BLUMEA 48: 515–522
Published on 28 November 2003 doi: 10.3767/000651903X489519

POLLEN OF SOUTHEAST ASIAN ALCHORNEA (EUPHORBIACEAE), WITH AN OVERVIEW OF THE POLLEN FOSSIL RECORD

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SUMMARY

In order to evaluate pollen morphological descriptions of *Alchornea* in the literature, which are almost completely based on African and American species, the pollen of eight Southeast Asian species of *Alchornea* was investigated, using light and scanning electron microscopy. Very little variation appeared to be present in the Asian material. Slightly deviating from the scabrate ornamentation type are *A. kelungensis* (psilate) and *A. rugosa* (striate-rugulate). The scabrate type is also found in *A. castaneaefolia* (Brazil), *A. hirtella* (Liberia) and *A. obovata* (Colombia). The operculate *Alchornea* pollen type, which can be easily recognised using light microscopy, seems to represent a diagnostic character for the tribe Alchornieae (pollen of *Bossera* unknown). Its characteristic appearance resulted in a relatively extensive fossil record. The earliest records are from the Middle Eocene of Venezuela and Nigeria, while records for Australia and Borneo date from the mid-Tertiary and the Neogene (Miocene–Pliocene), respectively. These records suggest that the tribe Alchornieae has an African–American Gondwanic origin, and reached its pantropic distribution at least in the mid-Tertiary.

Key words: *Alchornea*, Euphorbiaceae, fossil record, pollen, SE Asia.

INTRODUCTION

The Alchornieae are a tribe of nine genera (c. 96 spp.), *Alchornea*, *Aparisthmium*, *Bocquillonia*, *Bossera*, *Caelebogyne*, *Conceveiba*, *Gavarretia*, *Orfilea* and *Polyandra*, belonging to subfamily Acalyphoideae of the Euphorbiaceae (Radcliffe-Smith, 2001). Of these genera, *Alchornea* is the largest and most widespread, containing c. 60 species and having a pantropical distribution. The other genera are much smaller, containing from 1 to 14 species. They are restricted to America, Madagascar, Australia or New Caledonia.

Pollen morphologically, subfamily Acalyphoideae is the most heterogeneous of the five subfamilies of the Euphorbiaceae (Punt, 1987; Takahashi et al., 1995, 2000; Nowicke et al., 1998, 1999; Nowicke & Takahashi, 2002). Pollen of tribe Alchornieae was described by Punt (1962: 7 genera, 14 species, illustrated with drawings), Taka-

1) Dr. Lolita J. Bulalacao was the head of the Palynology Unit of the Botany Division of the National Museum, Manila, Philippines, and studied *Alchornea* pollen at the Nationaal Herbarium Nederland, Leiden during the summer of 2001, when she was already suffering from a severe illness. She died on 16 October 2002. The second author took it on him to complete the study, remembering a brave woman.

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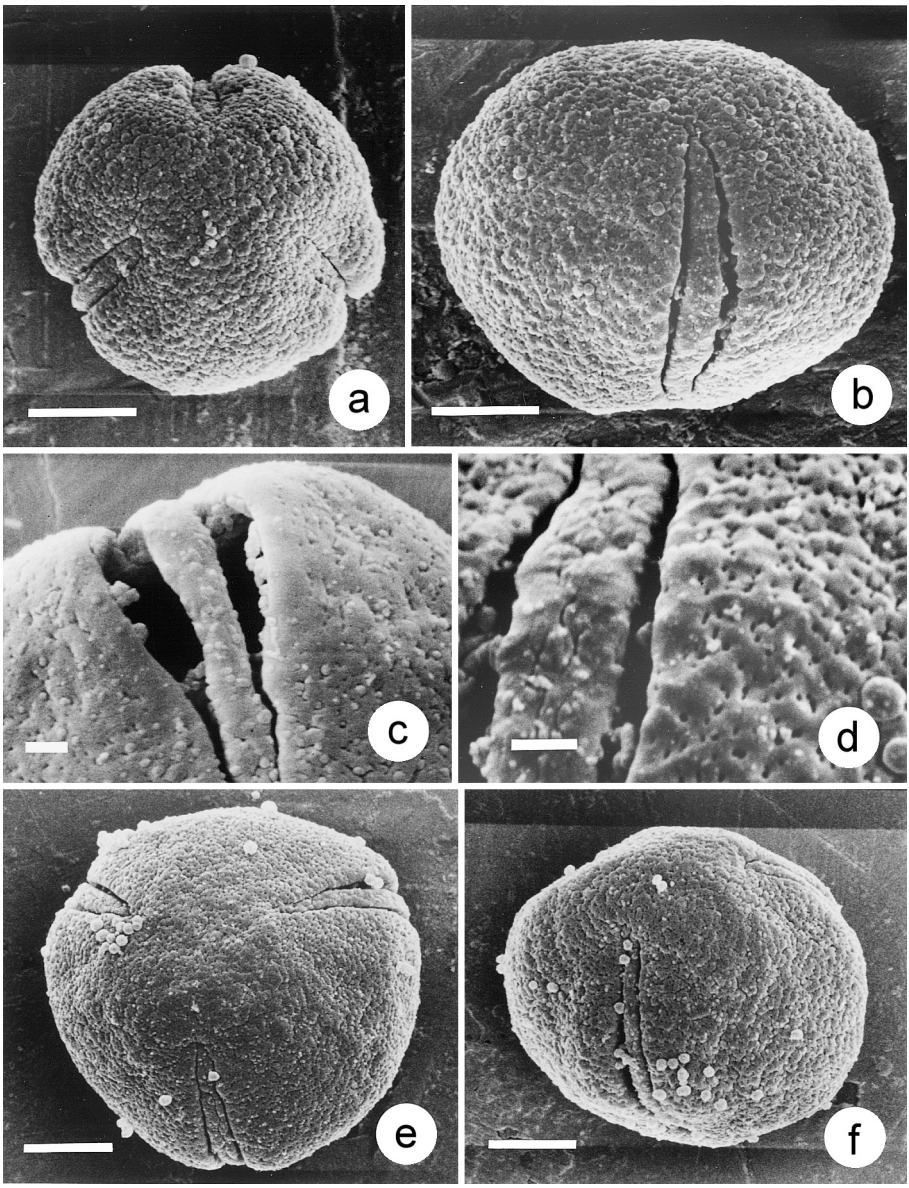

Fig.1. Scanning electron micrographs of *Alchornea* pollen. — a–c. *A. borneensis* Pax & K. Hoffm. a. Polar view; b. equatorial view; c. detail showing ornamentation, operculum and two Ubisch bodies (at the right). — d. *A. kelungensis* Hayata, detail showing ornamentation and operculum. — e, f. *A. parviflora* Müll.Arg. e. Polar view; f. equatorial view (note the Ubisch bodies). — Scale bars: a, b, e, f = 5 μm; c, d = 1 μm.

hashi et al. (1995: 5 genera, 15 species, illustrated with SEM and TEM images) and Takahashi et al. (2000: 7 genera, 29 species, illustrated with SEM and TEM images). No material of *Bossera* and *Polyandra* was available. The most exhaustive of these studies, Takahashi et al. (2000), includes 13 *Alchornea* species of which only two come from SE Asia: *A. kelungensis* (= *A. trewioides*; Ishigaki Island, east of Taiwan) and *A. rugosa* (New Guinea). Few pollen floras are available for Southeast Asian regions. None treat more than three *Alchornea* species: Ikuse (1956; no illustrations), Ting (1949; with drawings) and Yu & Long (1982; with LM images). To complement the data in these works, a special study was made of the pollen of a number of Southeast Asian *Alchornea* species, concurrently with a taxonomic revision of *Alchornea* in Malesia and Thailand (Bulalacao & Van Welzen, in prep.).

MATERIAL AND METHODS

Mature male flower buds were removed from the following herbarium material (all in L):

- *Alchornea adenophylla* Pax & K. Hoffm., *Meijer 7128*, Sumatra, Indonesia
- *Alchornea borneensis* Pax & K. Hoffm., *SHEA 27713*, Kalimantan, Indonesia
- *Alchornea kelungensis* Hayata, *Tanaka & Shimada 13513*, Taiwan
- *Alchornea parviflora* Müll.Arg., *Merrill 2095*, Palawan, Philippines
- *Alchornea rhodophylla* Pax & K. Hoffm., *SF 39080*, Penang, Malaysia
- *Alchornea rugosa* (Lour.) Müll.Arg., *Cheviwat & Nimanog 44*, Thailand
- *Alchornea rugosa* (Lour.) Müll.Arg., *Maxwell 87-443*, Thailand
- *Alchornea rugosa* (Lour.) Müll.Arg., *Meijer 1782*, Java, Indonesia
- *Alchornea tiliifolia* (Benth.) Müll.Arg., *Kerr 18467*, Thailand
- *Alchornea trewioides* (Benth.) Müll.Arg., *Walker & Tawada 7175*, Ishigaki Isl., Japan

All samples were prepared for light microscopy (LM) and scanning electron microscopy (SEM), according to the techniques described by Van der Ham (1990). Ten pollen grains per sample were measured. The terminology used follows Punt et al. (1994).

RESULTS

Pollen of Southeast Asian species of *Alchornea* — Fig. 1, 2; Table 1

Pollen grains isopolar, suboblate to prolate spheroidal. Equatorial outline obtusely triangular. Polar axis (P) = 16 (20.5) 27 µm, equatorial diameter (E) = 18 (22.8) 30 µm, P/E = 0.86 (0.90) 1.03.

Aperture system 3-colporate. Ectoapertures distinct operculate colpi, 6–16 µm long. Operculum elongate, towards the poles hardly or not connected to the non-apertural sexine. Margo absent. Endoapertures lalongate, often indistinct pori or colpi without costae, 1–4 by 6–13 µm. Fastigium-like cavities present, filled with relatively long columellae (Fig. 2h).

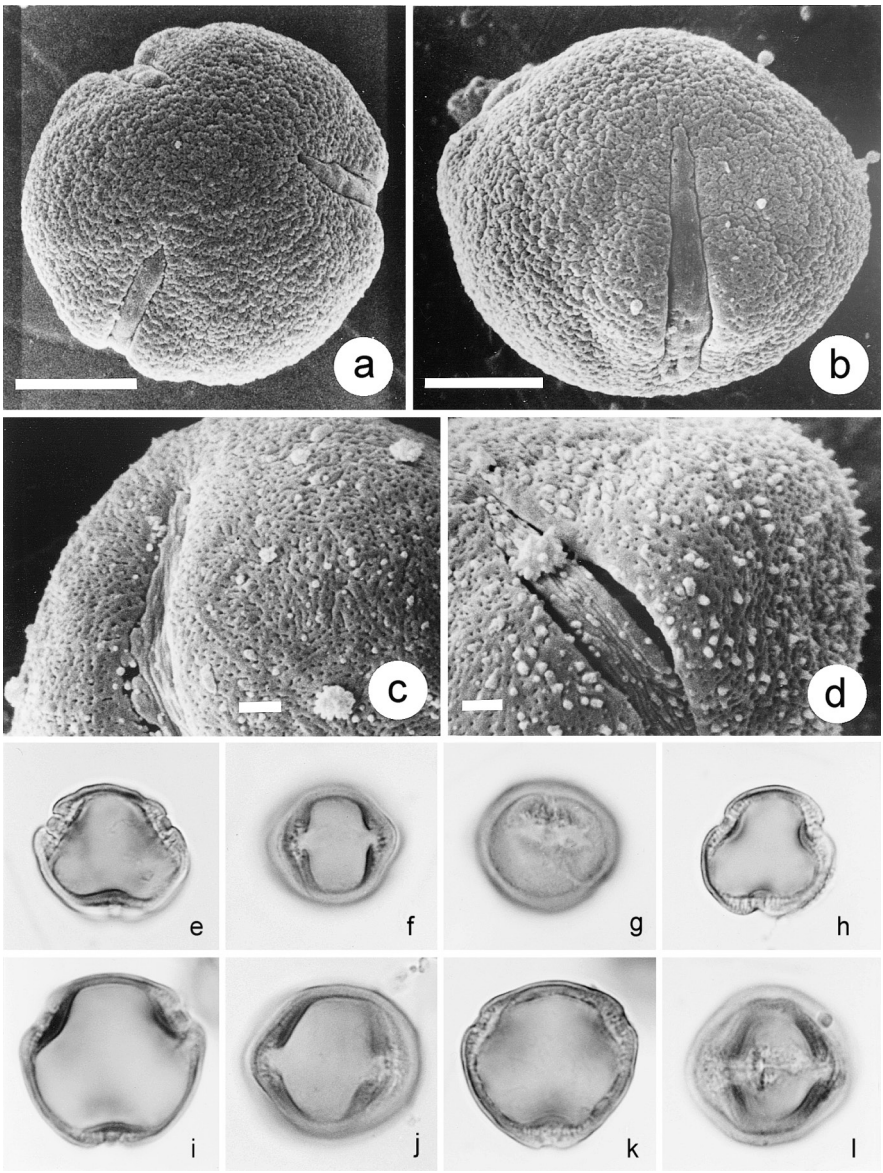

Fig. 2. Scanning electron (a–d) and light (e–l) micrographs of *Alchornea* pollen. — a, b. *A. rhodophylla* Pax & K. Hoffm. a. Polar view; b. equatorial view. — c. *A. rugosa* (Lour.) Müll. Arg. (*Maxwell 87-443*), detail showing ornamentation and operculum (note the Ubisch bodies). — d. *A. rugosa* (Lour.) Müll. Arg. (*Meijer 1782*), detail showing ornamentation and operculum (note the Ubisch body on the operculum). — e–g. *A. rhodophylla* Pax & K. Hoffm. e. Polar view; f. equatorial view; g. equatorial view showing endoaperture. — h. *A. rugosa* (Lour.) Müll. Arg. (*Maxwell 87-443*), polar view (note the relatively long columellae near the apertures). — i, j. *A. tiliifolia* (Benth.) Müll. Arg. i. Polar view; j. equatorial view. — k, l. *A. trewioides* (Benth.) Müll. Arg. k. Polar view; l. equatorial view. — Scale bars: a, b = 5 μm; c, d = 1 μm; e–l = 1000 x.

Mesocolpial exine 2–3 μm thick. Sexine thicker, equal to, or thinner than nexine. Infratectum thin, columellate, thickening near the endoapertures, showing distinctly longer columellae at both lateral sides of the endoapertures (fastigium-like cavities).

Ornamentation mostly scabrate-perforate (Fig. 1c), sometimes almost psilate-perforate (*A. kelungensis*; Fig. 1d) or striate-rugulate (*A. rugosa*; Fig. 2c, d). Operculum with hardly any perforations, usually scabrate or indistinctly striate, sometimes psilate (*A. kelungensis*) or more distinctly striate (*A. rugosa*). Psilate to scabrate Ubisch bodies often present (Fig. 1c, e, f; 2c, d).

Pollen data of the individual species are provided in Table 1.

Table 1. Pollen data of Southeast Asian *Alchornea* species. P = length of polar axis, E = equatorial diameter. All sizes are in μm.

	P	E	P/E	colpus length	endoaperture size	ornamentation
A. adenophylla	16.0	20.6	0.92			scabrate-perforate
A. borneensis	20.3	22.0	0.92	7–11	1–2 by 8–10	scabrate-perforate
A. kelungensis	23.0	26.2	0.88		2 by 8	psilate-perforate
A. parviflora	19.5	22.7	0.86	6–12	1–3 by 8–10	scabrate-perforate
A. rhodophylla	21.6	23.7	0.91	13–15	1–4 by 8–10	scabrate-perforate
A. rugosa	18.5	20.0	0.92	11–12	1–3 by 7–13	striate-rugulate
A. tiliifolia	23.9	26.7	0.89	14–16	2–4 by 7–10	scabrate-perforate
A. trewioides	21.8	21.2	1.03	10–12	2–3 by 6–10	scabrate-perforate

DISCUSSION

Genus Alchornea

Within the group of Southeast Asian species studied, very little pollen morphological variation occurs. Slightly deviating from the scabrate species are *A. kelungensis* (psilate) and *A. rugosa* (all three collections striate-rugulate). In comparing with the species studied by Takahashi et al. (1995, 2000), the scabrate ornamentation type occurring in most Southeast Asian species is found in *A. castaneaefolia* (Brazil), *A. hirtella* (Liberia) and *A. obovata* (Colombia); in the pollen of the other African and American species illustrated, the ornamentation elements are much more discrete. The occurrence in the Southeast Asian species studied of relatively long columellae in fastigium-like cavities at both lateral sides of each endoaperture, as described for the first time by Takahashi et al. (1995, 2000), is confirmed in the present study. The presence of a double columellate infratectum could not be demonstrated, as no transmission electron microscopy (TEM) examination was carried out.

Tribe Alchornieae

In the introduction, the paper by Takahashi et al. (2000) was cited as the most exhaustive of the studies dealing with Alchornieae, describing 29 species from seven of the

nine genera, while no material of the monotypic genera *Bossera* and *Polyandra* was available. However, Punt (1962, p. 82) referred to a photograph of a pollen grain of *Polyandra bracteosa* (only known from the type) in the original description of the genus (Léal, 1951). However, the photograph is actually an informative drawing of a pollen grain. It shows a 3-colporate, operculate pollen grain of c. 33 µm.

The eight known genera of the Alchornieae share a characteristic pollen type: 3-(or 4-)colporate pollen grains with distinctly operculate colpi (Léal, 1951; Punt, 1962; Takahashi et al., 2000), which can easily be recognised using light microscopy. Punt (1962) included species of two genera in his *Alchornea* pollen type that do not belong to the tribe Alchornieae: *Adenophaedra* and *Neotrewia*, and which do not possess pollen with operculate colpi (Fernández-González & Lobreau-Callen, 1996; Nowicke & Takahashi, 2002). Thus, the operculate *Alchornea* pollen type seems to represent a diagnostic character for the tribe Alchornieae.

Fossil record of the Alchornea pollen type

The characteristic appearance of the operculate pollen grains of the tribe Alchornieae, using light microscopy, has resulted in a relatively extensive fossil record of the *Alchornea* pollen type. The fossil pollen has usually been attributed to the genus *Alchornea*, but actually it should be compared with the pollen of the entire tribe Alchornieae, as the genera are hard to separate. The earliest records (as *Psilatricolporites operculatus*) are those from the lower and upper part of the Middle Eocene of Venezuela and Nigeria, respectively (Germeraad et al., 1968; Muller, 1970). Slightly younger are the Late Eocene records from Brazil (Muller, 1981). Graham (1976, 1988a, b, 1989, 1991a, b), Graham & Dilcher (1998) and Graham & Jarzen (1969) gave records for the Oligocene, Miocene and Pliocene of Costa Rica, Mexico, Panama and Puerto Rico. Martin (1974, 1978) found the *Alchornea* pollen type in the mid-Tertiary of Australia, comparing it with the extant Australian genus *Caelebogyne*, while Germeraad et al. (1968) recognised it in unspecified Neogene (Miocene–Pliocene) sediments in Borneo. These records suggest that the tribe Alchornieae has an African–American Gondwanic origin, and reached its pantropic distribution at least in the mid-Tertiary.

ACKNOWLEDGEMENTS

Thanks are due to Bertie Joan van Heuven and Vernie Sagun for assistance, Ben Kieft for the plates, Peter van Welzen for taxonomic guidance, and the Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO) for a visitor grant (B85-345) to the first author.

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