

Pollen morphology of the genus *Lasianthus* (Rubiaceae) and related taxa from Asia

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Abstract Pollen morphology of 16 Asian species including two subspecies and one variety of the genus *Lasianthus* and five species from five related genera was examined by light microscopy and scanning electron microscopy. *Lasianthus* Jack is eurypalynous. The pollen grains are small to medium in size and spheroidal or subprolate in shape, with a few being prolate. Pollen morphology is remarkably diverse, particularly in aperture and exine ornamentation. The apertures are usually (3–)4–(–5)-zonoaperturate, being porate and pororate. The number of apertures varies from three to five, with the majority of species being 3–4 zonoaperturate. The exine is usually perforate, finely reticulate or coarsely reticulate. Pollen data appear to be morphologically informative and useful for distinguishing among species of *Lasianthus*, and for elucidating the relationships among some species.

Key words *Lasianthus*, pollen morphology, Rubiaceae.

Lasianthus Jack of the family Rubiaceae is a large genus with more than 180 species. It has a pantropical distribution, occurring in Asia, Africa and America, with one species in Australia (Zhu, 2001a). The greatest number of species is found in tropical Asia (Robbrecht, 1988).

The genus *Lasianthus* was first described by Jack in 1823 (Jack, 1823). Most *Lasianthus* species are shrubs, including some small trees. They grow almost exclusively in the understory of primary forests, with occasional records from secondary or seriously disturbed forests or forest edges. The genus is an ecologically important element in tropical forests of Asia (Zhu, 2001a), making up a quantitatively important component of the vegetation.

Hooker (1880) recognized some 52 species from British India, which was the first regional floristic work in Asia. Subsequent regional floristic accounts have been published for the former “Indo-Chine” (Pitard, 1924) and Thailand (Craib, 1934). Later Yamazaki (1964) revised the genus for the Ryukyu Islands and Liu & Chao (1964) treated the Taiwanese species. Deb & Gangopadhyay (1989, 1991) published a revision of the genus for India, and Ridsdale (1998) for Sri Lanka as well as Zhu (2001b) for Thailand. Zhu (1994) revised the Chinese species of the genus, and Lo (1999) treated the genus for *Flora of China*, recognizing 34 species and ten varieties. Zhu (1998, 2002) revised the Chinese species again

and recognized a total of 33 species, four subspecies and three varieties in China.

Wight (1846) attempted the first infrageneric classification of *Lasianthus*, dividing the genus into two groups (i.e., *Bracteosae* and *Nudiflorae*), which were not typified or given a specific rank. Subsequent infrageneric classifications were made by Hooker (1880), Ridley (1923), and Gangopadhyay and Chakrabarty (1992). Hooker’s system, comprising four sections (i.e., *Stipulares*, *Bracteatae*, *Nudiflorae* and *Pedunculatae*), was commonly accepted, despite the absence of exclusive characters distinguishing any of these sections. Deb and Gangopadhyay (1989) removed sect. *Pedunculatae* Hook. f. and treated it in the genus *Litosanthes* Bl., but later Gangopadhyay & Chakrabarty (1992) returned the taxa that had previously been in the sect. *Pedunculatae* from *Litosanthes* back to *Lasianthus* again. Lo (1999) and Zhu (1994, 1998, 2001b) treated the genus without recognizing any infrageneric taxa, and Zhu (2002) treated the genus *Litosanthes* as a synonym of *Lasianthus*.

The current classifications of *Lasianthus* are mainly based on traditional macromorphology. Recent molecular work revealed the phylogenetic relationships of *Lasianthus* and other related genera (Bremer, 1996; Andersson & Rova, 1999; Bremer & Manen, 2000; Piesschaert et al., 2000; Xiao & Zhu, 2007). A group of genera (*Lasianthus*, *Saldinia* and *Trichostachys*) was recognized at tribal level as Lasiantheae Bremer & Manen on a strongly supported branch (Bremer & Manen, 2000), which was supported by further molecular work (Xiao & Zhu, 2007),

and is currently accepted.

Determining infrageneric relationships in *Lasianthus* is extremely difficult because the delimitation of some species is obscure (Zhu, 1994, 2002). In addition, flowers and fruits are small and are often missing from herbarium specimens, leaving taxonomists few distinct diagnostic characters. The majority of the characters used to determine species are quantitative features of the vegetative organs, such as leaves, stipules and bracts. Except for *L. fordii* Hance (Wang et al., 1997), no palynological data is available for this genus. The present study, therefore, aims to examine the major pollen characteristics of the genus and provide additional support to classification treatments of difficult species or section division currently recognized within *Lasianthus*.

1 Material and methods

Pollen of 16 species including two subspecies and one variety of *Lasianthus* and five species of related genera were included in this study, and examined and summarized in Table 1. Specimens were examined from the following herbaria: Xishuangbanna Tropical Botanical Garden (HITBC) and Kunming Institute of Botany, Chinese Academy of Sciences (KUN) (abbreviations according to Holmgren et al., 1990). A list of voucher specimens for pollen samples is given in Appendix I.

For light microscopy (LM), pollen samples were acetolysed (Erdtman, 1960), mounted in glycerol jelly and sealed with paraffin. Measurements of equatorial diameter (E) and polar axis (P) of individual pollen grains were based on 20 grains per sample.

For scanning electron microscopy (SEM), the acetolysed samples were mounted on glass cover slips and attached to aluminium stubs. After sputter coating with gold, pollen grains were examined and photographed under SEM (KYKY-10000B, Science Instrument Company, Beijing) at 15 kV. Descriptive terminology of the pollen follows Punt et al. (1994) and Lens et al. (2000).

2 Results

2.1 General description of *Lasianthus* pollen grains

Pollen grains of *Lasianthus* were generally isopolar, but some showed a slight heteropolarity (e.g., *L. rhinocerotis* Bl.).

The size of pollen grains varied from small to

medium. The most common size had P (a polar axis) = 40–42 μm and E (an equatorial axis) = 37–39 μm . The smallest grains (*L. formosensis* Matsum.) had P = 19.56 μm and E = 15.75 μm . The largest grains (*L. japonicus* Miq.) had P = 53.13 μm and E = 45.38 μm .

Three distinct shape classes were recognized: prolate (P/E: 1.33; Figs. 1, 2), spheroidal (P/E: 1.11; Figs. 4, 5) and subprolate (P/E: 1.17; Figs. 15, 20), of which spheroidal pollen grains were the most common, making up 74% of the specimens investigated. Prolate pollen grains were only found in *L. formosensis*, while subprolate pollen grains were observed in three taxa: *L. chinensis* (Champ.) Benth., *L. attenuatus* Jack, and *L. japonicus* ssp. *longicaudus* C. Y. Wu & H. Zhu. The polar views of the grains were usually circular, e.g. in *L. hookeri* (Fig. 7), triangular, quadrangular or pentangular with convex sides in *L. hainanensis* Merr. (Figs. 11, 12), *L. biermannii* King ex Hook. f. (Fig. 23) and *L. rhinocerotis* (Fig. 26).

Pollen grains were usually zonoaperturate, most of which were pororate. Aperture number varied from three up to five. Approximately 63% of the pollen were 3- and 4-aperturate in the same sample examined. Three-porate pollen was seen in *L. rhinocerotis* ssp. *xishuangbannaensis* H. Zhu & H. Wang. Colporate pollen with long colpi, extending nearly to the two poles, was observed in *L. formosensis*.

The compound apertures consisted of an ectoporus and an endoporus. In *L. rhinocerotis* ssp. *xishuangbannaensis* (Fig. 5), the endoporus and ectoporus were congruent with a circular ecto-aperture present (termed congruent apertures by Lens et al., 2000).

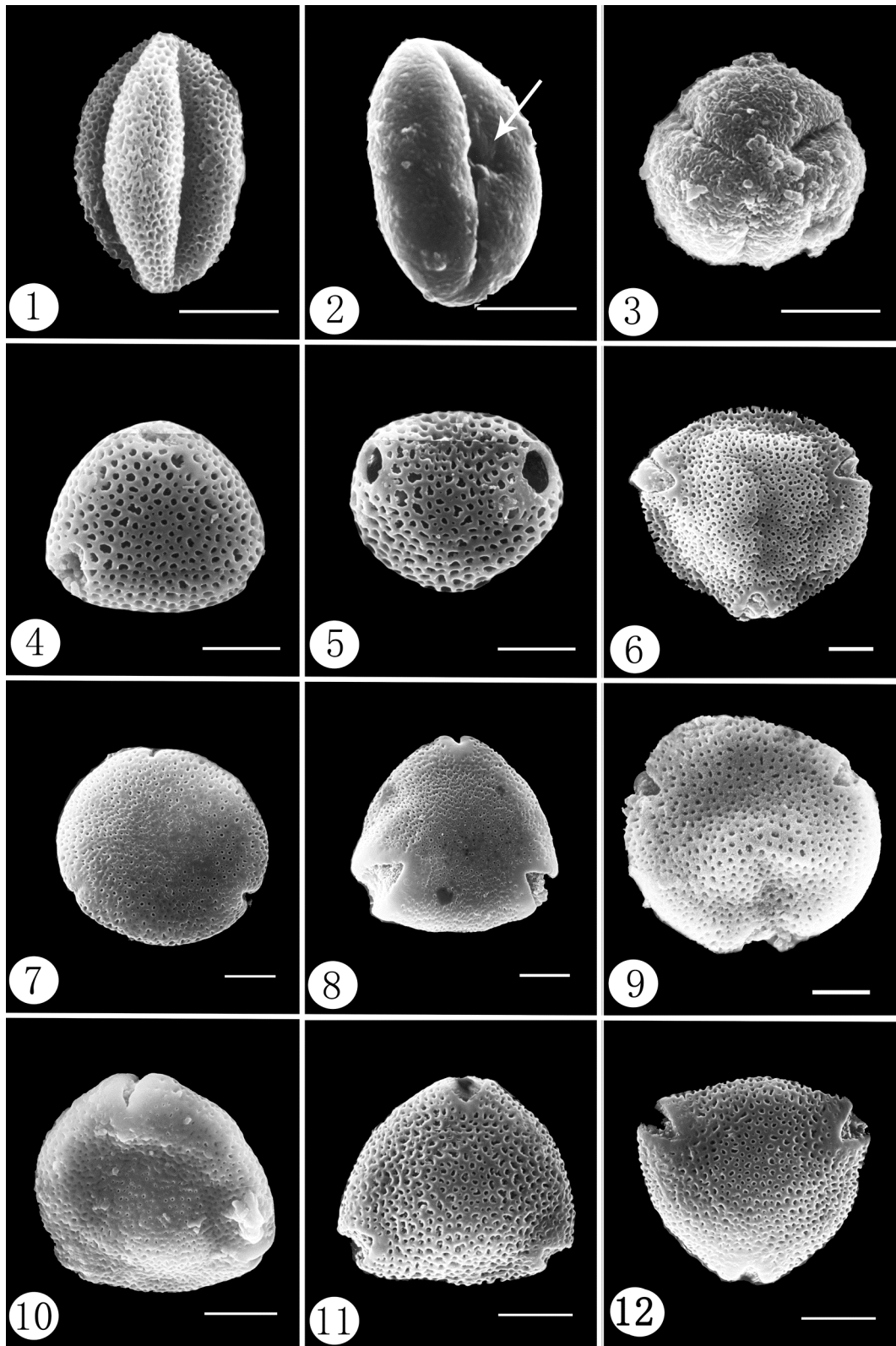
The ectopori were usually elongated and elliptic. The ends of the ectopori were obtuse (Figs. 31, 35), or acute (Figs. 23, 27, 30). Sometimes the margin of the ectoaperture was irregular with sexine bulges (Figs. 28, 31), or was very smooth (Figs. 30, 32). Ectoaperture membranes were often covered with irregular microverrucae (Figs. 27, 28), or could not easily be observed due to closing of ectopori. The endoaperture was irregular in shape, and was difficult to observe under both LM and SEM.

All grains were tectate with either perforate or reticulate tecta. Perforate tecta were present only in *L. attenuatus* (Fig. 36) and *L. japonicus* ssp. *longicaudus* (Fig. 37). Perforations were variable in size and shape and were smaller at the poles. The reticulate sexine was divided into two types according to variations in the diameter of the lumina. They were finely reticulate (lumina less than 1 μm in diameter) and coarsely reticulate (lumina greater than 1 μm in diameter). The

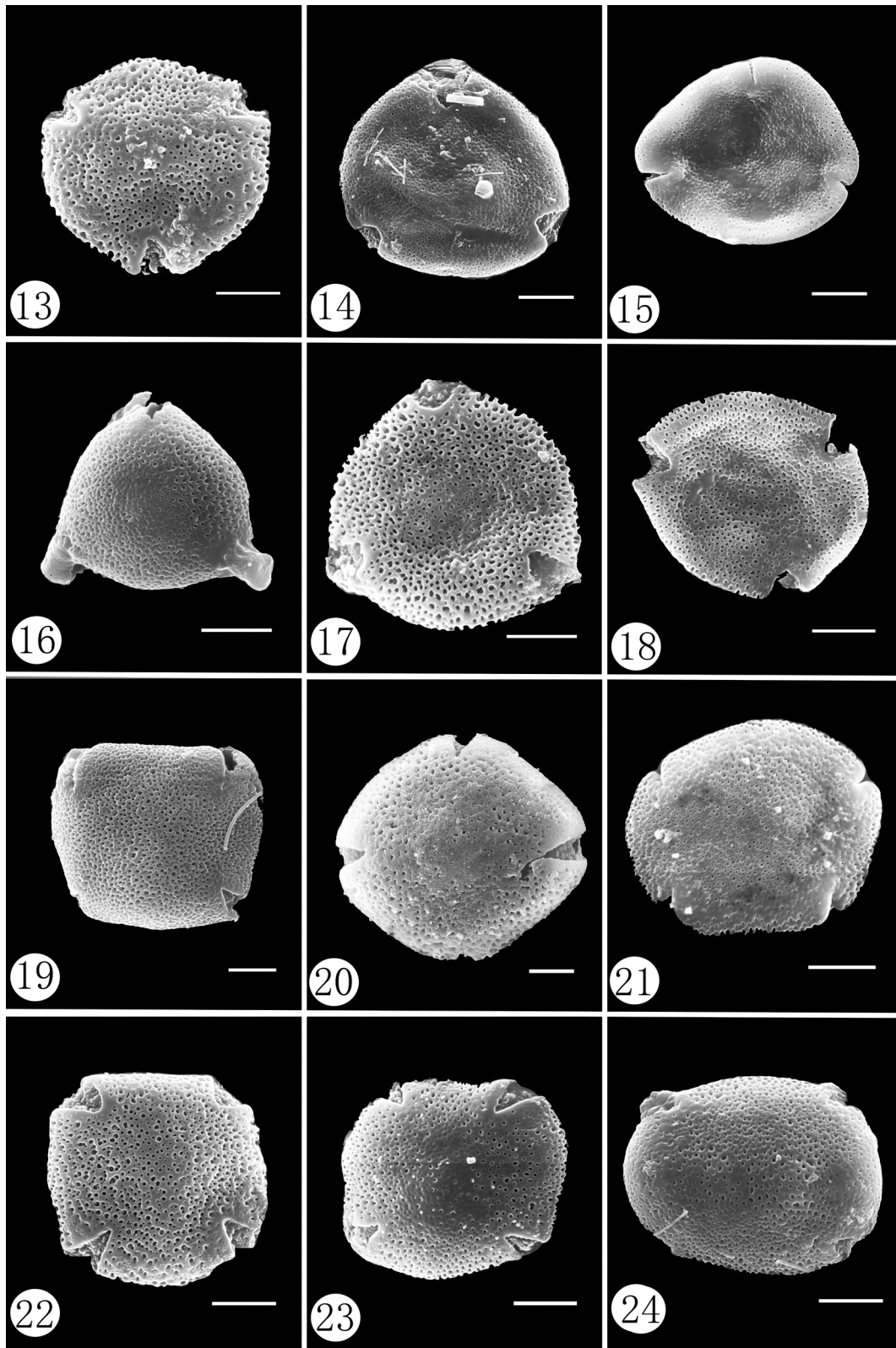
Table 1 Morphological characters of pollen grains of *Lasianthus* and related taxa

Species name	Polar axis (μm)	Equatorial axis (μm)	P/E	Shape	Aperture type	Ectoaperture	End of ectoaperture	Endoaperture	Exine type	Figure
<i>Lasianthus</i> species										
<i>L. atenuatus</i> Jack	40.25(31.75–48.50)	35.00(26.25–45.00)	1.17	SUBP	(3)–4-PORO	OP	O	*	P	10, 21, 36
<i>L. austroyunnanensis</i> H. Zhu	40.06(35.00–50.50)	36.69(22.50–40.50)	1.11	SPH	(3)–4-PORO	*	O	*	Coa-R	24, 45
<i>L. biernanii</i> King ex Hook. f.	40.50(30.00–45.00)	32.38(22.50–40.00)	1.06	SPH	(3)–4-PORO	OP	O, A	IR	Coa-R	23, 33
<i>L. chinensis</i> (Champ.) Benth.	35.38(22.50–47.50)	32.00(17.50–42.50)	1.16	SUBP	(3)–4-PORO	ELP	A	*	Coa-R	9, 20, 31
<i>L. chrysoeureus</i> Miq.	41.56(17.50–50.75)	37.94(12.50–48.25)	1.06	SPH	(3)–4-PORO	OP	O	*	Coa-R	17, 46
<i>L. fordii</i> Hance	31.44(25.00–40.75)	29.69(22.50–31.25)	1.13	SPH	3-PORO	OP	O, A	IR	Fin-R	16, 34
<i>L. formosensis</i> Matsum.	19.56(15.00–22.50)	15.75(12.50–17.50)	1.33	PRO	3-COLP	ELP	A	*	Fin-R	1–3, 38
<i>L. hainanensis</i> Merr.	38.25(35.00–40.50)	32.69(25.50–42.50)	1.14	SPH	3-PORO	ELP	O, A	*	Fin-R	11, 12, 42
<i>L. hookeri</i> C. B. Clarke ex Hook. f.	40.63(18.75–50.00)	38.75(16.25–41.25)	1.17	SUBP	3-PORO	*	*	*	Fin-R	7, 40
<i>L. hookeri</i> var. <i>dunniana</i> H. Zhu	41.44(22.50–52.50)	38.63(19.50–42.50)	1.04	SPH	3-(4)-PORO	ELP	O, A	*	Coa-R	19, 41
<i>L. inodorus</i> Bl.	37.50(29.50–45.25)	33.94(27.50–39.50)	1.12	SPH	(3)–4-PORO	OP	O, A	*	Fin-R	13, 22, 32, 43
<i>L. japonicus</i> Miq.	53.13(31.00–65.00)	45.38(28.50–61.25)	1.08	SPH	(3)–4-PORO	OP	O	*	Coa-R	14, 44
<i>L. japonicus</i> ssp. <i>longicaudus</i> C. Y. Wu & H. Zhu	38.44(25.00–47.50)	31.19(20.00–41.00)	1.17	SUBP	(3)–4-PORO	ELP	A	*	P	15, 37
<i>L. lucidus</i> Bl.	40.50(25.00–50.00)	32.63(20.00–40.00)	1.06	SPH	3-(4)-PORO	ELP	A	IR	Fin-R	25, 47
<i>L. schmidii</i> K. Schum.	43.19(27.50–55.00)	37.00(23.75–48.50)	1.11	SPH	(3)–4-PORO	OP	O	IR	Fin-R	28, 29
<i>L. sikkimensis</i> Hook. f.	41.94(30.50–48.00)	36.44(25.00–43.50)	1.13	SPH	(3)–4(-5)-PORO	OP	O	*	Coa-R	18, 35, 48
<i>L. rhinocerotis</i> Bl.	39.44(25.00–56.25)	33.56(22.50–50.00)	1.04	SPH	(3)–4(-5)-PORO	ELP	A	*	Coa-R	6, 26, 27
<i>L. rhinocerotis</i> ssp. <i>xishuangbannaensis</i> H. Zhu & H. Wang	27.06(22.50–30.75)	23.94(18.75–28.50)	1.11	SPH	3-POR	CP	O	CP	Coa-R	4, 5, 39
<i>L. rigidus</i> Miq.	42.44(25.00–52.50)	38.06(20.50–45.00)	1.12	SPH	(3)–4-PORO	ELP	A	*	Fin-R	8, 30
Related genera										
<i>Brachyotome walllichii</i> Hook. f.	49.06(42.50–62.50)	39.88(27.50–57.50)	1.13	SPH	(3)–4-PORO	ELP	A	*	Fin-R	49, 50
<i>Psychotria henryi</i> Lévl.	51.75(23.75–67.50)	45.19(20.00–62.50)	1.10	SPH	3-PORO	OP	O	RECP	Coa-R	52, 53
<i>Prismatomeria</i> sp.	42.25(37.50–47.50)	37.94(32.50–42.50)	1.06	SPH	(3)–4(-5)-PORO	ELP	A	RECP	Coa-R	55, 56, 57
<i>Saprosma ternatum</i> Hook. f.	47.13(32.50–53.75)	40.19(27.50–47.50)	1.17	SUBP	(3)–4(-5)-PORO	OP	O, A	*	Fin-R	51, 54
<i>Urophyllum chinensis</i> Merr. & Chun	22.50(20.00–25.00)	19.50(15.00–23.75)	1.20	SUBP	3-COLP	ELP	O	IR	P	58, 59, 60

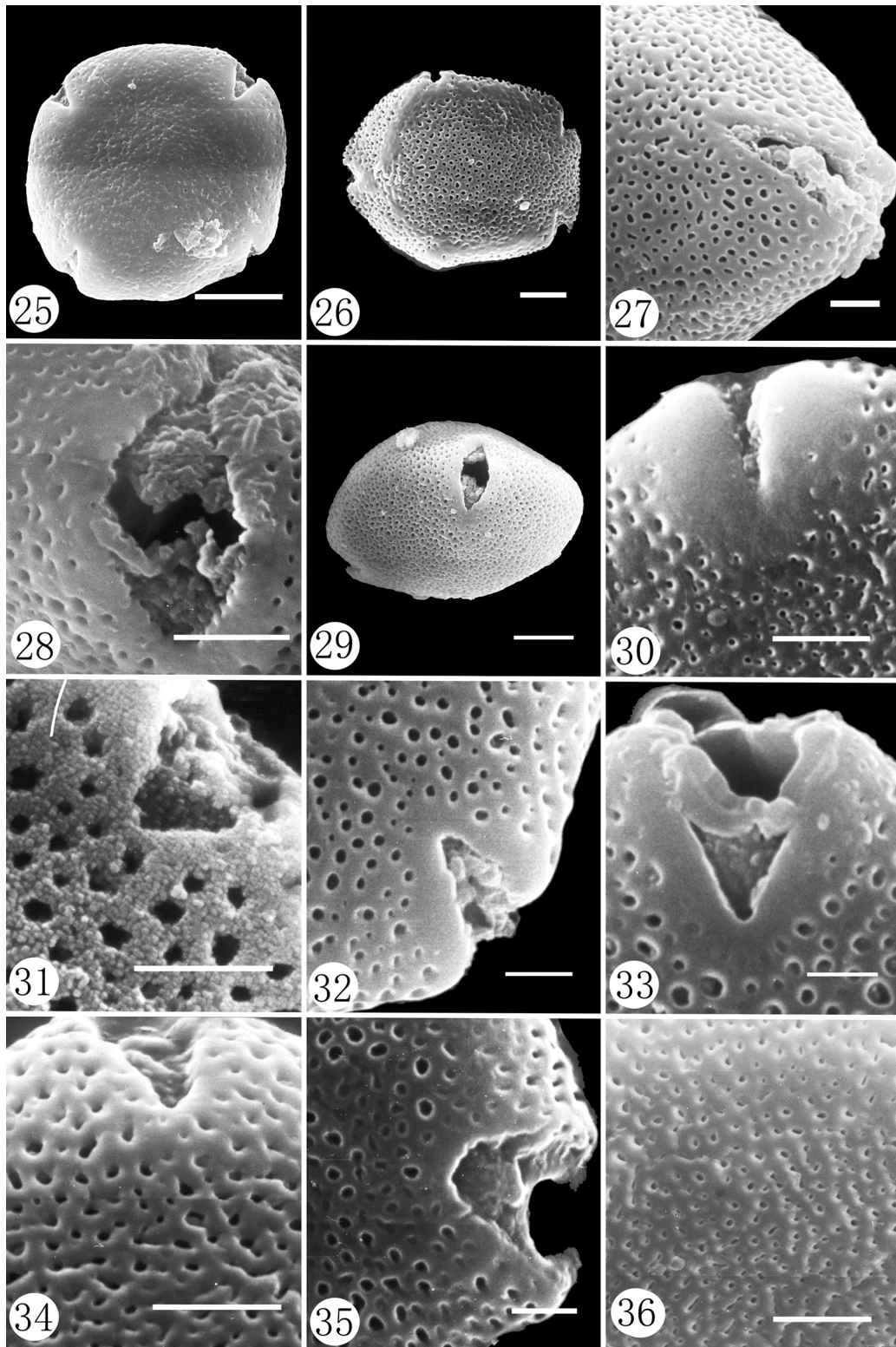
A, acute; Coa-R, coarsely reticulate; COLP, colporate; CP, circular porus; ELP, elongated porus; Fin-R, finely reticulate; IR, irregular; O, obtuse; OP, oval porus; P, perforate; POR, zonoporate; PRO, zonoporate; PRO, prolate; RECP, rectangular porus; SPH, spheroidal; SUBP, subprolate; *, present but morphological features could not be seen clearly.



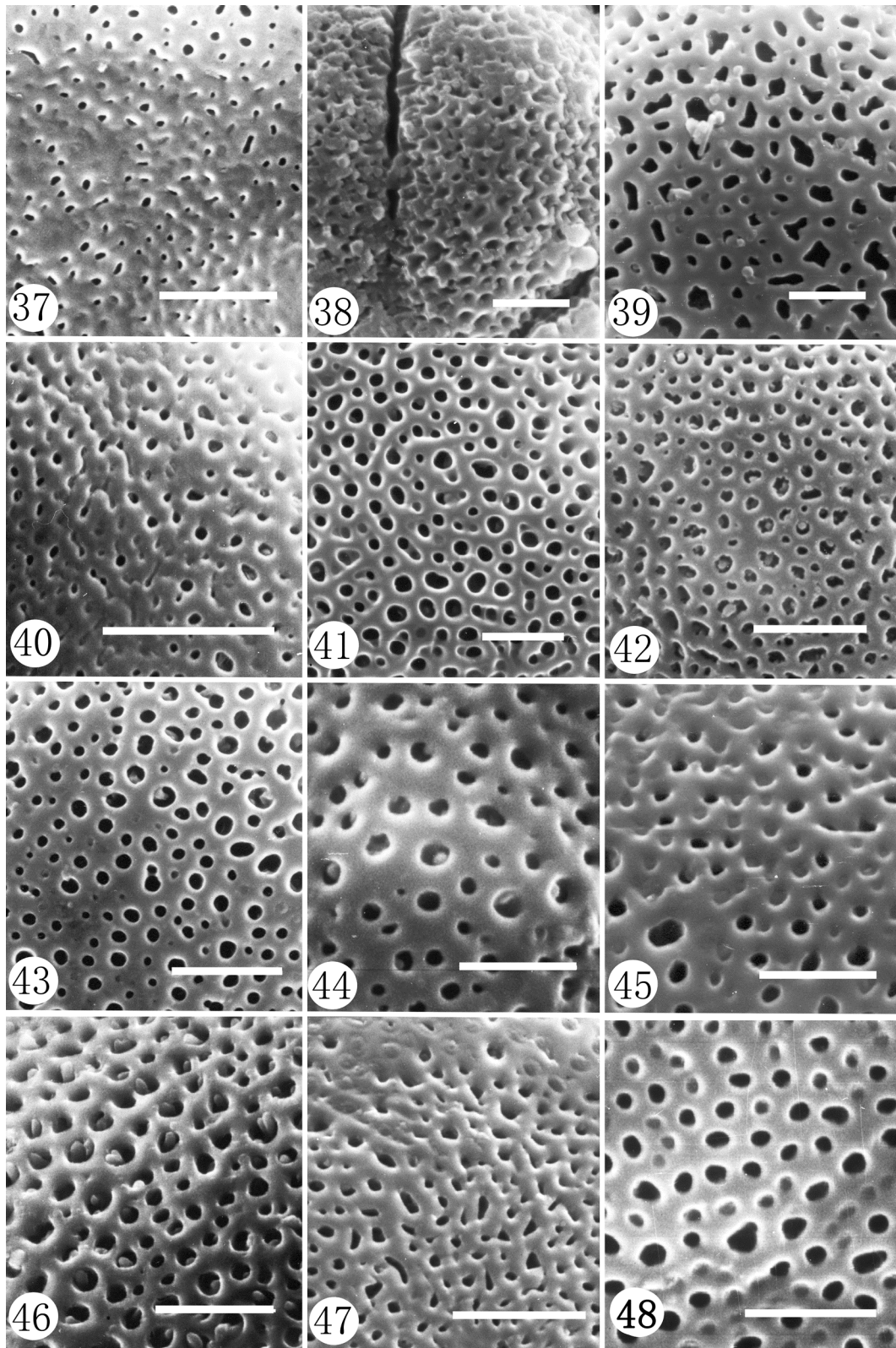
Figs. 1–12. SEM of *Lasianthus* pollen. 1–3. *L. formosensis*. 1. Equatorial view. 2. Equatorial view indicating 3-zonocolporate aperture (arrow). 3. Polar view. 4, 5. *L. rhinocerotis* ssp. *xishuangbannaensis*. 4. Polar view. 5. Equatorial view with 3-zonopororate aperture. 6–12. Polar view and 3-zonopororate aperture. 6. *L. rhinocerotis*. 7. *L. hookeri*. 8. *L. rigidus*. 9. *L. chinensis*. 10. *L. attenuatus*. 11, 12. *L. hainanensis*. Scale bars = 10 μ m.



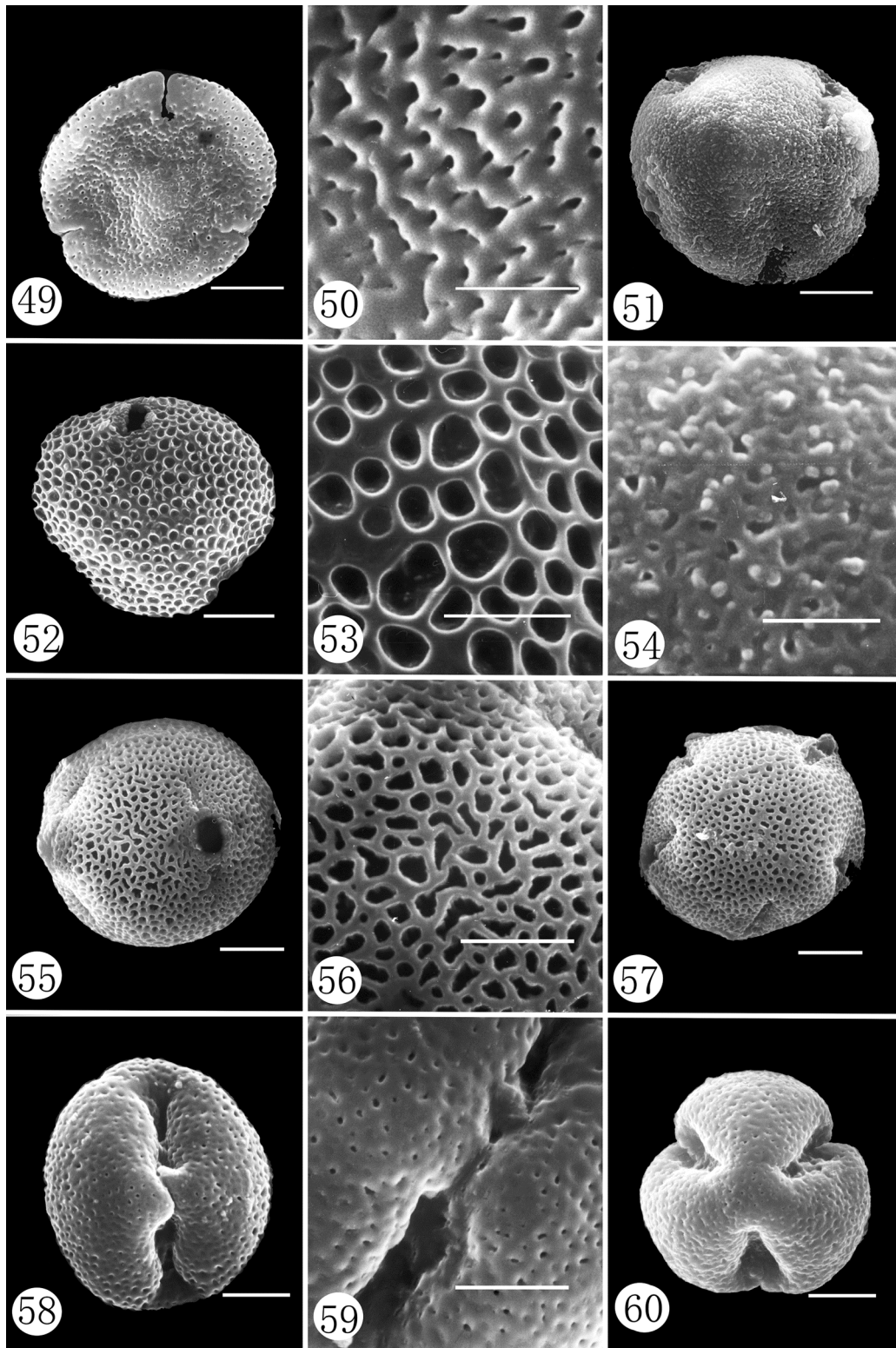
Figs. 13–24. SEM of *Lasianthus* pollen. 13–18. Polar view and 3-zonopororate aperture. 13. *L. inodorus*. 14. *L. japonicus*. 15. *L. japonicus* ssp. *longicaudus*. 16. *L. fordii*. 17. *L. chrysoneurus*. 18. *L. sikkimensis*. 19–24. Polar view and 4-zonopororate aperture. 19. *L. hookeri* var. *dunniana*. 20. *L. chinensis*. 21. *L. attenuatus*. 22. *L. inodorus*. 23. *L. biermannii*. 24. *L. austroyunnanensis*. Scale bars = 10 μ m.



Figs. 25–36. SEM of *Lasianthus* pollen. 25. *L. lucidus*, polar view and 4-zonopororate aperture. 26, 27. *L. rhinocerotis*. 26. Polar view with 5-zonopororate aperture. 27. Same under higher magnification, showing mesocolpium. 28, 29. *L. schmidtii*. 28. Higher magnification of the mesocolpium. 29. Equatorial view. 30–35. Higher magnification of the mesocolpium. 30. *L. rigidus*. 31. *L. chinensis*. 32. *L. inodorus*. 33. *L. biermannii*. 34. *L. fordii*. 35. *L. sikkimensis*. 36. *L. attenuatus*, higher magnification of the exine sculpture. Scale bars = 10 μm for whole pollen grains; =5 μm for details of the exine sculpturing.



Figs. 37–48. SEM of *Lasianthus* pollen. Features of exine ornamentation. 37. *L. japonicus* ssp. *longicaudus*, higher magnification of the exine sculpturing. 38. *L. formosensis*. 39. *L. rhinocerotis* ssp. *xishuangbannaensis*. 40. *L. hookeri*. 41. *L. hookeri* var. *dunniana*. 42. *L. hainanensis*. 43. *L. inodorus*. 44. *L. japonicus*. 45. *L. austroyunnanensis*. 46. *L. chrysoeurus*. 47. *L. lucidus*. 48. *L. sikkimensis*. Scale bars = 5 μ m.



Figs. 49–60. SEM pollen morphology of other five related genera. **49, 50.** *Brachytome wallichii*. **49.** Polar view with 3-zonopororate aperture. **50.** Finely reticulate with sexine. **51, 54.** *Saprosma ternatum*. **51.** Polar view with 5-zonopororate aperture. **54.** Finely reticulate with sexine. **52, 53.** *Psychotria henryi*. **52.** Polar view with 3-zonopororate aperture. **53.** Coarsely reticulate with sexine. **55–57.** *Prismatomeria* sp. **55, 57.** Polar view with (3–)4–(–)5-zonopororate aperture. **56.** Coarsely reticulate with sexine. **58–60.** *Urophyllum chinensis*. **58.** Equatorial outline view. **59.** Sunken colpi. **60.** Polar view with 3-zonopororate aperture. Scale bars = 10 μ m for whole pollen grains; =5 μ m for details of the exine sculpturing.

lumina were commonly elliptical, circular, or angular in shape (Figs. 39, 41, 44, 48). Some species exhibited granules on the inside of the lumina, such as *L. hainanensis* (Fig. 42), *L. japonicus* (Fig. 44) and *L. chrysonurus* (Fig. 46). The muri usually lacked suprategal ornamentation, except in *L. chinensis*, which had dense microverrucae (Fig. 31).

2.2 Pollen description of the related genera

2.2.1 *Brachytome wallichii* Pollen grains were medium (P: 49.06 μm ×E: 39.88 μm) in size and spheroidal (P/E: 1.13) in shape. Apertures were 3- or 4-colporate. The polar outline view was circular, with colpi narrow and slightly sunken (Fig. 49). The ectoaperture was usually elongated. The ends of the ectopori were acute. The sexine was finely reticulate (Fig. 50), with the muri protruding.

2.2.2 *Saprosma ternatum* Pollen grains were medium (P: 47.13 μm ×E: 40.19 μm) in size and subprolate (P/E: 1.17) in shape. Apertures were (3-)4-(5)-pororate. The polar outline view was circular with the colpi wide and short (Fig. 51). The ends of the ectopori were acute or obtuse. The sexine was finely reticulate (Fig. 54), with some micro-granules on the muri.

2.2.3 *Psychotria henryi* Pollen grains were large (P: 51.75 μm ×E: 45.19 μm) in size and spheroidal (P/E: 1.10) in shape. Apertures were 3-porate. The polar outline view was circular (Fig. 52). The ends of the ectopori were obtuse. The sexine was coarsely reticulate (Fig. 53), and the lumina were very large (mean 1–2.5 μm).

2.2.4 *Prismatomeria* sp. Pollen grains were medium (P: 42.25 μm ×E: 37.94 μm) in size and spheroidal (P/E: 1.10) in shape. Apertures were (3-)4-(5)-pororate. The polar outline view was circular (Figs. 55, 57). The ectoaperture was often elongated. The ends of the ectopori were acute. The sexine was coarsely reticulate (Fig. 56), with the irregular lumina in shape and size.

2.2.5 *Urophyllum chinensis* Pollen grains were medium (P: 22.50 μm ×E: 19.50 μm) in size and subprolate (P/E: 1.20) in shape. Apertures were 3-colporate. The polar outline view was circular to almost triangular (Fig. 60), with the colpi sunken (Fig. 59). The equatorial outline view was elliptic with comparatively acute apices (Fig. 58). Ectopori were very long, sometimes narrower at the center (Fig. 59). The ectocolpus margins were irregular. The ends of the ectopori were obtuse. The sexine was perforate, with the lumina irregular in shape and size, and the perforations present in the amb and near ectocolpus margins.

3 Conclusions and Discussion

Pollen grains showed a considerable morphological and structural polymorphism within the genus *Lasianthus* and among related genera. Pororate 3–4-zonoaperturate pollen grains, the most dominant type in *Lasianthus*, have been reported otherwise in the Rubiaceae. They have previously been seen in Gardenieae-Gardeniinae (Persson, 1993), Isertiaeae (Huysmans et al., 1993), Coptosapelteae (Huysmans, 1998) and Vanguerieae (Havard & Verdcourt, 1987). In addition, *L. formosensis* and *L. rhinocerotis* ssp. *xishuangbannaensis* had unique 3-colporate and 3-porate pollen grains, respectively.

There were three general types of exine ornamentation in the genus *Lasianthus*: perforate, finely reticulate and coarsely reticulate. Perforate pollen grains were less frequent, and seen only in *L. attenuatus* and *L. japonicus* ssp. *longicaudus*.

The pollen morphological characteristics of the five related taxa examined here were similar to those of *Lasianthus*, providing little diagnostic characteristics for distinguishing *Lasianthus* from these related genera.

However, the pollen studies did provide distinctive characters for some taxonomically difficult species. *Lasianthus formosensis* was previously distinguished from *L. fordii* only by the indumentum, which is usually with dense and much spreading tomentose hairs in the former and with thin or sparse and appressed pubescence in the latter. Indumentum, however, often found to be environmentally variable. The former species has even been reduced to a puberulent variety of the latter (Yamazaki, 1964). Zhu (2002) treated them as two separate species based upon differences in the length of lanceolate calyx lobes and the dense or sparse indumentum. Our palynological results indicate that *L. formosensis* has the less common 3-colporate pollen grains, which is conspicuously different from *L. fordii*, supporting the separation of the two species. Aperture or exine types can also be quite different in infra-specific taxa. For instance, *L. rhinocerotis* ssp. *rhinocerotis* has more diversified pororate pollen grains (3, 4 to 5-aperturate), whereas ssp. *xishuangbannaensis* has only 3-porate apertures. *Lasianthus japonicus* ssp. *japonicus* has common reticulate pollen tecta, while the ssp. *longicaudus* has uncommon perforate pollen tecta. Additionally, *L. chinensis* has unique pollen grains with dense microverrucae on the muri. Our results suggest that more detailed palynological work could be useful in resolving taxonomic issues within the genus *Lasianthus*.

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References

- Andersson L, Rova J. 1999. The *rps* 16 intron and the phylogeny of the Rubioideae (Rubiaceae). *Plant Systematics and Evolution* 214: 161–186.
- Bremer B. 1996. Phylogenetic studies within Rubiaceae and relationships to other families based on molecular data. *Opera Botanica* 7: 33–50.
- Bremer B, Manen JF. 2000. Phylogeny and classification of the subfamily Rubioideae (Rubiaceae). *Plant Systematics and Evolution* 225: 43–72.
- Craib WG. 1934. *Flora of Siamensis Enumeratio*. Bangkok: The Bangkok Times Press. 2 (1): 207–220.
- Deb DB, Gangopadhyay M. 1989. Review of the genus *Lasianthus* Jack (Rubiaceae). *Candollea* 44: 200–223.
- Deb DB, Gangopadhyay M. 1991. Taxonomic study of the genus *Lasianthus* Jack (Rubiaceae) in India. *Journal of Economic and Taxonomic Botany* 15: 265–308.
- Erdtman G. 1960. The acetolysis method: A revised description. *Svensk Totanisk Tidskrift* 54: 561–564.
- Gangopadhyay M, Chakrabarty T. 1992. A note on the status of *Lithosanthes* Bl. (Rubiaceae). *Journal of Economic and Taxonomic Botany* 16: 337–338.
- Havard A, Verdcourt B. 1987. A pollen survey of *Tapiphyllum* (Rubiaceae-Vanguerieae). *Kew Bulletin* 42: 605–609.
- Holmgren PK, Holmgren NH, Barnett LC. 1990. *Index Herbariorum Part I: The Herbaria of the World*. 8th ed. New York: New York Botanical Garden's Virtual Herbarium.
- Hooker JD. 1880. *Flora of British India*. London: Reeve L, Co Ltd. 3: 178–192.
- Huysmans S. 1998. Palynology of the Cinchonoideae (Rubiaceae): Morphology and development of pollen and orbicules. Ph.D. Dissertation. Leuven (Louvain): Botanical Institute, K. U. Leuven.
- Huysmans S, Robbrecht E, Smets E. 1993. Endoaperture morphology in the Coptosapelteae (Rubiaceae–Cinchonoideae). In: Furnkranz D, Schantl H eds. 11. Symposium Morphologie, Anatomie, Systematik, Kurzfassungen. Salzburg: University of Salzburg.
- Jack W. 1823. Account of the *Lansium* and some other genera of Malayan plants. *Transactions of the Linnean Society of London* 14: 125–126.
- Lens F, Jansen S, Huysmans S, Robbrecht E, Smets E. 2000. Pollen morphological variation in Vanguerieae (Ixoroideae Rubiaceae). *Grana* 39 (2–3): 90–102.
- Liu T-S, Chao J-M. 1964. Revision of the Taiwan Species of *Lasianthus* (Rubiaceae). *Taiwania* 10: 118–149.
- Lo HS (罗献瑞). 1999. *Lasianthus* Jack. In: *Flora Reipublicae Popularis Sinicae*. Beijing: Science Press. 71 (2): 70–106.
- Persson C. 1993. Pollen morphology of the Gardenieae–Gardeniinae (Rubiaceae). *Nordic Journal of Botany* 13: 561–582.
- Piesschaert F, Anderson L, Jansen S, Dessein S, Robbrecht E, Smets E. 2000. Searching for the taxonomic position of the African genus *Colletoeccema* (Rubiaceae): morphology and anatomy compared to an *rps* 16-intron analysis of Rubioideae. *Canadian Journal of Botany* 78: 288–304.
- Pitard J. 1924. *Lasianthus* Jack. In: Lecomte H eds. *Flore Generale de Indo-China*. Paris: Masson, Cie Editeurs. 3: 371–399.
- Punt W, Blackmore S, Nilsson S, Le Thomas A. 1994. Glossary of pollen and spore terminology. LPP contribution No. 1. Utrecht: Laboratory of Palaeobotany and Palaeobotany Foundation, University of Utrecht.
- Ridley HN. 1923. *Lasianthus* Jack in the Flora of the Malay Peninsula. London: Reeve L, Co Ltd. 2: 149–169.
- Ridsdale CE. 1998. Rubiaceae. In: Dassanayake MD, Clayton WD eds. *A revised handbook to the flora of Ceylon*. Rotterdam: Balkema Publishers. 12: 309–320.
- Robbrecht E. 1988. Tropical woody Rubiaceae. *Opera Botanica Belgica* 1: 132.
- Wang F-X, Qian N-F, Zhang Y-L. 1997. Pollen flora of China. 2nd ed. Beijing: Science Press. 355–369.
- Wight R. 1846. Notes on Indian Botany. *The Calcutta Journal of Natural History* 6: 494–518.
- Xiao L-Q, Zhu H. 2007. Paraphyly and phylogenetic relationship in *Lasianthus* (Rubiaceae) inferred from chloroplast *rps16* data. *Botanical Studies* 48: 227–232.
- Yamazaki T. 1964. Note on *Lasianthus* in Ryukyu. *Journal of Japanese Botany* 39: 348–352.
- Zhu H (朱华). 1994. A taxonomic study on the genus *Lasianthus* Jack in China. *Acta Phytotaxonomica Sinica (植物分类学报)* 32: 49–81.
- Zhu H (朱华). 1998. Notes on the genus *Lasianthus* Jack (Rubiaceae) from Asia. *Acta Botanica Yunnanica (云南植物研究)* 20: 149–159.
- Zhu H. 2001a. New plants of *Lasianthus* Jack (Rubiaceae) from Kinabalu, Borneo and its biogeographical implication. *Blumea* 46: 447–455.
- Zhu H (朱华). 2001b. A taxonomic revision of the genus *Lasianthus* Jack (Rubiaceae) from Thailand. *Acta Phytotaxonomica Sinica (植物分类学报)* 39: 116–150.
- Zhu H. 2002. A revision of the genus *Lasianthus* Jack (Rubiaceae) from China. *Systematics and Geography of Plants* 72: 63–110.

Appendix I Voucher information for taxa used in this study

- Lasianthus attenuatus* Jack, Mengla, Yunnan (云南勐腊), H. Zhu (朱华) 2059 (HITBC).
L. austroyunnanensis H. Zhu, Funing, Yunnan (云南富宁), Q. A. Wu (武全安) 9556 (KUN).
L. biermannii King ex Hook. f., Yongde, Yunnan (云南永德), T. P. Zhu (朱太平) 0079 (KUN).
L. chinensis (Champ.) Benth., Mengla, Yunnan (云南勐腊), G. D. Tao et al. (陶国达等) 0114 (HITBC).
L. chryseus Miq., Cangyuan, Yunnan (云南沧源), G. D. Tao & Y. W. Li (陶国达, 李锡文) 40052 (HITBC).
L. fordii Hance, Lingshui, Hainan (海南陵水), L. Deng (邓良) 3011 (KUN).
L. formosensis Matsum., Mengla, Yunnan (云南勐腊), H. Zhu (朱华) 2522 (HITBC).
L. hookeri C. B. Clarke ex Hook. f., Mengla, Yunnan (云南勐腊), H. Zhu (朱华) *s.n.* (HITBC).
L. hookeri var. *dunniana* H. Zhu, Mengla, Yunnan (云南勐腊), S. J. Pei (裴盛基) 59-9361 (HITBC).
L. inodorus Bl., Kinabalu, Borneo, H. Zhu (朱华) *s.n.* (HITBC).
L. japonicus Miq., Rongjiang, Guizhou (贵州榕江), Qiannan Team (黔南队) 2933 (KUN).
L. japonicus ssp. *longicaudus* C. Y. Wu & H. Zhu, Guangnan, Yunnan (云南广南), C. W. Wang (王启无) 88109 (KUN).
L. japonicus var. *lancilimbus* C. Y. Wu & H. Zhu, Yangshan, Guangdong (广东阳山), L. Deng (邓良) 1272 (KUN).
L. lucidus Bl., Jinghong, Yunnan (云南景洪), H. Zhu (朱华) 2508 (HITBC).
L. rhinocerotis Bl., Kinabalu, Borneo, H. Zhu (朱华) *s.n.* (HITBC).
L. rhinocerotis ssp. *xishuangbannaensis* H. Zhu, Jinghong, Yunnan (云南景洪), H. Zhu (朱华) 981101 (HITBC).
L. rigidus Miq., Cangyuan, Yunnan (云南沧源), G. D. Tao & X. W. Li (陶国达, 李锡文) 40023 (KUN).
L. schmidtii K. Schum., Yunnan (云南), C. W. Wang & Y. B. Zhang (王启无, 张音波) 86022 (KUN).
L. sikkimensis Hook. f., Mengla, Yunnan (云南勐腊), H. Zhu (朱华) 2180 (HITBC).
L. verticillatus (Lour.) Merr., Mengla, Yunnan (云南勐腊), H. Zhu (朱华) 1315 (HITBC).
L. hainanensis Merr. = *Saprosma merrillii* Lo, Hainan (海南), S. K. Lau (刘心祈) 26545 (KUN).
Brachytome wallichii Hook. f., Lüchun, Yunnan (云南绿春), Lüchun Team (绿春队) 838 (KUN).
Saprosma ternatum Hook. f., Xishuangbanna, Yunnan (云南西双版纳), Anonymous 8234 (KUN).
Prismatomeria sp., Yunnan (云南), Anonymous 623 (HITBC).
Psychotria henryi Lévl., Mengla, Yunnan (云南勐腊), G. D. Tao et al. (陶国达等) 0268 (HITBC).
Urophyllum chinensis Merr. & Chun., Thailand, Sino-Thai Botanic Exp. (中国-泰国植物调查队) 1726 (KUN).

亚洲茜草科粗叶木属及其相关属植物花粉形态研究

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摘要 利用光学显微镜和扫描电镜研究了茜草科粗叶木属*Lasianthus* 16种2亚种、1变种及相关的5属5种的花粉形态。粗叶木属的花粉属于广孢型, 单粒。一般中等大小, 绝大多数为圆球形, 少数为近长球形或长球形。花粉形态特征, 特别是在萌发孔和外壁纹饰上表现出多样化。根据孔沟的数目或是否具有内孔, 可以将萌发孔分为(3-)4-(5)孔沟和3孔。在所观察的这些种中, 萌发孔以3-4孔沟为主要类型, 比例为62.4%。外壁纹饰可分为细网状、粗网状和穴状。有部分种的花粉极面有穴状纹饰, 其余均为网状纹饰。网眼一般椭圆形、近圆形、三角形或者不规则形。少数外壁纹饰网脊上有颗粒状雕纹或模糊的颗粒, 网脊轮廓线呈波浪形, 一般凸出且平滑。大部分种的花粉具有沟膜, 沟膜上具有瘤状突起或小颗粒状, 沟边缘一般较平滑, 或粗糙, 有的种具有沟桥。

关键词 粗叶木属; 花粉形态; 茜草科