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SEM Studies on Spore in Taiwanese Fern Genera I. Athyrioids

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ABSTRACT: The spores of fifty-six Athyrioid fern species in eleven genera from Taiwan were examined under SEM. The surface ornamentation of each genus was described. Based on the palynological data, the taxonomy and systematic affinity of the genera and their subdivisions proposed by different workers are discussed.

KEYWORDS: Athyrioid, Spore ornamentation, Palynology, Taiwan.

INTRODUCTION

Palynological data are very useful for taxonomic purposes at all level of fern family and its below (Kramer and Tryon, 1990). However, botanists did not pay much attention to the spore of ferns until 1850's (Erdtman, 1971; Wagner, 1974). Since then, spore characters from light microscopy (LM) and electron microscope (EM), especially scanning electron microscopy (SEM), studies have played an important role in the studies of fern classification and phylogeny. As indicated in the world-wide comprehensive treatment of fern spores (Tryon and Lugardon, 1990), the integration of LM and EM studies in the generic level is needed for the delineation of systematic and evolutionary relationships of the genera. The LM studies of Taiwanese fern spores are extensive (Chen and Huang, 1974; Huang, 1981), but there are only a few SEM studies available (Liew, 1976a, b, c, 1977; Liew and Wang, 1976) for advancing our knowledge. In order to improve our understanding of the systematic relationships among Taiwanese fern genera, this SEM study of the Athyrioid ferns represents the first part of an ongoing project of redelimitating Taiwanese fern genera. The Athyrioids ferns were chosen because a reasonably satisfactory classification is still lacking (Tryon and Tryon, 1982), and the affinities between genera in this group is still uncertain. We studied the SEM image of Taiwan Athyrioid materials and compared their ornamentation of spore surfaces, and hoped the affinity between and within each genus resulted from this study can be used in the future improvement of fern taxonomy.

MATERIALS AND METHODS

Fifty-six species in eleven genera (Table 1) were examined. The delimitation and nomenclature scheme of the Athyrioid ferns and their genera were adapted from Kato and Kramer (1990). The Athyrioid ferns were placed under Dryopteridiaceae, subfamily Athyrioideae, tribe Physematieae, including *Hypodematium* and *Woodsia*. The last two genera could be classified into other families by other botanists (e. g. Wu and Ching, 1991; Shieh *et al.*, 1994). The species delimitation and nomenclature followed Kuo (1999).

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Table 1. List of voucher specimens.

Taxon	Voucher Specimen and Collecting Location	Relative Synonym
Athyrium Roth.		
A. anisopterum Christ	Nantou: Meifon, *Y. H. Chang 1649* (TAI) Pingtung: Chingshuiyin, *Y. C. Liu 2216* (NSYSU)	
A. arisanense (Hayata) Tagawa	Nantou: Hsinzengun, *M. L. Weng 388* (TAI)	
A. atkinsoni Beddome	Nantou: Hsinzengun, *Y. H. Chang 1656* (TAI)	Pseudocystopteris atkinsoni (Beddome) Ching
A. cryptogrammoides Hayata	Ilan: Nanhutashan, *Y. C. Liu 1917* (NSYSU)	
A. cumingianum (Presl) Milde	Pingtung: Shehchiehkengchi, *Y. C. Liu 1894* (NSYSU)	Anisocampium cumingianum Presl
A. drepanopterum (Kunze) A. Br. ex Milde	Nantou: Chunyan, *M. F. Kao 3745* (TAI)	
A. erythropodum Hayata	Chayi: Fenchihu, *C. M. Kuo 1654A* (TAI)	
A. foliolosum Sim.	Hsinchu: Kwanwu, *J. C. Wang and K. C. Yang 4838* (TAI)	
A. iseanum Rosenst	Nantou: Lushan, *M. T. Kao 7961* (TAI)	
A. kuratae Serizawa	Nantou: Zeiyanchi, *Y. H. Chang 2502* (TAI)	
A. nakanoi Makino	Taoyuan: Lalashan, *Y. H. Chang 2284* (TAI)	
A. nigripes (Bl.) Moore	Nantou: Tatachia, *C. C. Liu 423* (TAI)	
A. nipponicum (Mett.) Hance	Nantou: Salisenchi, *C. C. Liu 495* (TAI)	
A. oppositipinnum Hayata	Nantou: Salisenchi, *W. H. Hu 970* (TAI)	
A. reflexipinnum Hayata	Ilan: Nanhutashan, *Y. C. Liu 1945* (NSYSU)	
A. silvicolum Tagawa	Taichun: Sheueshantungfon, *Y. H. Chang 1670* (TAI)	
A. subrigescens (Hayata) Hayata ex H. Ito	Nantou: Salisenchi, *T. Y. Chiang 23093* (TAI); Hualein: Hoping Logging Trail, *M. F. Kao 1673* (TAI)	
A. tozanense (Hayata) Hayata	Nantou: Tatacha, *C. C. Liu 423* (TAI)	
A. vidalii (Fr. & Sav.) Nakai	Nantou: Meifon, *M. F. Kao 3704* (TAI)	
Diplazium Sw.		
D. amamianum Tagawa	Hualien: Shinchenshan, *M. F. Kao 3572* (TAI)	
D. contermina Christ.	Nantou: Meifon, *B. J. Wang 14883* (TAI)	Allantodia contermina (Chr.) Ching
D. dilatatum Bl	Pingtung: Maichu, *T. T. Chen 2310* (NSYSU)	Allantodia dilatata (Blume) Ching
D. doederleinii (Luerss.) Makino	Taipei: Wulai, *C. M. Kuo 16440* (TAI)	Allantodia doederleinii (Luerss.) Ching

Table. 1. Continued.

Taxon	Voucher Specimen and Collecting Location	Relative Synonym
D. donianum (Mett.) Tard.-Blot	Pingtung: Showka, *T. T. Chen 3676* (NSYSU)	
D. esculentum (Retz.) Sw.	Taoyuan: Hsiaowulai, *C. M. Kuo 15778* (TAI)	Callipteris esculentum (Retz.) J. Sm. Anisogonium esculentum (Retz.) Presl
D. incomptum Tagawa	Taipei: Wulai, *C. M. Kuo and W. H. Hu, 15661* (TAI)	Allantodia incompta (Tagawa) Ching
D. kawakamii Hayata	Pingtung: Tahanshan, *T. T. Chen 4502* (NSYSU)	Allantodia kawakamii (Hayata) Ching
D. lobatum (Tagawa) Tagawa	Taipei: Hoshan, *M. F. Kao 2107* (TAI)	
D. sp. closed to *D. lobatum.*	Taipei: Hsiangshan, *Y. H. Chang 680* (TAI)	
D. megaphyllum (Bak.) Christ	Hualein: Shinchenshan, *M. F. Kao 3407* (TAI)	Allantodia megaphylla (Bak.) Ching
D. mettenianum (Miq.) C. Chr.	Nantou: Shanlinchi, *M. F. Kao 1825* (TAI) Hsingchu: Litungshan, *Y. C. Liu 2286* (NSYSU)	Allantodia metteniana (Miq.) Ching
D. okinawaense Tagawa	Taoyuan: Tungyanshan, *Y. H. Chang 488* (TAI)	
D. petri Tard. -Blot	Pingtung: Chingshuiyin, *Y. C. Liu 2246* (NSYSU)	Allantodia petri (Tard.-Blot) Ching
D. prolifera (Lam.) Kaulf	Pintung: Beinanshan, *M. L. Weng s.n.* (TAI)	Callipteris prolifera (Lam.) Bory
D. pseudo-doederleinii Hayata	Nantou: Salisenchi, *T. Y. Chiang 26297* (TAI)	Allantodia pseudo-doederleinii (Hayata) Ching
D. pullingeri (Bak.) J. Sm.	Pingtung: Chingshuiyin, *Y. C. Liu 2218* (NSYSU)	Monomelangium pullingeri (Bak.) Tagawa
D. subsinuatum (Wall. ex Hook.& Grev.) Tagawa	Taipei: Syhshoushan, *M. F. Kao 3623* (TAI)	Triblemma lancea (Thunb.) Ching
D. taiwanense Tagawa	Taipei: Mientanshan, *Y. H. Chang 1617* (TAI)	
D. uraiense Rosenst	Taipei: Huantindan, *C. M. Kuo 15441* (TAI)	
D. wichurae Diels	Nantou: Chenyuanlanchi, *T. U. Chiang* 27029 (TAI)	Allantodia wichurae (Mett.) Ching
Dictydroma Ching		
D. formosana (Rosenst.) Ching	Taipei: Wulai, *M. F. Kao 3786* (TAI)	Diplazium formosanum Rosenst.
Diplaziopsis C. Chr.		
D. javanica (Blume) C. Chr.	Ilan: Fushan Botanical Garden, *M. L. Weng s.n.* (TAI)	Diplazium javanicum (Bl.) Makino
Deparia Hook et Grev.		
D. allantodioides (Bedd.) M. Kato	Ilan: Nanhutashan, *Y. C. Liu 1928* (NSYSU)	Lunathyrium pycnosorum (Chr.) Koidz. Athyrium pycnosorum Chr.

Table. 1. Continued.

Taxon	Voucher Specimen and Collecting Location	Relative Synonym
D. petersenii (Kunze) M. Kato	Pingtung: Tahashan, *T. T. Chen 4306, 4314* (NSYSU)	Athyriopsis japonica (Thunb.) Ching Athyrium japonica (Thunb.) Copel.
D. subfluvialis (Hayata) M. Kato	Nantou: Salisenchi, *T. Y. Chiang 26296* (TAI)	Dryoathyrium boryanum (Wild.) Change Athyrium boryanum (Wild.) Tagawa
Cornopteris Nakai		
C. decurrenti-alatum (Hook.) Nakai	Ilan: Yulin Hostel, *Y. C. Liu 1927* (NSYSU)	
C. fluvialis (Hayata) Tagawa	Ilan: Yulin Hostel, *Y. C. Liu 1946* (NSYSU); Pingtung: Chingshuiyin, *Y. C. Liu 1943* (NSYSU)	
C. opaca (Don) Tagawa	Pingtung, Chingshuiyin, *Y. C. Liu 2371* (NSYSU)	
Cystopteris Bernh.		
C. fragilis (L.) Bernh.	Ilan: Nanhutashan, *Y. C. Liu s.n.* (NSYSU)	
C. moupinensis Franchet	Ilan: Nanhutashan, *Y. C. Liu 1943* (NSYSU)	
Acystopteris Nakai		
A. japonica (Luerss.) Nakai	Ilan: Nanhutashan, *C. M. Kuo 15657* (TAI)	Cystopteris japonica Luerss.
A. tenuisecta (Blume) Tagawa	Hsingchu: Litungshan, *Y. C. Liu 2295* (NSYSU)	Cystopteris tenuisecta (Bl.) Mett.
Gymnocarpium Newman		
G. oyamense (Bak.) Ching	Kaohsiung: Kueiko-Yakou, *Y. C. Jeng s.n.* (TNM)	
G. remote-pinnatum (Hayata) Ching	Taichung: Pilushan, *H. S. Lin and C. K. Lin s.n.* (TNM)	
Hypodematium Kunze		
H. crenatum (Forsk.) Kuhn	Pingtung: Tahan Logging Trail, *Y. C. Liu 1619* (NSYSU)	included in Aspidiaceae or Hypodematiaceae
Woodsia R. Brown		
W. polystichoides Eaton	Nantou: Nankao, *Y. Tateishi et al. 18167* (TAI)	included in Woodsiaceae

Spores were collected from dry specimens, deposited in Herbarium of National Taiwan University (TAI), Herbarium of National Museum of Natural Science (TNM) and Herbarium of National Sun Yat-sen University (NSYSU). The spores were untreated and fixed on the alumni stubs from specimens, coating with gold about 15 nm thin by iron sputter (HITACHI E-101) and examined under a scanning electron microscope (HITACHI S2400) at 12-18 kV, 1,500-2,000X for whole spore and 8,000-10,000X for surface detail, photographed with Kodak TMX films. The terminology and classification of spore surface ornamentation followed Lellinger and Taylor (1997).

Genera Description of Spore Ornamentation

The spores of Athyrioid ferns are brown without chlorophyll, monolete, ellipsoid, bean-shape or rarely spheroid. The morphology of perispore is basically species-specific, but *Diplazium* species with rugate-retate types are not easily differentiated. There are three general perispore classes in Athyrioid ferns: bulliform, muriform and steliform.

Athyrium Roth (Figs. 1-12)

Nineteen species were examined, and the general perispore class is muriform. Three types of perispore macro-ornamentation are found:

1. Rugate type Figs. 1-4

Perispore are in thin fold, usually with incomplete, easily detached outer layers. There are two kinds of inner perispore surfaces, granulate in *A. foliolosum, A. kuratae, A. oppositipinnum, A. silvicolum, A. tozanense, A. vidalii* and *A. yakushimense*, and retate in *A. nigripes* and *A. subrigescens*. The inner perispore surface in *A. silvicolum* is covered with looser and relative large grains which more or less fusing with neighboring and is with minute grains at the bases of large grains.

2. Cristate-Retate type Figs. 5-10

Perispore muri-bearing folds are low except high in *A. nakanoi*. *Athyrium niponicum* has perispore varied from cristate to retate type (Figs. 5-6). Other seven species, *A. anisopterum, A. atkinsoni, A. cryptogrammoides, A. drepanopterum, A. iseanum, A. nakanoi,* and *A. reflexipinnum* have perispores in retate type (Figs. 7-10). The perispore surfaces of most species are plain, but *A. nakanoi* (Figs. 9-10) are bacillate and occasionally with pits.

3. Reticulate type Figs. 11-12

Perispore muri-bearing folds are wing-like and with fimbriate borders. The surfaces in the areolae are irregularly foveolate. This group has only one species, *A. cumingianum*.

Diplazium Swartz (Figs. 13-28, 56-57)

Twenty-one species were examined. The general perispores classes of *Diplazium* are bulliform, steliform and muriform. Six perispore macro-ornamentation types are found:

1. Baculate type Figs. 13-14

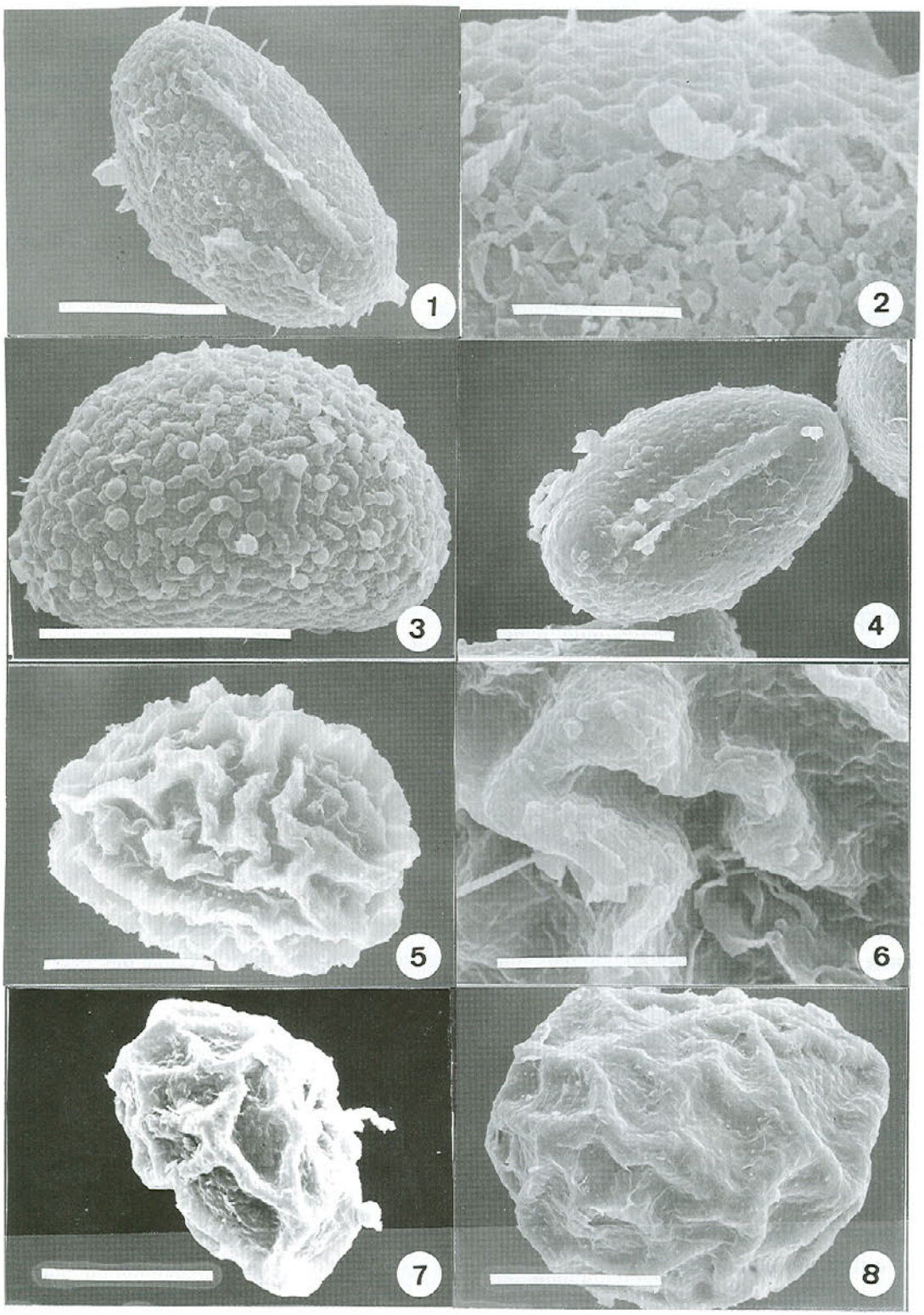
Perispore is stelliform and not folded. The stela apex is obtuse. The surface of perispore, including the apex of baculate process, is slightly rugate and papillate. There is only one species with this type: *D. subsinuatum*.

2. Echinate type Figs. 15-16

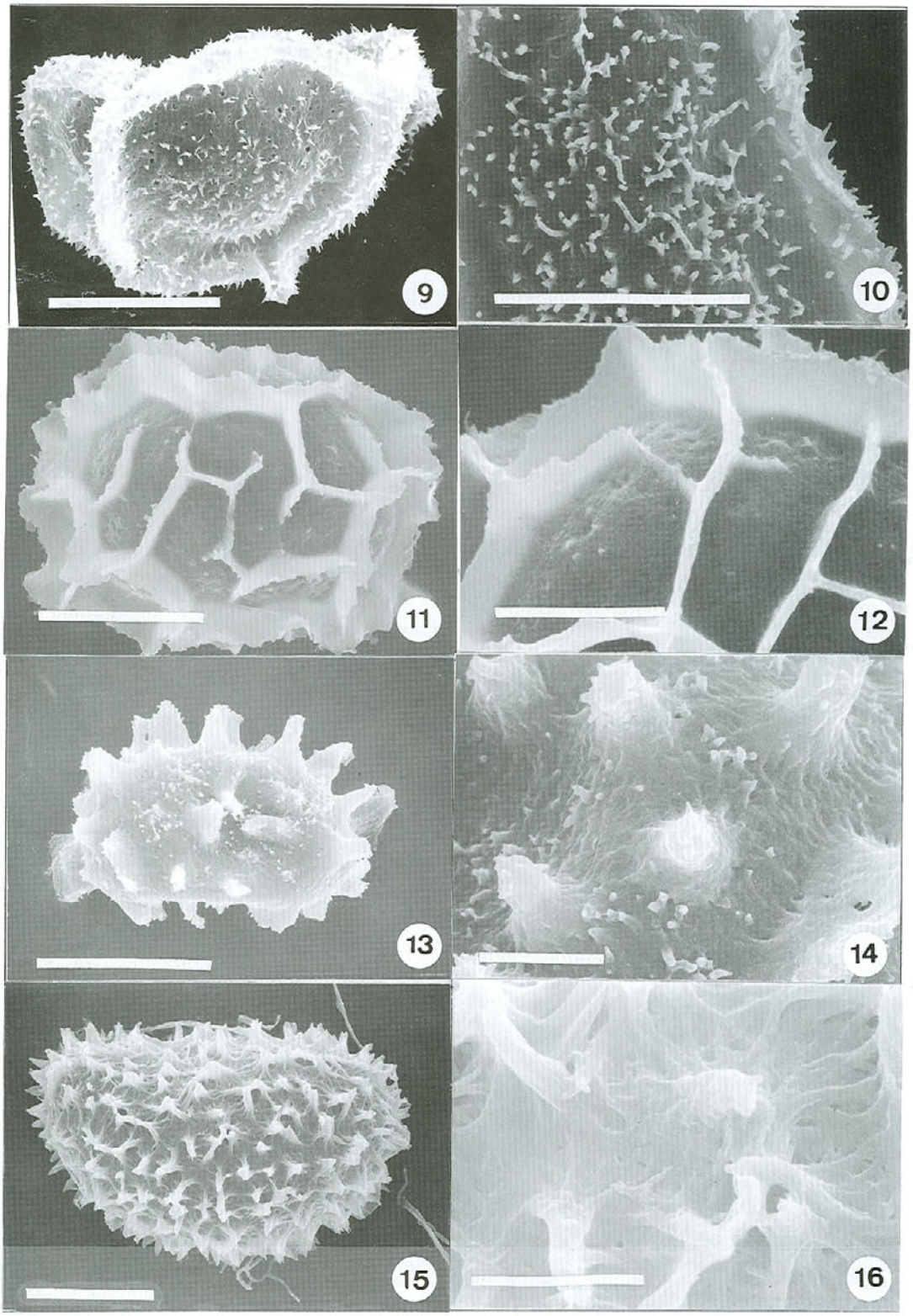
Perispore is stelliform and not folded. The stela is composed of several short spines, which united at apices. The surface micro-ornamentation is lacunate. There are two species in this group: *D. taiwanense* whose spines are horizontally flatted at bases, and *D. contermina* whose spines are ascending and narrow.

3. Reticulate type Figs. 17-18

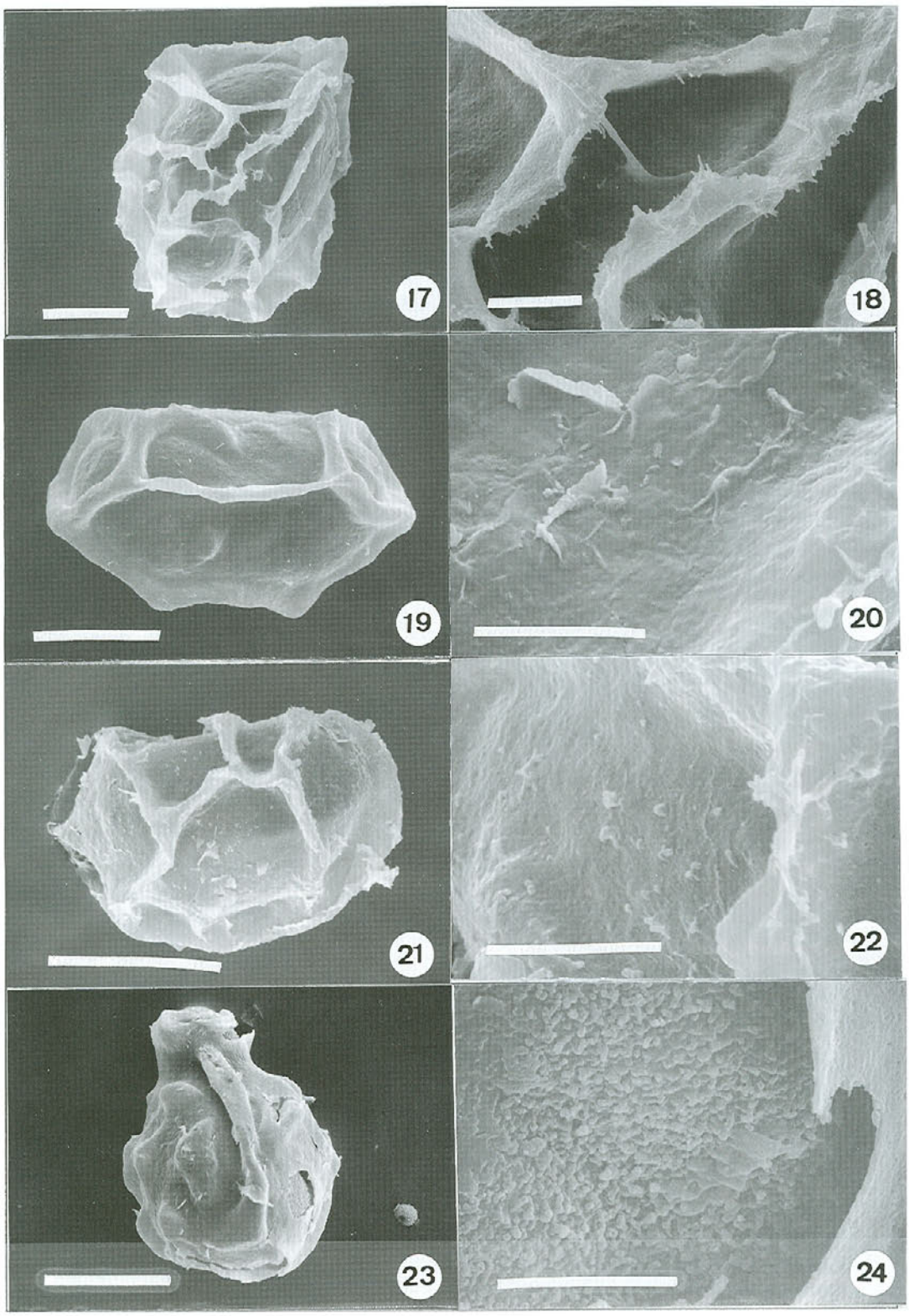
Perispore is muriform and with thin, narrow, wing-like folds. The borders of muri are fimbriate. Three species are in this group and the surfaces in the aerolae are different: *D. lobatum* is smooth to cristate; *D. okinawaense* is verrucate and *D. wichurae* is covered with fused fenestrate strands.



Figs. 1-8. *Athyrium* spore: Rugate Type: 1, 2. *A. oppositipinnum*. 3. *A. silvicolum*. 4. *A. tozanense*. Cristate-Retate Type: 5, 6. *A. niponicum*. 7. *A. atkinsoni*. 8. *A. iseanum*. Bar length = 5 μm in figs. 2, 6 and 20 μm in figs. 1, 3-5, 7, 8.



Figs. 9-12. *Athyrium* spore: Cristate-Retate Type: 9, 10. *A. nakanoi*. Reticulate Type: 11, 12. *A. cumingianum*. Figs. 13-16. *Diplazium* spore: Baculate Type: 13, 14. *D. subsinuatum*. Echinate Type: 15, 16. *D. contermina*. Bar length = 5 μm in figs. 10, 12, 14, 16 and 20 μm in figs. 9, 11, 13, 15.



Figs. 17-24. *Diplazium* spore: Reticulate Type: 17, 18. *D. lobatum*. Rugate-Retate Type: 19, 20. *D. petri*. 21, 22. *D. donianum*. Pustulate Type: 23, 24. *D. prolifera*. Bar length = 20 μm in figs. 17-19, 21, 23 and 10 μm in fig. 20 and 20 μm in figs. 22, 24.

4. Rugate-Retate type Figs. 19-22, 56-57

Perispore is muriform, and with obscure to low folds. Twelve species, *D. amamianum, D. dialatum , D. doedeileinii, D. donianum, D. incompta, D. kawakamii, D. megaphyllum, D. metterianum, D. petri, D. pseudo-doedeileinii, D. sp* aff. *lobatum* and *D. uraiense*, are in this group. Folds in *D. amamianum* and *D. incompta* are obscure or very few and low. Folds in *D. megaphyllum* and *D. metterianum* are many and net-like. Folds in other species are few. Besides *D. sp. aff. lobatum*, the outer perispore surfaces are smooth and sometimes with grains attached. The perispore surfaces, including wing-like folds, of *D. sp, aff. lobatum*, are covered with horizontal rods (Figs. 56-57). The inner perispore layers of most species are papillate with particles distinct. The perispore of *D. sp. aff. lobatum* is retate, with muri borders erosed, and larger than other *Diplazium* species.

5. Pustulate type Figs. 23-26

Perispore is bulliform. The folds are low, broad and separated. There are two species in this group, *D. prolifera* and *D. esculentum*. The inner layer surface are granulate with grains more or less connected; and the grains in *D. esculentum* are larger. The outer perispore layer of *D. esculentum* is easily detached.

6. Bacillate-Retate type Figs. 27-28

Perispore is muriform, retate type. The densely stranded surfaces of perispore are further bacillate. The inner surfaces are granulate. There is one species in this type, *D. pullingeri*.

Dictydroma Ching (Figs. 29-30)

One species, *D. formosona* was examined. The perispore is muriform, rugate type, and the surfaces are bacillate with some rod-structures sometimes united.

Diplaziopsis C. Chr. (Figs. 31-32)

One species, *D. javanica* was examined. The perispore is muriform, retate type and there are some granules on the surface.

Deparia Hooker and Greville (Figs. 33-37)

Three species in three sections were examined. Each section has its own perispore morphology:

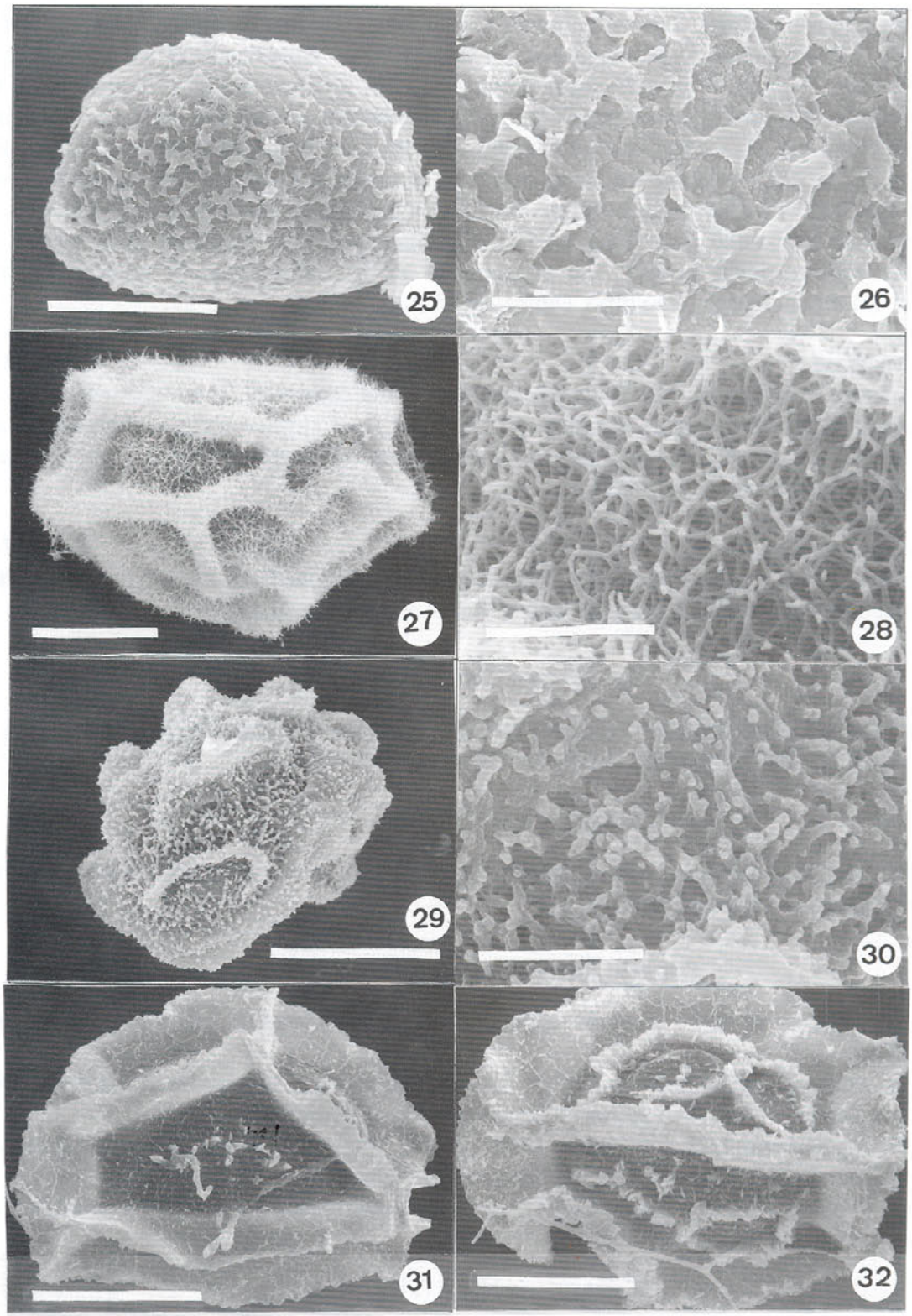
Sect. Athyriopsis, D. petersenii (Figs. 33-34). The spore is spheroid and the perispore is steliform, baculate type. The apices of stelate are obtuse, sometimes branched.

Sect. Dryoathyrium, D. subfluvialis (Figs. 35-36). The perispore is muriform, rugate type. The muri are short and curved, and the surface is granulate.

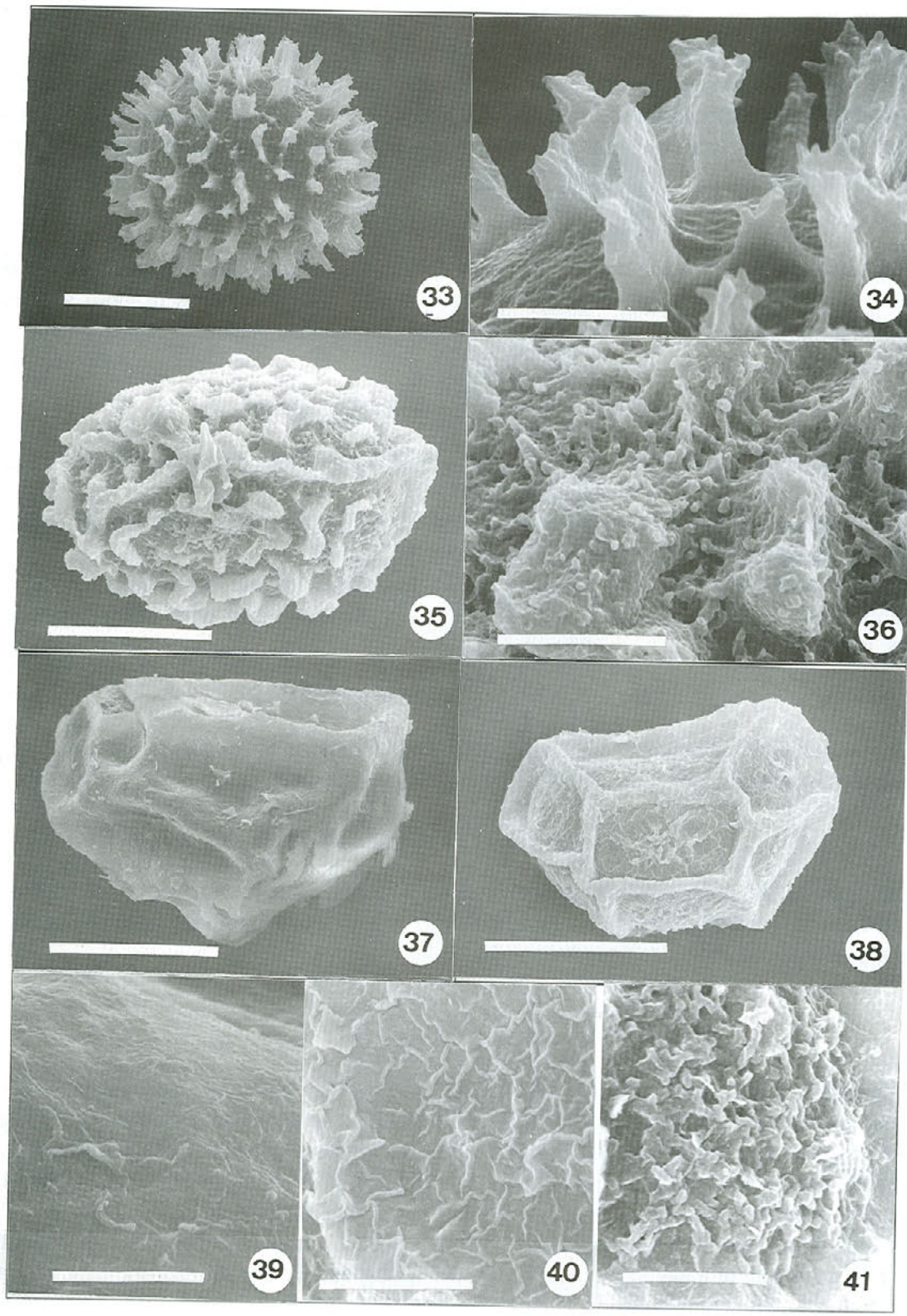
Sect. Lunathyrium, D. allantodioides (Fig. 37). The perispore is muriform, retate type. The muri are broad and the surface is plain.

Cornopteris Nakai (Figs. 38-41)

Three species were exmined. The perisore is muriform, retate type. The surfaces of perispore in the areolae are different in each species: *C. decurrenti-alatum* with smooth or few grains on the surface (Fig. 39); *C. opaca* with flat folds on the surface (Fig. 40); and *C. fluvialis* with bacillate perispore surface (Figs. 38, 41).



Figs. 25-28. *Diplazium* spore: Pustulate Type: 25, 26. *D. esculentum*. Bacillate-Retate Type: 27, 28. *D. pullingeri*. Figs. 29, 30. *Dictydroma* spore: Rugate Type: *D. formosana*. Figs. 31, 32. *Diplaziopsis* spore: Retate Type: *D. javanica*. Bar length = 5 μm in figs 26, 28, 30 and 20 μm in figs. 25, 27, 29, 31, 32.



Figs. 33-38. *Deparia* spore: Baculate Type: 33, 34. Sect. *Athyriopsis D. petersenii*. Rugate Type: 35, 36. Sect. *Dryoathyrium D. subfluvialis*. Relate Type: 37. Sect. *Lunathyrium D. allantodioides*. Figs. 38-41. *Cornopteris* spore: Retate Type: 38, 41. *C. fluvialis*. 39. *C. decurrenti-alatum*. 40. *C. opaca*. Bar length = 5 μm in figs. 34, 36, 39-41 and 20 μm in 33, 35, 37, 38.

Cystopteris Bernhardi (Figs. 42-45)

Two species in Taiwan and we examined both of them. The perispore is steliform, echinate type. The perispore surfaces in *C. fragilis* are fenestrate, and the net-like structures only slightly above the surfaces are the extension of the stelate. *C. moupinensis* has shorter spines, and the outer surfaces are generally broken around the spines to show the smooth inner layer surfaces.

Acystopteris Nakai (Figs. 46-47)

Two species in Taiwan and we examined both of them. The perispore is steliform, baculate type (bulbous in Tryon and Lugardon, 1990). The perispores of both species are quite similar and only minor differences present in the apices, where *A. japonica* has fewer and coarser warts.

Gymnocarpium Newman (Figs. 48-51)

Two species in Taiwan and we examined both of them. They have very different types of perispores:

1. *G. oyamense* has its perispore in steliform, verrucate type (Figs. 48-49). The wart-like stelate are composed of several fused strands with few caves.
2. *G. remote-pinnatum* has its perispore in muriform, rugate type (Figs. 50-51): The perispore folds are low and broad, and surfaces are granulate and with many more or less regular pits.

Hypodematium Kunze (Figs. 52-53)

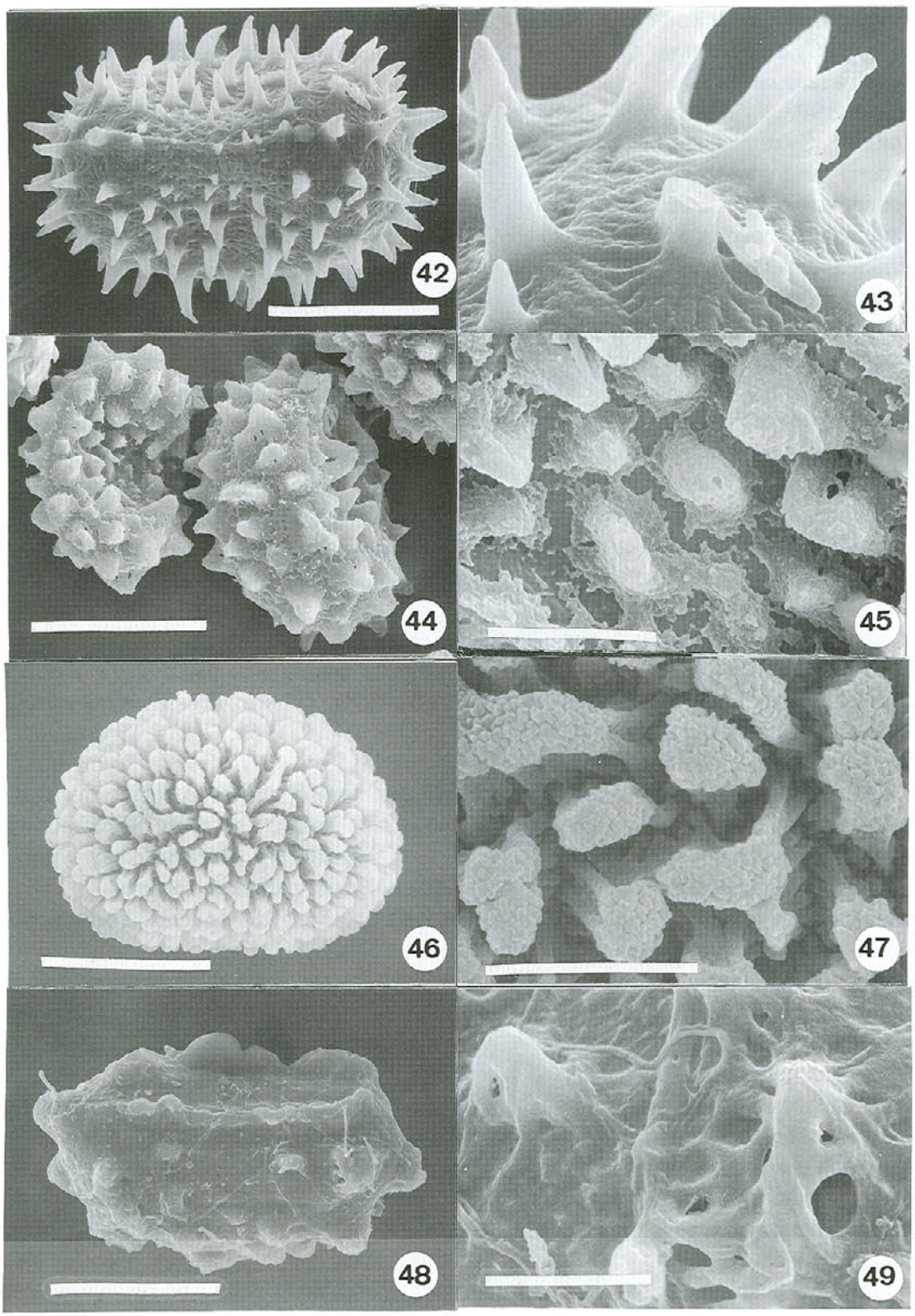
One species, *H. crenatum* was examined. The perispore is muriform, retate type. The surface is granulate and there is lots of pits in different size on it.

Woodsia R. Brown (Figs. 54-55)

One species, *W. polystichoides* was examined. The perispore is muriform, bisculpate type. The surface is basically papillate-granulate with many loose papillate appurtenances, and these appurtenances are more or less connecting.

DISCUSSION

Athyrioid ferns form a natural group and most botanists recognized it, with *Hypodematium* and *Woodsia* dubiously included. The systematic position of the genus *Hypodematium* was suggested to be allied with *Lastreopsis* (Ching, 1935; Holttum, 1954), Tectarioid ferns (Sledge, 1972), *Woodsia* (Copeland, 1947), the *Athyrium* group (Iwatsuki, 1964; Kato and Kramer, 1990), or *Dryopteris* (Tryon and Lugardon, 1990; Li *et al.*, 1988). The spores from Taiwan *Hypodematium crenatum* have a compact, tuberculate, pitted surface and papillate-rugulate inner layer. These characters, especially the pit morphology, suggested a connection to *Athyrium* group in Athyrioid ferns. Assessment of these characteristics of the spores along with other features is particularly needed to establish relationships with certainty. The affinity of the genus *Woodsia* was uncertain, being placed in its own family (Wu and Ching, 1991) or in Athyroid ferns (Kato and Kramer, 1990). *Woodsia polystichoides* has



Figs. 42-45. *Cystopteris* spore: Echinate Type: 42, 43. *C. fragilis*. 44, 45. *C. moupinensis*. Figs. 46, 47. *Acystopteris* spore: Baculate Type: *A. tenuisecta*. Figs. 48, 49. *Gymnocarpium* spore: Verrucate Type: *G. oyamense*. Bar length = 5 μm in figs. 43, 45, 47, 49 and 20 μm in figs. 42, 44, 46, 48.

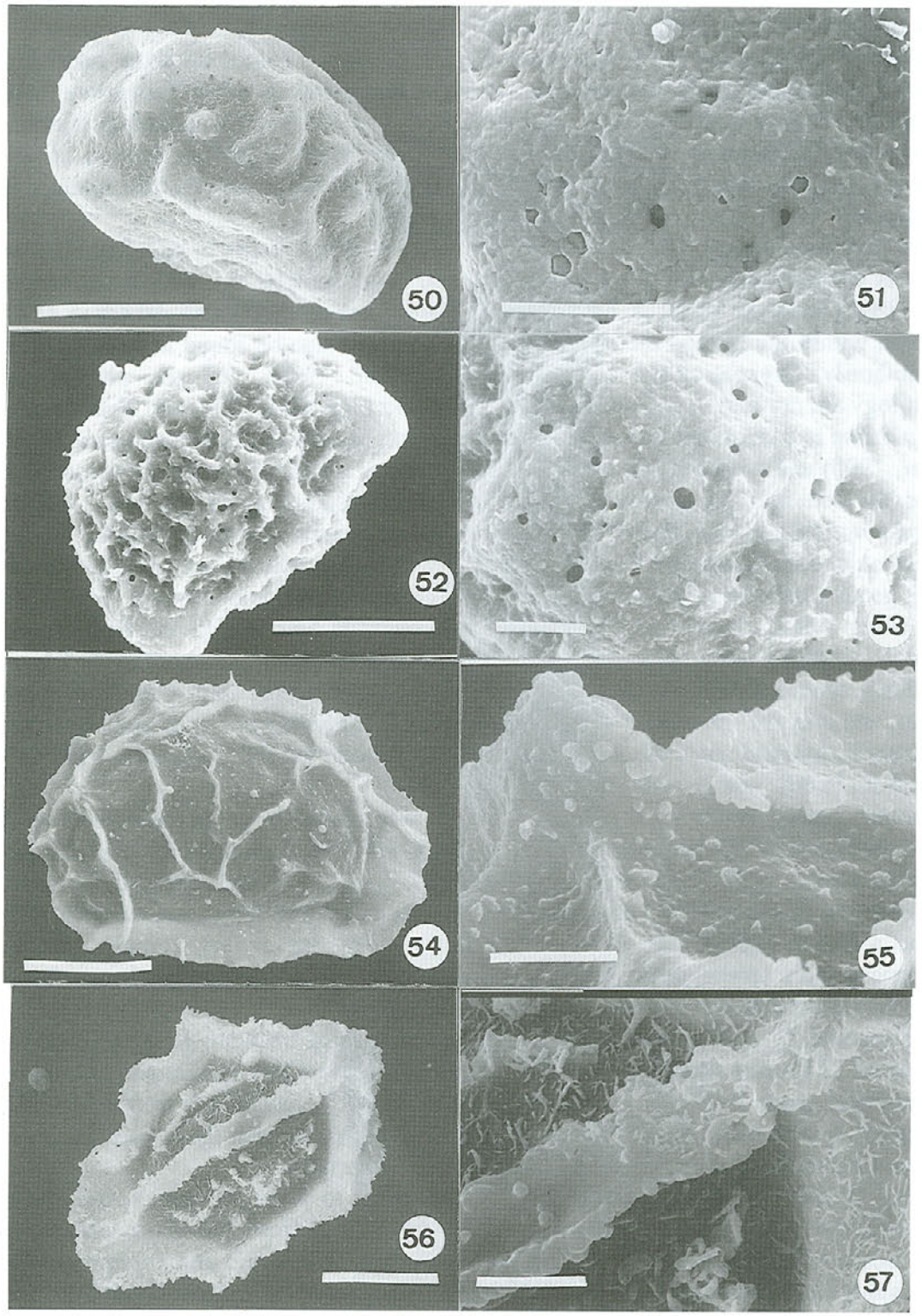
spore morphology most close to genus *Polystichum* in the tribe Dryopterideae, but some perispore features did suggest a link to *Diplazium* reticulate-type group. Hereafter, the authors could not propose a definite relationship of *Woodsia*. However, the spore ornamentation of *Woodsia* and *Hypodematium* did indicate they are bridges connecting different components of Dryopteridaceae *sensu lato*.

Wang (1997a) divided Athyrioid ferns without *Hypodematium* and *Woodsia* into three subfamilies, Cystopterioideae, Athyrioideae and Diplazioideae. Cystopterioideae contains *Cystopteris* and *Acystopteris*, and is characterized by elongated appurtenances, whose component has only one unit, on the spore surface. The spore morphology also suggested the Diplazoideae is more or less a natural group and the Athyrioideae is a less natural one. The *Diplazium* group includes genera *Diplazium, Diplaziopsis*, *Dictydroma* and *Cornopteris,* and the genus *Dictydroma* is more or less distinct with this subfamily. The spore ornamentation of *Diplaziopsis javanicum* is much similar to *Diplazium lobatum* and its allied species, so we suggested the genus is much close to *Diplazium*. *Cornopteris* is another genus near the genus *Diplazium* by its spore ornamentation. The distinction between Diplazoideae and Athyrioideae is not very obvious as some *Athyrium* and *Diplazium* are close to the each other on the basis of spore ornamentation. The spore morphology of *Athyrium* cristate-retate type species is similar to *Diplazium* rugate-retate type species. Also, *Athyrium cumingianum* would be the species with perispore characters somewhere bridging to genus *Diplazium*. The spore surface of *Deparia* sect. *Lunathyrium* is very similar to *Athyrium*, and sect. *Athyriopsis* is similar to *Diplazium subsinuatum*. *Gymnocarpium* was placed in the subfamily Athyrioideae by Wang (1997a) and the spore ornamentation placed the affinity of *Gymnocarpium* in an intermediate between *Cystopteris* and *Athyrium* groups.

The latest generic classification of Athyrioid ferns contains twelve genera of the world (Kato and Kramer, 1990) and eleven in Taiwan. However, generic classification varied from author to author (Copeland, 1947, 1958; Holttum, 1947, 1954, 1968; Ching, 1954, 1964, 1978; Wu and Ching, 1991; Alston, 1956; Sledge, 1962, 1973; Kato, 1977, 1984; Tryon and Tryon, 1982; Kato and Kramer, 1990; Wang, 1997a), with genera so similar to each other and some intermediate species or hybrids in between (Kato, 1977, 1984). The spore SEM morphology in this work did not provide with sound generic differentiating characteristics within each system, but some genera and sections did have their coherent perispore features.

Athyrium is a worldwide distributing genus contains about 180 species. The taxonomy is poor known and the classification of this genus is still doubtful (Kato and Kramer 1990). At the generic level, Kato (1977) enlarged it to include *Anisocampium*, *Pseudocystopteris* and *Kuniwatsukia*, the first two genera exist in Taiwan. *Pseudocystopteris* was established by Ching (1964) as an intermediate form between genera *Athyrium* and *Cystopteris*. The perispore ornamentation of *Athyrium atkinsoni* (= *Pseudocystopteris atkinsoni*) is retate, same as some *Athyrium* species, but different from the echinate perispore ornamentation of *Cystopteris*. The perispore morphology of *Athyrium cumingianum* (= *Anisocampium cumingianum*) is distinct from other *Athyrium* members and close to *Diplazium* group. Appending to the other morphological data, such as rhizome vascular arrangement, indusium structure, *A. cumingianum* is isolated in *Athyrium* and the genus *Anisocampium* may be better reestablished.

There are few studies about the subdivision of *Athyrium*. It would be reasoning from the hybridization with other genus (Kato, 1979) and within the genus (Schneller and Rasbach, 1984). Hsieh (1986) established two subgenera and Wang (1997b) classified *Athyrium* into fourteen sections. The spore ornamentation basically agrees with Hsieh's classification. The



Figs. 50, 51. *Gymnocarpium* spore: Rugate type: *G. remote-pinnatum*. Figs. 52, 53. *Hypodematium* spore: Relate Type: *H. crenatum*. Figs. 54, 55. *Woodsia* spore: Bisculpate Type: *W. polystichoides*. Figs. 56, 57. *Diplazium sp. aff. Lobatum*. Bar length = 5 μm in figs. 51, 53, 55, 57 and 20 μm in figs. 50, 52, 54, 56.

group with perispores in simple, rugate fold is belonged to subgenus Echinoathyrium excepting *A. yakushimense*. The group with perispore in cristate-retate fold is belonged to subgenus *Athyrium*, excepting *A. iseanum* and *A. cryptogramnoides*.

Athyrium anisopterum in Chingshuiyin, Pingtung Co. is a confusing taxon because of its elongated, erect, and truck-like rhizome, which is not found in other Taiwanese *Athyrium* populations. However, the perispore morphology of this collection is indistinguishable from the specimen collected in Meifon, Nantou Co. As different *Athyrium* species have quite different persispore characters, we thought these two populations may be best retained in the same species.

The perispore ornamentation of *Athyrium nakanoi* (Figs. 9-10) is peculiar because the surface is covered with bacillate appurtenants and some samples are with irregular-shaped, varied-sized pits on the surfaces, both character states were not known elsewhere in *Athyrium*. However, within the family, the bacillate appurtenant can also be found in some taxa within the subfamily Dryopteroideae (Tryon and Lugardon, 1990), and the pits of similar morphology are not rare in genera *Woodsia* (Tryon and Lugardon, 1990) and *Hypodematium*.

Diplazium is a taxonomicaly very difficult and quite insufficiently known genus (Kato and Kramer, 1990) and a natural subdivision is also lacking. Palynologically, Taiwanese species can be divided into six groups, three of which corresponding to the taxa, *Callipteris, Monomelangium,* and *Triblemma* recognized as distinct genera by some botanists.

Diplazium esculentum and *D. proliferum,* a new recorded species, are still classified into a distinct genus *Callipteris* (including *Anisogonium*) by some pteridologists (e.g. Wu and Ching, 1991; Wang 1997a). However, the pustulate type reported here is different from Tryon and Lugardon's (1990) photographs. The outer layer of *D. esculentum* perispore in the Tryon and Lugardon's material might be detached, as indicated by the spore non-folded and rugulated surfaces, and only the inner layer surface was shown. The identity of Tryon and Lugardon's *D. proliferum* is doubtful since the material came from Liberia but the *Callipteris* ferns are only known from Pacific and E. Asia (Wu and Ching, 1991).

Another special taxon is *D. pullingeri*, which was placed in genus *Monomelangium* by Ching (1964) as a bridge between genera *Asplenium* and *Diplazium* and closed to *Athyriopsis*. Our study agrees with Tryon and Lugardon's (1990) report, which showed the perispore morphology in this species is very unusual within the Athyrioid ferns, and an isolated genus may be a better choice. The perispore of this species has a very compact, meshwork arrangement. This arrangement might provide the connection clue toward some *Asplenium* species having similar, but less compact meshwork pattern.

The species, *D. subsinuatum*, has spore coving with large baculate perispore stela, which is visible on LM image (Huang, 1981). Ching (1978) proposed this species and *D. zeylanicum* to form a new genus *Triblemma*. The spore LM image of *D. zeylanicum* from China (Zhang, *et al.* 1990) is with a similar structure of the perispore. We suggest these two species might represent a rather distinct group isolated from others *Diplazium*.

Ching (1964) separated some species of *Diplazium* to form the genus *Allantodia* and established the subdivisions under the genus. The results from the spore ornamentation comparison could not hold the separation between genera *Allantodia* and *Diplazium*, also the present study found no correspondence existing between perispore morpholgy and sections.

Diplazium sp. aff. lobatum posed a particular interesting spore morphology. The perispore has its muri borders erosed, and the surface covered with horizontal, rod-like structures. The perispore of this taxon is quite similar to *Diplaziopsis javanica* and very different from *Diplazium lobatum*. In our observations, the population from which the specimen was

collected probably represents an undescribed species, and a further study of this taxon is needed to explore the distinction and relationship between genera *Diplazium* and *Diplaziopsis*. Although very unlikely, another possible identity of this taxon is an intergeneric hybrid between genera *Diplazium* and *Diplaziopsis*.

Kato (1984) divided the genus *Deparia* into four quite distinct sections, with three of them, *Lunathyrium*, *Athyriopsis* and *Dryoathyrium* occurring in Taiwan. The authors found spore surface ornaments close to *Athyrium* and have differences between sections. Tryon and Lugardon (1990), whose study included two species examined by the authors but collected elsewhere, shared the later view of differentiating sections.

The systematic position of genus *Cornopteris* is still in discussion. Wu and Ching (1991) considered *Cornopteris* next to *Allantodia* (= *Diplazium*). Kato (1977) placed it close to *Athyrium* and indicated a putative hybridization between them. Base on the spore surface characters, we suggested *Cornopteris* related to *Diplazium* more.

The perispore micro-ornamentation in genus *Cornopteris* provides a easy way of identifying different species. The macro-ornamentation in *Cornopteris* is retate to reticulate, but the ridges are not fixed in the same position and the areolate shape and size are not same in each spore. The micro-ornamentation is more stable and no intermediate case found between each types of micro-ornamentation, thus would be a good character to differ each species under the genus. We observed three kinds of surface fine structure in the areole: *C. decurrenti-alatum* has a very smooth surface and slight fold, *C. opaca* has spore with flat fold on the surface, and while *C. fluriallis* spore is clearly baculate to papillate.

The genus *Cystopteris* was last monographed by Blasdell in 1963. He divided the genus into two subgenera: subgenus *Cystopteris* has two sections, and subgenus *Acystopteris,* treated here as a distinct genus (Ching, 1978; Kato and Kramer, 1990). *Acystopteris* species have their spores with denser and blunt-tip baculate stelate, while *Cystopteris* species have spores with thinner and pointed spines. On the basis of spore ornamentation, the separation of the two genera was justified. Taiwan has two species of *Cystopteris* in two sections, and the spore ornamentation shows a clear difference between each other. However, when combining with other available data (Pearman, 1976; Tryon and Lugardon, 1990), it is not easy to define the difference between each section. *Cystopteris fragilis* is a world wide distributed species complex and the spore ornamentation is variable (Tryon and Lugardon, 1990), and the spore morphology in this study is also different from what has been reported.

There are two different types of spore ornamentation found in two specie of Taiwan *Gymnocarpium*. Comparing photographs from other reports (Pryer and Britton, 1983; Tryon and Lugardon, 1990), the spore of *G. oyamense* is about the same as other species in the world, and close to *Cystopteris moupinnum*. The spore morphology of *G. remote-pinnatum* is quite distinct within the genus with perispores slightly folded to cristate and pits over all the surfaces.

The spore morphology of Taiwanese *Hypodematium crenatum* is quite different from the materials reported elsewhere. Tryon and Lugardon (1990) examined two specimens of *H. crenatum* from Thailand and Kiangsu (China), and indicated that there were some different features between those two samples. These palynological data suggested the taxonomy of *H. crenatum*, a widespread and likely complex species (Iwatsuki, 1964), is needed.

The results of this study indicated that the spore ornamentation of Athyrioid ferns is stable, polymorphic, and more or less species-specific, thus a palynological basis for the classification of this family is provided. When more spore data are collected in the future, the taxonomy of this taxonomic difficult group can be much improved.

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臺灣蕨類屬之孢子掃瞄式電子顯微鏡研究(一)：蹄蓋蕨類

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摘　　要

以掃瞄式電子顯微鏡觀察臺灣產蹄蓋蕨類孢子表面飾紋，共計五十六種十一屬。依據孢粉學的資料，討論並檢討蹄蓋蕨類屬及屬下分類群之間的親源關係。

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