Spore Morphology of Malayan Dennstaedtiaceae sensu Holtttum

by

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Abstract

Spore morphology of 28 species belonging to 28 genera included by Holtttum (1954) in the Dennstaedtiaceae are described. Amongst the Malaysian taxa there are at least seven distinct spore-types. The disposition of the Malaysian genera in these spore-types does not conform with any of the existing systems of classification. Only spores of those genera assigned by Holtttum in the subfamilies Davallioideae, Dryopteridoideae and Tectarioideae show some degree of uniformity.

Introduction

The Dennstaedtiaceae as originally defined by Holtttum (1947, 1949, 1954) is a very large family of modern ferns, containing very diverse groups of genera and species. In the Peninsular Malaysia alone the family comprises not less than 48 genera and 203 species out of the total 124 genera and 389 species of its fern-flora. As has been shown in the excellent review by Pichi Sermolli (1973) and Mickel (1973), there seems to be a great controversy over the delimitation and classification of the taxa involved. Many authors, such as Christensen (1938), Ching (1940), Copeland (1947), Reimers (1954), Pichi Sermolli (1958), Nayar (1970) and others placed the 48 Malaysian genera involved in 5 or 10 separate families, whereas Holtttum (1954) included these genera in 11 subfamilies of the Dennstaedtiaceae, though later (1973) he more or less agrees with Pichi Sermolli’s system of classification. Furthermore, it is also evident that there is a great difference of opinion with regard to the disposition and affinity of the genera within each family or subfamily recognised by the above authors.

In an attempt to introduce a more natural system of classification of these taxa, many pteridologists (e.g. Atkinson, 1973; Lovis, 1973; Manton, 1961; Mickel, 1973; Sen & Sen, 1973; Sledge, 1973; Swain & Cooper-Driver, 1973; Van Cotthem, 1973; Walker, 1973, and others) have used modern and advanced techniques in their studies, previously unexploited by those who are responsible in drawing up the existing schemes of classification. Amongst these modern techniques are: anatomical, cytological, phytochemical, biochemical, developmental and palynological.

Of the palynological aspects, Erdtman & Sorsa (1971) have admirably summarised our present knowledge on the spore morphology of those genera included in the Dennstaedtiaceae by Holtttum. This work shows that of the total 3052 species so far recognised in the 48 genera occurring in Malaysia (Willis, 1973), spore descriptions of only 449 (= 14.7%) have been published by Harris (1955), Erdtman (1957), Nayar & Devi (1963, 1964a, 1964b, 1966, 1967, 1968a, 1968b), Nayar & Kaur (1963), Tardieu-Blot (1963a & b, 1965), and several others. Of these descriptions only a few were based on Malaysian specimens.
The present paper describes the spores of 28 species belonging to 28 genera, and is intended as a starting point for more intensive works to be done in the future.

Species Investigated

1. **DENNSTAEDETIODEAE**
   - Hypolepis bivalvis v.A.V.R.
   - Microlepia speluncae (L.) Moore
   - Orthiopetis kingii (Bedd.) Holtt.

2. **LINDSEAOIDEAE**
   - Isoloma diversgens (Hook. f. & Grev.) Sm.
   - Lindsea seandens Hook. f.
   - Sphenomeris chusana (L.) Copel.
   - Tapeinodium pinnatum (Cav.) Christ.

3. **DAVALLIOIDEAE**
   - Davalla divaricata Bl.
   - Humata heterophylla (Sm.) Desv.

4. **OLEANDROIDEAE**
   - Nephrolepis biserrata (Sw.) Schott.
   - Oleandra pistillaris (Sw.) Christ.

5. **PTERIDIOIDEAE**
   - Acrostichum aureum L.
   - Histiopteris stipulacea (Hook. f.) Copel.
   - Pieris viitata L.
   - Stenochlaena palustris (Burm.) Bedd.

6. **ASPLENIOIDEAE**
   - Asplenium nidus L. var. musifolia (Sm.) Bedd.

7. **BLECHNOIDEAE**
   - Blechnum orientale L.
   - Brainea insignis (Hook. f.) Sm.

8. **LOMARIOPSIDOIDEAE**
   - Bolbiis heteroelitta (Pr.) Ching
   - Egenolfa appendiculata (Willd.) Sm.
   - Elaphoglossum callifolium (Bl.) Moore
   - Lomagramma sumatrana v.A.V.R.
   - Teratophyllum aculeatum (Bl.) Mett.
   - var. montanum Holtt.

9. **DRYOPTERIDIOIDEAE**
   - Dryopteris sparsa (Don) O. Ktze.

10. **TECTARIOIDEAE**
    - Arcecypterys irregularis (Pr.) Holtt.
    - Heterogonium pinnatum (Copel.) Holtt.

11. **ATHYRIODEAE**
    - Athyrium pinnatum (Blanco) Copel.,
    - Cystopteris tenuisecta (Bl.) Mett.

Materials and Methods

In this study both fresh and herbarium materials were used. The fresh specimens were collected from various localities in Selangor and Pahang, and were identified with the help of Holttum's keys (1954). Voucher specimens are now deposited in the Herbarium, Department of Botany, University of Malaya, Kuala Lumpur (KLU). Dried and preserved materials were obtained from herbarium specimens available in the above Herbarium.

Spores containing materials were acetolysed, stained lightly with safranin, and mounted in glycerin jelly. The slides were then sealed permanently with paraffin wax. In some species, during acetolysis the perine was easily dissolved and the spores become shrivelled. In such cases, a lesser amount of concentrated sulphuric acid was added in the acetolysing mixture and heating was skipped. Although by this treatment, the spores did not become transparent, the perine remained intact and could be studied. Observation, measurement and photomicrography was carried out with a Leitz Dialux Microscope fitted with occular micrometer, Combi phot Automatic Camera System, achromatic condensor with N.A. 0.90, phaco achromatic objectives 40x /0.65 and 100X /1.30, and halogen lamp-housing model 100 Z.

For each species, measurement is based on 50 readings. This measurement is expressed in the text as length of polar axis (P) × longitudinal equatorial diameter (E1) × transverse equatorial diameter (E2) in monolet-bilateral spores and as P × E1 in triletetraedral spores. All measurements are exclusive of perine and any other processes.
Description of Spores

DENNSTAEDTIOIDEAE

1. Hypolepis bivalvis (Gunong Brinchang, Perak; Poore KLU 468; Plate 8, Figs. 4–7).

Spores monolete-bilateral, 30–46 × 48–61 × 33–46 μ. Amb oblong; proximal face flat, distal face hemispherical. Læsura 36–40 μ, margins thickened into protruding lips about 4 to 7 μ broad on either side of the læsura. Exine 2 μ thick, sexine thicker than nexine, with fine spinulose pattern. Perine thin and provided with minute spine-like processes.

2. Orthoöpteris kingii (Cameron Highlands, Pahang; Turnau KLU 2936; Plate 2, Fig 8).

Spores trilete-tetrahedral, 29–32 × 31–39 μ. Amb triangular in outline, with convex sides and broadly rounded corners. Proximal face conical, distal face convex to hemispherical. Læsura 15 μ, margins thickened into lips about 3 μ broad and tapering towards the tips. Exine 2 μ thick, sexine nearly as thick as nexine, smooth. Perine absent.

3. Microlepis speluncae (Templer Park, Selangor; Abd. Samat b. Abdullah KLU 2686; Plate 2, Figs. 6–7).

Spores trilete-tetrahedral, 25–33 × 30–33 μ. Amb triangular with strongly concave sides and broadly rounded corners. Proximal face slightly convex to flat; distal face hemispherical. Læsura 13 μ, margin thickened into lips of 2 μ broad and tapering towards the tips. Exine 2 μ thick, sexine as thick as nexine, densely granulose. Perine absent.

LINDSÆOIDEAE

4. Lindsaea scandens (Gunong Ulu Kali, Pahang; Abd. Samat b. Abdullah KLU 1846; Plate 2, Figs. 2–3).

Spores trilete-tetrahedral, 22–25 × 24–27 μ. Amb triangular, with slightly convex to straight sides. Proximal face conical with angular pole; distal face convex. Læsura 13 μ, margins thickened into lips of 1 μ broad. Exine 1 μ thick, not clearly subdivided into sexine and nexine, densely granulose. Perine absent.

5. Sphenomeris chusana (Fraser’s Hills, Pahang; Turnau KLU 2701; Plate 9, Fig. 3).


6. Isoloma divergens (Genting Simpah, Selangor; Mohd. Kassim b. Rajab KLU 139; Plate 2, Figs. 4–5).

Spores trilete-tetrahedral, 19–22 × 20–25 μ. Amb triangular with straight to slightly convex sides and broadly rounded corners. Proximal face conical with angular pole; distal face convex, Læsura 12 μ, margins thickened into lips of 1 μ broad. Exine 1.5 μ thick, sexine much thicker than nexine, smooth. Perine-like layer present, smooth, very closely adherent to the exine, and disintegrates very easily on acetolysis.

7. Tapeinidium pinnatum (Fraser’s Hills, Pahang; Khoo Eng Ee KLU 12307; Plate 9, Fig. 4).
Spores monolet-bilateral, 26–32 \( \times 28-46 \times 27-32 \) \( \mu \). Amb. oblong. Proximal face flat to slightly convex; distal face hemispherical. Laeura 32 \( \mu \), margins thickened into protruding lips of 6 \( \mu \) broad. Exine 1.5 \( \mu \) thick, sexine thicker than nexine, smooth. Perine thin with fine reticulate pattern, disintegrates easily on acetylosis.

DAVALLIOIDEAE

8. *Davalliadivaricata* (Fraser's Hills, Pahang; Khoo Eng Ee KLU 12309; Plate 6, Figs. 1–3).

Spores monolet-bilateral, 27–35 \( \times 36-50 \times 24-34 \) \( \mu \). Amb oblong. Proximal face concave; distal face convex. Laeura 28 \( \mu \), margins slightly thickened into lips of 2 \( \mu \) broad. Exine 2.5 \( \mu \) thick, sexine thicker than nexine, verrucose to rounded tuberculate; verrucae or tubercules crowded, 5–7 \( \mu \) in diameter and 2 \( \mu \) high. Perine absent.

9. *Humataheterophylla* (Lombong, Johore; Abd. Samat b. Abdullah KLU 1849; Plate 6, Figs. 4–8).

Spores monolet-bilateral, 22–36 \( \times 38-43 \times 28-32 \) \( \mu \). Amb oblong. Proximal face flat; distal face hemispherical. Laeura 18 \( \mu \), margins slightly thickened into lips of 1 \( \mu \) broad. Exine 3 \( \mu \) thick, sexine thicker than nexine, verrucose-tuberculose; tubercules crowded, round, 2 \( \mu \) high, 5–7 \( \mu \) broad and 10–16 \( \mu \) long. Perine absent.

OLEANDROIDEAE

10. *Oleandra pistillaris* (Fraser's Hills, Pahang; Khoo Eng Ee KLU 12310; Plate 4, Figs. 5–6).

Spores monolet-bilateral, 19–26 \( \times 27-32 \times 17-23 \) \( \mu \). Amb oblong. Proximal face flat; distal face hemispherical. Laeura 17 \( \mu \), margins slightly thickened into lips of 1 \( \mu \) broad. Exine 4–5 \( \mu \) thick, sexine thicker than nexine, smooth. Perine loosely wrinkled, anastomosing to form a reticulate patterns; folds about 4 \( \mu \) high, spinulose; spinules minutes, less than 1 \( \mu \) high, with pointed tips. Perine disintegrates very easily on acetylosis.

11. *Nephronepis biserrata* (Damansara Road, Kuala Lumpur, Selangor; Khoo Eng Ee KLU 12305; Plate 7, Figs. 3–4).

Spores monolet-bilateral, 25–30 \( \times 33-40 \times 23-29 \) \( \mu \). Amb oblong. Proximal face flat to slightly concave; distal face convex. Laeura 20 \( \mu \), margins thickened into lips of 1 \( \mu \) broad, tapering towards the tips. Exine 2 \( \mu \) thick, sexine thicker than nexine, verrucose to tuberculose; verrucae 1 \( \mu \) high and 4–6 \( \mu \) broad. Perine thin, more or less verrucose and easily disintegrates on acetylosis.

PTERIDIOIDEAE

12. *Histiopteris stipulacea* (Fraser's Hills, Pahang; Khoo Eng Ee KLU 12306; Plate 7, Figs. 1–2).

Spores monolet-bilateral, 38–48 \( \times 59-65 \times 43-46 \) \( \mu \). Amb oblong. Proximal face slightly concave; distal face convex. Laeura 40 \( \mu \), margins thickened slightly into lips of 6–10 \( \mu \) broad and tapering towards the tips. Exine 5 \( \mu \) thick, sexine thicker than nexine, densely verrucose-tuberculose; verrucae or tubercles granulose, 5 \( \mu \) high, 6 \( \mu \) broad, and 8–22 \( \mu \) long. Perine absent.

13. *Pterisvittata* (Fraser's Hills, Pahang; Khoo Eng Ee KLU 12306; Plate 1, Figs. 1–3).

Spores triletetrahemeral, 48–53 \( \times 61-65 \) \( \mu \). Amb triangular with nearly straight sides and rounded corners. Proximal face flat to slightly convex; distal
face hemispherical. Laesura 27 μ, margins thickened into lips of 3 μ broad and tapering towards the tips. Exine 3 μ thick, sexine much thicker than nexine, densely rugulose; rugulae up to 6 μ tall, sometimes coalescing to form a coarse reticulum. On the proximal face there are 3 ridges parallel and close to the laeura arms. Equator collar present; this is a collar-like ridge which protrudes as a flange around the spores, separating the proximal and the distal parts of the spores, up to 7 μ high, often interrupted. Perine absent.

14. *Acrostichum aureum* (Lukut, Negeri Sembilan; Turnau KLU 2925; Plate 2, Fig. 1).

Spores trilete-tetrahedral, 42–49 × 50–60 μ. Amb rounded triangular with slightly convex sides and broadly rounded corners. Proximal face conical with straight sides and angular pole; distal face hemispherical. Laeura 21 μ, margins thickened into lips of 1 μ broad and tapering towards the tips. Exine 2 μ thick, sexine thicker than nexine, granulose. Perine not seen.

15. *Stenochlaena palustris* (Damansara Road, Kuala Lumpur, Selangor; Khoo Eng Ee KLU 12311; Plate 7, Figs. 5–6).

Spores monolette-bilateral, 30–37 × 39–53 × 30–36 μ. Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laeura 29 μ, margins thickened into lips of 1 μ broad. Exine 3 μ thick, sexine thicker than nexine, provided with conical tubercles of 2 μ tall with rounded tips and base diameter of 2 μ. Perine absent.

**ASPLENIIOIDEAE**

16. *Asplenium nidus* var. *musifolia* (Damansara Road, Kuala Lumpur; Khoo Eng Ee KLU 12304; Plate 3, Figs. 1–2).

Spores monolette-bilateral, 27–36 × 30–50 × 27–32 μ. Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laeura 20 μ, margins thickened slightly into lips of 3 μ broad. Exine 1 μ thick, sexine as thick as nexine, smooth. Perine finely granulose, wrinkled into discontinuous, closely sinuous folds protruding up to 3 μ from the exine surface, with smooth crests.

**BLECHNOIDEAE**

17. *Blechnum orientale* (Ulu Gombak Road, Selangor; Khoo Eng Ee KLU 12308; Plate 3, Figs. 3–4).

Spores monolette-bilateral, 34–39 × 44–51 × 36–46 μ. Amb oblong. Proximal face flat; distal face hemispherical. Laeura 29 μ, margins thickened into lips 3 μ broad and tapering towards the tips. Exine 1 μ thick, sexine as thick as nexine, smooth. Perine sparsely granulose, loosely folded into sparse, thin indistinct folds protruding up to 3 μ from the exine surface, with smooth crests; disintegrates easily on acetolysis.

18. *Brainea insignis* (Tanjong Selantai, Johore; Abd. Samat b. Abdullah KLU 1869; Plate 10, Figs. 4–6).

Spores monolette-bilateral, 31–42 × 35–50 × 29 43 μ. Amb oblong to subspherical. Proximal face slightly convex; distal face hemispherical. Laeura 27 μ, margins thickened into lips of 1 μ thick and tapering towards the tips. Exine 2 μ thick, sexine as thick as nexine, smooth. Perine densely granulose, closely adherent to the exine nearly without folds or only with one or two indistinct short folds which protrude up to 2 μ from the exine surface; disintegrates easily on acetolysis.
LOMARIOPSIDOIDEAE

19. *Egenolfia appendiculata* (Kuah, Langkawi, Kedah; Abd. Samat b. Abdullah KLU 2316; Plate 10, Fig. 3).

Spores monolet-bilateral, 32–36 \( \times \) 31–39 \( \times \) 26–37 \( \mu \). Amb subspherical to circular in outline. Proximal face flat to slightly convex; distal face hemispherical. Laesura 19 \( \mu \), slightly thickened into lips of 1 \( \mu \) broad; in some spores forked in one end. Exine 1 \( \mu \) thick, sexine as thick as nexine, smooth. Perine with finely reticulate patterns, loose, lightly folded into very many elongated sharp ridges most of which radiate from the centre to the periphery of the spores and protruding up to 7 \( \mu \) from the exine surface; disintegrates on acetylation.

20. *Bolbitis heteroclitica* (Jengka Forest Reserve, Pahang; Turnau KLU 2894; Plate 10, Figs. 1–2).

Spores monolet-bilateral, 31–37 \( \times \) 35–42 \( \times \) 35–38 \( \mu \). Amb oblong to subspherical. Proximal face flat to convex; distal face hemispherical. Laesura 21 \( \mu \), margins slightly thickened into smooth lips of 1 \( \mu \) broad. Exine 1 \( \mu \) thick, sexine as thick as nexine, smooth. Perine sparsely covered with minute spinules, highly folded into sinuous and elongated ridges radiating from the centre to the periphery of the spores; folds protrude up to 12 \( \mu \) from the exine surface, with undulating crests; disintegrates on acetylation.


Spores monolet-bilateral, 47–60 \( \times \) 66–71 \( \mu \) (polar view not obtained). Proximal face convex to hemispherical; distal face hemispherical. Laesura 27–30 \( \mu \). Exine very thin, less than 1 \( \mu \) thick, not subdivided into distinct sexine and nexine. Perine densely crowded with minute spinules less than 1 \( \mu \) high, very sparsely folded into faint folds which protrude up to 19 \( \mu \) from the exine surface; with smooth crests; cracked up on acetylation.

22. *Lomagramma sumatranum* (22nd mile Bentong Road, Selangor; Turnau KLU 2914; Plate 9, Figs. 1–2).

Spores monolet-bilateral, 31–43 \( \times \) 50–58 \( \times \) 35–40 \( \mu \). Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laesura 29 \( \mu \), margins slightly thickened into lips of 1 \( \mu \) broad. Exine 2 \( \mu \) thick, sexine slightly thinner than nexine, finely granulose to spinulose. Perine absent.

23. *Elaphoglossum callifolium* (Tanah Rata, Pahang; Mahmud b. Sider KLU 4612; Plate 4, Figs. 1–2).

Spores monolet-bilateral, 18–30 \( \times \) 23–40 \( \times \) 18–22 \( \mu \). Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laesura 18 \( \mu \). Exine 1 \( \mu \) thick, sexine and nexine are not clearly differentiated, smooth. Perine minutely spinulose, sparsely folded into thin, sharp sinuous ridges protruding up to 7 \( \mu \) from the exine surface; disintegrates on acetylation.

DROOPTERIDOIDEAE

24. *Dryopteris sparsa* (Maxwell Hills, Perak; Evans KLU 2493; Plate 3, Figs. 5–6).

Spores monolet-bilateral, 22–27 \( \times \) 38–46 \( \times \) 28–31 \( \mu \). Amb oblong. Proximal face flat to slightly concave; distal face convex. Laesura 20 \( \mu \), margins thickened very slightly into lips of 1 \( \mu \) broad. Exine 1 \( \mu \) thick, sexine as thick as nexine, smooth. Perine smooth, fairly closely adherent to the exine, folded into lobate crowded ridges protruding up to 11 \( \mu \) from the exine surface; with many undulating crests; disintegrates on acetylation.
25. *Arcypteris irregularis* (Ulu Gombak Road, Selangor; Wee & Lim KLU 1975; Plate 5, Figs. 4–6).

Spores monolet-bilateral, 20–29 × 32–39 × 23–26 μ. Amb oblong. Proximal face flat; distal face hemispherical. Laesura 20 μ, margins faintly thickened into lips of 1 μ broad. Exine 1.5 μ thick, sexine as thick as nexine, smooth. Perine with very minute spinules, folded into a few elongated sharp, thin ridges radiating from the centre to the periphery of the spores; folds protrude up to 10 μ from the exine surface; disintegrates easily on acetylation.


Spores monolet-bilateral, 28–40 × 40–50 × 33–36 μ. Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laesura 27 μ, margins faintly thickened into lips of 1 μ broad. Exine 2 μ thick, sexine as thick as nexine, smooth, breaking up on acetylation. Perine minutely spinulose (spines less than 1 μ tall), highly folded up into elongated, closely sinuous ridges protruding up to 6 μ from the exine surface; disintegrates on acetylation.

**ATHYRIODAE**

27. *Athyrium pinnatum* (Genting Simpah, Selangor; Turnau KLU 2785; Plate 9, Figs. 5–6).

Spores monolet-bilateral, 20–27 × 33–44 × 24–25 μ. Amb oblong. Proximal face flat to convex; distal face hemispherical. Laesura 23 μ, margins faintly thickened into lips of 1 μ broad. Exine 2 μ thick, sexine as thick as nexine, smooth. Perine faintly granulose, closely adherent to the exine, with a few folds; folds appear as irregular ridges protruding up to 2 μ from the exine surface; disintegrates on acetylation.

28. *Cystopteris tenuisecta* (Cameron Highlands, Pahang; Poore KLU 256; Plate 8, Figs 1–3).

Spores monolet-bilateral, 30–45 × 45–60 × 31–45 μ. Amb oblong. Proximal face flat to slightly concave; distal face hemispherical. Laesura 30 μ, margins slightly thickened into lips of 1 μ broad. Exine 2 μ thick, sexine thicker than nexine, densely finely spinulose. Perine folded; folds anastomose to form dense reticulum, provided with numerous rod-like protuberances about 3–4 μ high; tips of rods peltately lobed.

**Discussion**

Spore morphology of 28 Malaysian species included by Holttum (1954) in the Dennstaedtiaceae shows a great diversity of form, size and structure. Based on whether the spores are monolet-bilateral or trilette-tetrahedral, with or without perine, and perine if present smooth or variously patterned, etc., there seem to be at least seven distinct types of spores. These spore-types are:

Type-1: Spore trilette-tetrahedral, provided with well-developed equatorial collar (*Pteris vittata*).

Type-2: Spore trilette-tetrahedral, without equatorial collar, without or occasionally with a thin spinulose perine (*Acrastichium aureum*, *Isoloma diversgens*, *Lindseae scandens*, *Microlepia speluncae*, and *Orthopteris kingii*).

Type-3: Spore monolet-bilateral, provided with folded or reticulate perine, plano-convex or concave-convex in equatorial view (*Asplinum nidus* var. *musifolia*, *Blechnum orientale*, *Dryopteris sparsa*, *Elaphoglossum callifolium*, *Heterogonium pinnatum*, *Oleandra pistillaris*, *Arcypteris irregularis*, and *Teratophyllum aculeatum*).
Type-4: Spore monolette-bilateral, without or occasionally with very thin perine, exine provided with low, flattish, roundish or conical protuberances (*Davallia divaricata, Histiopteris stipulacea, Humata heterophylla, Nephrolepis biserrata, and Stenochlaena palustris*).

Type-5: Spore monolette-bilateral, plano-convex, perine provided with spine-like or rod-like blunt processes (*Cystoiopteris tenuisecta, Hypolepis bivalvis*).

Type-6: Spore monolette-bilateral, concave-convex or plano-convex, with or without perine; perine if present thin, hardly folded and easily dissolved on acetolysis (*Athyrium pinnatum, Lomagrimma sumatrana, Sphenomeris chusana, and Tapeinidiium pinnatum*).

Type-7: Spore monolette-bilateral, biconvex or sometimes plano-convex, provided with folded, reticulate or finely patterned perine (*Bolbitis heteroclita, Brainea insignis, and Egenolfia appendiculata*).

In the Dennstaedtioidaeceae, Holtttum included *Dennstaedtia, Hypolepis, Microlepia* and *Orthoiopteris*. *Hypolepis* with a monolette-bilateral spore of type-5 seems to be out of place in this subfamily, since the other three genera have triletetrahtedral spores of type-2. Furthermore, the perine in *Hypolepis* is provided with spine-like or rod-like minute processes, while the perine of *Dennstaedtia* and *Orthoiopteris*, if present, is not so patterned, and in *Microlepia* the spores are without perine. Erdtman & Sorsa (1971) included these four genera in the family Pteridaceae in which 52 out of 65 genera have exclusively triletetrahtedral spores, 7 possess mainly trilette but occasionally also monolette spores, and 6 genera with exclusively monolette-bilateral spores. Apart from *Hypolepis*, the other five genera which have exclusively monolette-bilateral spores are:— *Humblottella, Tapeinidiium, Sphenomeris, Paeasia, and Lonchitis*. Perine of these genera, if present, is very thin, hardly folded and is easily detached from the exine on acetolysis, unlike that of *Hypolepis*. In Holtttum’s classification, *Tapeinidiium* and *Sphenomeris*, on the other hand, were grouped together with *Lindsaea, Schizoloma* and *Isoloma* in the Lindseaeoideae. Spore morphology does not support this grouping, since both *Isoloma* and *Lindsaea* have a triletetrahtedral spore of type-2, whereas *Sphenomeris* and *Tapeinidiium* have a monolette-bilateral spore of type-6.

Of the Davallioideae, the four genera (i.e. *Araiooegia, Davallia, Humata*, and *Leucostegia*) assigned by Holtttum (1954) in this subfamily have a more or less similar spore-type, namely monolette-bilateral, without perine, and the exine is provided with low flattish verrucae or tubercles (spore type-4). For these features, the spores of *Nephrolepis, Histiopteris* and *Stenochlaena* agree very well. Holtttum (1954), on the other hand, placed *Nephrolepis* together with *Oleandra* in the Oleandroideae. Spores of *Oleandra* are, however, different from those of *Nephrolepis* by being provided with folded perine, the detailed structure of which matches very well with that of *Elaphoglossum, Arcypetis*, and *Teratophyllum* (spore type-3). *Histiopteris* and *Stenochlaena* together with *Acrostichum, Pteridium* and *Pteris* were included by Holtttum (i.e.) in the Pteridoideae. *Acrostichum* and *Pteridium* possess a triletetrahtedral spores of type-2, whereas *Pteris* has spores of type-1.

The genus *Asplenium* (included by Holtttum in the Asplenioidae) has spores which are very much similar to those of *Blechnum* and *Heterogonium* (spore type-3). However, *Blechnum* was assigned by Holtttum in the Blechnoideae together with *Brainea* and *Woodwardia*. While spores of *Woodwardia* match very well with those of *Blechnum*, that of *Brainea* being monolette-bilateral, biconvex and provided with folded, granulose-reticulose perine, agree well with the spores of *Bolbitis* and *Egenolfia* (spore type-7). The last two mentioned genera were placed together with *Elaphoglossum, Lomagrimma, Lomariopsis* and *Teratophyllum* in the Lomariopsidoideae by Holtttum. While spores of *Elaphoglossum* and *Teratophyllum*
are very much similar to that of Oleandra and Tectaria (spore type-3), those of Lomagramma, being without perine, agree well with the spores of Athyrium, Sphenomeris and Tapeinodium (spore type-6). According to Erdtman & Sorsa (1971), some species of Lomariopsis possess perinourous spores similar to those described as type-3, while others have a spore of type-6.

In the Dryopteridioideae, Holttum assigned Acrophorus, Diacalpe, Didymochlaena, Dryopteris, Polystichum and Polystichopsis. These genera have more or less uniform spores which match very well with those of Asplenium, Blechnum and Heterogonium (Spore type-3). Similarly, the spores of ten genera included by Holttum in the Tectarioideae (Acreperis, Ctenitis, Cyclopetelis, Heterogonium, Hypodematum, Lastreopsis, Pleocnemia, Pteridrys, Quercifilix and Tectaria) agree well with each other and more or less similar to those of spore type-3.

Of the Athyroideae, Holttum place two Malaysian genera, namely Athyrium and Cyatopterus. As has been indicated above, the spores of Athyrium belong to spore type-3, whereas those of Cyatopterus to spore type-5.

The above discussion seems to indicate that apart from the Davallioideae, Dryopteridioideae and Tectarioideae, the other subfamilies of the Dennstaedtiaceae as defined by Holttum, show very diverse types of spores and that spore morphology does not lend any support to the disposition of various genera either in the different subfamilies as recognized by Holttum (1954) or in the various families as subscribed by Copeland (1947), Reimers (1954), Pichi Sermolli (1958) and others.

However, this does not imply that the classification of the genera included by Holttum in the Dennstaedtiaceae should match well with the spore types, but rather that it demonstrates that more palynological studies, especially on those of the tropical taxa should be done, so that morphological characters of the spores could be considered along with other attributes in constructing a more natural system of classification.

Finally, it should be emphasised here that, since the number of species of which the spores have been studied in detail, is very small, and that, it is also well known that even within a single genus the spore morphology may vary considerably, the above findings should be considered with great caution.

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References


Plate 1. Figs. 1–3: *Pteris vittata*; 1 — pr.p.v. spore in the centre is in optical section; 2 — oblique view; 3 — detailed structure of distal polar wall of perine layer.

(abbrev. in legends: pr.p.v. = proximal polar view, oblique view, d = distal)
Plate 2. Fig. 1 — *Acrostichum aureum*, pr.p.v.; figs. 2 & 3 — *Lindsaea scandens*, pr.p.v. & c.v. respectively; figs. 4 & 5: *Isoloma divergens*, 4 — pr.p.v., 5 — optical section of 4; figs. 6 & 7: *Microlepia speluncae*, 6 — pr.p.v., 7 — optical section of 6; fig. 8 — *Orthiopteris kingii*, optical section of pr.p.v.
Plate 7. Figs. 1 & 2: Histiopteris stipulacea, 1 — e.v., 2 — obl.pr.p.v.; figs. 3 & 4 Nephrolepis biserrata, 3 — pr.p.v., 4 — e.v.; 5 & 6: Stenochlaena palustris, 5 — pr.p.v. in optical section, 6 — e.v. in optical section.
Plate 9. Figs. 1–2: Lomagramma sumatrana, 1 — e.v., 2 — obl.pr.p.v.; fig. 3 — Sphenomeris chusana, obl.e.v.; fig. 4 — Tapeinidium pinnatum, obl.e.v.; figs. 5 & 6: Athyrium pinnatum, 5 — obl.pr.p.v., 6 — e.v.
Plate 10. Figs. 1 & 2 — Bolbitis heteroclitica, obl.e.v.; fig. 3 — Egenolfia appendiculata, d.p.v., figs. 4–6: Brainea insignis, 4 — obl.e.v., 5 — pr.p.v. in optical section, 6 — d.p.v.