ON SOME ASIAN AND AFRICAN SPECIÉS OF FOLIOCEROS BHARADWAJ

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ABSTRACT

Seven species of Folioceros Bharad., F. miyabenus (St.) comb. nov., F. falsinervius (Lindbg.) comb. nov., F. incurvus (St.) comb. nov., F. glandulosus (L. et L.) comb. nov., F. pinnilobus (St.) comb. nov., F. buitenzorgius (St.) comb. nov. and F. weistii (Khanna) comb. nov. from Asian and African countries have been described in detail. The morphological details of different parts in the gametophyte and the sporophyte together with the variations in these and in other species of the genus described by me earlier (Bharadwaj, 1965, 1971), have been compared and discussed to conclude that the species of Folioceros fall into three groups chiefly separated from each other on the basis of differences in spore characters viz., the baculate ornamentation with dentate-apexed bacula and indistinct to ill-defined tetrad mark in spores alongwith pinnately lobed fronds in F. fuciformis, F. vesiculosus F. miyabenus, F. incurvus and F. assamicus, with baculate spores having smooth-apexed bacula, a defined tetrad mark and strap-shaped or elongated fronds in F. glandulosus and F. pinnilobus, or the spinose ornamentation with distinct tetrad mark in spores and broadly expanded fronds in F. amboenensis (Schffn.) Bharad., F. mamillisporus (Bharad.) Bharadwaj, F. dixitianus (Mahabale) Bharad., F. weistii and F. buitenzorgius. Within each of these groups the variations in the nature of sex distribution, height of the mature antheridia, the density of stomata, the spore diameter, the size and incidence of ornament-units and the length of complete (4-celled) elaters appear to be useful for species delimitation.

INTRODUCTION

In continuation of my study of species of Folioceros (Bharadwaj, 1971), it has been possible to include therein, five Asian species of Aspiromitus St., or Anthoceros (Mich.) L., occurring in the neighbouring countries viz., Asp. miyabenus St., Asp. buitenzorgius St., A. falsinervius Lindbg., A. weistii Khanna and A. glandulosus L. et L. and two African species viz., Asp. incurvus St. and Asp. pinnilobus St., all now referrable to Folioceros. By now, detailed information regarding as many as 14 species of Folioceros has accumulated. A comparative appraisal of these species reveals that they present different combinations of variable morphological characters, both qualitatively as well as quantitatively.

MATERIAL AND METHODS

Aspiromitus miyabenus St. Collected and determined by Hattori in 1946 (Hattori Exsicc. Ser. 2, 1947, No. 55) from Kiushiu, Japan.

Anthoceros falsinervius Lindbg. and A. glandulosus L. et L. Collected, determined and sent by W. Meijer, Herbarium Bogoriense, Kebun Raya, Indonesia.

Anthoceros vesiculosus Austin alim glandulosus L. et L. original Herb. Nees; Nos, 15049, 15052 of Fondation Stephani, Genève, from Java,

Aspiromitus buitenzorgius St. Type material of Stephani, No. 14575, of Fondation Stephani, Genève, collected from Botanical Garden of Buitenzorg, Batavia, Java by V. Schiffner.

Aspiromitus incurvus St. Type material of Stephani, No. 14579 of Fondation Stephani, Genève, collected from Bibundi in Cameroon, West Africa by Jungner.

Aspiromitus pinnilobus St. Lectotype material of Stephani, No. 14580 of Fondation

Stephani, Genève, collected from Samoa by Rechinger.

Anthoceros Weistii Khanna, materia originalis (Verdoorn Hepaticae selectae et criticae Ser. VIII, 353, 1945).

The usual method of study, as described earlier for dry material, consisted of soaking in boiling hot water. Spores were studied after, as well as without, acetolysis (ERDTMAN, 1933). The measurements given in this paper are from fresh preparations in glycerin jelly. The observations recorded here for various organs pertain to their similar location or state of maturity in different species, e.g. the fronds studied have been taken from well developed thalli, chloroplasts have been studied from dorsal cells of the lobes in the fronds, t.s. of involucres is from their middle region, spores have been measured in polar view from the mature ones only and the stomatal count is from the upper half of the capsule.

DESCRIPTIONS

Folioceros miyabenus (St.) comb. nov.

Text-figs. 1, 6, 8, 12; Pl. 1, Figs. 1-3

Syn. Aspiromitus miyabenus St. in Stephani 1916

Diagnosis emend: Planta monoica. Frons ad 2 cm longa furcata anguste linearis grosse cavernosa, rami incisolobati, margine crenulati et cellulis digitatim aggregatis limbati. Involucra cavernosa cum cavis in duo ordinum, lamellata. Capsula stomata media. Sporae $35~\mu~(30\text{-}37~\mu)$, fulvae, baculosae, bacula $2~\times~1\text{-}4~\mu$, multifida aut similiter virgula, cicatrix tetradi parum perspicua. Elateres $430~\mu~(350\text{-}550~\mu)$ longi, septati, spadici, anguste foramini. Androecia octandria, paria. Antheridia corporum $145~\mu~(238\text{-}155~\mu)$ longorum.

Thallus—The thallus is monoecious. It consists of fronds not forming regular rosettes. Fronds are longish (Text-fig. 1), i.e. much narrower than long, bearing large number of small or large, flat lamellae on the dorsal surface and with the margin dissected due to large number of small, pinnately arranged lobes whose apical region is more or less swollen. The margin of the lobes is irregularly dentate due to unequally longish marginal cells, similar to those in F. assamicus (Bharadwaj, 1971).

Internally the thallus is cavernous. The surface cells contain mostly one chloroplast of any geometrical shape. Within each, a number of large and small hayaline regions are visible (Text-fig. 6). No centralized pyrenoid body could be distinguished.

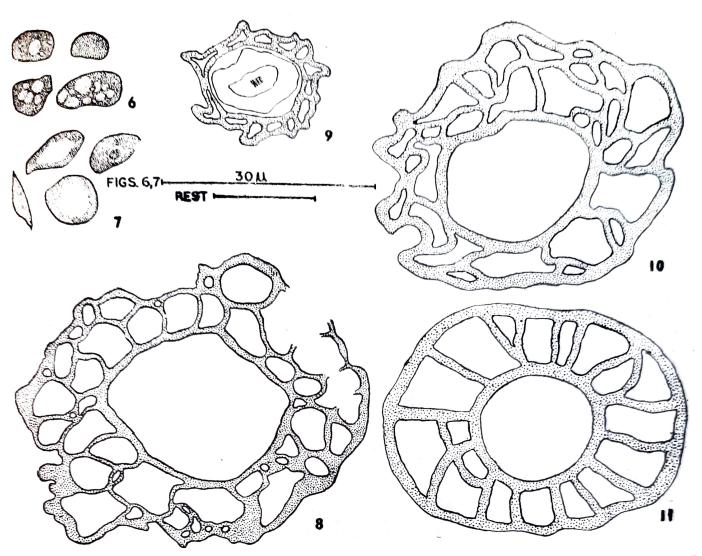
Androecia—Androecia are present on the same fronds as bear the sporogonia. They may be found near the bases of the involucres or posteriorly at the base of the side lobes. Androecia are circular to subcircular, sunk within the thallus for most of their part but for a small portion raised above the general surface like a mound. In the centre of the mound is usually seen a nearly circular opening. Inside the androecia a bunch of 6-8 antheridia at the same stage of development are found. There is no evidence of a secondary basal cushion. An antheridium is built on the same pattern as in other species of Anthoceros. The body of mature antheridium is $138~\mu$ to $155~\mu$ in height with $145~\mu$ mean. The antheridial stalk is 2 cells high.

Involucre—The involucre is cavernous (Text-fig. 3), the cavities being in two layers. The surface is irregularly ridged and bears lamellate outgrowths.

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Text-figs. 1-5, 1. Frond of F. miyabenus; 2a, b. female and male fronds of F. incurvus; 3a, b. female frond and a lobule of F. pinnilobus; 4a, b, c. female, male fronds and marginal spongy bodies of F. glandulosus; 5. Female frond of F. buitenzorgius.



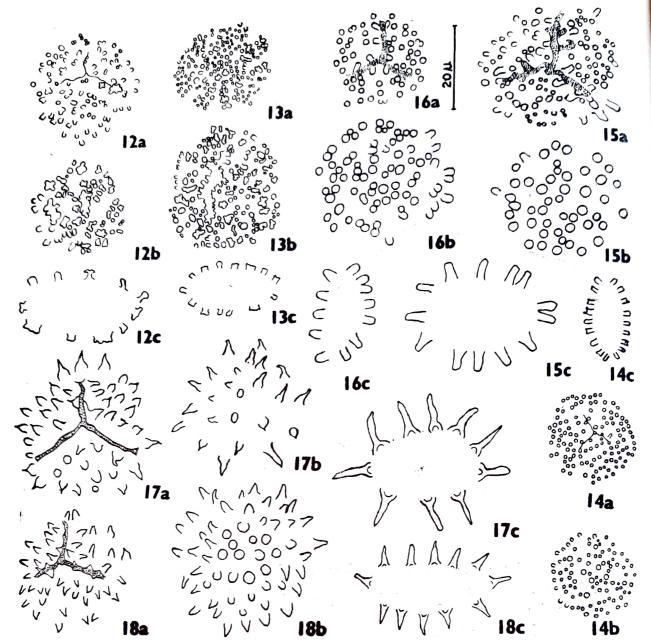
Text-figs. 6-11. 6, 7. Chloroplasts in F. miyabenus and F. glandulosus; 8-11. T. s. of involucres in F. miyabenus, F. falsinervius, F. weistii, F. incurvus.

Capsule—The epidermis is stomatiferous. The number of stomata is 15 per sq. mm of the epidermal surface. Stomata are 69 μ (mean) long. Opposite grooves in the capsule wall lodging the lines of dehiscence, are shallow.

Spore—The spore is brown and subcircular in polar view. Tetrad mark is seen indistinctly as composed of thin ridges, (Text-fig. 12). The spore exine is ornamented with 2 μ high and 1.5 μ wide bacula with their tips truncate or divided. A number of bacula may be confluent (Text-fig. 12b). The bacula are smaller and sparser on the proximal face than those on the distal face (Text-fig. 12; Pl. 1, Figs. 5, 6). The average diameter of the spores in polar view is 35 μ (mean) ranging between 30 μ and 37 μ .

Elater—The elaters are brown, slender, vermiform and usually four-celled with tapering ends (Pl. 1, Fig. 4). The walls of the elater cells are substantially regularly thickened enclosing a darker lumen of variable width, it being wider nearer the transverse cell walls. On an average a mature, complete, four celled elater is 430 μ long, the length ranging between 350 μ to 550 μ and the width between 5.0 μ and 10.0 μ .

Comparison—Among the closely comparable species in view of the qualitative similarity in spores, are F. assamicus and F. falsinervius. However, the former differs qualitatively in being dioecious and quantitatively in the size of antheridial body being bigger, the bacula and elaters being smaller and the stomata sparser. The latter differs in having bigger antheridial body but distinctly smaller bacula of the spores.



Text-figs. 12-18. Spores in proximal (a) and distal (b) views and showing some ornamentation-units (c) along equator. 12. F. miyabenus, 13. F. falsinervius, 14. F. incurvus, 15. F. pinnilobus, 16. F. glandulosus, 17. F. buitenzorgius, 18. F. weistii.

Folioceros falsinervius (Lindbg.) comb. nov.

Text-figs. 9, 13; Pl. 1, Figs. 4,5

Syn. (after Meijer 1954)

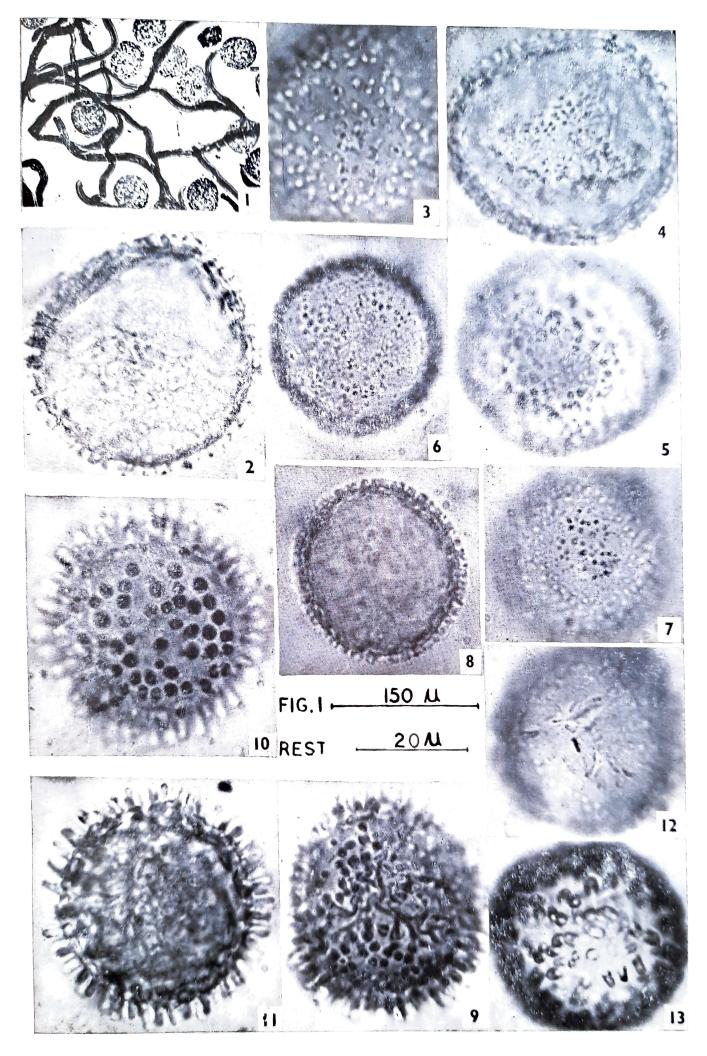
Anthoceros falsinervius Lindenb. ex Meissner in Bot. Zeitg. 6: 463, 1948.

Anthoceros falsinervius var. lyratus Gottsche in Natuurk. Tijdschr. Ned. Indle 4: 575, 1853; Sande Lacoste, Syn. Hep. Javan. 100, 1856.

Aspiromitus falsinervis (Ldbg.) St. in Stephani, Sp. Hep. V. 1916.

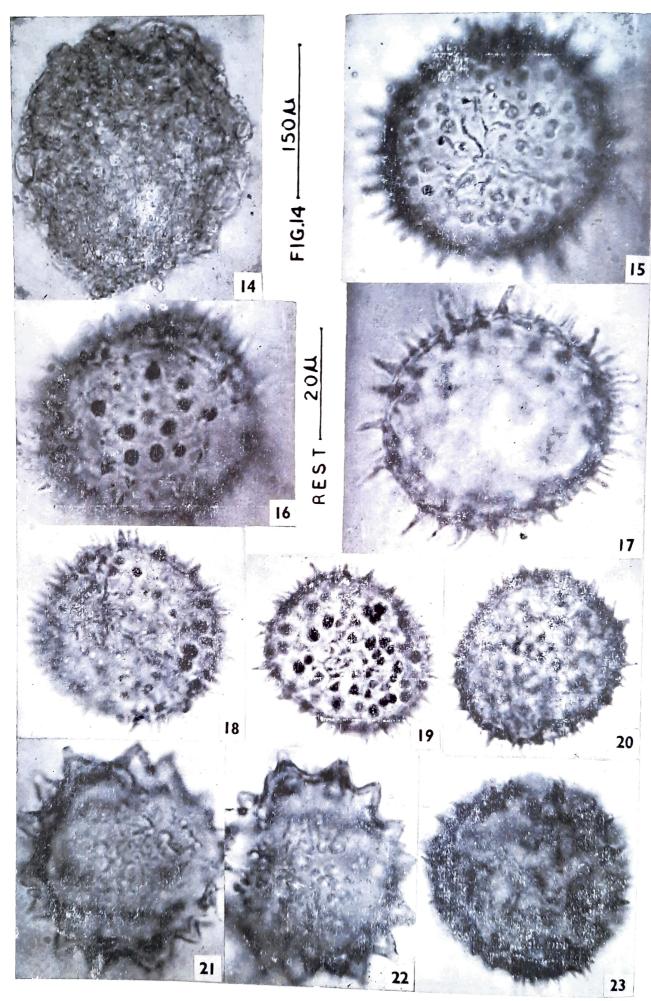
Arpiromitus gracilis Goebel in Ann. Jard. bot. Buitenz. 39: 61, 1928—Anthoceros indonesicus Proskauer in Bull. Torrey bot. Club. 79: 347, 1951.

Remarks—Meijer (1954) has already given a good taxonomic description of this plant but for certain additional details which I needed for my comparative study. For-



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Bharadwaj—Plate 1



Bharadwaj—Plate 2

tunately Dr. Meijer had sent some material of this species to Late Dr. S. K. Pande which I have utilized to supplement Meijer's earlier description.

Diagnosis emend: Planta monoica, terricola et rupicola. Frons ad 3 cm longa, linearis, grosse cavernosa, marginibus irregulariter inciso-lobulatis, lobulis margine cellarum longarum. Involucra cavernosa. Capsula stomata media. Sporae 35 μ (33-38 μ), fulvae baculosae, bacula extrema dividua, cicatrix tetradi non perspicua. Elateres 420 μ (250-500 μ) longi, septati, fulvae, anguste foramini. Androecia numerosa, alveolis parvis, polyandria (ad 25 in utroque alveolis.) Antheridia corporum 175 μ longorum.

Thallus—In the thallus the chloroplasts are usually circular or subcircular. The pyrenoid body is not visible.

Involucre—The involucre is ridged on the surface (Text-fig. 9) and internally a single layer of cavities is seen.

Capsule—In the epidermis of the capsule 15 stomata per sq. mm of the surface have been found. The stomata are 65 μ (mean) in length.

Spore—The spore is brown. It is subcircular in polar view. Tetrad mark is not apparent, instead a triangular, caved-in area is to be seen (Pl. 1, Fig. 4). The spores have baculate ornamentation, the bacula are of various shapes (Text-fig. 13c). Often they are confluent (Text-figs. 13a, b). The apex of the baculum is either rounded or dentate. The bacula are smaller and sparser proximally but larger and denser distally. The bacula are 1.5μ high and $1-2 \mu$ wide. The mature spores are 35μ in diameter (mean) with the range of variation being 30μ to 38μ .

Elater—The elaters are brown, slender, vermiform and usually four-celled with tapering ends. The wall is uniformly thickened enclosing a dark, uneven-floored lumen. Complete elaters are 420 μ long on an average, the range of variation in length being from 350 μ to 500 μ and in width 5-10 μ .

Comparison—Among the comparable species having qualitatively similar spore, is F. assamicus which differs in being dioecious, having bigger bacula, smaller elater and sparser stomatal distribution.

F. fuciformis appears to be very close on the basis of scanty information available so far which is not conclusive.

Folioceros incurvus (St.) comb. nov.

Text-figs. 2, 11, 14, 19; Pl. 1, Figs. 6-8

Syn. Aspiromitus incurvus St. in Stephani 1916

Diagnosis emend: Planta dioica majuscula. Frons ad 3 cm longa, grosse cavernosa, repetito-furcata, ramis anguste linearibus, regulariter profundeque pinnulatis. Involucra cavernosa, cum cavibus in uno ordino, levia. Capsula nonstomatifera. Sporae 28.5 μ (26-30 μ), fulvae, minuteque baculosae, bacula extrema dividua, cicatrix tetradi parum perspicua. Elateres 450 μ (350-460 μ) longi, septati, fulvi, angusta foramini. Androecia magna, alveolis polyandris (ad 20 in utroque alveolis). Antheridia corporum 155 μ (150-170 μ) longorum.

Thallus—The plant is dioecious. The fronds are long and narrow. The female fronds are broader than the male fronds. The truncate lobes are more characteristically pinnately arranged in the male fronds (Text-fig. 2). The surface of the fronds is smooth. The marginal cells in the lobes are broad with their free wall thin and slightly convex. Internally the fronds are copiously cavernose.

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Usually there is only one chloroplast per cell in the fronds. It is variously shaped and always lacks a differentiated pyrenoid body.

Androecia: Androecia occur in linear rows pertaining to the apical notches in the anterior region of the male fronds (Text-fig. 2b). They are sunken in the thallus and possess a small, central opening in the maturer ones. The exact number of antheridia produced in a chamber could not be exactly ascertained but they were certainly not many and presumably 20 per chamber.

The antheridium is stalked, with the body wall built by 4 tiers of cells as found in Anthoceros and Folioceros. The body of mature dehisced antheridium is 155 μ (mean) high.

Involucre—The involucre is cavernous, the cavities being in a singler layer (Text-fig. 11). The surface is irregularly, shallowly ridged. Surface lamellae are absent.

Capsule—The epidermis is non-stomatiferous.

Spore—The spore is very light brown and subcircular in polar view. Tetrad mark is small and made up of sinuous rays. The spore surface is baculate with bacula being about 2μ high and bifurcate at the tip (Text-fig. 14). The bacula are slightly smaller in width as well as height on the proximal face than those on the distal face (Pl. 2, Figs. 6-8). The average diameter of the spore along one of the rays is 28.5μ (mean) ranging between 26μ and 30μ .

Elaters—The elaters are light brown, slender, vermiform and usually four-celled with tapering ends (Text-fig. 19). The wall of the elater cells is substantially, regularly thickened enclosing darker granular inclusions of various sizes in the lumen. On an average, a mature, complete, four called elater is $400\,\mu$ long, the length ranging between 350 to $460\,\mu$. 5 celled elaters have also been observed. The width of elater cells is 5-8.5 μ but at the joints it is upto 12.5 μ .

Comparison—On the basis of qualitative features in spore, F. incurvus belongs to the group of species having baculum with dentate apex viz., F. assamicus, F. miyabenus, F. falsinervius, F. fuciformis and F. vesiculosus. However, as compared to these species, the spore in F. incurvus is the smallest in diameter, the bacula are also thinner and most striking of all the features, is that stomata are absent from the capsule epidermis.

General Remarks—An outstanding feature of the species is the absence of stomata on the capsule epidermis. This fact had been observed by Stephani as apparent from the inscription on the type sheet but not stated in the diagnosis of the species published by him. It seems that the material labelled as Anthoceros pinnatus St., collected by P. Dusèn from Cameroon and located in Herbarium of University of Wisconsin and referred to as an a anomalous specimen by Proskauer (1957), is in all probability F. incurvus.

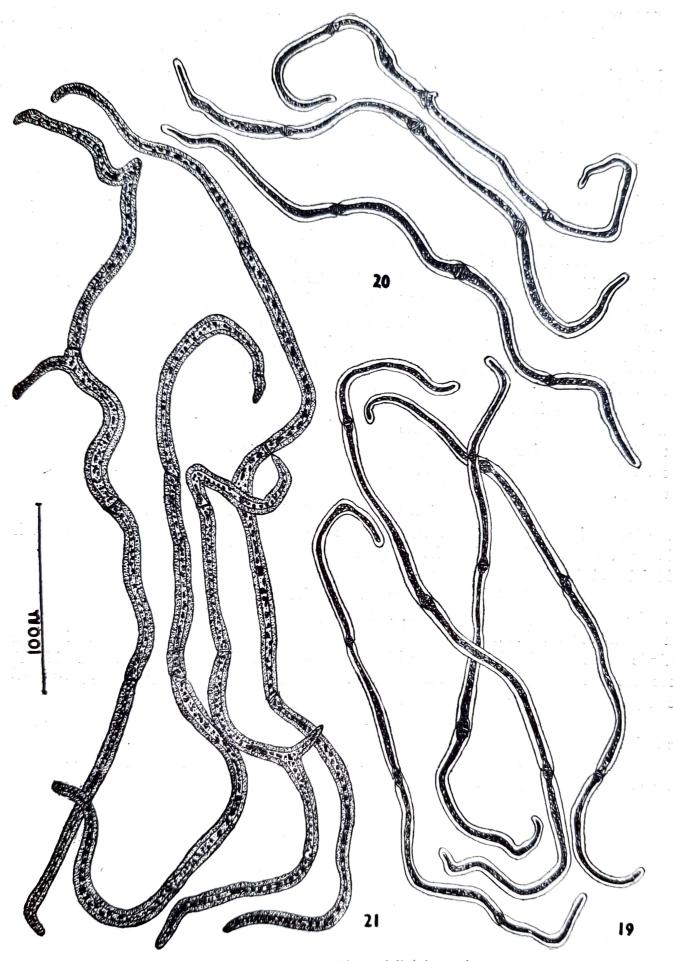
Folioceros pinnilobus (St.) comb. nov.

Text-figs. 3, 15, 20; Pl. 9-11

Syn. Aspiromitus pinnilobus St. in Stephani 1916

Diagnosis emend—Planta dioica (?) minor, brunnea. Frons ad 1.5 cm longa, grosse cavernosa, lobata, lobulis contiguis. Involucra cavernosa in uno ordinibus, levia. Capsula stomatifera. Sporae 33 μ (30-38 μ) fulvae, baculosae, bacula $4.0 \times 2.5 \mu$ similiter virgulae, cicatrix tetradi parum perspicua. Elaters 320 μ (280-400 μ) longi, septati, fulvae, anguste foramini. Androecia desunt.

Thallus—The fronds are small, with the margin deeply lobed (Text-fig. 3a). The lobes are contiguous and bear detachable lobules (Text-fig. 3b). The surface of the fronds



Text-figs. 19-21. Elaters in F. incurvus, F. pinnilobus and F. buitenzorgius.

is smooth. The cells along the margin are broader than long with outer wall slightly convex. Internally the thallus is cavernous.

Chloroplasts are round to polygonal and without any centralized pyrenoid body. Androecia—In all the 10 fronds studied, only sporogonia were present without any indication of androecia. Stephani (1916) in his diagnosis of the species mentions androecia to be numerous in the branches and also to be containing four antheridia in each. Inspite of keen search not one frond was found to be bearing even a single androecium. Evidently the species in likely to be a dioecious one in which male fronds seem to have escaped collection along with the capsule bearing ones.

Involucre—The involucre is smooth on the surface and internally a single layer of cavities is seen,

Capsule—In the epidermis of the capsule 15 stomata per sq mm of the surface have been found. The stomata are 66μ (mean) in length.

Spore—The spore is light brown in colour and often subcircular in outline in polar view. A thin trilete mark is often discernible. The exine is ornamented with bold bacula (Text-fig. 15; Pl. 1, Figs. 9-11) which are 4μ high and 2.5μ broad. The tips of the bacula are truncate or rounded and the width at the base and near the apex is almost the same. The bacula are smaller in height as well as the width and also sparser on the proximal face than those on the equator and the distal face. The average diameter of the spores in polar view is 33μ , ranging from $30-38\mu$.

Elaters—The elaters are light brown slender, vermiform and usually four celled with tapering ends (Text-fig. 20). The walls of the elater cells are thickened enclosing narrow to wide lumen with small or big inclusions. On an average a mature, complete, four celled elater is $320~\mu$ long, the length ranging between $280~\mu$ to $400~\mu$ and the width between $5~\mu$ to $10~\mu$.

Comparison—F. pinnilobus has boldest bacula in spores among the baculate spored species. In the nature of bacula it comes close to F. glandulosus, However, the bacula in the latter are smaller in height. The marginal spongy bodies in F. glandulosus are also very individualistic.

General remarks—The sheet accompanying the specimen no. 14580 Fondation Stephan at the conservatory in Genève bears the inscriptions—"Anthoceros pinnato-lobatus St nsp. frons angusta pinnata, pinnis multilobulatis, lacunosis; Inovol. lacunosa; Sporae 36 \mu hispidae nigrie; Elaters longi solidi 400\mu—Rechinger 3727". Another inscription connected with this specimen states-"Anthoceros pinnilobus steph. 1908 (in Rechinger); (Lecto) type Rechinger 3027, Upolo; Proskauer Determ. Anno 1954".

As compared to the diagnosis of the species given by Stephani (1916 and the inscriptions) my study reveals slight differences in that the thallus margin bears detachable lobules, the spores are light brown, baculate and measuring $33\,\mu$ (mean) and that the elaters are only $320\,\mu$ (mean) long.

Folioceros glandulosus (L. et L.) comb. nov.

Text-figs. 4, 7, 16; Pl. 1, Figs. 12-13; Pl. 2, Fig. 14

Syn. Anthoceros glandulosus L. et L. 1832

Aspiromitus glandulosus (L. et L.) St. in Stephani 1916

Remarks—Dr. Meijer sent a material identified by him as A. glandulosus L. et L. which

as far as ascertained by me agrees with the diagnosis of the species given by Stephani as Aspiromitus glandulosus (L. et L.) St.

Diagnosis emend—Planta dioica, terricola. Frons ad 10 mm longa, lamellata, cavernosa breviter lobata, lobis spathulatis, truncatis, margine cum lobulis rotundatis. Involucra cavernosa, Capsula copiosa stomatifera. Sporae 31 μ (26-36 μ), baculosae, bacula 3.0 \times 2.5 μ similiter virgulae, cicatrix tetradi parum perspicua. Elateres 300 μ (260-350 μ) longi, septati spadici, latum foraminis. Androecia numerosa, in ramis propriis, polyandria (ad 20 in utroque alveolis). Antheridia corporum 177 μ (170-185 μ) longorum.

Thallus—The thallus is dioecious. The fronds are small and of longish type (Text-fig. 4). The anterior margin of the fronds is crenulate being densely beset with circular multicellular truncate spongy bodies of various sizes (Text-fig. 4c; Pl. 2, Fig. 12). The surface of the frond is usually full of lamellae. Lateral lobes are arranged irregularly in a pinnate fashion. Internally the thallus is cavernous. Chloroplasts are fragmented in the cells nearer the margin but large and single in the cells of the posterior regions. Chloroplast is of an irregularly roundish or oval shape, denser on the margin and lighter towards inside. In some cases the lighter area has some denser particles in the centre (Text-fig. 7).

In the scanty material available for study the fronds are either sterile or they bear androecia (Text-fig. 4b) and sporogonia on separate fronds.

Androecia—Androecia are sparse and in one row in the maturer posterior parts of the fronds but closer and in as many rows as the growing points in the younger regions of the fronds. A greater portion of the androecium is sunken in the thallus. The portion raised above the thallus has a small circular pore in maturer androecia but is unbroken in young ones. In a young androecium dissected out by me upto 20 antheridia in various stages of development were seen. Mature antheridium has a two tiered stalk and four tiered body wall. The height of the body (dehisced or fully mature) averages 177μ ranging between 170μ and 185μ .

Involucre—The involucre is deeply ridged and lamellate. Internally a single layer of cavities is seen.

Capsule—On the epidermis of the capsule 22 stomata per sq mm of the surface have been found. The stomata are 55 μ (mean) in length.

Spore—The spore is brown in colour and roundly triangular in polar view. Of a trilete tetrad mark there is just an indication (Text-fig. 16a: Pl. 1, Fig. 12). The exine is ornamented with very bold bacula (Text-fig. 16b, c; Pl. 1, Fig. 13) which are $2.7-3.0 \mu$ high and $2.0-2.5 \mu$ broad, distally and around the equator. The tips of the bacula are truncate or rounded and the width at the base and near the apex is almost the same. The bacula are smaller and sparser on the proximal face than those on the equator and the distal face. The average diameter of the spores in polar view is 31μ , ranging from $26 \text{ to } 36 \mu$.

Elaters—The elaters are dark brown, slender but very wide at the middle septum, vermiform and usually four-celled with tapering ends. The walls of the elater cells are thickened; lumen is wide with finely irregular cavity surface. On an average, a mature, complete four-celled elater is 300μ long, the length ranging between $260~\mu$ to $350~\mu$ and the width between 5 to $12.5~\mu$.

Comparison—F. glandulosus stands out by virtue of its very characteristic spore ornamentation from all the species described by me. F. pinnilobus (St.) comb. nov. has qualitatively similar spore but its bacula are distinctly longer.

Folioceros buitenzorgius (St.) comb. nov.

Text-figs. 5, 17, 21; Pl. 2, Figs. 15-17

Syn. Aspiromitus buitenzorgius St. in Stephani 1916

Diagnosis emend:—Planta dioica (?) major. Frons ad 2 cm longa, cavernosa, longa furcata, furcis planis levibus, margine breviter incisolobulatis. Involucra cavernosa. Capsula media stomatifera. Sporae 45 μ (40-50 μ) fuscae, spinosae, spinis ad 8 μ longis. Etateres 470 μ (400-550 μ) longi, septati, spadici anguste foramini. Androecia desunt.

Thallus—The fronds are expansive with deeply furcate branches (Text-fig. 5). In each branch the margin is shallowly incised into lobes. The thallus surface is smooth. Internally the thallus is cavernose. The chloroplasts are roundish to variously polygonal, usually single or fragmented in the thallus cells. In the cortical cells of the capsule 12 or more chloroplasts occur. The chloroplasts lack a differentiated, centralized pyrenoid body.

Androecia—In all the fronds of the type material studied by me, only sporogonia were borne without any evidence of androecia. According to Stephani (1916, p. 971) the plant is autoecious and the androecia are small, sparse, situated near the involucres and the cavity contains two antheridia. In view of my experience of the conditions occurring in most of the species of Folioceros studied by me so far, this species could be dioecious or markedly protandrous if at all monoecious, although the possibility of the former being the case is greater.

Involucre—The involucre is smooth on the surface and internally a single layer of cavities is seen.

Capsule—On the epidermis of the capsule only 15 stomata per sq mm of the surface have been found. The stomata are 55 μ (mean) in length.

Spores—The spore is brown in colour and circular in polar view. Proximally a thin but well defined tetrad mark is present. (Text-fig. 17a; Pl. 2, Fig. 15). The rays appear as if subtending short branches probably due to the too close presence of spines. Distally the spines are very sparse (Text-fig. 17b; Pl. 2, Fig. 17). The spines in the contact area are only half as long as those on the equator or distal face. The larger spines are 6-7 μ in height with a small, bulbous base subtending a long, pointed, spine with the apex often slightly bent (Text-fig. 17c; Pl. 2, Fig. 16). The average diameter of the spore in polar view is 45 μ , ranging from 40-50 μ .

Elaters—The elaters are brown, vermiform and usually four-celled, often with short branches. The ends are pointed. The wall is thickened enclosing a dark lumen with tubercular—inner surface (Text-fig. 21). Complete elaters are 470 μ (mean) ranging in length from 400-550 μ . The width of the elater cells is 6-10 μ but at joints it may be upto 12.5 μ .

Comparison—Among the spinose spored species of Folioceros well described so far, F. buitenzorgius has spores with longest spine and smallest bulbous base as compared to F, amboenensis, F. mamillisporus and F. spinisporus having spores with biggest bulbous base and F. dixitianus having spores with mediumly bulbous base as well as spine. F. buitenzorgius also has sparser stomatal distribution as compared to F. spinisporus or F. dixitianus. F. weistii (Khanna) comb. nov. described here has organizationally similar though smaller spines in the spores and the elaters are shorter as compared to F. buitenzorgius.

General remarks—Meijer examined the type material in 1953 and has remarked on the type sheet kept in the Herbarium at Genève that Asp. buitenzorgius St. = Asp. argillaceus St. Meijer (1954) puts Asp. buitenzorgius as a synonym of A. argillaceus, the latter appearing first in Stephani's treatise (1916). Meijer (1954) noted that A. argillaceus seemed to be closely

related to A. amboinensis Schffn.; the most reliable difference between them was in the spores which are distinctly hispidly papillose in the former. Proskauer (1951) studied the isotype material of A. weistii as well as that of Asp. argillaceus St. and found them to be identical. Meijer (1954) put Anthoceros weistii Khanna as a synonym of A. argillaceus on the basis of his own study of the type material supporting Proskauer's earlier finding. However, as my studies now reveal, F. buitenzorgius and A. weistii are not the same although they are very close to each other.

Folioceros weistii (Khanna) comb. nov.

Text-figs. 17, 18; Pl. 2, Figs. 18-20

Syn. Anthoceros weistii Khanna in Khanna, 1932

Diagnosis emend: Planta dioica. Plantae fimininae 30-50 mm diametro, lobatae, lobis leviter dentatis. Plantae masculinae 20-76 mm diametro. Frons grosse cavernosa. Involucra cavernosa, cum cavibus in duo ordino. Capsula media stomatisera. Sporae 45 μ (33-53 μ), suscae, spinosae, spinis ad 5.0 μ longis. Elateres 400 μ (350-460 μ) longi, septati, suscae, angusta foramini. Androecia alveolis polyandris. Antheridia 163-215 μ (cum caulis) longa.

Thallus—The few fronds examined are all of the expansive type with smooth surface. Internally the fronds are cavernose. No male plants were present in the material examined but as already observed by Khanna (1932) the plants are dioecious.

Involucre—The involucre is ridged on the surface and internally the cavities are in two or more layers (Text-fig. 10).

Capsule—On the epidermis of the capsule 15 stomata per sq mm occur. The stomata are 60 μ (mean) in length.

Spores—The spore is usually circular in polar view. Proximally a small but well defined tetrad scar (Text-fig. 18a) is seen. The rays are beset with spines. The spore is ornamented with 4-5 μ long spines which have a short, apical, pointed, often slightly bent portion mounted on a drawn out conical basal part (Text-fig. 18c). Distally the spines are fairly closely distributed (Text-fig. 18b; Pl. 2, Fig. 18). The average diameter of the spore is 43 μ , ranging from 38-48 μ .

Elaters—The elaters are brown and vermiform and usually four-celled with pointed ends. The wall is uniformly thickened enclosing a dark lumen with granular contents. Complete elaters are 400 μ (mean) long ranging from 350-460 μ . The width is 6-12.5 μ .

COMPARISONS

Gametophyte—The Thallus is cavernous in all the species of Folioceros described by me so far (incl. Bharadwaj, 1965, 1971). Some are monoecious and others are dioecious. In appearance the thallus in different species is of two sorts, i.e. (1) the fronds are narrow and long but either strap-shaped as in F. glandulosus, and F. pinnilobus or linear pinnate type as in F. vesiculosus, F. miyabenus, F. assamicus, F. falsinervius, F. incurvus, and F. fuciformis; (2) the fronds are broadly expansive type, i.e. anteriorly broad, e.g. in F. mamillisporus, F. dixitianus, F. amboenensis, F. spinisporus, F. buitenzorgius and F. weistii.

The difference in the two types of thalli is often easily apparent. These thalli appear to be typical of their groups of species because they are fertile, bearing antheridia as well as sporogonia and are apparently normal. It is possible that under abnormal conditions of growth these may present varied appearance but it is improbable that similar treatments would

obviate the difference noted between normal thalli and would produce identical abnormal thalli.

The thalli in F. miyabenus and F. falsinervius have lamellate outgrowths on the dorsal surface. In F. glandulosus and F. pinnilobus small, spongy, circular, discoid outgrowths from the margin are found and in F. assamicus, F. miyabenus and F. falsinervius (Meijer, 1954, Fig. 6b) the marginal, 1 cell thick border, composed of elongated cells is the characteristic feature.

The chloroplast possesses a centrally grouped pyrenoid body in F. spinisporus, F. mamillisporus, F. dixitianus and F. buitenzorgius and F. weistii but lacks it in F. pinnilobus, F. falsinervius, F. glandulosus, F. miyabenus, F. assamicus and F. incurvus.

The androecium, and the structure of the antheridial wall is similar in all the species considered here wheresoever studied. The height of the antheridial body is variable (Table 1). There seem to be three size categories viz., 145μ , 160μ and 175μ in the species with baculate spores and two categories of 130μ and 170μ for F. mamillisporus and F. dixitianus having spinose spores. In the number of antheridia produced per androecium, the variations tend to fall into 3 categories viz., 8, 20-25 and 60 antheridia per chamber.

The involucre is cavernous in all the specimens but in F. miyabenus and F. weistii the cavities are in two rows whereas in F. incurvus, F. assamicus, F. falsinervius and F. dixitianus they are in a single row. In F. miyabenus and F. assamicus lamellate outgrowths from the surface of the involucre have been noted. The involucre is fluted in F. miyabenus, F. falsinervius and F. weistii.

In the sporogonia, the capsular epidermis is mostly stomatiferous. The number of stomata varies from complete absence in F. incurvus to few (10 per sq. mm) in F. assamicus, medium (15 per sq. mm) in F. pinnilobus, F. miyabenus, F. falsinervius, F. biutenzorgius, F. weistii and presumably in F. vesiculosus also, and high (20-26 per sq. mm) in F. dixitianus (26 per sq. mm) and F. spinisporus. The stomata are smallest (55 μ) in length in F. spinisporus and F. buitenzorgius, of medium length (65 μ) in F. pinnilobus and F. falsinervius but longest (77 μ) in F. miyabenus and F. assamicus. F. fuciformis might fall in the last group. The stoma in F. dixitianius is medium sized (62 μ).

The spores in mature conditions are brown in F. falsinervius, F. miyabenus and light brown in F. pinnilobus, F, fuciformis F. incurvus. By size (equatorial diameter of mature spores in polar view) the spores fall into three groups i.e. 27-30 μ (mean) in F. incurvus; 31-36 μ (mean) in F. glandulosus, F. pinnilobus, F. assamicus, F. miyabenus, F. falsinervius F. fuciformis and F. vesiculosus; 37-45 μ mean in F. buitenzorgius, F. weistii, F. mamillisporus, F. dixitianus and F. spinisporus. In the last group, the spores are dark brown to black.

The ornamentation of the spore exine is either baculate or spinose. However, there is significant variation in the size and shape of the bacula or the spines in different species. In respect of the size of ornament-units among species having baculate spores, F. pinnilobus and F. glandulosus have boldest bacula, F. miyabenus, F. assamicus and F. fuciformis have medium-sized bacula and F. falsinervius has shortest bacula while F. incurvus has thinnest bacula. The bacula of F. glandulosus and F. pinnilobus have truncate or rounded apex. However, in F. miyabenus, F. falsinervius, F. incurvus and F. assamicus the bacula usually have dentate apex Normally the bacula on distal face are bolder and denser than those on the proximal face in each species. Among species having spinose spores, F. mamillisporus has bolder spines but fewer in number as compared to F. dixitianus (Pl. 2, figs. 21-23), F. weistii and F. buitenzorgius. The last species has the longest spines. The spines in the last four species are built on similar pattern, i.e. with an apparently hollow bulbous, base, topped with a concial spine of varied length.

In most of the species having dentate-baculate spores a clear tetrad mark is not to

		(6)		-	×									
			An	Antheridium	m		Spore (Mature)	fature)	,	Elater size		Ca	Capsule	
Name of	Sexuality	Thallus Type	Per	Body ir	Body height in μ	Diamet	Diameter in μ	Bacula or spines	Leng	Length in μ	width	-	Stoma length	Special features
Species			cham- ber	mean	range	mean	range	size (1×b) (biggest)	mean	range	range	per sq. mm	$\lim_{\mu} \frac{\mu}{\mu}$	· ·
*						Spores	baculate	Spores baculate (dentate)						,
F. miyabenus	Monoecious	longish	8	145	138-155	32	30-37	2×1 -4 μ	430	350-550	5-10	15	69	lamellae
F. falsinervius	Monoecious	pinnate longish	25	175	C.	32	30-38	$1.5 \times 1.2 \mu$	450	350-500	5-10	15	65	.
$oldsymbol{F.}$ vesiculosus	Monoecious	pinnate. longish	20	۰.	c.	36	c.	ر د. د.	۵.	350-500	۸.	few	٥.	
F. fuciformis	Monoecious	pinnate linear	21	180	۵.	34	32-40	c. c.	316	c.	۰.	۵.	ر. ر	
F. incurvus	Dioecious	pinnate	20	155	150-170	28	26-30	$1.5\times0.5~\mu$	400	350-460	5-8.5	absent	٠.	
F. assamicus	Dioecious	pinnate longish pinnate	œ	160	150-175	32	33-38	$2 \times 1.5 - 3.0 \ \mu$	350	300-410	5-10	10	70	. ,
					, 25	pores b	aculate	pores baculate (laevigate)						
$F.\ glandulosus$	Dioecious	longish	20	177	170-185	31	26-36	$3\times2.5~\mu$	300	260-350	5-12.5	22	55 8	spongy
$F.\ pinnilobus$	Dioecious(?) longish	longish		6		33	30-38	$4 \times 2.5 \ \mu$	320	280-400	5-10	12	66 d	bodies iamaliae, detachable lobules
		D				Sp	Spores spinose	nose						, *
F. amboenensis	Monoecious	expansive	٥.	۵.	. a.	ca30	25-35	c.	250	د.	٠.	۸.	٠.	
F. spinisporus	Monoecious	expansive	25	٥.	د.	38	35-42.5	η 9×9	480	400-550	5-8.5	22	55	
F. mamillisporus	Monoecious	expansive	25	130	125-145	43.5	40—50	$5.5 \times 6 \mu$	320	225-410	6-12.5	22	56	
F. dixitianus	Dioecious	expansive	09	170	160-180	37	35-43	$4.5 \times 4 \mu$	550	470-630	0.6-9	26	62	
F. buitenzorgius	Dioecious	expansive	۵.	c.	۵.	45	40-50	$8\times2.5~\mu$	470	400-550	6-12.5	15	55	
F. weistii	Dioecious	expansive	٠.	٠.	c	43	38-48	$5.0 \times 2.5 \mu$	400	350-460	6-12.5	15	09	

be seen. In F, glandulosus and F, pinnilobus it is masked by bacula. On the other hand, in F, amboenensis F, mamillisporus, F, divitianus and F, buitenzorgius having spinose spores, a tetrad mark consisting of three, thin rays is well formed and clearly distinguishable.

The elaters in species with baculate spores or spinose spores show hardly any difference in the structure. However, in F. assamicus the two-and three-celled elaters are as frequent as the four-celled normal elaters. In F. falsinervius, F. pinnilobus, F. miyabenus, F. mamillisporus, F. dixitianus and F. buitenzorgius four-celled elater is the general rule. In their length, that of complete units, the elaters fall into three categories with average length of $300-350\,\mu$, $400-480\mu$ and $500-600\,\mu$. The contents of the lumen are mostly tuberculate but for F. dixitianus and F. weistii where they are finer, consisting of granules.

DISCUSSION

Between the various species of the genus Folioceros considered here, qualitative differences in general have been noted in the ornamentation of the spores separating the species into three distinct groups, viz. (1) spores with bacula having dentate apices, (2) spores with bacula having smooth apices and (3) spores with spines having a bulbous base. Associated with this major distinction are a number of other features such as in the shape of the fronds, and the presence of ill-defined or distinct tetrad mark in the spores. I consider the differences in the features of spore to be of great taxonomic significance as these are known to be genetically controlled and thus constant. The difference in the shape of fronds being associated with the major difference in spore characters, also assumes taxonomic significance. With regard to this difference in the shape of the thalli in the three groups, I fully agree with Proskauer (1953) in considering the difference between linear pinnate or strap-shaped thalli and broadly radiating expansive thalli to be significant.

The above discussion leads to the conclusion that there are three distinct groups of species in Folioceros, primarily separable from each other on the basis of differences in spore ornamentation and the development or otherwise of haptotypic characters, i.e. the tetrad mark. Secondarily the difference in the shape of the fronds also separates these groups. The species of group (1) are F. assamicus, F. fuciformis, F. vesiculosus, F. falsinervius and F. miyabenus where the bacula have often multifid apex and the tetrad mark is scarcely distinguishable. The species of group (2) are F. pinnilobus and F. glandulosus where the bacula have smooth apex and the tetrad mark is definable though not well demarcated. The frond-type also differs between these two groups, the former having linear pinnately lobed appearance and the latter having longish, strap-shaped appearance. The species of group (3) are F. amboenensis F. mamillisporus, F. spinisporus, F. dixitianus, F. buitenzorgius and F. weistii having spinose spores and broadly expansive fronds.

Between the species in each group quite a number of features show quantitative variation tending to fall into a number of definable categories. For taxonomic purposes the significant characteristics appear to be those pertaining to the thalli being monoecious or dioecious, the height of the mature antheridial body, the density of stomata on capsule wall, the spore diameter, the size of ornament-units on the spore exine and the length of elaters. So far there is no report to indicate that any of the above mentioned characteristics are indeterminable or inconsistent in a pure species population. Varied combinations of these variables can be utilized for diagnosing the species. There are also some special features associated with the species, e.g. the circular, marginal spongy bodies in F. glandulosus, the detachable lobules in F. pinnilobus and the marginal palisade of longish cells in F. assamicus,

F. miyabenus and F. falsinervius which are additional characteristics distinguishing the species in the genus Folioceros.

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EXPLANATION OF PLATES

PLATE 1

- 1-3. F. miyabenus—1. Elaters, 2. Spore proximal, 3. Spore distal.
- 4-5. F. falsinervius—4. spore proximal, 5. spore distal (acetolysed).
- 6-8. F. incurvus—6. spore proximal, 7. spore diatal, 8. spore equatorial (acetolysed).
- 9-11. F. pinnilobus—9. spore proximal, 10. spore distal, 11. spore equatorial (acetolysed).
- 12-13. F. glandulosus—12. spore proximal, 13. spore distal (acetolysed).

Plate 2

- 14. F. glandulosus-Marginal spongy body.
- 15-17. F. buitenzorgius-15. Spore proximal, 16. spore distal, 17. spore equatorial (acetolysed).
- 18-20. F. weistii—18. spore proximal, 19. spore distal, 20. spore equatorial (nonacetolysed).
- 21-22. F. mamillisporus—21. spore equatorial, 22. spore proximal (nonacetolysed).
- 23. F. dixitianus—spore proximal (nonacetolysed).