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DISTICHOUS AND PSEUDODISTICHOUS MOSSES

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In revising the family *Phyllogoniaceae* for the Flora Malesiana, I found that in many species which so far were included in this family, the leaves are, contrary to expectation not distichously disposed. As that type of phyllotaxis is regarded as the main diagnostic character of the family, it was a surprise to me that other bryologists had not noticed this fact. For this reason I have paid special attention to the phyllotaxis of the species belonging to the *Phyllogoniaceae*.

In BROTHERUS, Natürl. Pflanzf. ed. 2, 11 (1925) 175, the family includes three genera, viz. *Phyllogonium* Brid., *Orthorrhynchium* Reichdt. and *Eucatagonium* (Broth.) Fleisch. The first genus, *Phyllogonium*, comprises, as far as I could check, distichophyllous species only (Fig. 5*a*). The leaves are inserted alternately on the complanate branches, the distances between the consecutive leaves in both rows being equal. The genus is restricted to S. America and Africa (Congo), and is characterized by the well-marked alar cells and by the strongly ampliate leaf bases.

The last-mentioned genus, *Eucatagonium*, also occurs in S. America, and further in Africa and Australia. In 1922 Fleischer transferred the genus to the family *Phyllogoniaceae*. Before this change it was regarded as a subgenus of *Catagonium* C. Muell., a genus belonging to the *Plagiotheciaceae;* this family includes several complanate mosses. Fig. 5*b* shows two branches of *Eucatagonium politum* (Hook. f. et Wils.) Broth. At first sight it is clear that the phyllotaxis is totally different from that in *Phyllogonium:* the leaves are not regularly arranged in two rows. However, these irregularities are easily overlooked. As a matter of fact, Fig. 3, which is a copy of fig. 565 of BROTHERUS, Natürl. Pflanzf. ed. 2, 11 (1925) 176, does not show them. In comparing figures 5*b* and 3 one undoubtedly sees the difference: in Fig. 3 the distances between the consecutive leaves on each side of the stem are equal, whereas in Fig. 5*b* they are unequal and even the alternation is not always regular.

If in Fig. 5*b* the leaves are not distichously disposed, what then is the phyllotaxis? To answer this question I have attempted to determine what the result would be, if a radially symmetric stem with a phyllotaxis belonging to the so-called main series is compressed. The main series in phyllotaxis is formed by the Fibonacci numbers 1, 2, 3, 5, 8, 13, 21 etc., in which any term is the sum of the two preceding terms. Each term indicates the number of contact parastichies and simultaneously the possible number of orthostichies Schoute's

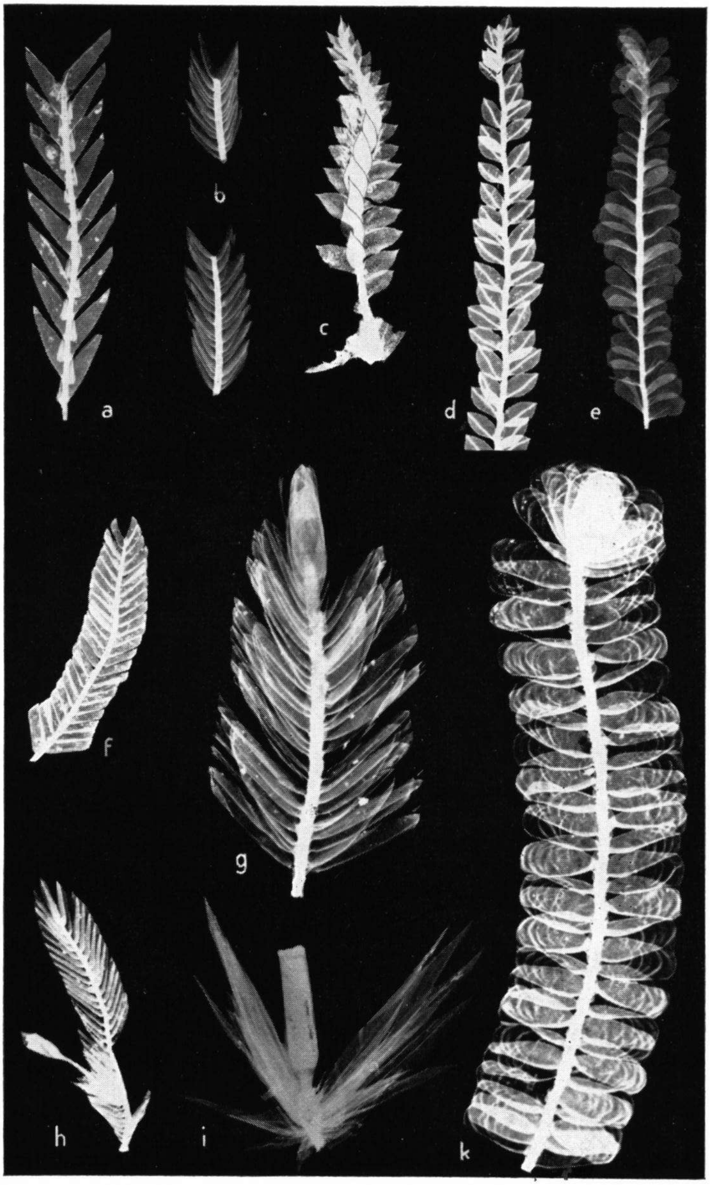

Fig. 5. Stems and in h. and i. capsules of different mosses ($\times$ 6). a. *Phyllogonium serra*. b. *Eucatagonium politum*. c. *Cyathophorella hookeriana*. d. *Thamnium ellipticum*. e. *Homaliodendron beccarianum*. f. *Orthorrhynchium elegans*. g. *Orthorrhynchium philippinense*. h. Capsule of *O. elegans*. i. Capsule of *O. philippinense*. k. *Neckeropsis lepineana*.

investigations have shown that it are these numbers of parastichies, and no others, which nearly always occur in higher plants. Alexander Braun, observing the divergences in phyllotaxis at a much earlier

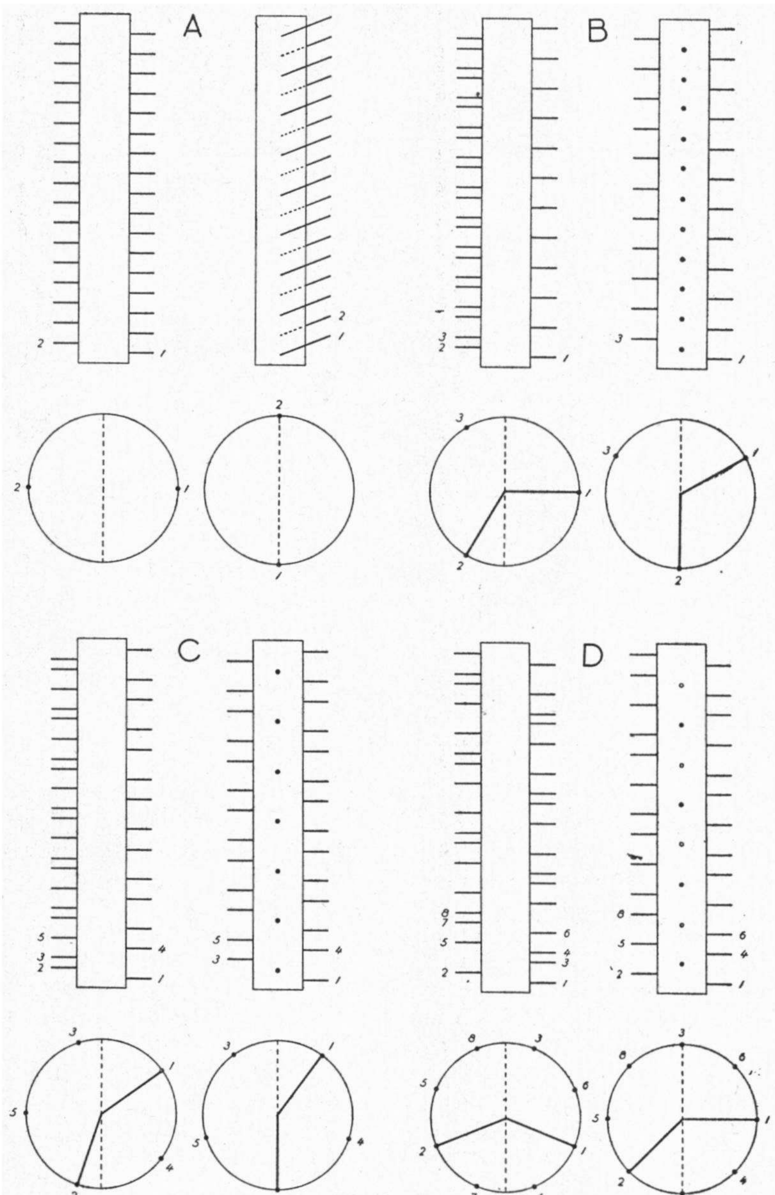

Fig. 1. Phyllotaxis with 2 (A), 3 (B), 5 (C), or 8 (D) orthostichies on complanate stems. The figures on the left relate to stems without median leaves, the figures on the right to those with either one or two rows of median leaves.

date, found the same numbers of orthostichies in the greater part of the mosses.

Fig. 1 demonstrates what will happen if the number of orthostichies is respectively 2, 3, 5 or 8, when the radially symmetric stem becomes a complanate one: the leaves, so far as they are found on different sides of the median line, are then shifted either to the left or to the right.

a. Leaves disposed in two orthostichies. (Fig. 1A). The leaves are distichously inserted, as is seen in *Phyllogonium* (Fig. 5*a*). However, there is a second possibility, *viz.* if the leaves are inserted in the median line; in the complanate stem the leaves are then found on the dorsal and the ventral side. This case with all the leaves pointing in one direction, is often realized in *Rhizogonium novae-hollandiae* Brid.

b. Leaves disposed in three orthostichies (Fig. 1B). In this case the number of leaves on one side of the median line may become twice as large as that on the other side. I did not find this type of phyllotaxis in complanate mosses. However, the other possibility *viz.* that one of these orthostichies is found in the median line, is realized in several mosses. Fig. 5*c*. shows the two rows of lateral leaves and the single row of ventral median leaves (amphigastria) in *Cyathophorella hookeriana* (Griff.) Fleisch.

c. Leaves disposed in five orthostichies. (Fig. 1C). Let us first consider the transitional case, *i.e.* that with one orthostichy in the median line. The lateral leaves are apparently disposed in two rows, and in each row the distances between the consecutive leaves are in the ratio 2:3:2:3 etc. If none of the five orthostichies is in the median line, the distances between the consecutive leaves on one side would be in the ratio 1:2:1:2, on the other side 2:3:2:3. Neither arrangement agrees with Fig. 5*b* of *Eucatagonium*, nor did I discover this arrangement in any other complanate moss.

d. Leaves disposed in eight orthostichies. In the transitional case there are two rows of median leaves, a dorsal and a ventral one (Fig. 1D to the right). If leaf number 1 is ventrally inserted, then leaf number 5 is dorsally placed, and on both sides the ratio of the distances between the consecutive leaves is 2:3:2:3. If median leaves are absent, the ratio of the distances between the consecutive leaves is on both sides 1:2:3:2:1 etc. This very characteristic ratio varies on the two sides in this way that if on one side it is 1:2:3:2:1 etc. it is on the other side 3:2:1:2:3 etc. If we measure in Fig. 5*b* of *Eucatagonium* the distances between the consecutive leaves on either side, then we find that the ratio is indeed 1:2:3:2:1 etc., and if on one side of the stem two leaves are near to each other, there is a large gap between the two leaves on the opposite side. My conclusion therefore is that the leaves of *Eucatagonium* are not really distichous, but that they are arranged in eight orthostichies. For this reason we will call them pseudodistichous.

That this arrangement is also present in the genus *Catagonium* and in other genera of the *Plagiotheciaceae*, may be taken as an indication that *Eucatagonium* is closely allied to *Catagonium*, of which it was originally regarded as a subgenus. There are other reasons for assuming a close relation between the two genera: the leaf cells in *Eucatagonium* are thin-walled and long-linear just as in *Catagonium*, whereas in *Phyllogonium* the leaf cells have incrassate and pitted walls, and are much shorter linear to rhombic. The capsule of *Eucatagonium* is borne on a well-developed seta, whereas in *Phyllogonium* the seta is short or absent. In my opinion, Fleischer who was not aware of the pseudodistichous leaves, made a mistake in transferring the (sub-) genus *Eucatagonium* to the *Phyllogoniaceae;* its correct place is near the genus *Catagonium* in the *Plagiotheciaceae.*

For the sake of completeness I wish to add that it is not necessary to accept precisely 8 orthostichies, for with 13 or 21 (the next Fibonacci numbers of the main series) orthostichies too we arrive at a

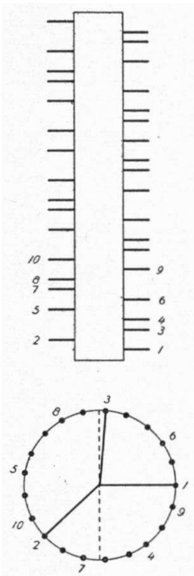

Fig. 2. Phyllotaxis without orthostichies, the divergence between the consecutive leaves is 137° 29′, the Fibonacci angle.

disposition which agrees with the observation. The differences between the dispositions obtained in the case of 8 and 13 orthostichies are very small indeed. To demonstrate the comparatively small size of these differences I have given in Fig. 2 the situation in the case of a phyllotaxis with the limiting angle of the main series, the so-called Fibonacci angle, *i.e.* 137° 29′. The resulting disposition in a complanate stem is in that case nearly the same as the one we arrive at with an angle of 135° (*i.e.* with 8 orthostichies), at least if we confine our attention to a short part of the stem. Only if a much longer part of the stem is considered, we observe a slight deviation of the ratio mentioned above, *viz.* 1:2:3:2:1. Our final conclusion is this: if the arrangement remains regular along the whole length of the branch, the leaves are disposed in 8 orthostichies, but if there is a slight shifting, we have a closer approximation to the limiting angle of the main series. In this case it is not possible to determine whether the number of orthostichies is 13, 21, 34 or even higher.

Further study of the phyllotaxis in complanate mosses has shown that pseudodistichous leaves, *i.e.* leaves that are in reality in 8 or more rows, occur in several families, especially in the *Neckeraceae* and the *Plagiotheciaceae* (see Fig. 5*d* *Thamnium ellipticum* (Bosch et Lac.) Kindb. and Fig. 5*e* *Homaliodendron beccarianum* (Hamp.) Broth.).

Let us now consider the third genus, *Orthorrhynchium*, which occurs in the Malaysian region. In the herbaria several specimens have been named *O. philippinense* C. Muell., but a re-examination clearly showed that two different species have been included under this name. The leaves of the first moss (Fig. 5*f*) proved to be perfectly distichous, but this moss is incorrectly referred to *O. philippinense* C. Muell.; it is in reality *O. elegans* (Hook. f. et Wils.) Reichdt. which was originally described from Australia. *O. beccari* C. Muell. from New Guinea is also the same species.

The other *Orthorrhynchium* specimens, included under the name *O. philippinense* C. Muell. are totally different (Fig. 5*h*). They are pseu-

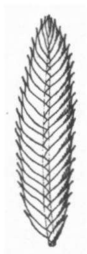

Fig. 3. *Eucatagonium politum* (fig. 565 from BROTHERUS, Natürl. Pflanzf. ed. 2, 11).

dodistichous, *i.e.* the leaves are arranged in 8 or more rows. The question is now whether this moss really belongs to *Orthorrhynchium*. The phyllotaxis seems to make this improbable. In search for other discrepancies, I turned my attention to the capsule of this *Orthorrhynchium* species which hitherto was unknown. However, the specimen collected by Carr (no 11944) in New Guinea proved to bear capsules. The seta is short or nearly absent, and the capsule itself is long and cylindrical (Fig. 5*i*). The capsule of *O. elegans* (Fig. 5*g*) has a well developed but short seta and is ovoid. In my opinion these two points of difference (the difference in phyllotaxis and that in shape and development of the capsule) sufficiently prove that this part of *O. philippinense* C. Muell. will have to be removed from the genus *Orthorrhynchium*. But to what other genus should we transfer the species? Now in Journ. of Bot. 43 (1905) 342 A. and E.S. GEPP recognized that *O. philippinense* C. Muell. from the Philippine Islands and *Neckera* *phyllogonioides* Sull. from Luzon are conspecific. It is for this reason that in BARTRAM's Mosses of the Philippines (1938) 232 this species is named *O. phyllogonioides* (Sull.) E. G. Britt. ex Bartr. To my opinion it is better to transfer this part of *O. philippinense* C. Muell. for the present to the genus *Neckera* and to accept for the species the name *Neckera phyllogonioides* Sull.

Let us wind up with a few remarks on another dilemma. In a key to the genera of the *Neckeraceae* one finds:
1. Leaves in 4 rows......*Homaliodendron, Neckeropsis.*
2. Leaves in 8 rows......*Neckera, Himantocladium.*

The arrangement of the leaves in 8 rows is easily recognizable; there may be some difficulty only if a few leaves are not directed laterally, but an arrangement in 4 rows did not agree with the theory of phyllotaxis. There are two possibilities; either there are 4 rows, and then the phyllotaxis is of the first accessory series 1, 3, 4, 7, 11, etc., or the 4 rows do not really exist. To solve this problem, I have calculated the disposition of the leaves in the case of 4 orthostichies (Fig. 4A) and in that of 7 orthostichies (Fig. 4B). The ratio of the

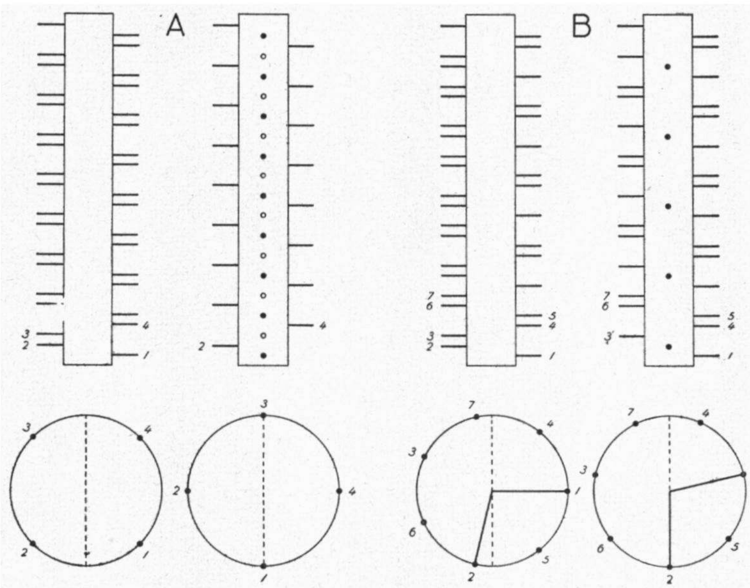

Fig. 4. Phyllotaxis with 4 (A) or 7 (B) orthostichies on complanate stems.

distances between consecutive leaves is 1:3:1:3 or 1:3:3:1 and 1:2:1:3:1 etc. respectively. Neither of these dispositions occur in *Neckeropsis* (Fig. 5*k*), but our figure clearly shows that the ratio is the same as in Fig. 5*b*, which relates to *Eucatagonium*. The conclusion in this case is also that the arrangement in 4 rows is a fiction; the moss is not tetrastichous, but pseudo-tetrastichous; in reality it is octostichous.

The above considerations may serve to show that in mosses a morphological study of the phyllotaxis may refrain us from drawing false taxonomic conclusions and that at least in some moss families the phyllotaxis may be of taxonomic importance.