson, D.M. (2003) Phylogenetic significance of spiral and distichous architecture in the Annonaceae. *Systematic Botany* 28: 503–511.

King, G. (1893) The Annonaceae of British India. *Annals of the Royal Botanic Garden (Calcutta)* 4: 1–169 + pl. 1–220.

Le Thomas, A. (1980) Ultrastructural characters of the pollen grains of African Annonaceae and their significance for the phylogeny of primitive angiosperms (first part). *Pollen & Spores* 22: 267–342.

Linnaeus, C. (1753) *Species plantarum* 1. Salvius, Stockholm.

Merrill, E.D. (1904) New or noteworthy Philippine plants, 2. *Department of the Interior, Bureau of Government Laboratories* 17: 1–47. + pl. 1–3.

Merrill, E.D. (1915) Studies on Philippine Anonaceae, 1. *Philippine Journal of Science, section C, Botany* 10: 227–264.

Miquel, F.A.W. (1865) Annonaceae Archipelagi Indici. *Annales Museum Botanicum Lugduno-Batavum* 2: 1–45 + pl. 1–2.

Mols, J.B., Gravendeel, B., Chatrou, L.W., Pirie, M.D., Bygrave, P.C., Chase, M.W. & Keßler, P.J.A. (2004a) Identifying clades in Asian Annonaceae: Monophyletic genera in the polyphyletic Miliuseae. *American Journal of Botany* 91: 590–600.

Mols, J.B., Co, D.L.V., Gravendeel, B., Chatrou, L.W., Pirie, M.D., Van der Ham, R.W.J.M., Van Marle, E.J. & Keßler, P.J.A. (2004b) Morphological character evolution in the miliusoid clade (Annonaceae). *In*: Mols, J.B. (ed.), *From Miliusa to Miliuseae to miliusoid: Identifying clades in Asian Annonaceae*. PhD Thesis, Leiden University, pp.

37–75.
Okada, H. & Ueda, K. (1984) Cytotaxonomical studies on Asian Annonaceae. *Plant Systematics and Evolution* 144: 165–177.
Punt, W., Hoen, P.P., Blackmore, S., Nilsson, S. & Le Thomas, A. (2007) Glossary of pollen and spore terminology. *Review of Palaeobotany and Palynology* 143: 1–81.
Richardson, J.E., Chatrou, L.W., Mols, J.B., Erkens, R.H.J. & Pirie, M.D. (2004) Historical biogeography of two cosmopolitan families of flowering plants: Annonaceae and Rhamnaceae. *Philosophical Transaction of the Royal Society B: Biological Sciences* 359: 1495–1508.
Robinson, C.B. (1908) Alabastra Philippinensia – 1. *Bulletin of the Torrey Botanical Club* 35: 63–75.
Scheffer, R.H.C.C. (1885) Sur quelques plantes nouvelles ou peu connues de l'Archipel Indien. *Annales du Jardin Botanique de Buitenzorg* 2: 1–31.
Sinclair, J. (1953) Notes on Siamese Annonaceae. *Gardens' Bulletin, Straits Settlements* 14: 40–44.
Sinclair, J. (1955) A revision of the Malayan Annonaceae. *Gardens' Bulletin, Straits Settlements* 14: 149–516.
Van der Ham, R.W.J.M. (1990) Nephelieae pollen (Sapindaceae): Form, function, and evolution. *Leiden: Nationaal Herbarium Nederland, Leiden Botanical Series* 13.
Van Heusden, E.C.H. (1992) Flowers of Annonaceae: Morphology, classification, and evolution. *Blumea, supplement* 7: 1–218.
Van Heusden, E.C.H. (1995) Revision of the Southeast Asian genus *Stelechocarpus* (Annonaceae). *Blumea* 40: 429–438.
Van Heusden, E.C.H. (1997) Revision of the Southeast Asian genus *Sageraea* (Annonaceae). *Nordic Journal of Botany* 17: 39–54.
Van Setten, A.K. & Koek-Noorman, J. (1992) Fruits and seeds of Annonaceae: Morphology and its significance for classification and identification. *Bibliotheca Botanica* 142: 1–101.
Van Steenis, C.G.G.J. (1948) Remarks on some generic names used for Malaysian phanerogams 1. *Bulletin du Jardin Botanique de Buitenzorg, sér. 3* 17: 457–464.
Walker, J.W. (1971) Pollen morphology, phytogeography, and phylogeny of the Annonaceae. *Contributions from the Gray Herbarium* 202: 3–131.
Weerasooriya, A.D. & Saunders, R.M.K. (2010) Monograph of *Mitrephora* (Annonaceae). *Systematic Botany Monographs* 90: 1–167. + colour pl. 1–4.