

## MOLECULAR AND MORPHOLOGICAL ANALYSIS SUPPORTS THE TRANSFER OF THE MONOTYPIC INDONESIAN GENUS *SEPTOGARCINIA* KOSTERM. TO *GARCINIA* (CLUSIACEAE)

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### ABSTRACT

SARI, R., CRAYN, D., DILLON, N., GADEK, P. & ABELL, S. 2023. Molecular and morphological analysis supports the transfer of the monotypic Indonesian genus *Septogarcinia* Kosterm. to *Garcinia* (Clusiaceae). *Reinwardtia* 22(2): 111–129. — Based on molecular phylogenetic analysis and an assessment of fruit and pollen characters, the transfer of *Septogarcinia sumbawaensis* Kosterm., endemic to Sumbawa Island, Indonesia and the sole member of the genus *Septogarcinia*, to *Garcinia* is strongly supported. The formal transfer of *S. sumbawaensis* to *Garcinia* (as *G. sumbawaensis*; the current name is *G. septogarcinia*) was based on morphological studies only. Phylogenetic analysis of nuclear internal transcribed spacer (ITS) sequences supports a placement of *G. septogarcinia* in *Garcinia* Section *Brindonia*. The distinctive dehiscent fruit, cited by Kostermans as justification for erecting *Septogarcinia*, is interpreted as an autapomorphy for this species in *Garcinia*. Pollen exine ornamentation is similar to *G. griffithii*, *G. gummi-gutta* var. *gummi-gutta*, *G. mestonii*, *Garcinia* sp. (Maluku) and *Garcinia* sp. (Batulanteh, Sumbawa).

**Key words:** Batulanteh, *Septogarcinia sumbawaensis*, Sumbawa.

### ABSTRAK

SARI, R., CRAYN, D., DILLON, N., GADEK, P. & ABELL, S. A. 2023. Analisis molekuler dan morfologi mendukung perpindahan marga monotipik Indonesia *Septogarcinia* Kosterm. to *Garcinia* (Clusiaceae). *Reinwardtia* 22(2): 111–129. — Berdasarkan analisis molekuler dan penilaian terhadap karakter buah dan serbuk sari, perpindahan *Septogarcinia sumbawaensis* Kosterm., endemik di Pulau Sumbawa, Indonesia dan anggota tunggal dari marga *Septogarcinia*, ke *Garcinia* sangat didukung kuat. Perpindahan secara formal *S. sumbawaensis* ke *Garcinia* (sebagai *G. sumbawaensis*; nama saat ini adalah *G. septogarcinia*) hanya didasarkan atas studi morfologi. Analisis filogenetik dari sekuens *internal transcribed spacer* (ITS) inti sel mendukung hubungan kekerabatan yang dekat antara *Garcinia septogarcinia* dengan *Garcinia* Seksi *Brindonia*. Perbedaan karakter buah yang terbelah, dikutip oleh Kostermans sebagai dasar untuk memisahkan *Septogarcinia*, diinterpretasikan sebagai otomorfi untuk jenis ini dalam *Garcinia*. Ornamenasi eksin serbuk sari mirip dengan *G. griffithii*, *G. gummi-gutta* var. *gummi-gutta*, *G. mestonii*, *Garcinia* sp. (Maluku) dan *Garcinia* sp. (Batulanteh, Sumbawa).

**Kata kunci:** Batulanteh, *Septogarcinia sumbawaensis*, Sumbawa.

## INTRODUCTION

*Septogarcinia* Kosterm. (Clusiaceae) was erected by Kostermans (1962) for a single species *S. sumbawaensis* Kosterm. based on material from Sumbawa Besar Island, Nusa Tenggara Barat, Indonesia (Figs. 1 & 2). Kostermans noted that *Septogarcinia* exhibited an unusual character state for Clusiaceae –fruits dehiscent (Fig. 3) at maturity– but in other respects was very similar to *Garcinia* L. He considered the dehiscent fruit of *S. sumbawaensis* to be morphologically similar to those found in the genera *Tovomita* Aubl. and *Rheedia* L. *Rheedia* fruit, however, do not dehisce. Another genus in Clusiaceae that has dehiscent fruit is *Clusia* L. but Kostermans did not compare *Septogarcinia* with *Clusia*.

Kostermans (1962) considered *Septogarcinia* to be related to *G. septata* from Celebes (Sulawesi). However, the name *G. septata* has not been published, nor are there any known specimens annotated with this name. It is possible that Kostermans was referring to *G. segmentata* Kosterm. (Kostermans, 1956) which was collected from South Sulawesi. This species has fleshy fruits that shrink when dried causing the fruits to split into many segments.

*Septogarcinia sumbawaensis* was informally included in *Garcinia* by Corner (1976), Jones (1980), and Stevens (2007) based on a suite of morphological characters. Corner (1976) noted that the flesh covering the seeds is typical of *Garcinia*, Jones (1980) found that the pollen is similar to that of *Garcinia* species in Section *Brindonia*, and Stevens (2007) assessed inflorescence characters and concluded that *Septogarcinia* could not be separated from *Garcinia*. Despite the morphological evidence none of these authors formally transferred *Septogarcinia* to *Garcinia*.

The morphological analysis of *Garcinia* by Ruhfel *et al.* (2013) placed *Septogarcinia* sister to *G. morella* (Gaertn.) Desr. but with weak support. Medellín-Zabala & Marinho (2015) followed previous studies of *Garcinia*, mainly by Sweeney (2008) and Ruhfel *et al.* (2013) and undertook a morphological study using the isotype of *S. sumbawaensis*. On the basis of these studies, Medellín-Zabala and Marinho transferred *S. sumbawaensis* to *Garcinia* as *G. sumbawaensis* (Kosterm.) Medellín-Zab. & L. Marinho (Medellín-Zabala & Marinho, 2015). However, Nazre (2018) considered that *G. sumbawaensis* and *G. sumbawensis* Lauterb. were synonyms. Turner & Jennings (2021) disagreed and provided clear morphological evidence that *G. sumbawaensis* (Kosterm.) Medellín-Zab. & L. Marinho and *G. sumbawensis* Lauterb. are distinct taxa. Further they considered *G. sumbawaensis* (Kosterm.) Medellín-Zab. & L. Marinho to be a later homonym of *G. sumbawensis* Lauterb. and erected the replacement name *G. septogarcinia* I.M. Turner & L.V.S. Jenn. for *G.*

*sumbawaensis*. Although POWO does not accept this, we do and use the name *G. septogarcinia* henceforth.

Despite *S. sumbawaensis* having been transferred to *Garcinia*, its taxonomic status has not been tested against a molecular dataset and its relationships and position within *Garcinia* remains unresolved. In this study we use a phylogenetic analysis of molecular and morphological data to evaluate the taxonomic status of *Septogarcinia*, in particular its position in relation to *Garcinia*.

## MATERIALS AND METHODS

### Molecular Analysis

#### DNA extraction, ITS amplification and sequencing

Total genomic DNA was extracted from silica gel-dried leaf material or herbarium specimens of 75 taxa using the DNeasy Kit (Qiagen, Germany). Extractions were performed according to the manufacturer's instructions, with a minor modification: at the second wash using AW2 buffer samples were centrifuged at 13,000 rpm instead of 14,000 rpm. The ITS regions were amplified by polymerase chain reaction (PCR) using forward primer ITS-I (Urbatsch *et al.*, 2000) and reverse primer ITS4 (White *et al.*, 1990) on a Bio-Rad TM-100 Thermal Cycler (BIO-RAD, Hercules, California, USA). Removal of unincorporated primers and degradation of unincorporated nucleotides from PCR products was done using the FastAP kit (Thermo Fisher, California, USA) following the manufacturer's instructions. The dried templates were sequenced at the Australian Genome Research Facility (AGRF, Brisbane) by capillary electrophoresis on AB3730xl instruments (Life Technologies, California, USA).

Herbarium vouchers were deposited in the Australian Tropical Herbarium (CNS) except for two samples from India (*G. indica* and *G. talbottii*) which were deposited in Krishna Mahavidyalaya Herbarium, Shivaji University, Maharashtra, India (SUK), and one sample of *Garcinia* sp. (Batam Island) that was deposited in Herbarium Bogoriense (BO). GenBank accession numbers for all sequences are provided in Table 1.

#### Alignment and phylogenetic analysis

The sequences were aligned using Multiple Alignment using Fast Fourier Transform (MAFFT, Katoh *et al.*, 2002; Katoh & Standley, 2013) in Geneious® version 9.1.6 software (Kearse *et al.*, 2012). Phylogenetic analyses were undertaken using Bayesian Inference (BI) in Geneious® version 9.1.6. (Kearse *et al.*, 2012) with the following settings: General-Time-Reversible (GTR) substitution model, rate variation = gamma, gamma categories = 4, chain length = 1,000,000, heated chains = 4, heated chain temperature = 0.2, subsampling fre-



Fig. 1. Map of Indonesia and the position of Sumbawa Island as indicated by the arrow and the box (Google Earth Data SIO, NOAA, U.S. Navy, NGA, GEBCO Landsat/Copernicus IBCAO U.S.).



Fig. 2. Map of Nusa Tenggara Barat Province showing the location of Sumbawa Island (Google Earth Data SIO, NOAA, U.S. Navy, NGA, GEBCO Landsat/Copernicus IBCAO U.S. 8°08'15" S, 116°46'27" E).



Fig. 3. The dehiscent fruit of *G. septogarcinia* at maturity, split from the base as indicated by the arrow. Photo by A. Aris.

Table 1. Details of samples used in the molecular study.

Species	Origin	Collector No.	Garden/Herbarium Accession No.	Sample Source
<i>Clusia major</i> L.	C. America	R. Sari RI1403	-	FBG
<i>Cratoxylum sumatranum</i> (Jack) Blume	Jambi, Sumatra, Indonesia	R. Sari RI1437	XIX.F.116	BBG
<i>Mammea siamensis</i> T.Anderson	Maluku, Indonesia	R. Sari RI1443	VII.D.85	BBG
<i>Pentadesma butyracea</i> Sabine	Africa	R. Sari RI1444	VI.C.246a	BBG
<i>Garcinia balica</i> Miq.	Lesser Sunda Island, Indonesia	R. Sari RI1438	XIX.N.23	BBG
<i>G. bancana</i> Miq.	Bangka Belitung, Sumatra, Indonesia	R. Sari RI1366	VI.C.392b	BBG
<i>G. binucao</i> (Blanco) Choisy	Philippines	R. Sari RI1378	VI.C.161	BBG
<i>G. brassii</i> C.T.White	N. Queensland, Australia	S.J. Worboys 825	CNS-130985	ATH
<i>G. celebica</i> L.	E. Java, Indonesia	R. Sari RI1410	XII.G.2	PBG
<i>G. cymosa</i> (K.Schum.) I.M.Turner & P.F.Stevens	New Guinea	R. Sari RI1394	XXIV.A.92	BBG
<i>G. daedalanthera</i> Pierre	N. Sulawesi, Indonesia	R. Sari RI1369	VI.C.429	BBG
<i>G. dulcis</i> (Roxb.) Kurz.	Kai Island, Maluku, Indonesia	R. Sari RI1404	XVII.K.II.40	PBG
<i>G. echinocarpa</i> Thwaites	Sri Lanka	R. Sari RI1380	VI.A.36	BBG
<i>G. fruticosa</i> Lauterb.	S. Papua, Indonesia	R. Sari RI1395	VI.C.217	BBG
<i>G. graminea</i> Kosterm.	Papua New Guinea	S.A. James	SAJ1369	ATH
<i>G. gummi-gutta</i> (L.) N. Robson var. <i>gummi-gutta</i> (yellow fruit)	India	R. Sari RI1425	20050100	SW
<i>G. gummi-gutta</i> (L.) N.Robson var. <i>gummi-gutta</i> (red fruit)	India	R. Sari RI1424	20050099	SW
<i>G. hombroniana</i> L.	Belitung Island, Sumatra, Indonesia	R. Sari RI1370	IX.D.286	BBG
<i>G. humilis</i> (Vahl.) C.D.Adams	S. America	R. Sari RI1438	-	PU
<i>G. intermedia</i> (Pittier) Hammel	S. America	R. Sari RI1433	-	SW
<i>G. jensenii</i> W.E.Cooper	N. Queensland, Australia	W.E. Cooper	CNS-G01401	ATH
<i>G. kola</i> Heckel	C. Africa	R. Sari RI1428	20100018	SW
<i>G. kydia</i> Roxb.	Kalimantan, Indonesia	R. Sari RI1393	VII.D.84	BBG
<i>G. lateriflora</i> Blume	Java, Indonesia	R. Sari RI1442	IX.D.278B	BBG
<i>G. latissima</i> Miq.	S. Papua, Indonesia	R. Sari RI1381	VI.C.338	BBG
<i>G. leggeae</i> W.E.Cooper	N. Queensland, Australia	W.E. Cooper	CNS-G01399	ATH
<i>G. lirii</i> C.E.Chang	Taiwan	W.H. Hu	4503	TBG
<i>G. livingstonei</i> Anderson	Tropical Africa	R. Sari RI1382	VI.A.30	BBG
<i>G. loureiri</i> Pierre	Vietnam	R. Sari RI1397	VI.C.60	BBG

<i>G. malaccensis</i> Hook.f. ex T.Anderson	Jambi, Sumatra, Indonesia	R. Sari RI1371	2012000038	BBG
<i>G. mangostana</i> L.	Java, Indonesia	R. Sari RI1372	XIII.E.10	BBG
<i>G. megaphylla</i> Verdc.	Brazil, S. America	R. Sari RI1386	VI.A.45	BBG
<i>G. mestonii</i> F.M.Bailey	N. Queensland, Australia	W.E. Cooper	CNS-G01403	ATH
<i>G. multiflora</i> Champ. ex Benth.	Taiwan	S.H. Wu	-	TBG
<i>G. nervosa</i> Miq.	Jambi, Sumatra, Indonesia	R. Sari RI1374	IX.D.269	BBG
<i>G. nigrolineata</i> Planch.	Bangka Island, S. Sumatra, Indonesia	R. Sari RI1398	VI.C.37	BBG
<i>G. picrorhiza</i> Miq.	Ambon Island, Maluku, Indonesia	R. Sari RI1405	VI.A.27	BBG
<i>G. porrecta</i> Wall.	W. Java, Indonesia	R. Sari RI1388	VI.A.79	BBG
<i>G. porrecta</i> Wall. var. <i>schizogyna</i> Boerl.	Ambon Island, Maluku, Indonesia	R. Sari RI1389	VI.A.50	BBG
<i>G. prainiana</i> King	Malaysia	R. Sari RI1432	-	SW
<i>G. rigida</i> Miq.	N. Sulawesi, Indonesia	R. Sari RI1375	XXIII.A.221	BBG
<i>G. russellii</i> W.E.Cooper	N. Queensland, Australia	W.E. Cooper	CNS-G196	ATH
<i>G. schomburgkiana</i> Pierre	Thailand	R. Sari RI1431	20050097	SW
<i>G. septogarcinia</i> I.M. Turner & L.V.S. Jenn.	Batudulang, Sumbawa Besar, NTB, Indonesia	R. Sari RI1461	-	BSB
<i>G. sizygiifolia</i> Pierre	Sarawak, Malaysia	R. Sari RI1399	VI.C.325	BBG
<i>Garcinia</i> sp. (Batam Is.)	Batam Island, Indonesia	I.P. Astuti	-	BI
<i>Garcinia</i> sp. (Kai Is.)	Kai Island, Maluku, Indonesia	R. Sari RI1455	XVII.K.II.10	PBG
<i>Garcinia</i> sp. (E. Java)	E. Java, Indonesia	R. Sari RI1421	XVII.J.II.27-a	PBG
<i>Garcinia</i> sp. (Halmahera Is.)	Halmahera Island, Maluku, Indonesia	R. Sari RI1415	XVII.K.II.39	PBG
<i>Garcinia</i> sp. (Buru Is.)	Buru Island, Maluku, Indonesia	R. Sari RI1414	XVII.J.II.16	PBG
<i>Garcinia</i> sp. (N. Sumatra)	N. Sumatra, Indonesia	R. Sari RI1413	IX.D.299	BBG
<i>Garcinia</i> sp. (C. Kalimantan)	C. Kalimantan, Indonesia	R. Sari RI1422	XVII.J.II.33-ab	PBG
<i>Garcinia</i> sp. (E. Kalimantan)	E. Kalimantan, Indonesia	R. Sari RI1446	XVII.J.II.26	PBG
<i>Garcinia</i> sp. (S. Morotai)	S. Morotai, N. Maluku, Indonesia	R. Sari RI1478	XVII.J.II.14-a	PBG
<i>Garcinia</i> sp. (Seram Is.)	Seram Island, Maluku, Indonesia	R. Sari RI1450	VI.C.379	BBG
<i>Garcinia</i> sp. (Bukit Lawang)	Bukit Lawang, N. Sumatra, Indonesia	R. Sari RI1477	-	MRT
<i>Garcinia</i> sp. (Bengkulu)	Bengkulu, Sumatra, Indonesia	R. Sari RI1447	XIX.F.102	BBG
<i>Garcinia</i> sp. (Batudulang)	Batudulang, Sumbawa Besar, NTB, Indonesia	R. Sari RI1462	-	BSB
<i>Garcinia</i> sp. 1 (Maluku)	Maluku, Indonesia	R. Sari RI1368	XVII.K.II.31	PBG
<i>Garcinia</i> sp. 2 (Maluku)	Maluku, Indonesia	R. Sari RI1423	XVII.K.II.35-ab	PBG
<i>Garcinia</i> sp. 1 (Papua)	Papua, Indonesia	R. Sari RI1376	IX.D.283	BBG
<i>Garcinia</i> sp. 2 (Papua)	Papua, Indonesia	R. Sari RI1377	IX.D.295	BBG

<i>Garcinia</i> sp. 3 (Papua)	Papua, Indonesia	R. Sari RI1406	IX.D.295a	BBG
<i>Garcinia</i> sp. 4 (Papua)	Papua, Indonesia	R. Sari RI1419	IX.D.302	BBG
<i>Garcinia</i> sp. 5 (Papua)	Papua, Indonesia	R. Sari RI1449	IX.D.303	BBG
<i>Garcinia</i> sp. 6 (Papua)	Papua, Indonesia	R. Sari RI1445	XVII.J.II.24	PBG
<i>Garcinia</i> sp. 1 (S. Sulawesi)	S. Sulawesi, Indonesia	R. Sari RI1408	IX.D.287a	BBG
<i>Garcinia</i> sp. 2 (S. Sulawesi)	S. Sulawesi, Indonesia	R. Sari RI1420	IX.D.274	BBG
<i>Garcinia</i> sp. 1 (W. Sumatra)	W. Sumatra, Indonesia	R. Sari RI1448	IX.D.294	BBG
<i>Garcinia</i> sp. 2 (W. Sumatra)	W. Sumatra, Indonesia	R. Sari RI1451	VI.C.463	BBG
<i>G. subelliptica</i> Merr.	Taiwan	W.H. Hu	4502	TBG
<i>G. tetrandra</i> Pierre	Philippines	R. Sari RI1391	VI.C.108	BBG
<i>G. warrenii</i> F.Muell.	N. Queensland, Australia	D. Warmington	-	CNS
<i>G. xanthochymus</i> Hook.f. ex T.Anderson	India	R. Sari RI1392	VI.A.52	BBG
<i>G. zichii</i> W.E.Cooper	N. Queensland, Australia	W.E. Cooper	CNS 138512.1	ATH

quency = 1,000, burn-in = 200,000 and random seed = 4,654. *Clusia rosea* was used as the out-group.

## Morphological Analysis

### Pollen

Sampling of taxa for the pollen study was based on the availability of male flowers. Male flowers of 72 species were obtained fresh, or from herbarium or spirit material. Fresh samples were air dried and spirit samples oven dried at 40°C in tea bags prior to preparation for microscopy. The presence of mature, fully formed pollen grains was confirmed in 32 of the 72 samples using light microscopy (Wild M7 S, Wild Heerbrugg, Pty. Limited, Australia; Nikon Eclipse E100, Nikon Corporation, Tokyo, Japan) (Table 1). Pollen from these 32 samples was mounted on IA023 carbon tabs (PSA, Thuringowa, Australia) on aluminium stubs, coated with gold using a SPI Module Sputter Coater (SPI, West Chester, Pennsylvania, USA) then observed and imaged using a JEOL JSM 6300 (CAE, Austin, Texas, USA) scanning electron microscope operating at 5 kV with Semaphore imaging software.

### Fruit

The scoring of fruit morphological characters was carried out using the naked eye on fresh material in the field. Measurements were made using a ruler and calipers.

### Morphological character scoring

Variation in pollen and fruit morphology was scored as four characters as follows. The morphological character matrix is provided as Table 2.

1. Pollen ornamentation. Six states were observed and scored: psilate (0), surface smooth; scabrate (1), sculptural elements of

varying shapes, <1 µm in diameter; verrucate (2), sculptural elements wart-like (usually broader than high and never constricted at the base), >1 µm in diameter; echinate (3), sculptural elements pointed, >1 µm high; gemmate (4) sculptural elements the same width as height and constricted at their bases, >1 µm high; pilate (5) sculptural elements rod-like with swollen or knob-like heads (capita), >1 µm high (Moore *et al.*, 1991). All character states are illustrated in Fig. 4 (A–F).

2. Pollen aperture. Seven states were observed and scored: monocolpate (0), having a single elongated aperture (colpus); tricolpate (1); tetracolpate (2); tetraporate (3), having four pore-like apertures; tetra-pentacolpate (4); penta-hexacolpate (5); hexacolpate (6) (Moore *et al.*, 1991). All character states are illustrated in Fig. 5 (A–G).
3. Fruit segmentation: non-segmented (0), exocarp smooth, without grooves; segmented (1), fruit segmented or grooved.
4. Fruit dehiscence: indehiscent (0); dehiscent (1).

Of the 32 taxa included in the pollen study, 14 were included in the molecular analysis. Ancestral state reconstruction of the pollen and fruit characters was undertaken using maximum likelihood in Mesquite ver. 3.40 (Maddison & Maddison, 2018) using the Bayesian tree from the molecular analysis pruned to include only those taxa for which the morphological data were scored (*i.e.* taxa in Table 1) and the following settings: current probability models, max. number of mappings per character per tree = 50. The proportional likelihood of each character state is indicated for each node using pie graphs.

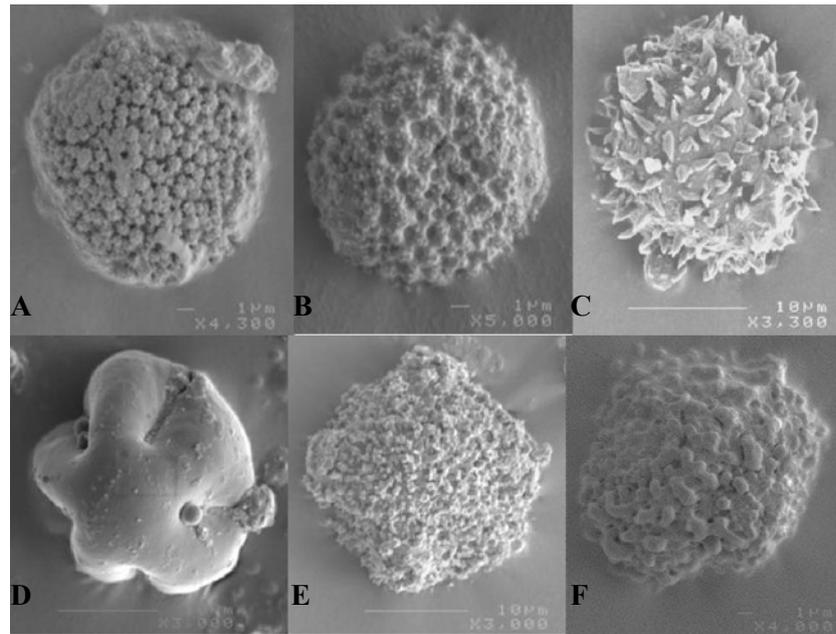


Fig. 4. Pollen ornamentation in *Garcinia* observed in this study. A. Gemmate (*G. binucao*). B. Pilate (*G. griffithii*). C. Echinate (*G. latissima*). D. Psilate (*G. nervosa*). E. Scabrate (*G. porrecta*) and F. Verrucate (*G. hombroniana*). Micrographs by R. Sari.

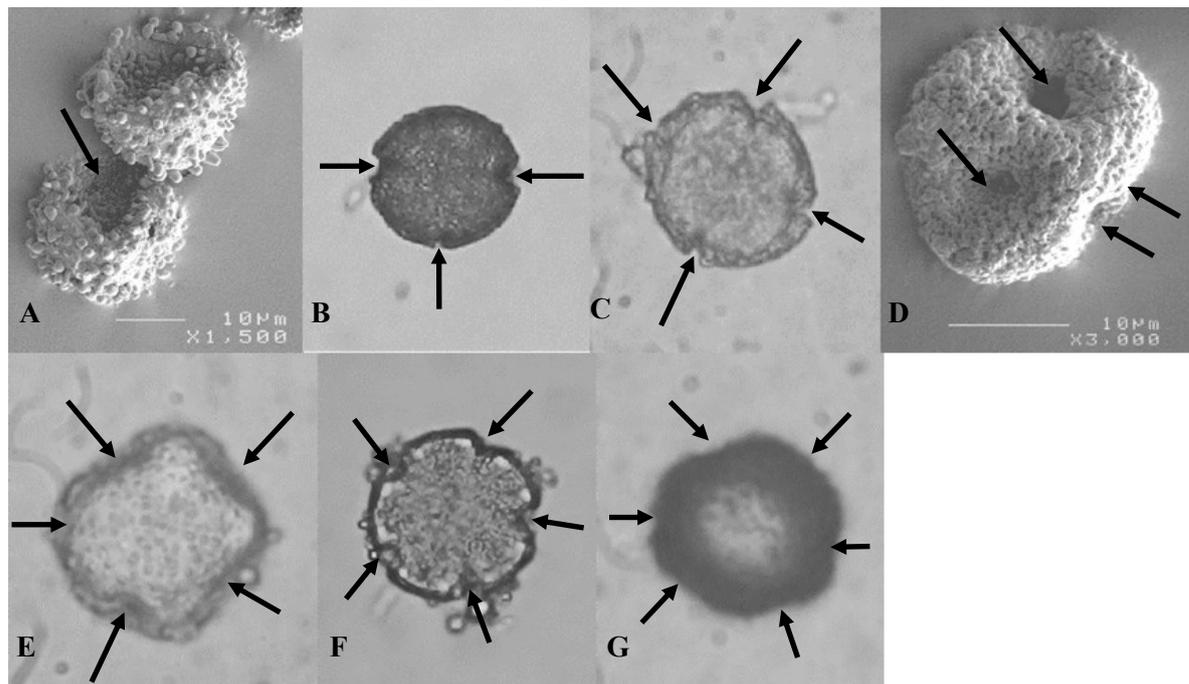


Fig. 5. Pollen apertures observed in this study as indicated by arrows. A. Monocolpate (*G. zichii*, SEM). B. Tricolpate (*G. griffithii*, light microscope 100 $\times$ ). C. Tetracolpate (*G. binucao*, light microscope 100 $\times$ ). D. Tetraporate (*Garcinia* sp. (Batudulang, Sumbawa, SEM). E. Tetra-pentacolpate (*G. malaccensis*, light microscope 100 $\times$ ). F. Penta-hexacolpate (*G. nervosa*, light microscope 40 $\times$ ). G. Hexacolpate (*G. warrenii*, light microscope 100 $\times$ ). Micrographs by R. Sari.

## RESULTS

### Molecular Analysis

The aligned ITS sequences generated in this study ranged in length from 761–1,808 bp, with 87.2% pairwise identity. Bayesian analysis of these data resolved two major lineages with maximum support among the ingroup: (1) *Cratoxylum* + *Mammea* (posterior probability, PP, 1.0); and (2) *Garcinia* + *Pentadesma* (PP 1.0) (Fig. 6). The position of *Pentadesma* is unresolved at the base of *Garcinia*, potentially rendering *Garcinia* non-monophyletic. Within the *Garcinia* clade 11 subclades were resolved, although some lineages were unresolved on polytomies such as *Garcinia* sp. (Halmahera Island, Indonesia), *Garcinia* sp. 6 (Papua, Indonesia), *G. echinocarpa* (Sri Lanka), *G. mestonii* (N. Queensland, Australia), *G. bancana* (Bangka Belitung, Sumatra, Indonesia) and *Garcinia* sp. (Seram, Maluku, Indonesia).

*Garcinia septogarcinia* clustered within a maximally supported clade comprising species assigned to Section *Brindonia* according to Jones (1980). This clade includes 10 samples representing described species, and four samples of unknown species identity. Together, these 14 samples represent a wide geographical range, including Australia (*G. leggae*, *G. mestonii*), India (2 samples of *G. gummi-gutta* var. *gummi-gutta*, representing red-fruited and yellow-fruited forms), Indonesia (*G. bancana*, *G. nigrolineata*, *Garcinia* sp. (Bengkulu), *Garcinia* sp. (Bukit Lawang), *Garcinia* sp. 1 (W. Sumatra), *Garcinia* sp. (Seram Is.), Malaysia (*G. szygiiifolia*, from Sarawak, Borneo), Philippines (*G. binucao*, *G. tetrandra*, the latter also widely distributed in Sulawesi), and Vietnam (*G. loureiri*). Within this clade *G. septogarcinia* is sister to *G. szygiiifolia*.

### Morphological Analysis

The pollen of *G. septogarcinia* is tetracolpate with pilate ornamentation. Among the 21 taxa examined in this study this combination of character states is found in two other taxa: *G. mestoni* and *G. gummi-gutta*. Tetracolpate pollen is also found in *G. binucao*, which has scabrate ornamentation. Pilate pollen ornamentation is found in three other taxa: *G. echinocarpa*, *Garcinia* sp. (Maluku), and *Garcinia* sp. (Batudulang, Sumbawa Besar) (Table 3).

The ancestral state reconstruction of pollen ornamentation is shown in Fig. 7. Three character states are autapomorphic, namely: state 1, psilate (*G. nervosa*); 2, verrucate (*G. hombroniana*); and 4, gemmate (*G. zichii*). The other character states are spread among the clades and are not monophyletic. In this analysis, the pollen ornamentation of *S. sambawaensis* (5, pilate) is resolved as ancestral for the Section *Brindonia* clade which includes *G. septogarcinia* (marked with an asterisk in Fig. 7) with a high proportional likelihood

of 0.97525734 (other proportional likelihoods are state 0: 0.00123573; 1: 0.01972518; 2: 0.00124669; 3: 0.0013019; 4: 0.00123317). Within the *Brindonia* clade, scabrate pollen is resolved as ancestral for a subclade comprising *G. leggae*, *G. binucao* and *G. tetrandra*.

Of the pollen aperture character states only state 6, hexacolpate, occurred in a single clade (Fig. 8). The proportional likelihood is 0:0.00081357; 1: 0.01300851; 2: 0.9829738\*; 3: 0.0007924; 4: 0.00078478; 5: 0.00079117; 6: 0.00083577. Character states 3, tetraporate and 4, tetra-pentacolpate are each autapomorphic, for *Garcinia* sp. (Sumbawa, NTB, Indonesia) and *G. malaccensis* respectively, which are sisters in the tree. All other character states have evolved more than once and are shared among the taxa. The pollen aperture of *G. septogarcinia* is categorized as state 2, tetracolpate.

“Fruit segmented” is found only in sister taxa *G. septogarcinia* and *G. gummi-gutta* var. *gummi-gutta* (Fig. 9). “Fruit dehiscent” was only found in *G. septogarcinia* (Table 2, Fig. 10) in this study but it might occur in some other species that have not been included here such as *G. segmentata* Kosterm. which Kostermans considered a close relative of *S. sambawaensis*.

### Variation within *G. septogarcinia*

During field work undertaken during this study the first author discovered two variants of *G. septogarcinia* distinguished by characters of the fruit (colour, shape, and texture of the stigma) and leaves (pedicel length and colour, and lamina dimensions) (Table 4, Fig. 11). Flowers of variant 2 were not available so floral morphology could not be compared. Further field, herbarium and laboratory studies are required to determine the appropriate taxonomic status of these variants.

## DISCUSSION

The morphological and molecular analyses confirmed previous morphological studies that showed *S. sambawaensis* belongs in the genus *Garcinia*. In our molecular analysis, ITS was used as previous studies showed it is an appropriate marker to analyse phylogenetic relationships in *Garcinia* (Sari, 2000; Nazre *et al.*, 2007; Sweeney, 2008). Most specimens were successfully amplified in the PCR, but several failed such as *G. atroviridis* and *G. gibbsieae*. This may be due to poor primer match or the use of herbarium specimens for DNA extraction in a few species. For the next study it is recommended to design additional primers for *Garcinia* and to obtain fresh or silica gel-dried samples for the remaining taxa where possible. We also attempted to locate material of *G. sambawaensis* Lauterb. in a few herbaria but it appears that the only material of *G. sambawaensis* is in the Wroclaw Herbarium in Poland (see Turner & Jen-

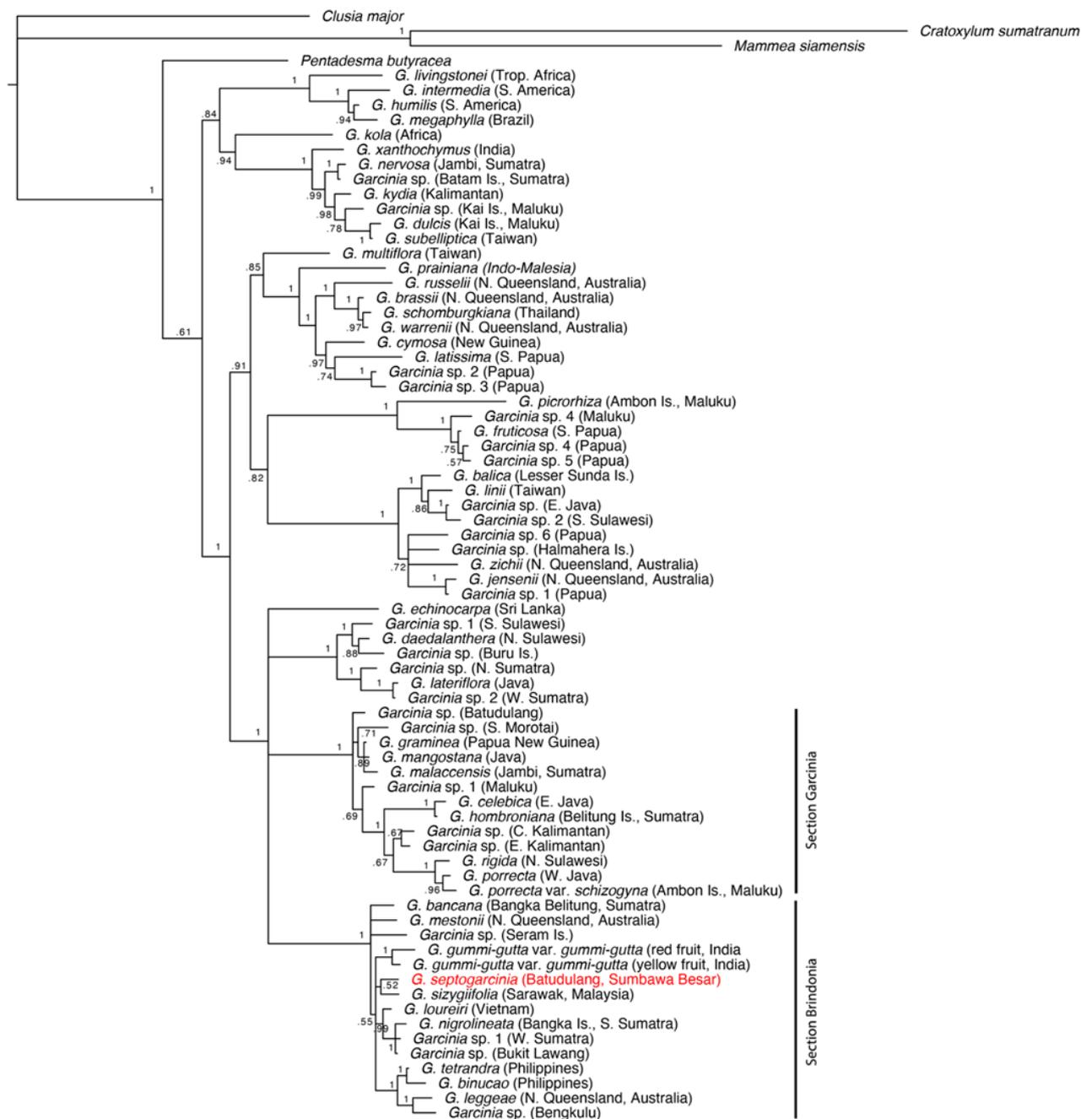


Fig. 6. A strict consensus tree of 71 samples of *Garcinia* based on Bayesian analysis of ITS sequence data showing *G. septogarcinia* (in red) nested within *Garcinia* Section *Brindonia*. Sections *Brindonia* and *Garcinia* are marked by the two lines. Numbers associated with nodes are posterior probability values.

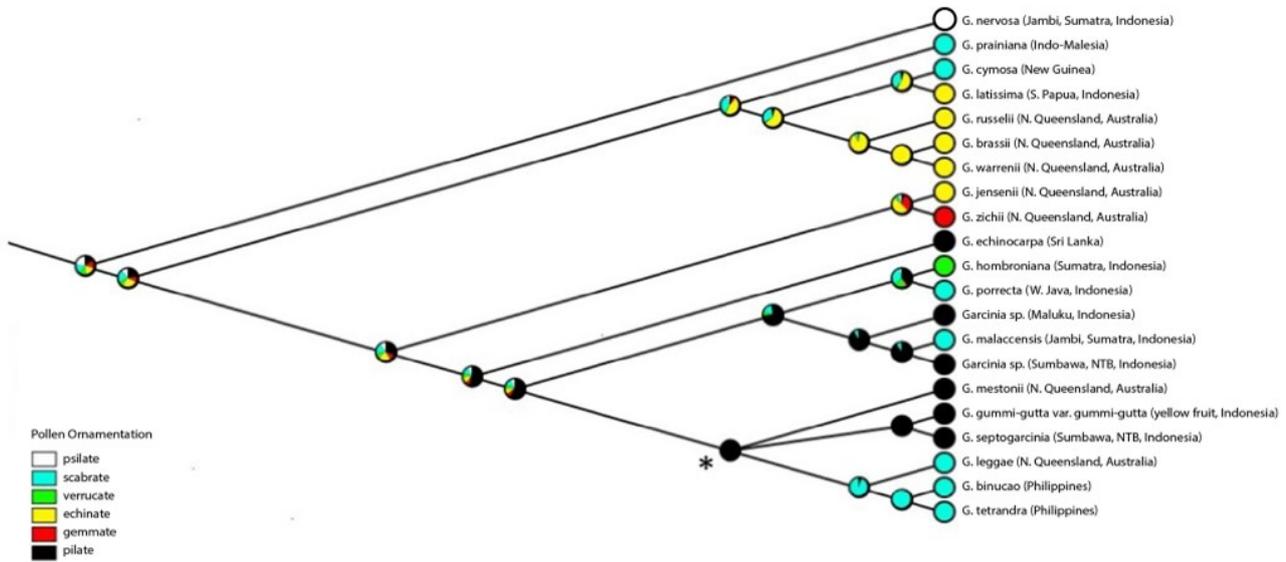


Fig. 7. Ancestral state reconstruction analysis of pollen ornamentation in 21 species of *Garcinia*.

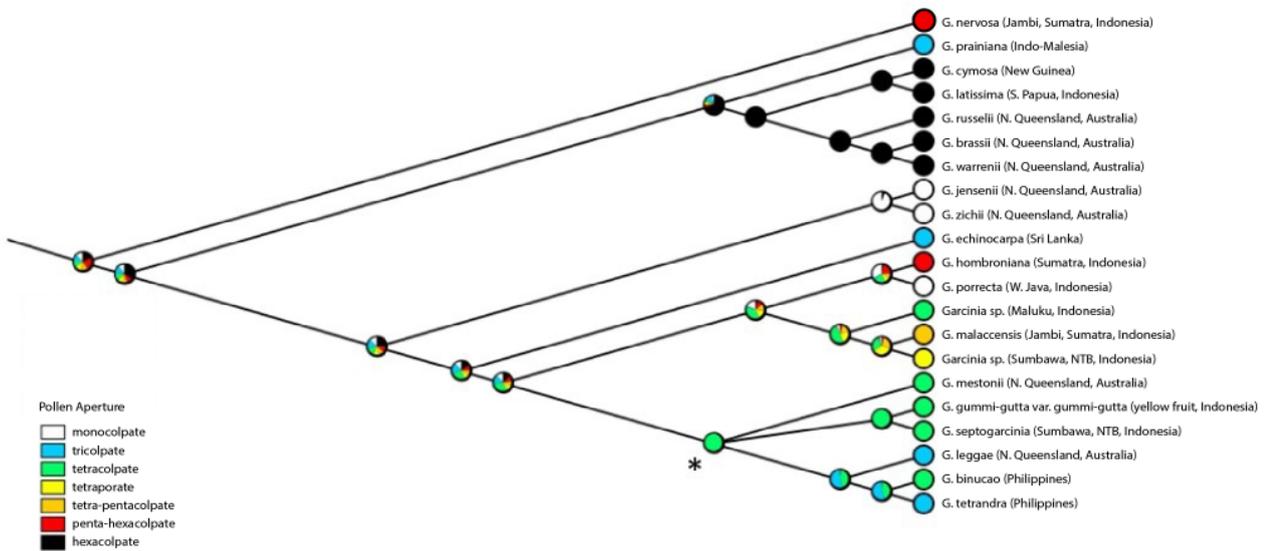


Fig. 8. Ancestral state reconstruction analysis of pollen aperture in 21 species of *Garcinia*.

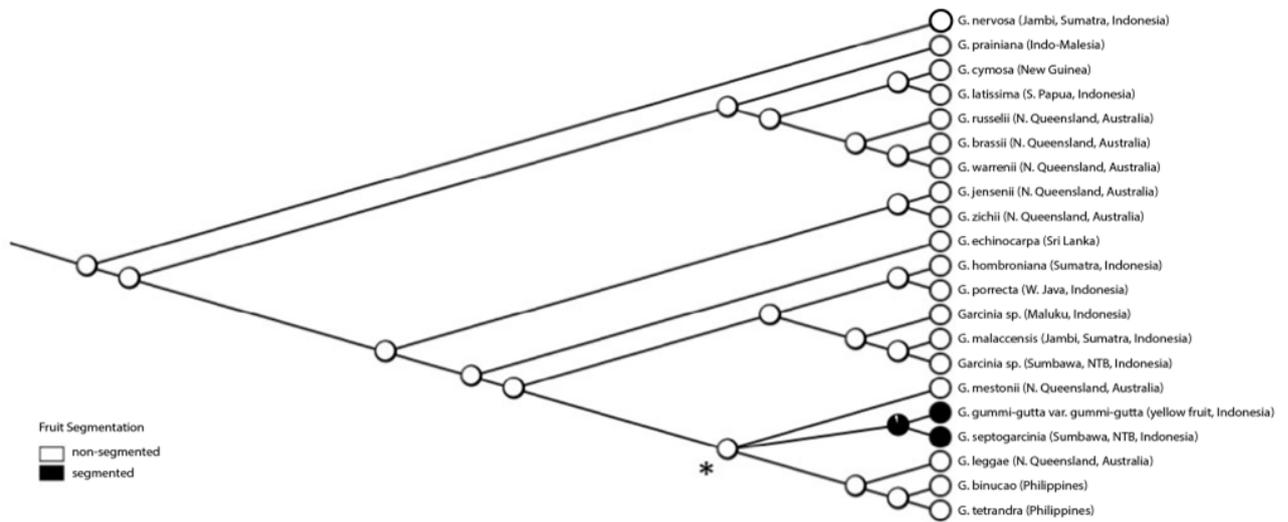


Fig. 9. Ancestral reconstruction of segmented fruit of 21 species of *Garcinia*.

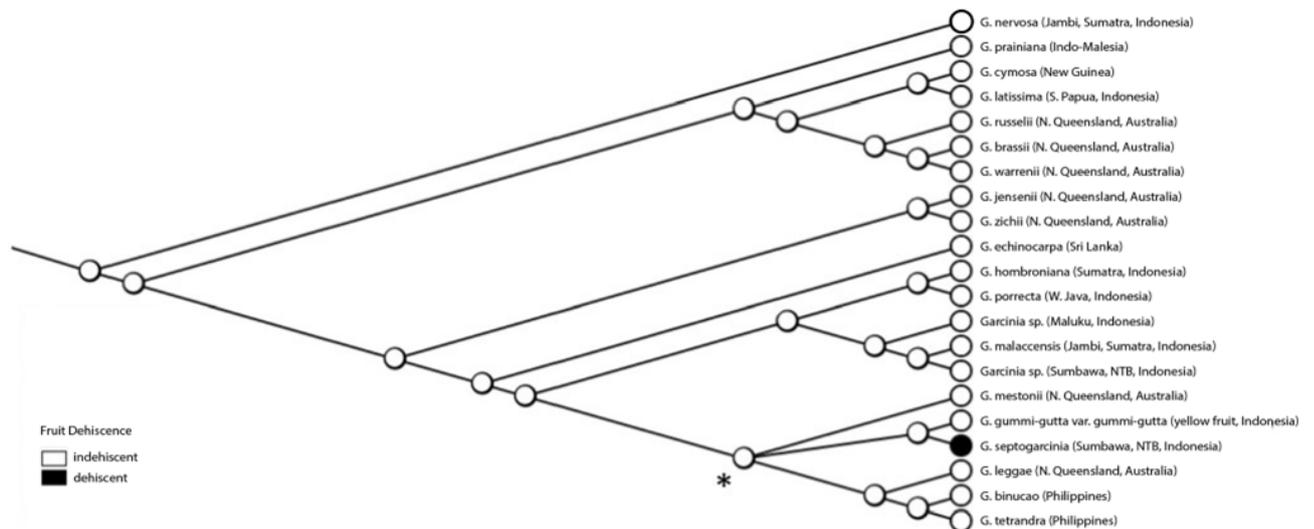


Fig. 10. Ancestral state reconstruction analysis of fruit dehiscence in 21 species of *Garcinia*.

Table 2. Morphological character matrix. The source of material for pollen were from herbarium specimen (H), spirit collections (S) or fresh (F). Fruit characters were observed on fresh fruit or taken from the literature.

Species	Pollen ornamentation	Pollen apertures	Fruit segmentation	Fruit dehiscence	Pollen source material
<i>Garcinia binucao</i> Choisy	1	2	0	0	H
<i>G. brassii</i> C.T.White	3	6	0	0	S
<i>G. cymosa</i> (K.Schum.) I.M.Turner & P.F.Stevens	1	6	0	0	F
<i>G. echinocarpa</i> Thwaites	5	1	0	0	F
<i>G. gummi-gutta</i> (L.) N.Robson var. <i>gummi-gutta</i> (yellow fruit)	5	2	1	0	F
<i>G. hombroniana</i> Pierre	2	5	0	0	H
<i>G. jensenii</i> W.E.Cooper	3	0	0	0	H
<i>G. latissima</i> Miq.	3	6	0	0	H
<i>G. leggeae</i> W.E.Cooper	1	1	0	0	S
<i>G. malaccensis</i> Hook.f.	1	4	0	0	F
<i>G. mestoni</i> F.M.Bailey	5	2	0	0	S
<i>G. nervosa</i> (Miq.) Miq.	0	5	0	0	H
<i>G. porrecta</i> Laness.	1	0	0	0	F
<i>G. prainiana</i> King	1	1	0	0	F
<i>G. russellii</i> W.E.Cooper	3	6	0	0	S
<i>Garcinia</i> sp. (Batudulang, Sumbawa Besar)	5	3	0	0	F
<i>Garcinia</i> sp. (Maluku)	5	2	0	0	F
<i>G. septogarcinia</i> I.M.Turner & L.V.S.Jenn.	5	2	1	1	F
<i>G. tetrandra</i> Pierre	1	1	0	0	F
<i>G. warrenii</i> F.Muell.	3	6	0	0	H
<i>G. zichii</i> W.E.Cooper	4	0	0	0	H

nings, 2021). The condition of the specimen seems inadequate to obtain DNA suitable for Sanger sequencing, however future studies using phylogenomic approaches may have a greater chance of successfully obtaining sequence data.

The pollen characters in this study support Jones' (1980) findings of similarity between *G. septogarcinia* (as *Septogarcinia sumbawaensis*) and some *Garcinia* species. Despite the limited availability of male flowers used in this study, the

pollen of *G. septogarcinia* is most similar to species in Section *Brindonia* (Jones, 1980). However, reticulate ornamentation does not occur only in Section *Brindonia* but also in species of Section *Garcinia*. For instance, *Garcinia* sp. from Batudulang, Sumbawa, which obviously belongs to Section *Garcinia*, has pollen similar to that of *G. septogarcinia*. Pollen ornamentation in *G. septogarcinia* is similar to six other species included in this study, three of them in Section *Brindonia*

Table 3. The pollen ornamentation and aperture of 21 *Garcinia* species.

Species	Ornamentation	Apertures
<i>G. binucao</i>	Scabrate	Tetracolpate
<i>G. brassii</i>	Echinate	Hexacolpate
<i>G. cymosa</i>	Scabrate	Hexacolpate
<i>G. echinocarpa</i>	Pilate	Tricolpate
<i>G. gummi-gutta</i> var. <i>gummi-gutta</i> var. fruit yellow	Pilate	Tetracolpate
<i>G. hombroniana</i>	Verrucate	Penta-hexacolpate
<i>G. jensenii</i>	Echinate	Monocolpate
<i>G. latissimi</i>	Echinate	Hexacolpate
<i>G. leggeae</i>	Scabrate	Tricolpate
<i>G. malaccensis</i>	Scabrate	Tetra-pentacolpate
<i>G. mestonii</i>	Pilate	Tetracolpate
<i>G. nervosa</i>	Psilate	Penta-hexacolpate
<i>G. porrecta</i>	Scabrate	Monocolpate
<i>G. prainiana</i>	Gemmate	Tricolpate
<i>G. russelii</i>	Echinate	Hexacolpate
<i>G. tetrandra</i>	Scabrate	Tricolpate
<i>G. warrenii</i>	Echinate	Hexacolpate
<i>G. zichii</i>	Gemmate	Monocolpate
<i>Garcinia</i> sp. (Batudulang, Sumbawa Besar)	Pilate	Tetraporate
<i>Garcinia</i> sp. 1 (Maluku)	Pilate	Tetracolporate
<i>G. septogarcinia</i>	Pilate	Tetracolpate

(see also Jones, 1980). However, the similarity between pollen characters of *G. septogarcinia* and *Garcinia* sp. (Batudulang, Sumbawa) revealed that pollen characteristics in *Garcinia* might have some exceptions as infrageneric grouping delimitation characters. One of those, *Garcinia* sp.1 (Maluku), was provisionally named *G. cylindrocarpa* by Kostermans in the Type Specimen Collection in the Herbarium Bogoriense but this name has not yet been published. Further studies of pollen in *Garcinia* will likely yield additional morphological characters that support the infrageneric groupings.

SEM is a suitable technique to analyse the pollen that provides detailed images of the outer morphological characters. Despite some anthers having been contaminated with fungi, there was

plentiful pollen. Another challenge was that the pollen from the herbarium specimens, particularly the immature ones, tended to be brittle and easily damaged in the coating process rendering some of the features difficult to observe as has been reported previously (Sari, 2000). In this study, the flowers of *G. septogarcinia* were dried at room temperature from fresh flowers and the pollen was well-coated, and using mature pollen resulted in a positive outcome for pollen analysis using SEM.

Examination of the morphological characters of *G. septogarcinia*, and the ancestral state reconstruction analyses, are consistent with a placement of *Septogarcinia* within *Garcinia*. *Garcinia septogarcinia* is most readily distinguished from other species in having dehiscent, segmented fruit.

Table 4. Characteristics of the green- and red-fruited variants of *G. septogarcinia*.

Character	Variant 1	Variant 2
<i>Leaves</i>		
Leaf blade length (cm)	8.6–9.4	8.5–8.7
Leaf blade width (cm)	6.0–6.4	5.0–5.6
Pedicel length (cm)	2.0–2.3	3.0–3.1
Pedicel colour	green	green with a red flush
<i>Fruit</i>		
Young fruit colour	green	red
Mature fruit colour	yellowish green	red
Fruit shape	subglobular to subconical	subconical
Stigma surface texture	smooth	corrugated

However, segmented indehiscent fruit occurs in some other species of *Garcinia* including in at least three OTU's in the same cluster as *G. septogarcinia*: *G. gummi-gutta* var. *gummi-gutta* (yellow fruited and red fruited forms) and *Garcinia* sp. (Bukit Lawang) (Fig. 12). Other species that have segmented fruit are *G. atroviridis* Griff. ex T.Anderson, *G. cowa* Roxb. ex Choisy and *G. griffithii* T.Anderson which are mainly distributed in SE Asia (Corner, 1952). Among these three species, dehiscent fruits occur only in *G. atroviridis*. Compared to *G. septogarcinia* the fruit of *G. atroviridis* is much bigger (ca. 7.9–10.5 cm diameter; Sari & Sutrisno, 2005), dehisces differently, and is green when young, ripening yellow. In *G. septogarcinia* the fruit dehisces septically from the base toward the top of the fruit (acropetally) and the seeds remain attached to the placenta when the segments fall (Kostermans, 1962), while in *G. atroviridis* the whole fruit drops to the ground when fully ripe causing the fruit to split septically into segments containing the seeds (David Warmington, Cairns pers. comm. 2018). Kostermans remarked that the splitting in *Septogarcinia* was a unique character that differentiated it from other *Garcinia*. Unfortunately, the DNA sample of *G. atroviridis* could not be amplified in this study therefore its relationships remain unknown.

Other morphological characters not analysed in the present study provide further insights into the relationships of *G. septogarcinia*. The yellow, sticky exudate of *G. septogarcinia* appears to be plesiomorphic in *Garcinia*. Sticky latex is a distinct character of the family Clusiaceae, and the latex glands and canals are found in all parts of the fruit (Stevens, 2007). The decussate arrangement of leaves and branches, the presence of two black

dots (glands) at the base of the petiole, the petiole base that clasps the twig, and dioecy are all common characters of this genus (Sari, 2000; Cooper, 2013).

Both male and female flowers of *G. septogarcinia* are sessile, have four small bracts, and four sepals and petals. The sepals are green and in pairs, connected via a short tube. Four petals is the most common flower character in *Garcinia* (Stevens, 2007). Certain sections in *Garcinia* have three or five petals, but flowers of other taxa in the same cluster with *G. septogarcinia* in the phylogenetic tree, *G. bancana*, *G. gummi-gutta* var. *gummi-gutta* (yellow fruit), *G. leggeae*, *G. mestonii* and *G. nigrolineata*, have four sepals and petals (Fig. 13).

The results of the morphological and the molecular analyses indicate that *G. septogarcinia* strongly clusters within *Garcinia* Section *Brindonia*, and that the dehiscent fruit character is autapomorphic for this species. Therefore, the results strongly support the recent placement of *Septogarcinia* in the synonymy of *Garcinia* (Medellín-Zabala & Marinho, 2015).

#### Comments of the status of *G. sumbawensis* Lauterb. versus *G. sumbawaensis* (Kosterm.) Medellín-Zab. & L.Marinho.

In 1923 Lauterbach described *Garcinia sumbawensis* Lauterb. from the same island as *Septogarcinia sumbawaensis* Kosterm. and tentatively placed it in section *Discostigma* (Lauterbach, 1923, p. 26). Nazre (2018) considered *G. sumbawensis* Lauterb. to be conspecific with *G. sumbawaensis* (Kosterm.) Medellín-Zab. & L.Marinho (= *Septogarcinia sumbawaensis*). A comparison of the morphology of the two species based on the



Fig. 11. Comparison of fruits and leaves of *G. septogarcinia* variant 1 and variant 2. A. Fruits of variant 1. B. Fruits of variant 2. C. Polar view of fruits of variant 1 (left) and variant 2 (right). D. Lateral view of fruits of variant 1 (left) and variant 2 (right). E. Leaves of variant 1. F. leaves of variant 2. Photos by R. Sari.



Fig. 12. Fruits of *Garcinia*. A. Young fruit of *G. septogarcinia*. B. Young fruit of *G. gummi-gutta* var. *gummi-gutta* (fruit yellow). C. Mature fruit *G. gummi-gutta* var. *gummi-gutta* (fruit red). D. Young fruit of *Garcinia* sp. (Bukit Lawang). Photos by R. Sari.



Fig. 13. Flowers of *Garcinia*. A. Female flower of *G. septogarcinia*. B & C. Two types of male flowers of *G. septogarcinia*. D. Bract, sepals, and petal of female flower of *G. septogarcinia*. E. Female flower of *G. gummi-gutta* var. *gummi-gutta* (yellow fruit). F. Male flower of *G. mestonii*. G. Male flower of *G. leggeae*. H. Male flower of *G. bancana* and I. Male flower of *G. nigrolineata*. Photos by G. Sankowsky, R. Jensen, R. Sari.

protologues and observations by the first author is presented in Table 5.

*Garcinia sumbawensis* was described as having leaves 8–10 × 3–4 cm, petiole 8–12 mm long, leaf tip 5 mm long (Lauterbach, 1923) whereas *G. sumbawaensis* is described by Kostermans (1962; as *Septogarcinia sumbawaensis*) as having leaves 7–13 × 5–6.5 cm, petiole 1.5–2 cm (15–20 mm), and apex obscurely acuminate. Based on these data the leaves of *G. sumbawensis* are smaller and have significantly shorter petioles with a distinct leaf tip compared with *G. sumbawaensis*.

According to Lauterbach (1923) the male flowers of *G. sumbawensis* are ca. 15 mm, the outer sepals 2 mm, the inner sepals 4 mm, the petals 8 mm long and 5 mm wide in the upper third, the androecium 3.5 mm and the anthers 0.7 mm. Kostermans (1962) stated that the male flower of *G. sumbawaensis* (as *Septogarcinia sumbawaensis*) has a light green calyx, sepals 4, pairwise opposite, persistent, obovate to rotundate, the lower ones 3–4 mm long, attached much lower than the 8 mm long upper ones. To generate comparable data, we examined male flowers on an herbarium

specimen (BO.0120127, Herbarium Bogoriense) collected by Kostermans. The male flowers were observed to be 15 mm in diameter, the outer sepals 2.5 mm long, the inner sepals 4 mm long, the petals 8 mm long and 4.5 mm wide, the androecium 4 mm long and the anthers 1 mm long. Based on field observations the male flower diameter was 18–22 mm, the sepals 3.5–5 mm long, petals 6–7.2 mm long and 2.5–5 mm wide, stamen bundles 6.5 mm in diameter, and flowers fragrant. Female flowers of *G. sumbawensis* were not available for comparison.

The male flowers of *G. sumbawensis* seemed to be close to *G. terpnophylla* Thwaites of Sri Lanka which is considered as a transition to the sections *Mangostana* or *Peltostigma* (Lauterbach, 1923). Section *Mangostana* was recognised by Choisy (1824), Vesque (1894), Pierre (1883) and Engler (1925) and Section *Peltostigma* by the last three (not Choisy). The two sections were merged as Section I *Garcinia* by Jones (1980). This section is marked by having four stamen bundles in the male flower which do not occur in *G. sumbawaensis*. Section *Brindonia* is characterised by numerous

Table 5. Comparison of morphological characters in *Garcinia sumbawaensis* (Kosterm.) Medellín-Zab. & L.Marinho (= *G. septogarcinia*) and *G. sumbawensis* Lauterb. based on the species protologues, examination of specimen BO.0120127 (Herbarium Bogoriense) and field observations.

Character	<i>Garcinia sumbawaensis</i> (Kosterm.) Medellín-Zab. & L.Marinho (= <i>G. septogarcinia</i> )			<i>Garcinia sumbawensis</i> Lauterb.
	Kostemans, 1962	This study - BO.0120127	This study – field observations	Lauterbach, 1923
<i>Leaves</i>				
Leaf length (cm)	7–13	3.35-14	4.75-12.15	8–10
Leaf width (cm)	5–6.5	3.45-7.85	2.55-6.6	3–4
Petiole length (mm)	15–20	14-28	0.55-0.95	8–12
Leaf tip	obscurely acuminate	rotundate, acute, acuminate	rotundate, acute, acuminate	5 mm long
<i>Male flower</i>				
Diameter (mm)	NA	15	18–22	15
Outer sepal length (mm)	3–4	2.5	3.5	2
Inner sepal length (mm)	8	4	5	3
Petal length (mm)	NA	8	6–7.2	8
Petal width (upper third) (mm)	NA	4.5	2.5–5	5
Androecium length (mm)	NA	4	NA	3.5
Anther length (mm)	NA	1	0.5–0.6	0.7

free stamens (Sweeney, 2008). These two anther characters clearly can be differentiated.

Whereas Nazre (2018) considered *G. sumbawensis* and *G. sumbawaensis* to be conspecific, the comparison above indicates that they are distinct, as Turner & Jennings (2021) argued. Indeed, they are treated as such in the Plants of the World Online (POWO, 2023).

From the protologue, it seems that *G. sumbawensis* was found in Sambor, 1,300 m above sea level (Lauterbach, 1923). The name Sambor does not exist today on the island nor do authorised people recognise the name. It may possibly be Tambora, a mountain on Sumbawa Island which reaches a height of up to 4,300 m ([https://en.wikipedia.org/wiki/Mount\\_Tambora](https://en.wikipedia.org/wiki/Mount_Tambora)). The highest peak in Batulanteh forest is 1,200 m above sea level which is lower than the altitude where *G. sumbawensis* was recorded. The precise location of

Sambor remains unresolved, and it would be interesting to find out whether it was collected from the same location where *S. sumbawaensis* grows.

## CONCLUSION

The results of analyses of morphological and molecular data support the transfer of *Septogarcinia* to the synonymy of *Garcinia* (Medellín-Zabala & Marinho, 2015). Further, comparisons of published morphological data and new observations in the herbarium and field indicate that *G. sumbawensis* Lauterb. should be maintained as a species distinct from *G. sumbawaensis* Kosterm. (= *G. septogarcinia*), and revealed the existence of two variants of *G. septogarcinia* distinguished on leaf and fruit characters. Further research is required to determine the appropriate taxonomic status of these two variants.

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## REFERENCES

- CHOISY, I. D. 1824. *Guttiferae*. In: DE CANDOLLE, A. P., *Prodromus Systematis Naturalis Regni Vegetabilis*, Vol. 1. Treuttel et Wurtz, London. Pp. 557–564.
- COOPER, W. E. 2013. A taxonomic revision of *Garcinia* L. (Clusiaceae) in Australia, including four new species from tropical Queensland. *Austrobaileya* 9: 1–29.
- CORNER, E. J. H. 1952. *Wayside Trees of Malaya*. Government Printing Office, Singapore.
- CORNER, E. J. H. 1976. *The Seeds of Dicotyledons*. Cambridge University Press, Cambridge.
- LAUTERBACH, A. 1923. Beiträge zur flora von Papuasien IX. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 58: 1–181.
- ENGLER, A. 1925. *Guttiferae*. In ENGLER, A. & PRANTL, K. A. E. (Eds.) *Natürlichen Pflanzenfamilien*. 2<sup>nd</sup> ed. Vol. 21. Engelmann, Leipzig. Pp. 154–237.
- JONES, S. W. 1980. Morphology and Major Taxonomy of *Garcinia* (Guttiferae). University of Leicester, Leicester [PhD. Thesis].
- KATOH, K., MISAWA, K., KUMA, K. & MIYATA, T. 2002. MAFFT: A novel method for rapid multiple sequence alignment based on fast fourier transform. *Nucleic Acids Research* 30(14): 3059–3066.
- KATOH, K. & STANDLEY, D. M. 2013. MAFFT Multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780.
- KEARSE, M., MOIR, R., WILSON, A., STONES-HAVAS, S., CHEUNG, M., STURROCK, S., BUXTON, S., COOPER, A., MARKOWITZ, S., DURAN, C., THIERER, T., ASHTON, B., MEINTJES, P. & DRUMMOND, A. 2012. Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–9.
- KOSTERMANS, A. J. G. H. 1956. New and critical Malaysian plants IV. *Reinwardtia* 4: 3–5.
- KOSTERMANS, A. J. G. H. 1962. *Septogarcinia* Kostermans, gen. nov. *Reinwardtia* 6: 167–169.
- MADDISON, W. P. & MADDISON, D. R. 2018. Mesquite: a modular system for evolutionary analysis. Available at <https://mesquiteproject.org>.
- MEDELLIN-ZABALA, D. M. & MARINHO, L. C. 2015. *Garcinia sumbawaensis* comb. nova (Clusiaceae) based on *Septogarcinia sumbawaensis*. *Annales Botanici Fennici* 52: 82–83.
- MOORE, P. D., WEBB, J. A. & COLLINSON, M. E. 1991. *Pollen Analysis*. Blackwell Science, Oxford.
- NAZRE, M., CLYDE, M. M., & LATIFF, A. 2007. Phylogenetic relationships of locally cultivated *Garcinia* species with some wild relatives. *Malaysian Applied Biology* 36(1): 31–40.
- NAZRE, M., NEWMAN, M. F., PENNINGTON, R. T. & MIDDLETON, D. J. 2018. Revision of *Garcinia* section *Garcinia* (Clusiaceae). *Phytotaxa* 373(1): 1–52.
- PIERRE, L. 1883. *Flore Forestiere de la Cochinchine*. Vols. 4–6, pl. 65–92. Paris.
- POWO. 2023. *Plants of the World Online*. Facilitated by the Royal Botanic Gardens, Kew. <http://www.plantsoftheworldonline.org/>. (Accessed 26 February 2023).
- RUHFEL, B. R., STEVENS, P. F. & DAVIS, C. C. 2013. Combined morphological and molecular phylogeny of the Clusioid Clade (Malpighiales) and the placement of the ancient rosoid macrofossil *Paleoclusia*. *International Journal of Plant Sciences* 174: 910–936.
- SARI, R. 2000. Review on *Garcinia* (Clusiaceae) Based on Molecular Systematics. James Cook University, Cairns [M.Sc. Thesis].
- SARI, R. & SUTRISNO, 2005. Studi etnobiologi asam gelugur (*Garcinia atroviridis* Griff. ex T.Anders.) sebagai sumber asam hidroksisisitrat di Sumatera Utara. *Proceeding Silaknas*. IPB. Bogor.

- STEVENS, P. F. 2007. Clusiaceae-Guttiferae. In: KUBITZKI, K. (Ed.) *The Families and Genera of Vascular Plants*. Vol. IX. Springer, Berlin. Pp. 48–66.
- SWEENEY, P. 2008. Phylogeny and floral diversity in the genus *Garcinia* (Clusiaceae) and relatives. *International Journal of Plant Sciences* 169(9): 1288–1303.
- TURNER, I. M. & JENNINGS, L. V. S. 2021. A new name for Indonesian *Garcinia* (Clusiaceae) species with dehiscent fruit. *Annales Botanici Fennici* 58: 361–362.
- URBATSCH, L. E., BALDWIN, B. G. & DONOGHUE, M. J. 2000. Phylogeny of the cone-flowers and relatives (Heliantheae: Asteraceae) based on nuclear rDNA Internal Transcribed Spacer (ITS) sequences and chloroplast DNA restriction site data. *Systematic Botany* 25: 539–565.
- VESQUE, J. 1894. *Guttiferae*. Paris: Masson. (DC., Mon. Phan., Vol.8). Pp. 133–140.
- WHITE, T. J., BRUNS, T., LEE, S., TAYLOR, J. 1990. *Amplification and direct sequencing of fungal ribosomal RNA Genes for Phylogenetics*. In INNIS, M. A., GELFAND, D. H., SNINSKY, J. J. & WHITE. T. J. (Eds). *PCR - Protocols and Applications – A Laboratory Guide*. Academic Press, San Diego. Pp. 315–322.

