Pollen morphology of the tribes Naucleeae and Hymenodictyaeae (Rubiaceae – Cinchonoideae) and its phylogenetic significance

JEF VERELLEN1, STEVEN DESSEIN1,3, SYLVAIN G. RAZAFIMANDIMBISON2, ERIK SMETS FL3,4 and SUZY HUYSMANS1*

1Laboratory of Plant Systematics, Institute of Botany and Microbiology, K.U.Leuven, Kasteelpark Arenberg 31, BE-3001 Leuven, Belgium
2National Botanic Garden of Belgium, Domein van Bouchout, BE-1860 Meise, Belgium
3The Bergius Foundation at the Royal Swedish Academy of Sciences, P.O. Box 50017, SE-104 05 Stockholm, Sweden
4National Herbarium of the Netherlands, Leiden University Branch, P.O. Box 9514, 2300 RA Leiden, the Netherlands

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The tribe Naucleeae has recently been recircumscribed on the basis of both morphological and molecular [rbcL, trnT-F], internal transcribed spacer (ITS) evidence, and has been found to be the sister group of the tribe Hymenodictyaeae Razafim. & B. Bremer. In order to find pollen morphological support for this new classification, the pollen and orbicules of 65 species, representing 23 Naucleeae and the two Hymenodictyaeae genera, were investigated by scanning electron and light microscopy. Naucleeae pollen is very small (< 20 µm) to small (20–30 µm) and its shape in equatorial view is suboblate to spheroidal or, more rarely, subprolate. Three compound apertures are present, each comprising a long and narrow ectocolpus, a circular to slightly lolongate mesoporus, and an often H-shaped endoaperture. The sexine ornamentation is perforate, rugulate, or (micro)reticulate, and supratectal elements are always absent. Apart from the variation in sexine ornamentation, the tribe is rather stenopalous. The pollen of Hymenodictyaeae is very similar to that of Naucleeae. The H-shaped endoapertures often observed probably form a synapomorphy for the clade comprising Naucleeae and Hymenodictyaeae. Our pollen morphological observations are not in conflict with the widened delimitation of Naucleeae. Unambiguous pollen support for the recent subtribal or generic concepts of Naucleeae could not be found because of a lack of variation of pollen characters within the tribe. Orbicules are invariably present in the ten Naucleeae taxa investigated. They are spheroidal and smooth or irregularly folded. © 2007 The Linnean Society of London, Botanical Journal of the Linnean Society, 2007, 153, 329–341.


INTRODUCTION

Naucleeae, as circumscribed by Razafimandibison & Bremer (2002), is a mainly palaeotropical tribe of the subfamily Cinchonoideae (Rubiaceae) comprising 26 genera and c. 180 species. The tribe’s highest diversity is found in South-east Asia, followed by Madagascar and Africa. Only five species, representing two genera, occur in Central, North, and South America. Members of Naucleeae are morphologically well recognizable by the many-flowered globose inflorescences and the epigynous floral nectaries deeply embedded in hypanthia (Bremer, Andreason & Olsson, 1995; Razafimandibison & Bremer, 2001, 2002; Razafimandibison, 2002).

Naucleeae is sister to the tribe Hymenodictyaeae Razafim. & B. Bremer (Razafimandibison & Bremer, 2001). Razafimandibison & Bremer (2001) described the latter tribe to accommodate the genera Hymenodictyon Wall. and Paracorynanthe R. Capuron, previ-
ously placed by Andersson & Persson (1991) in their polyphyletic tribe Coptosapelteae. These genera differ from the Naucleaceae genera in having elongate inflorescences and lenticellate capsular fruits containing bilaterally flattened, elongate, accrescent placentas (S.G. Razafimandimbison & B. Bremer, unpubl. data). The Naucleaceae–Hymenodictyeae clade forms the sister group to the rest of Cinchonoideae (Andersson & Antonelli, 2005).

The results of the phylogenetic studies by Razafimandimbison & Bremer (2001, 2002), based on molecular (internal transcribed spacer (ITS), rbcL, and trnT-F) and morphological data, strongly suggested a much broader circumscription for Naucleaceae than previously proposed, including all members of Naucleaceae sensu Ridsdale (1978), together with Cephalanthus L., Hallea J.-F. Leroy, Mitragyna Korth., Uncaria Schreb. (as shown by Bremer et al., 1995), and also Corynanthe Welw. and Pausinystalia Pierre ex Dupouy & Beille. Their analyses also showed that Naucleaceae can be subdivided into six highly supported and morphologically distinct subtribes: Breoniniae, Cephalantheinae, Corynantheinae, Naucleiniae, Mitragyninae, and Uncarinae. A seventh subtribe, the Adininiae, was only poorly supported. Razafimandimbison & Bremer (2002) also proposed changes to the delimitation of some of the Naucleaceae genera. Corynanthe was restricted to Corynanthe paniculata Welw., the other species of the genus being transferred to the reinstated genus Pseudocinichona A. Chev. ex Perrot. Hallea J.-F. Leroy (Leroy, 1975) was merged with Mitragyna, and Neobreonia Ridsdale with Breonia A. Rich. The generic delimitations and infratribal taxa adopted here are as circumscribed by Razafimandimbison & Bremer (2002).

The pollen morphology of Naucleaceae and Hymenodictyeae is very poorly documented. Only the pollen of Hallea and Mitragyna has been studied extensively. Leroy (1975) segregated the genus Hallea from Mitragyna, partly on the basis of palynological evidence from only two species. This study was later elaborated by Huysmans, Robbrecht & Smets (1994), who studied the pollen of all ten species of Hallea and Mitragyna. They concluded that Hallea and Mitragyna could not be split on the basis of pollen morphology, although they accepted the separation on the basis of other morphological evidence.

As pollen morphology has been proven to provide useful taxonomic characters in other groups of Rubiaceae (for example, Johannsson, 1992; Andersson, 1995; Rova & Andersson, 1995; Andreasen & Bremer, 1996; Delprete, 1996; De Block & Robbrecht, 1998; Huysmans, Robbrecht & Smets, 1998; Huysmans et al., 1999; Dessein et al., 2002, 2005a), we decided to conduct a thorough investigation of the pollen and orbicule morphologies of Naucleae and its sister Hymenodictyeae. This article addresses the following questions: (1) are the new delimitations of Naucleae (sensu Razafimandimbison & Bremer, 2002) and the sister group relationship between Naucleaceae and Hymenodictyeae supported by pollen data?; (2) are there any pollen morphological synapomorphies for the seven subtribes proposed by Razafimandimbison & Bremer (2002)?; and (3) are the newly proposed generic circumscriptions supported by pollen morphology?

**MATERIAL AND METHODS**

This study is based on the examination of 123 specimens, encompassing 65 species belonging to 25 genera of Naucleaceae and Hymenodictyeae. Some of these observations were extracted from the Master’s thesis of Huysmans (1993); in the material list, these samples are indicated with an asterisk. Mitragyna s.l. (Hallea J.-F. Leroy included) was not investigated here, as extensive pollen data of Mitragyna s.s. and Hallea were published by Huysmans et al. (1994). No pollen observations were made for Diyaminuclea Ridsdale and Khasiaclinea Ridsdale as suitable material was lacking. Pollen samples were taken from specimens from the following herbaria: A, AS, BR, L, MO, P, S, TAN, and TEF (abbreviations according to Holmgren, Holmgren & Barnett, 1990). The identifications of all specimens used were verified.

All specimens were acetylated following Reitsma’s (1969) ‘wetting agent’ method. Prior to acetylation (10 min in a heating block at 90 °C), flowers were hydrated in an Agepon solution (1:200) and dehydrated in pure acetic acid. After acetylation, the pollen sample from each specimen was split into two subsamples, one part for light microscopy (LM) and the other for scanning electron microscopy (SEM) observations and storage. Pollen for SEM was rinsed in 70% ethanol, mounted on a stub, air-dried, and coated with gold for 2 min using a SPI-Module™ sputter coater. Pollen grains were broken by adding small glass beads to the pollen suspension and shaking it with a vortex, as described by Huysmans et al. (1994). Digital images were taken with a Jeol JSM 5800 scanning electron microscope. Grains for LM studies were mounted in Kaisr’s glycercine jelly and sealed with paraffin. The slides were observed using a Leitz Dialux 20 light microscope with a ×100 oil immersion lens.

In order to check for the possible presence of orbicules on the inner locule wall of the anthers, entire anthers were critically point dried (Balzers, CPD 030) after hydration in Agepon solution and dehydration in an acetone series. The dried, entire anthers were mounted on stubs with double adhesive carbon strips before further preparation. If undehisced, a longitudinal section of each theca was made using a razor.
blade. To be able to observe the inner locule wall, the pollen grains were gently removed using a cactus needle.

Both the polar axis diameter (P) and equatorial diameter (E) were measured under LM in at least ten mature pollen grains. P/E values were calculated for each measured pollen grain. All other measurements were performed on digital SEM images using CARNOY software (Schols et al., 2002). Pollen terminology follows the online edition of Punt et al. (1994) at http://www.bio.uu.nl/~palaeo/glossary/index.htm/. Pollen size classes are as proposed by Dessein et al. (2005a): very small, <20 µm; small, 20–30 µm; medium, 30–40 µm. For shape classes in equatorial view (P/E), we adopted the wide definitions of Nilsson & Pragowski (1992): suboblate, 0.75–0.88; spheroidal, 0.88–1.14; subprolate, 1.14–1.33; prolate, 1.33–2.00. Measurements of the lumina refer to the lumina at the mesocolpium. Tribal, subtribal, and generic concepts are as proposed by Razafimandimbison & Bremer (2002). After each genus in the ‘Results’ section, the number of species investigated relative to the number of estimated species is given in parentheses.

RESULTS

GENERAL POLLEN OBSERVATIONS

Naucleeae and Hymenodictyeae are relatively stenopalynous. Variation was mainly observed in sexine ornamentation and, to a lesser extent, in pollen size and shape, and aperture morphology. Table 1 summarizes the pollen morphological characters at a generic level.

Pollen is always shed as monads. The pollen size in Naucleeae varied from very small (<20 µm) to small (20–30 µm), although the majority of the genera had very small-sized pollen. The largest pollen grains were observed in Adina Salisb. and Cephalanthus. Pollen shape in equatorial view ranged from suboblate to subprolate, with pollen of most species and genera being spheroidal. Suboblate and subprolate pollen grains sometimes occurred in the same genus, as in Breonia, Ludekia, and Nauclea. A few prolate grains were observed in Adina. The amb was usually circular, more rarely subtriangular.

All Naucleeae taxa investigated were three-colporate. Only in Hymenodictyon floribundum (Hochst. & Steud.) B. L. Robinson and Neonauclea forsteri (Seem. ex Havil.) Mer. were a few four-colporate pollen grains observed. From the outside, an ectocolpus and mesoporus were observed in all genera (Figs 1–6). In most cases, the ectocolpus was long and narrow. A relatively short ectocolpus was observed in Myrmecononauclea Merr. (Fig. 5) and some species of Neonauclea Merr. Because the colpi were usually long, the apocolpium index was low (see Table 1). The colpus ends varied from acute (i.e. Figs 2, 3, 7) to obtuse (Figs 4, 11). The colpus membrane was coarse, granular, or smooth. The mesoporus was located in the middle of the colpus (at the equator), and was circular (Fig. 1) or somewhat longer than wide (Figs 2–6). The mesoporus was usually small and rarely exceeded 2 µm in diameter. A mesoporus exceeding 2 µm was observed in Ochreinauclea Ridsdale & Bakh. f. H-shaped endoapertures were observed in Breonadia Ridsdale, Corynanthe, Haldina Ridsdale, Hymenodictyon, Neonauclea, Pausinystalia, Pseudocinchona, and Uncaria (Fig. 18). The inner ornamentation of the sporoderm was not observed with SEM for all genera studied, and so H-shaped endoapertures might also occur in other genera. A distinct endoaperture seemed to be lacking in Neonauclea and Nauclea.

The sexine was semitectate and simplicolumellate (Figs 16–18). Supratectal elements were almost absent. The most common sexine ornamentations in Naucleeae were microreticulate (Figs 1–3, 5–7, 14), rugulate (Fig. 15), and perforate (Figs 8, 9, 11). A reticulate sexine pattern (lumina >1 µm) was only observed in the genus Ludekia (Figs 4, 10) and in some Pausinystalia species. Usually, there was no differentiation of the sexine towards the poles or apertures (Figs 7, 10, 11–15). In some species, however, the lumina or perforation size was smaller towards the colpi and/or at the poles (Figs 8, 9). For all genera investigated, the inner surface of the nexine was granular (Figs 17, 18).

GENERAL ORBICULE OBSERVATIONS

Orbicules in Naucleeae were small and spheroidal, or sometimes slightly lobed. A central indentation in the orbicule body was rare, but occurred in Nauclea. The surface of the orbicules was always smooth. Orbicules can lie freely upon the locule wall (Figs 19–21, 23, 24) or can be embedded (Fig. 22). According to the orbicule typology as proposed by Huysmans et al. (1997) and Vinckier, Huysmans & Smet (2000), they belong to type IV (irregularly folded orbicules) in Burttdavya Hoyle and type IIIa (smooth spheroidal orbicules without a central perforation) in all other genera investigated.

GENERIC POLLEN AND ORBICULE DESCRIPTIONS

Adina Salisb. (2/3) (Figs 1, 19): Pollen very small to small (P, 16–31 µm; E, 15–24 µm); shape in equatorial view spheroidal, subprolate, or rarely prolate; amb circular to subtriangular. Apertures 3, colporate with long and narrow ectocolpi; colpus ends acute to obtuse; colpus membrane coarse to granular; mesoporus

<table>
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<tr>
<th>Genus</th>
<th>P value (µm)</th>
<th>E value (µm)</th>
<th>P/E value</th>
<th>Shape</th>
<th>Apocolpium index</th>
<th>Sexine ornamentation</th>
<th>Lumina size (µm)</th>
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<td><strong>Nauclaeae</strong></td>
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<td>18–(20.0)–23</td>
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<td>Microreticulate–rugulate</td>
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<td>16–(22.2)–31</td>
<td>15–(19.2)–24</td>
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<td>Rugulate</td>
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<td>Microreticulate</td>
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<td>Microreticulate</td>
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<td>Perforate–microreticulate</td>
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<td>13–(14.7)–16</td>
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<td>Perforate–microreticulate</td>
<td>0.10–(0.45)–0.83</td>
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“–”, data not available; E, equatorial diameter; P, polar axis diameter; S, spheroidal; SO, suboblate; SP, subprolate; x/y, number of species studied for each genus over total number of species in the genus.
Figures 1–15. Figs 1–6. Equatorial view of pollen grains. Figs 7–15. Polar view of pollen grains. Figure 1. Adina pilulifera. Figure 2. Breonia macrocarpa. Figure 3. Cephalanthus tetrandra. Figure 4. Ludekia benardoi. Figure 5. Myrmeconauclea stipulacea. Figure 6. Uncaria africana. Figure 7. Breonia macrocarpa. Figure 8. Cephalanthus tetrandra. Figure 9. Gyrostipula comoriensis. Figure 10. Ludekia benardoi. Figure 11. Metadina trichotoma. Figure 12. Myrmeconauclea stipulacea. Figure 13. Neolamarcia cadamba. Figure 14. Pertusadina eurhyncha. Figure 15. Uncaria africana.

circular to slightly lolongate without distinct annulus; endoaperture unknown. Sexine pattern rugulate to microreticulate, without differentiation towards colpi or poles; supratectal elements absent; lumina 0.14–0.63 µm in diameter.

Orbicules present, 1 µm or less in diameter, spheroidal, sometimes slightly lobed, without central perforation, not embedded in the locule wall; surface smooth (Fig. 19).

**Adinauclea Ridsdale (1/1) (Fig. 20):** Pollen very small (no measurements); shape in equatorial view spheroidal; amb circular. Apertures 3, colporate with long ectocolpi; colpus ends acute; colpus membrane coarse; mesoporous not observed; endoaperture unknown. Sexine pattern distinctly rugulate with interwoven rugae, without differentiation towards colpi or poles; supratectal elements absent; lumina 0.12–0.29 µm in diameter.

Orbicules present, 1 µm or less in diameter, spheroidal without central perforation, sometimes aggregated, not or only slightly embedded in the locule wall; surface smooth (Fig. 20).

**Breonadia Ridsdale (1/1):** Pollen very small to small (P, 15–20 µm; E, 17–22 µm); shape in equatorial view suboblate to spheroidal; amb circular. Apertures 3, colporate with long and narrow ectocolpi; colpus ends acute; colpus membrane granular; mesoporous circular, without distinct annulus; endoaperture present, H-shaped. Sexine pattern microreticulate, without differentiation towards colpi, but lumina sometimes slightly smaller at poles; supratectal elements absent; lumina 0.33–0.74 µm in diameter.

Orbicules: no observations.

**Breonia A. Rich. ex DC. (4/20) (Figs 2, 7):** Pollen very small to small (P, 19–23 µm; E, 19–21 µm);
shape in equatorial view spheroidal to subprolate; amb circular. Apertures 3, colporate, with long and narrow ectocolpi; colpus ends mostly acute; colpus membrane granular; mesoporus circular to slightly lolongate with a distinct, more or less smooth annulus; endoaperture unknown. Sexine pattern microreticulate, without differentiation towards colpi or poles; supratectal elements absent; lumina 0.18–0.56 µm in diameter.

Orbicules present, 1 µm or less in diameter, often in aggregates of several orbicules; individual orbicules spheroidal, often slightly embedded in the locule wall; surface smooth.

*Burttdavya Hoyle* (1/1): Pollen very small to small (P, 16–19 µm; E, 18–23 µm); shape in equatorial view suboblate to spheroidal; amb circular. Apertures 3, colporate with long ectocolpi; colpus ends acute to obtuse; colpus membrane granular; mesoporus circular to slightly lolongate, sometimes with an annulus; endoaperture unknown. Sexine pattern microreticulate to rugulate, without differentiation towards colpi or poles; supratectal elements absent; lumina 0.38–0.88 µm in diameter.

Orbicules present, 0.80–1.90 µm in diameter, irregularly shaped, not embedded in the locule wall; surface folded (Huysmans et al., 1997: figs 22, 23).

*Cephalanthus L.* (5/6) (Figs 3, 8, 16, 21): Pollen very small to small (P, 20–25 µm; E, 19–27 µm); shape in equatorial view spheroidal; amb circular to subtriangular. Apertures 3, colporate with long ectocolpi; colpus ends acute; colpus membrane granular; mesoporus lolongate with annulus; endoaperture unknown. Sexine pattern perforate, sometimes microreticulate, with perforations/lumina slightly smaller towards colpi and at poles; supratectal elements absent; perforations/lumina 0.12–1.05 µm in diameter (the largest lumina were measured in *Cephalanthus glabratus* K. Schum.).

Orbicules present, smaller than 1 µm in diameter, spheroidal, sometimes in aggregates, not embedded in locule wall; surface smooth (Fig. 21).

*Corynanthe Welw.* (1/1): Pollen very small (P, 12–16 µm; E, 13–16 µm); shape in equatorial view spheroidal or more rarely suboblate; amb circular with sunken colpi. Apertures 3, colporate, with long and narrow ectocolpi; colpus ends obtuse; colpus membrane granular; mesoporus lolongate, without distinct annulus; endoaperture H-shaped with costa. Sexine pattern perforate to microreticulate, without differentiation towards colpi or poles; supratectal elements absent; perforations/lumina 0.11–0.50 µm in diameter.

Orbicules: no observations.

*Gyrostipula J.-F. Leroy* (2/2) (Figs 9, 22): Pollen very small (P, 13–19 µm; E, 13–21 µm); shape in equatorial view suboblate to spheroidal; amb circular. Apertures 3, colporate, with long and narrow ectocolpi; colpus ends acute; colpus membrane granular; mesoporus circular to lolongate, without or with indistinct annulus; endoaperture unknown. Sexine pattern microreticulate without differentiation towards colpi or poles, sometimes with interwoven muri; supratectal elements absent; lumina 0.14–0.54 µm in diameter.

Orbicules present, 1 µm or less in diameter, sometimes in small aggregates, spheroidal, slightly embedded in the locule wall; surface smooth (Fig. 22).

*Haldina Ridsdale* (1/1): Pollen very small (P, 13–16 µm; E, 12–16 µm); shape in equatorial view spheroidal to subprolate; amb circular. Apertures 3, colporate, with long and narrow ectocolpi; colpus ends acute; colpus membrane granular but smooth around mesoporus; mesoporus circular to slightly lolongate without distinct annulus; endoaperture faint, H-shaped with costa; inner nexine surface granular. Sexine pattern microreticulate, without differentiation towards colpi, with the lumina somewhat smaller at the poles; supratectal elements absent; lumina 0.20–0.46 µm in diameter.

Orbicules: no observations.

*Hymenodictyeon Wall.* (4/26): Pollen very small to small (P, 11–24 µm; E, 13–22 µm); shape in equatorial view suboblate to spheroidal, rarely subprolate; amb circular or subtriangular. Apertures 3 or exceptionally 4, colporate, with long and narrow ectocolpi; colpus ends obtuse; colpus membrane granular; mesoporus circular to slightly lolongate or lolongate with or without annulus; endoaperture faint, probably H-shaped, with costa. Sexine pattern perforate or microreticulate, sometimes with smaller perforations/lumina towards the colpi and at the poles; supratectal elements absent; perforations/lumina 0.12–0.80 µm in diameter.

Orbicules: no observations.

*Janotia J.-F. Leroy* (1/1) (Fig. 23): Pollen very small (P, 11–13 µm; E, 12–13 µm); shape in equatorial view suboblate to spheroidal; amb circular. Apertures 3, colporate, with long and narrow ectocolpi; colpus ends unknown; colpus membrane unknown; mesoporus unknown; endoaperture unknown. Sexine pattern microreticulate to perforate; supratectal elements absent; perforations/lumina 0.22–0.55 µm in diameter.

Orbicules present, smaller than 1 µm, spheroidal, sometimes in aggregates, not embedded in locule wall; surface smooth (Fig. 23).
**Ludekia Ridsdale** (2/2) (Figs 4, 10): Pollen very small (P, 11–19 μm; E, 11–21 μm); shape in equatorial view spheroidal, rarely suboblate or subprolate; amb circular. Apertures 3, colporate, with relatively broad and long ectocolpi; colpus ends acute; colpus membrane coarse; mesoporus with rather distinct annulus; endoaperture unknown. Sexine pattern (micro)reticulate, without differentiation towards colpi or poles; supratectal elements absent; lumina 0.65–1.23 μm in diameter.

Oribuciles present, 1 μm or less in diameter, spheroidal, often in aggregates, embedded in locule wall; surface smooth.

**Metadina Bakh. f.** (1/1) (Figs 11, 24): Pollen very small (P, 11–19 μm; E, 12–17 μm); shape in equatorial view suboblate to spheroidal; amb circular. Apertures 3, colporate, with relatively broad ectocolpi; colpus ends obtuse to acute; colpus membrane coarse; mesoporus circular to lolongate with or without distinct annulus; endoaperture unknown. Sexine pattern perforate to microreticulate, sometimes with interwoven muri, without differentiation towards colpi or poles; supratectal elements absent; perforations/lumina 0.13–0.60 μm in diameter.

Oribuciles present, smaller than 1 μm, spheroidal, never distinctly aggregated and lying freely upon locule wall; surface smooth (Fig. 24).

**Myrmeconuclea Ridsdale** (3/3) (Figs 5, 12): Pollen very small to small (P, 13–23 μm; E, 14–25 μm); shape in equatorial view spheroidal; amb circular. Apertures 3, colporate, with narrow and relatively short ectocolpi; colpus ends acute; colpus membrane usually smooth, sometimes slightly granular; mesoporus circular or slightly lolongate, without annulus; endoaperture indistinct. Sexine pattern microreticulate, without differentiation towards colpi or poles; supratectal elements absent; lumina 0.24–1.06 μm in diameter (the largest lumina were measured in *Myrmeconuclea stipulacea* Ridsdale).

Oribuciles: no observations.

**Nauclea Korth.** (9/9): Pollen very small to small (P, 13–25 μm; E, 16–24 μm); shape in equatorial view spheroidal, suboblate, or subprolate; amb circular. Apertures 3, colporate, with long and narrow ectocolpi; colpus ends acute; colpus membrane coarse or granular; mesoporus circular to lolongate with indistinct annulus (mesoporus often remarkably large in *Nauclea officinalis*); endoaperture unknown. Sexine pattern microreticulate to perforate, often with interwoven muri, without differentiation towards colpi or poles; supratectal elements absent; perforations/lumina 0.13–(0.35)–0.61 μm in size (the largest lumina were found in *Nauclea parva* Merr., the smallest ones in *Nauclea tenuiflora* Merr.).

Oribuciles present, 0.60–1.10 μm in diameter, mostly spheroidal, sometimes with perforations, sometimes in small aggregates; surface smooth (Huysmans et al., 1997: figs 24, 25).

**Neolamarckia Bosser** (1/2). (Fig. 13): Pollen very small (P, 13–15 μm; E, 14–16 μm); shape in equatorial view spheroidal or sometimes suboblate; amb circular to subtriangular. Apertures 3, colporate with long ectocolpi; colpus ends acute or obtuse; colpus membrane granular; mesoporus lolongate with pronounced smooth annulus; endoaperture unknown. Sexine pattern microreticulate to slightly rugulate, without differentiation towards colpi or poles; supratectal elements absent; lumina 0.16–0.41 μm in diameter.

Oribuciles: no observations.

**Neonauclea Merr.** (8/65): Pollen very small to small (P, 11–23 μm; E, 13–22 μm); shape in equatorial view suboblate to spheroidal; amb circular to subtriangular. Apertures 3, colporate (in *Neonauclea forsteri*, a single four-colporate grain has been observed) with long or short (*Neonauclea borneensis* Ridsdale, *Neonauclea excelsa* Merr., *Neonauclea formicaria* Merr., and *Neonauclea forsteri*) and narrow ectocolpi; colpus ends acute; colpus membrane smooth or finely granular; mesoporus circular without annulus; endoaperture indistinct, H-shaped, with costa in *Neonauclea forsteri*. Sexine pattern microreticulate, without differentiation towards the colpi, sometimes changing to perforate at poles; lumina 0.17–0.74 μm in diameter (the largest lumina were found in *Neonauclea formicaria*).

Oribuciles: no observations.

**Ochreinauclea Ridsdale & Bakh. f.** (1/2): Pollen very small (P, 11–13 μm; E, 12–13 μm); shape in equatorial view suboblate to spheroidal; amb circular. Apertures 3, colporate, with long and narrow ectocolpi; colpus ends acute or obtuse; colpus membrane coarsely granular; mesoporus circular to lolongate, rather large (> 2 μm), usually with an annulus; endoaperture unknown. Sexine pattern microreticulate to slightly rugulate, with interwoven muri without differentiation towards colpi or poles, or lumina slightly smaller at poles; supratectal elements absent; lumina 0.23–0.66 μm in size.

Oribuciles: no observations.

**Paracorynanta R. Capuron ex Bosser** (2/2): Pollen very small (P, 15–18 μm; E, 17–20 μm); shape in equatorial view spheroidal or sometimes suboblate; amb subtriangular. Apertures 3, colporate, with long and narrow ectocolpi; colpus ends acute or obtuse; colpus
membrane granular; mesoporus slightly lolongate with distinct annulus; endoaperture unknown. Sexine pattern perforate to microreticulate, with perforations/lumina smaller towards colpi and at the poles; supratectal elements absent; perforation/lumina 0.10–0.53 \( \mu \)m in diameter.

**Orbicules:** no observations.

**Pausinystalia Pierre ex Dupoux & Beille (3/5):**

Pollen very small (P, 8–13 \( \mu \)m; E, 10–15 \( \mu \)m); shape in equatorial view suboblate or spheroidal; amb circular or subtriangular. Apertures 3, colporate with long ectocolpi; colpus ends obtuse; colpus membrane slightly granular; mesoporus circular, often not as wide as ectocolpus, without clear annulus; endoaperture distinct, H-shaped. Sexine pattern (micro)reticulate or perforate, with the lumina decreasing in size towards the colpi, sometimes also smaller at the poles; supratectal elements absent; lumina 0.20–1.19 \( \mu \)m in diameter (remarkably large lumina were observed in *Pausinystalia lane-poolei* (Hutch.) Hutch. ex Lane-Poole ssp. lane-poolei).

**Orbicules:** no observations.

**Pertusadina Ridsdale (2/4) (Fig. 14):**

Pollen very small (P, 11–15 \( \mu \)m; E, 11–16 \( \mu \)m); shape in equatorial view spheroidal, sometimes suboblate; amb circular. Apertures 3, colporate with long and narrow ectocolpi; colpus ends acute; colpus membrane granular; mesoporus circular to slightly lolongate with indistinct smooth annulus; endoaperture unknown. Sexine pattern microreticulate, sometimes with interwoven muri, without differentiation towards colpi but often with slightly smaller lumina at poles; lumina 0.20–0.54 \( \mu \)m in diameter.

**Orbicules:** no observations.

**Pseudochinchona A. Chev. ex E. Parrot (2/2):**

Pollen very small (P, 13–18 \( \mu \)m; E, 14–19 \( \mu \)m); shape in equatorial view spheroidal or suboblate; amb circular with sunken colpi. Apertures 3, colporate, with long and narrow ectocolpi; colpus ends obtuse or acute; colpus membrane granular; mesoporus lolongate, with smooth annulus; endoaperture H-shaped with costa. Sexine pattern perforate to almost microreticulate, with perforations smaller towards colpi and poles; supratectal elements absent; perforations/lumina 0.10–0.70 \( \mu \)m in diameter.

**Orbicules:** no observations.

**Sarcocephalus Afzel. ex R. BR. (2/2):**

Pollen very small (P, 15–19 \( \mu \)m; E, 17–20 \( \mu \)m); shape in equatorial view suboblate to spheroidal; amb circular or subtriangular. Apertures 3, colporate, with long and narrow ectocolpi; colpus ends acute, sometimes slightly obtuse; colpus membrane granular; mesoporus circular to lolongate, mostly with distinct annulus; endoaperture presumably lolongate in *Sarcocephalus pobeguinii* (Hua ex Pobé). Sexine pattern microreticulate to rugulate, with interwoven muri, without differentiation towards colpi or poles; lumina 0.28–0.67 \( \mu \)m in size.

**Orbicules:** no observations.

**Sinoadina Ridsdale (1/1):**

Pollen very small (P, 15–19 \( \mu \)m; E, 13–16 \( \mu \)m); shape in equatorial view spheroidal to subprolate; amb circular. Apertures 3, colporate with long and narrow ectocolpi; colpus ends acute; colpus membrane granular; mesoporus circular to slightly lolongate, without annulus; endoaperture unknown. Sexine pattern rugulate to almost striate, without differentiation towards colpi or poles; lumina 0.15–0.45 \( \mu \)m in size.

**Orbicules:** no observations.

**Uncaria Schreb. (5/34) (Figs 6, 15, 17, 18):**

Pollen very small (P, 13–21 \( \mu \)m; E, 14–18 \( \mu \)m); shape in equatorial view spheroidal to suboblate; amb circular with sunken colpi. Apertures 3, colporate with long and very narrow ectocolpi; colpus ends acute; colpus membrane granular with smooth zone around mesoporus; mesoporus lolongate, without annulus; endoaperture, H-shaped with costa. Sexine pattern microreticulate with interwoven muri or rugulate with slender and long striae on reticulum, without differentiation towards colpi or poles; supratectal elements absent; lumina 0.17–0.65 \( \mu \)m in size.

**Orbicules:** no observations.

**DISCUSSION**

**TRIBAL LEVEL**

Naucleae are fairly stenopalynous; especially in pollen size and shape, number and type of apertures, and sexine characteristics, the variation is limited. The only pollen character that varied considerably within the tribe was the sexine ornamentation. Perforate, rugulate, microreticulate, and reticulate sexine patterns were observed. The pollen morphologies of the genera that were transferred from Coptosapteleae sensu Andersson & Persson (1991) (*Mitragyna sensu* Ridsdale, *Uncaria*, *Corynanthe*, and *Pausinystalia*) and Cephalantheae (*Cephalanthus* to Naucleae by Razafimandimbison & Bremer (2001) agreed well with the pollen found in Naucleae sensu Ridsdale (1978). The emendation of Naucleae proposed by Razafimandimbison & Bremer (2001, 2002) is thus not in conflict with the pollen morphological evidence. However, a pollen morphological synapomorphy for Naucleae could not be found. Indeed, most pollen features observed in Naucleae were also commonly found in...
other genera of Rubiaceae. Tricolporate pollen was the basic pollen type in Rubiaceae (Dessein et al., 2005a). A tendency towards pluriporate grains, as found in the tribes Psychotrieae (Johansson, 1992), Isertieae (Huysmans et al., 1998), Rubieae (Huysmans et al., 2003), and Spermacoaeae (Dessein et al., 2002, D2005b) was not seen in Naucleeae.

The pollen morphology of Hymenodictyeae was very similar to that of Naucleeae. The sister group relationship between the two tribes seemed to be supported by the shared presence of the H-shaped endoapertures. Our palynological evidence added support for merging Hymenodictyeae in Naucleeae, as proposed by Andersson & Antonelli (2005).

The H-shaped endoapertures observed in both Naucleeae and Hymenodictyeae have only been recorded in two distant Rubiaceae genera: Burchellia (Gardenieae, Ixoroideae) and Molopanthera (associated with Henriquezieae, Ixoroideae; Rova et al., 2002) (Dessein et al., 2005a).

Orbicules were found in all ten genera investigated. They were small, spheroidal, with a smooth surface, and could be aggregated and slightly embedded in the locular wall. The orbicules could also have a folded surface, as observed in Burtttdavya nyasica (Naucleinae). According to the typology of Huysmans et al. (1997), Vinckier et al. (2000), and Vinckier & Smets (2002), the orbicules found in Naucleeae can be classified as type IIIa (smooth, spheroidal orbicules without a central indentation) and type IV (angular, irregularly folded orbicules) in Burtttdavya. Type IIIa orbicules were the most common type in both Cinchonoeae and Ixoroideae. They occurred in Pavetteae (Vinckier et al., 2000), Cinchonoeae, Isertieae, and Rondeletieae (Huysmans et al., 1997). The irregularly folded orbicules of type IV have so far only been observed in Burtttdavya of Naucleeae and Alibertia pilosa of Gardenieae (Vinckier et al., 2000).

**INFRATRIBAL AND GENERIC LEVEL**

The second aim of this article was to verify whether the recently modified subtribal concepts proposed by Razafimandimbison & Bremer (2002) were supported by palynological data. Therefore, we attempted to identify pollen morphological synapomorphies that supported the current division of Naucleeae into seven subtribes. We also wished to determine whether the Naucleeae genera could be distinguished on the basis of pollen morphology alone. Very few if any characters could be detected to support the subtribal and generic delimitations.

In the subtribe Naucleinae, three different sexine ornamentations were observed. Microreticulate patterns were most common, but a tendency towards rugulate patterns was observed in the genera Burtttdavya, Neolamarckia, and Sarcocephalus. The largest grains were found in Nauclea, where subprolate grains were also observed. The lumina size was largest in the genus Burtttdavya.

Adiniae was heterogeneous in pollen size (largest grains in Adina) and sexine ornamentation. The genus Ludekia was remarkable because of its larger lumina compared with the other genera. It was the only genus, together with Pausinystalia (Corynantheinae), in which a reticulate sexine pattern was detected. Pollen shape was variable and ranged from suboblate to prolilate in Adina. The tendency towards rugulate patterns was also observed in this subtribe, namely in Adina, Adinauclea, and Sinoadina.

Breonia was exceptional in the subtribe Breoniinae because it had larger pollen than the other three genera (Breonadia, Gyrostipula, and Janotia), with a tendency towards a subprolate shape.

The single genus Cephalanthus in the subtribe Cephalanthinae had an equatorial diameter exceeding 25 μm. As a consequence, this subtribe was characterized by the largest pollen grains in the tribe.

Both Mitragyna s.s. and Hallea had the H-shaped endoapertures found in the other Naucleeae and Hymenodictyeae taxa investigated. They could not be distinguished on the basis of their pollen morphologies. The subtribe Mitragyninae does not seem to have any pollen synapomorphies.

The genus Uncaria in the subtribe Uncarinae was characterized by a tendency towards rugulate sexine patterns and subprolate grains. Yet, it should be mentioned that only four of the 34 species of the genus Uncaria were studied.

Pausinystalia of the subtribe Corynantheinae had the smallest pollen in the tribe (not exceeding 15 μm). The pollen grains of the other two genera of this subtribe, Corynanthe and Pseudocinchona, were slightly larger. The sexine pattern was often (micro)reticulate.

The resurrection of the genus Pseudocinchona, making Corynanthe monospecific, as proposed by Razafimandimbison & Bremer (2002), was not supported or contradicted by pollen morphology.

**CONCLUSION**

Nauclea is a stenopalous tribe, characterized by very small to small, tricolporate pollen with an ectocolpus, a circular to lalongate mesoporus, and an often H-shaped endoaperture. Sexine patterns are perforate, (micro)reticulate, or somewhat rugulate. Orbicules are present; they are small, spheroidal, and with a smooth surface. They belong to type IIIa and type IV. Our pollen morphological observations are not in conflict with a recent widened delimitation of Nauclea. H-shaped endoapertures probably form a synapomorphy for the Naucleae–Hymenodictyeae clade. Pollen
morbidity is of little value in distinguishing the sub-tribes and genera of Naucleae.

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SPECIMENS EXAMINED
Collections indicated with an asterisk were studied by Suzy Huysmans and presented in her Master’s thesis (Huysmans, 1993). ‘SF’ stands for ‘Service Forestier’.

Adina pilulifera (Lam.) Franch. ex Drake, Clemens & Clemens 3066 (A), Vietnam; Tsang 29239 (L.), Vietnam; Adina rubella Hance, Wilson 1949 (A), China.

Adinauclea fagifolia (Tejjsm. & Binn. ex Havil.) Ridsdale, Van Steenis 1939 (A), Indonesia.

Breonadia salicina (Vahl) Hepper & J.R.I.Wood, de Koning et al. 8640 (BR), Mozambique; Antanimilanja 4587 (L.), Madagascar.

Breonia fragifera Capuron ex Razafim., Perrier de la Bâthie 14215bis (P), Madagascar; Breonia macrocarpa Homolle, SF-18116 (P), Madagascar; Breonia richardsonii Razafim., SF-14359 (TEF), Madagascar; Breonia decaryana Homolle, Razafimandimbiso 257 (TAN), Madagascar.

Burttavaya nyasica Hoyle, Schlieben 5581 (BR), Tanzania.

Cephalanthus glabratrus (Spreng.) K. Schum., Zardini & Valazquez 18861 (MO, AS), Paraguay; Cephalanthus natalensis Oliv., Bolus 7679 (MO), South Africa; Cephalanthus occidentalis L., Flores & Martinez 1724 (MO); Cephalanthus salicifolius Humb. & Bonpl., Meyerand & Rogers 1889 (MO); Cephalanthus tetrandra (Roxb.) Ridsale & Bakht. f., collector unknown s. n. (MO).


Gyrostypa comoriensis J.-F. Leroy, collector unknown 16 (P), Comoro Islands; Gyrostypa foveolata (Capuron) J.-F. Leroy, Razafimandimbison 270 (TAN, MO), Madagascar; SF-27633 (TEF), Madagascar.

Haldina cordifolia (Roxb.) Ridsdale, Abdul Rashid Manhas s. n. (BR-S.P. 862493), India; Geesink et al. 6726 (L.), Thailand; Shaik Mokim s. n. (L.), Burma.

Hymenodictyon biafranum Hiern, Thomas 422* (VR), Cameroon; Hymenodictyon decaryii Homolle, Phillipson 2778* (VR), Madagascar; Hymenodictyon orixense (Roxb.) Mabb., Fox in PNH 4795* (BR), Philippines; Hymenodictyon floribundum (Hochst. & Steud.) B. L. Robinson, Runyinya 603* (BR), Rwanda.

Janotia macrostipula (Capuron) J.-F. Leroy, SF-2071 (TAN, MO), Madagascar.

Ludekia bernardoi (Merr.) Ridsdale, Sulit 22889 (A), Philippines; Ramos 1707 (L.), Philippines; Ludekia borneensis Ridsdale, Yee Puan Ching S40171 (L.), Borneo.

Metadina trichotoma (Zoll. & Moritzi) Bakh. f., Bapel 1909 (S), Burma; Merrill 9383 (MO), Philippines; Krukoff 4128 (BR), Sumatra; Parkinson 4350 (MO), Thailand; Maxwell 88-228 (L.), Thailand.

Myrmeconaulceae stipulacea Ridsdale, Chai S37274 (L.), Malaysia; Myrmeconaulceae strigosa (Korth.) Merr., Slooten 2229 (L.), Borneo; Ridsdale 1954 (L.), Malaysia; Myrmeconaulceae sp., Kostermans 12872 (L.), Borneo.

Nauclea diderrichii (De Wild.) Merr., Louis 6123 (BR), R. D. Congo; Letouzey 5190 (BR), Cameroon; Nauclea officinalis (Pierre ex Pit.) Merr. & Chun, Smitinand & Bonpl., Soejarto et al. 8438 (L.), Philippines; Kostermans & Kuswata 68 (L.), Indonesia; Nauclea parva (Havil.) Merr., Haviland 134 (L.), Indonesia; Nauclea robinsonii Merr., Mendoza 61–450 (L.), Philippines; Nauclea subdita (Korth.) Steud., Endert 4085 (L.), Indonesia, Thakur Rap Chad 6173 (L.), India; Nauclea tenuiflora (Havil.) Merr., Sauveur 3348 (L.), New Guinea; Nauclea vanderguchtii (De Wild.) E. M. A. Petit, Le Testu 8308 (BR), Gabon; Louis 13736 (BR), R. D. Congo; Nauclea xanthoxylo- lon (A. Chev.) Aubrév., Tisserant 931 (BR), R. D. Congo.

Neolamarckia cadamba (Roxb.) Bosser, de Wilde & de Wilde 16959 (MO), Indonesia.

Neonauclea bartlingii (DC.) Merr., Mendoza 18462 (L.), Philippines; Neonauclea borneensis Ridsdale, Otthman et al. S41394 (L.), Malaysia; Neonauclea calycina (Bartl. ex DC.) Merr., Schmutz 3370 (L.), Lesser Sunda; Krukoff 4098 (BR), Sumatra; Neonauclea excelsa (Blume) Merr., de Wilde & de Wilde-Duyfes 20499 (L.), Indonesia; Neonauclea formicaria (Elmer) Merr., Madulid et al. 117820 (L.), Philippines; Neonauclea forsteri (Seem. ex Havil.) Merr., Mauri- asi & collectors 13859 (L.), Solomon Islands, Moerenhout 1831-4 (BR); W. Beer’s collectors 7271 (L.), Solomon Islands; Neonauclea maluensis (Valeton) S. Moore, Kalkman B3688 (BR), New Guinea; Neo-
nauclea obversifolia (Valeton) Merr. & L.M.Perry, Kalkman BW3688 (L.), New Guinea.

Ochreinaulea maingayii (Hook. f) Ridsdale, Kuntner 6424 (BR), Malaysia, Boschproeftasting 794 (L.), New Guinea.

Paracorynanthe antankarana Capuron ex J.-F. Leroy, SF-28718* (P), Madagascar; Paracorynanthe uropetala Capuron, SF-6788* (P).

Pausinystalia johimbe (Schumann) Pierre ex Beille, Le Testu 9075* (BR), Gabon; Zenker 1059* (WAG), Cameroon; Zenker 2883* (BR), Cameroon; Kennedy 2071* (BR), Nigeria; Pausinystalia lane-poolei (Hutch.) Hutch. ex Lane-Poole 3753 (BR), Gabon; Michelson 729* (BR), R. D. Congo; Michelson 1014* (BR), R. D. Congo; Michelson 1035* (BR), R. D. Congo; Pierce 792* (BR), R. D. Congo; Pierce 1048* (BR), R. D. Congo; Pausinystalia lane-poolei (Hutch.) Hutch. ex Lane-Poole ssp. lane-poolei, Voorhoeve 133 (BR), Liberia; Pausinystalia macroceras (K. Schum.) Pierre ex Beille, Bequaert 6694* (BR), R. D. Congo; Gérad 3900* (BR), R. D. Congo; Hart 289* (BR), R. D. Congo; Hart 862* (BR), R. D. Congo; Louis 4124* (BR), R. D. Congo; Toussaint 2175* (BR), R. D. Congo; Le Testu 8994* (BR), Gabon; Pausinystalia talbotti Wernham, Thomas 6843* (BR), Cameroon; Thomas & Nemb 5903* (WAG).

Pertusadina euryncha (Miq.) Ridsdale, Boschproeftasting 24 E3 F.T 844 (L.), Indonesia; Dr King’s Collector 7850 (BR), Malay Peninsula; Pertusadina multiflora (Havil.) Ridsdale, Elmer 15428 (L.), Philippines.

Pseudocinchona mayumbensis (Good) Raym.-Hamet, Louis 1737* (WAG), Gabon; Louis 2095* (WAG), Gabon; Wilks 1038* (WAG), Gabon; Wilks 820* (WAG), Gabon; Pseudocinchona pachyceras A. Chev., Eurard 1899* (BR), R. D. Congo; Lebrun 1542* (BR), R. D. Congo.

Sarcocephalus latifolius (Sm.) E. A. Bruce, Lebrun 2300 (BR), R. D. Congo; Billiet & Jadin 4069 (BR), R. D. Congo; Sarcocephalus pohbeguini Hua ex Pobé-G., Malaisse 4608 (BR), R. D. Congo; Bruneel 1906 (BR), R. D. Congo.

Sinoadina racemosa (Siebold & Zucc.) Ridsdale, Pierot s.n. (BR-S.P. 862487), Japan; von Siebold s.n. (L.), Japan; Tector s.n. (L.), Japan.

Uncaria africana G. Don, Meuanglango & Lelioyo 371 (BR), Tanzania; Friis et al. 7144 (BR), Ethiopia; Friis et al. 565* (BR), Ethiopia; Kisena 1472 (BR), Tanzania; Toussaint 476 (BR), Ethiopia; Eurard 2057 (BR), R. D. Congo; Ridsdale, Letouze 6111 (BR), Cameroon; Le Testu 1138 (BR), Gabon; Uncaria gambir (Hunther) Roxb., Corbisier-Baland 2055* (BR), R. D. Congo; Uncaria guianensis (Aubl.) J. F. Gmel., Taylor et al. 12870 (MO), Guiana; Uncaria hirsuta Havi., Odashima 17849* (BR), Taiwan; Uncaria talbotti Wernham, de Wilde 1076 (BR), Ivory Coast.

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