CYTOLOGY OF HYMENOPHYLLACEAE

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(With Plates 14–17 and Twenty Text-figures)

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Over 600 species of filmy ferns are placed in the family Hymenophyllaceae which are included in two large and comprehensive genera *Hymenophyllum* and *Trichomanes* whose limits are sometimes ill-defined. Recently, following Presl and van den Bosch, Copeland (1947) has segregated the family into thirty-three smaller units, each including a group of closely related species, and considered as a distinct genus. This splitting has not so far been universally accepted, and has still to stand the test of time. Consequently in the present cytological investigation older conservative nomenclature has been followed, but the generic names according to Copeland's system are indicated in parentheses.

The only work on the cytology of the Hymenophyllaceae is that of Manton (1950) and Manton & Sledge (1954) as a part of the former's stimulating work on the cytology of the Pteridophyta. In the present paper eight species and two varieties have been investigated, mostly from the subtropical region of the Darjeeling Himalayas. This area lies at 27° 3′ N. latitude and 88° 16′ E. longitude on the outer Himalayan range, and receives an average rainfall of about 120 in. annually, of which 100 in. fall during the principal rainy months from June to October. The species are distributed within an altitude of 5000–9000 ft. The only exception is that of *Trichomanes insigne* forma γ, which is met with farther west on the outer Himalayan range in the Mussoorie Hills, an area which receives lesser rainfall of about 86 in. annually. In this region it is the only species met with in nature commonly distributed along the ravines.

Methods

The collections were made during the months of July and August 1954 and 1955, as the sporogenesis occurs during the rainy season. The pinnules bearing young sori were fixed in acetic alcohol (1:3) for 24–72 hr. on bright sunny days, generally before 12 a.m., and then preserved in 75% alcohol after thorough washing with 95% alcohol. The aceto-carmine squash preparations for the study of chromosome numbers were made soon after, since it was found difficult to liberate spore mother cells with ease from sporangia when the material had been stored for over 4–5 days, as the sporangia lose their plasticity. Definite chromosome numbers were established after counting them in a good many spore mother cells. The preparations were made permanent by the method suggested by McClintock (1929). All the illustrations of chromosomes given under text-figures are from actual photographic prints bleached according to the procedure given by Manton (1950) and are for the purpose of elucidating the photographs reproduced as plates.

The specimens whose cytology is investigated have been deposited in the herbarium of the Panjab University, Amritsar, India. It is a pleasure to express our sincere thanks to Mr A. H. G. Alston, of the British Museum, London, for identifying some of the specimens for us.

Observations

Hymenophyllum exsertum Wall. (= *Mecodium exsertum* (Wall.) Copel.)

The species is very common at Darjeeling, growing practically everywhere in dense, moist, shady places underneath the clusters of *Gleichenia glauca*. The species is described to be widely distributed in India, being reported from the Khasya Hills (2000–9000 ft.), the Western Ghats of Madras Presidency, and from Ceylon (Beddome, 1892).

The chromosome number $n = 21$ tallies with that recently published by Manton & Sledge (1954) from Ceylon (Pl. 14, fig. 1; Text-figs. 1, 2). The chromosomes are significantly larger than in most of the ferns, and their chiasmatic configurations include X's, O's, Y's and V's. An interesting feature is the variation in size of the complements in plants from different sources, as observed on a comparison of Text-figs. 1 and 2, which represent print drawings at exactly the same magnification from material under identical conditions of fixation and staining. Meiosis is normal, and 128 spores per sporangium are produced.

Hymenophyllum polyanthos Swartz (= *Mecodium polyanthos* (Swartz) Copel.)

The species grows epiphytically quite commonly in Darjeeling on Sanchal Road, below Ghoom, in the Lebong forest, and on the way to Sandakphu at an altitude of 10,000 ft.

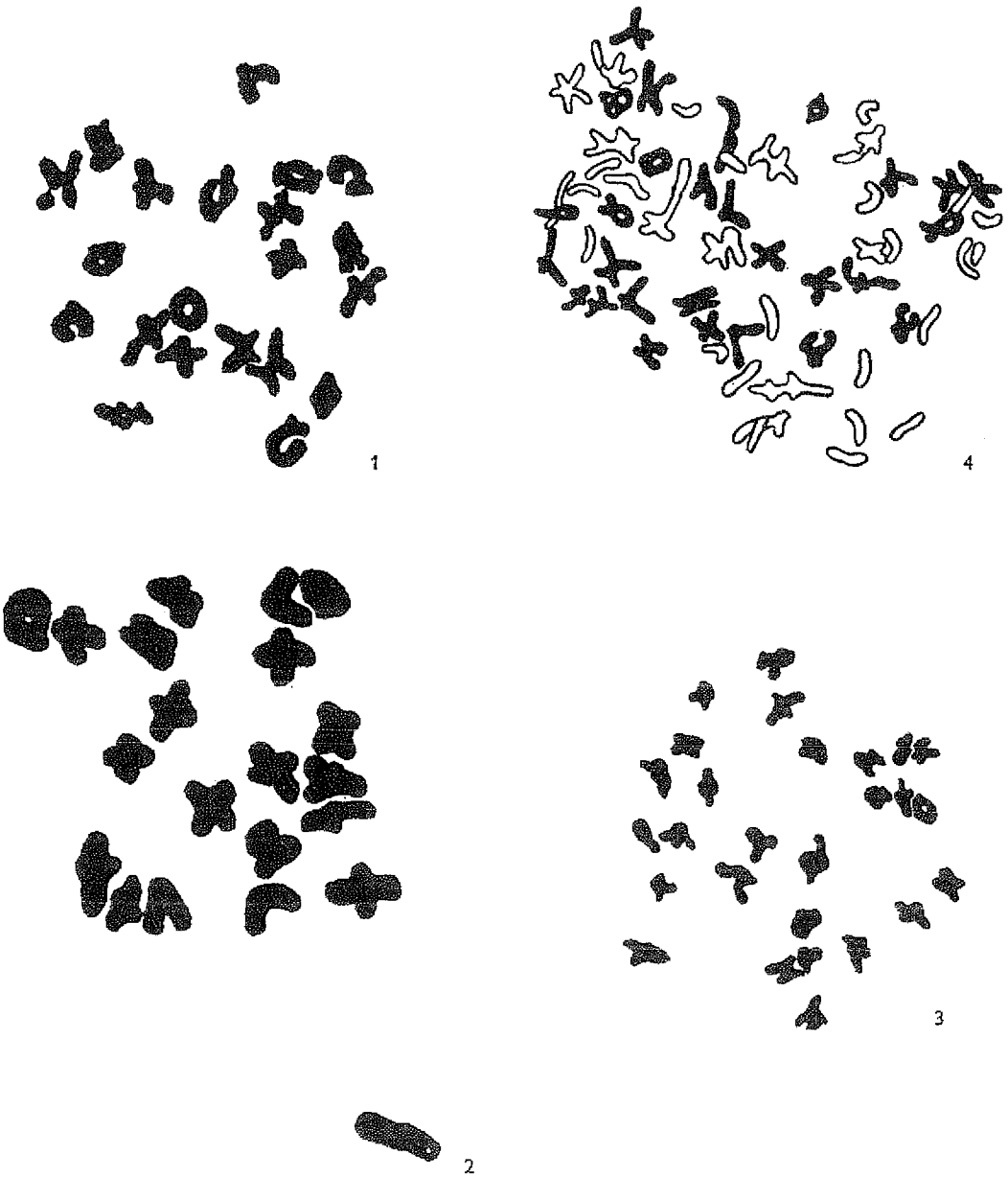
The Himalayan species unmistakably show the haploid chromosome number to be 27 in several spore mother cells (Pl. 14, fig. 2; Text-fig. 3). Sporogenesis is normal, and 128 well-filled and apparently viable spores are produced within a sporangium.

This chromosome number is at variance from that reported by Manton & Sledge (1954) for plants under the same name from Ceylon. They report the n number to be 28, and on this basis and on a comparison with the chromosome number in other species have deduced one of the monoploid base numbers for the genus to be 7. It is interesting in this connexion to note what Beddome states for the plants referred to this species growing in Ceylon: 'This has generally been considered a quite distinct species by Botanists in Ceylon and S. India, but Mr Clarke says it runs into the type in Northern India, and cannot be separated. With only Ceylon and S. Indian specimens in view, it is difficult to consider them all forms of one species, but after seeing the Himalayan forms, I quite agree with Mr Clarke that they cannot be separated as species.' It seems there is a taxonomic difficulty which requires clarification, but the two types are quite distinct cytologically.

Hymenophyllum javanicum Spreng. (= *Mecodium australe* (Willd.) Copel.)

Commonly found in Birch Hill Road forest and the forests below Lebong at Darjeeling. Grows as an epiphyte near the base of tree trunks or on rocks in rather moist places. The species is reported to occur widely not only in India and Ceylon but also in Burma, the Malaya Peninsula, Australia, New Zealand, etc.

Meiosis is very irregular in Darjeeling specimens. At diakinesis univalents, bivalents, trivalents and even occasional quadrivalents are observed (Pl. 14, fig. 3; Text-fig. 4). The

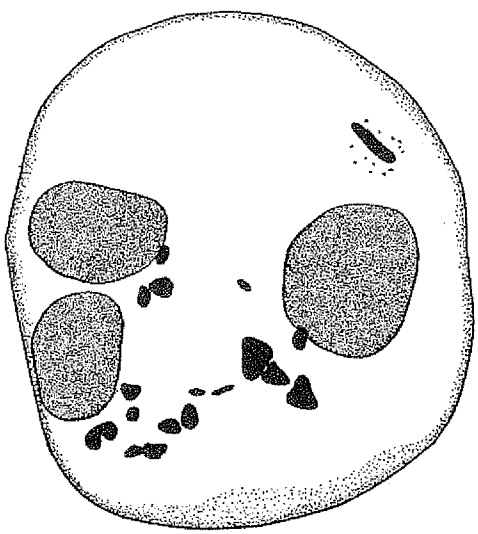


Text-figs. 1–4. 1, 2. *Hymenophyllum exsertum*, $n=21$, $\times 940$. 3. *H. polyanthos*, $n=27$, $\times 756$. 4. *H. javanicum*, $2n=108$, $\times 885$. (Barring Text-fig. 2 the others are explanatory diagrams to Figs. 1, 2, 3 respectively.)

$2n$ chromosome number is 108. For illustration the constitution in only two mother cells is represented below:

No. of mother cell	Univalents	Bivalents	Trivalents	Quadrivalents	$2n$ number
1	21	28	9	1	$2n=108$
2	28	25	10	0	$2n=108$

At metaphase I a number of univalents are observed scattered outside the equatorial plate. At anaphase the bivalents disjoin normally, but the behaviour of trivalents and univalents is typical. Trivalents either move to the poles in a body or disjoin unequally. On the other hand, the univalents arrange themselves on the equator and divide longitudinally (Pl. 14, fig. 4). The daughter chromatids may not be included in any of the two daughter nuclei and form micronuclei inside the mother cell. At anaphase II the univalents, being unable to divide for the second time, are again left out in the cytoplasm, and are later distributed at random in the resulting tetrad. These are often seen as micronuclei inside the spores (Pl. 15, fig. 6), and their number and size varies in each case. As a result of this irregular division the four nuclei in a mother cell are often highly unequal (Pl. 15, fig. 5). Occasionally three nuclei and a scattered group of chromosomes may be observed within a sporocyte (Text-fig. 5). The resulting spores are shrivelled and vary in number from 48 to 64 within a sporangium. This form is obviously an apomict and multiplies vegetatively.

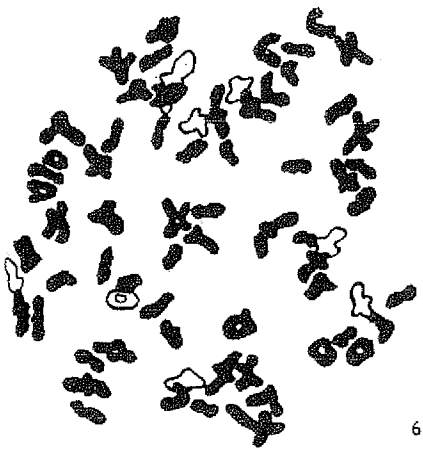


Text-fig. 5. *H. javanicum*. A mother cell with three unequal nuclei and a few scattered chromosomes, × 1120.

Manton & Sledge (1954) have investigated the same species from Ceylon after it had been removed and transplanted to Kew. They reported complete absence of pairing and found the $2n$ chromosome number to be 72. Obviously this form is a diploid, while the Darjeeling one which we have investigated is a triploid. The absence of pairing in the Ceylon specimens grown at Kew, the above authors suspect, may be merely a case of modification or metabolic failure due to altered climatic conditions; and they cautiously add that to be certain on the point specimens in their natural habitat should be investigated. We may state that the formation of bivalents and trivalents in the $3n$ Darjeeling plants gives an indirect hint that the surmise of the above authors may probably be correct.

Trichomanes radicans Sw. (= *Vandenboschia radicans* (Swartz) Copel.)

This is a very pretty species commonly met with in the Lebong forest and on the way to Takda forest, forming festoons under shady damp rocks on which it creeps. It often climbs tree trunks to a height of 7–8 ft.



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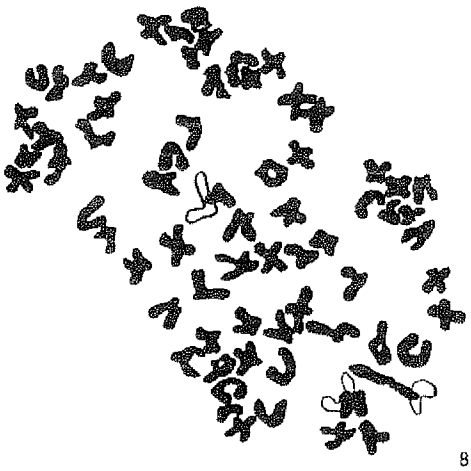

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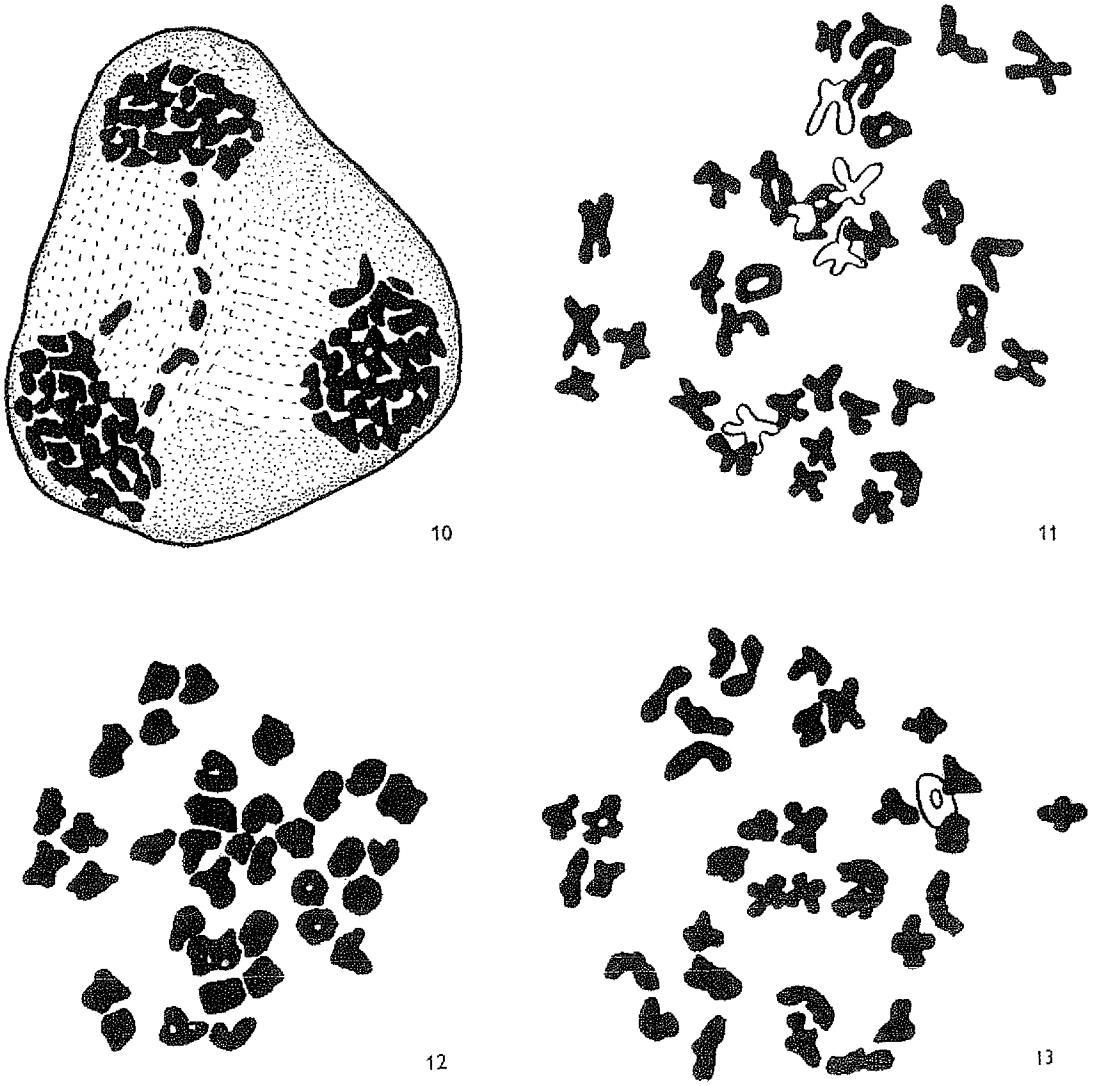
Text-figs. 6–9. 6. *Trichomanes radicans*, $n = 72$, × 940, 7. Diploid *T. auriculatum* $n = 36$; 8. An abnormal mother cell in the same with 72 bivalents. 9. Triploid *T. auriculatum*, $2n = 108$. 7–9, × 877. (Explanatory diagrams to Pl. 15, Figs. 7–10 respectively.)

The haploid chromosome number is 72 (Pl. 15, fig. 7; Text-fig. 6), and agrees with that reported by Manton (1950) for the species collected from Ireland. Meiosis is normal, as is evident from the production of normal tetrads and well-filled spores.

Trichomanes auriculatum Bl. (= *Vandenboschia auriculata* (Bl.) Copel.)

This graceful species is fairly common in the Birch Hill and Lebong forests at Darjeeling. It possesses a stout rhizome which is creeping or scandent on damp rocks or tree trunks. In the eastern Himalayas it is quite well distributed, being reported by Beddome (1892) from Sikkim, Bhotan, and the Khasya Hills between 2000 and 7000 ft.



Text-figs. 10–13. 10. Laggards at anaphase II in triploid *T. auriculatum*, ×2240. 11. *T. pyxidiferum*, $n=36$, ×1560; *T. plicatum*, $n=36$, ×1560. 13. *T. insigne* forma *a*, $n=36$, ×1560. (11–13 are E.D. to Figs. 14–16 respectively.)

In the Darjeeling area two cytologic forms, a diploid and a triploid, which to all appearances are morphologically indistinguishable, are met with. In the diploid the meiosis is perfectly regular, and 36 bivalents are counted at metaphase (Pl. 15, fig. 8; Text-fig. 7). The preparation was not so satisfactory from a photographic point of view;

nevertheless, 36 bivalents could be clearly observed. The normal production of spores in this is 64 per sporangium, and these are well filled, equal in size and apparently viable.

Occasionally a tetraploid mother cell occurs among the numerous diploid ones, clearly showing 72 bivalents (Pl. 15, fig. 9; Text-fig. 8). Some of these are closely associated to give quadrivalent configurations. In what way such mother cells are formed could not be investigated. In the triploids the mother cells at metaphase show abnormal chromosome pairing resulting in the formation of trivalents, bivalents and univalents (Pl. 15, fig. 10; Text-fig. 9). The $3n$ chromosome number is 108. The frequency of the irregular associations may be judged from the following data representing two mother cells:

No. of mother cell	Univalents	Bivalents	Trivalents	$2n$ number
1	22	25	12	$2n=108$
2	28	25	10	$2n=108$

The disjunction of chromosomes during first and second meiotic divisions are characteristic of triploids. In Pl. 16, figs. 11 and 12, are seen irregularities at metaphase and anaphase I. In the latter univalents are observed splitting. Irregularities at anaphase II are seen in Text-fig. 10. Ultimately in the tetrads micronuclei are observed (Pl. 16, fig. 13). The unbalanced distribution of hereditary material results in empty and abortive spores which may be up to 64 in number. The remarkable similarity between the diploids and triploids leads us to believe in the autotriploid nature of the latter. It seems likely that they have originated by the combination of a diploid and a haploid sex cell. The occasional occurrence of tetraploid mother cells with 72 bivalents among the diploid individuals may be an indication of the formation of diploid spores and hence diploid gametophytes and sex cells. It is not unlikely that further search may even reveal tetraploid individuals within the population. The triploids thrive well and reproduce apomictically.

Trichomanes pyxidiferum L. (= *Vandenboschia pyxidifera* (L.) Copel.)

The species is distributed in the Sanchal forest and on the roadside to Sandakphu, growing in tufts along with mosses on damp rocks in shady places.

Meiosis in this species is perfectly normal, and 36 large bivalents are clearly discernible at metaphase (Pl. 16, fig. 14; Text-fig. 11).

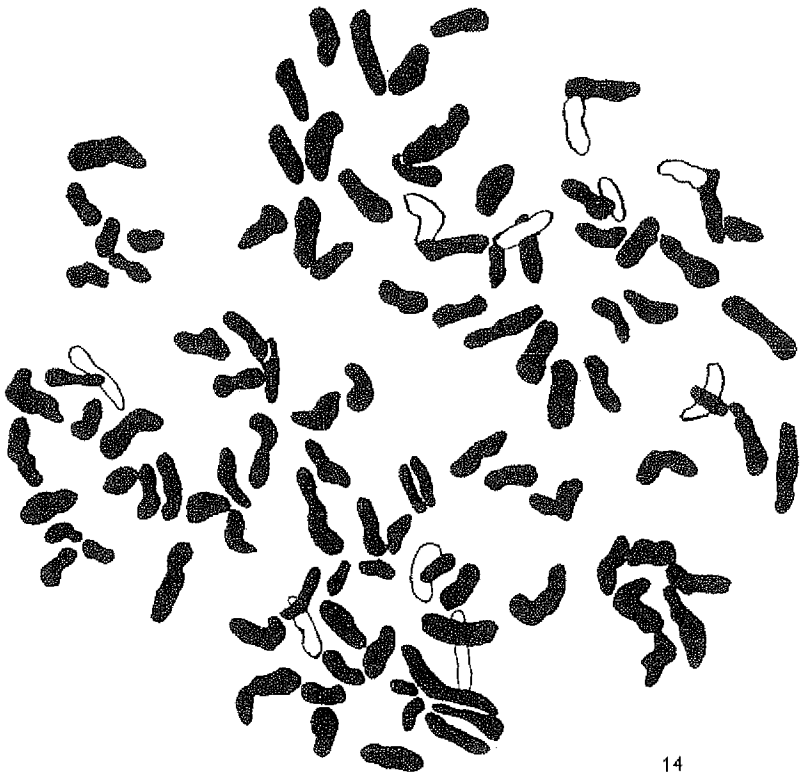
Trichomanes plicatum v.d.B. (= *Crepidomanes plicatum* (v.d.B.) Copel.)

Beddome (1892) considers it to be a member of *Trichomanes bipunctatum* complex and ranks it as a variety, but there is a good deal of justification in separating it as a distinct species both on cytologic and morphologic grounds. The species was collected from Lebong forest growing epiphytically on the bark of a maple tree. It is not common in the area.

Meiosis is perfectly regular. Thirty-six bivalents have been counted in several aceto-carmine preparations at metaphase (Pl. 16, fig. 15; Text-fig. 12). Sixty-four spores are produced within a sporangium all of which appear viable.

Trichomanes insigne v.d.B.

The plants identified by Alston under this name are segregated by us into three forms, two of which are morphologically similar but cytologically different and the third morphologically somewhat different from the first two. They are treated here as forma α, β and γ,



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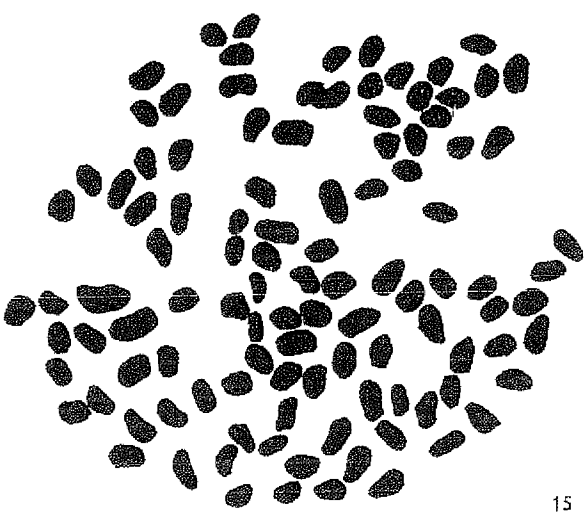

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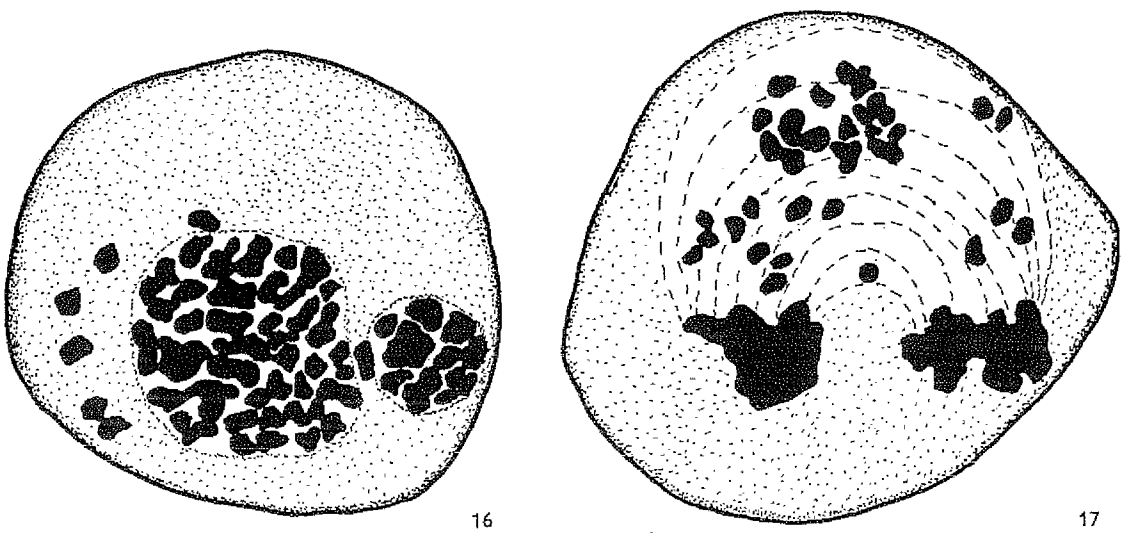
Text-figs. 14, 15. *T. insigne*, forma β at 'diakinesis' and 'metaphase' respectively showing complete asynapsis. $2n=108$, $\times 1800$ and $\times 2640$ respectively. (Text-fig. 15 is E.D. to Fig. 18.)

respectively. All these were formerly included under the polymorphic species *T. bipunctatum* as variety *insigne* by Beddome (1892).

Forma α. Both the forms α and β grow plentifully in Darjeeling. They are small plants growing in very hygrophytic environments near the ravines, and like the form γ lack roots. The rhizome is directly covered over with root-hairs.

Thirty-six bivalents are clearly counted at metaphase in forma α (Pl. 16, fig. 16; Text-fig. 13). At anaphase a few chromosomes may lag behind but ultimately reach the poles. Meiosis is normal, and 64 spores are formed within a sporangium.



Text-figs. 16, 17. 16. *T. insigne*, forma β, interkinesis to form two nuclei with a few scattered chromosomes; 17. *T. insigne*, curved spindle at first division. Both ×1460.

Forma β. This form is entirely different cytologically from the previous one. The mother cells show complete 'asynapsis' at metaphase I, and 108 completely separate univalents are organized (Pl. 17, fig. 18; Text-fig. 15). In view of this abnormality earlier substages of the prophase were studied, and it was noted that the chromosomes paired and formed bivalents and trivalents at zygotene, though the pairing was limited (Pl. 17, fig. 19). This condition continued in the pachytene, but at diplotene all the previously formed spirals between the paired chromosomes regress, the chromosome pairs fall apart, and numerous univalents appear. Signs of chiasmata or crossing-over points between paired chromosomes are observed in solitary instances, but it is not possible to assert if they are real chiasmata or merely contact points of relational coiling. The chromosomes at this stage are rather longish and 'mitotic' in appearance. The fibre attachment points, which are mostly median or submedian, are visible (Text-fig. 14). Soon, however, at diakinesis they undergo marked condensation, becoming ovoid (Pl. 17, fig. 18). This is followed by a short period of interkinesis when the chromosomes become enveloped in a thin nuclear membrane. Commonly a single 'interkinetic nucleus' is not able to include all the chromosomes, and hence two or three nuclei of different sizes may be organized (Text-fig. 16). This stage is short-lived, and soon after this the chromosomes prepare to divide mitotically to form diads.

The separate nuclei, when more than one are present in the mother cell, do not form their individual spindles but a single fusion spindle is organized. Usually this is kite-shaped but sometimes it may be in the form of a bow (Text-fig. 17). The chromosomes which lie at the centre divide homotypically, and daughter chromosomes reach their respective poles. This is followed by cytokinesis resulting in the formation of diads (Pl. 17, fig. 19). Quite often the division of the chromosomes is incomplete or delayed so that the daughters fail to reach the poles and in such cases organize micronuclei within the diads. Usually, however, the diads are well filled and green in fresh material and number 32 within a sporangium. Occasionally improper cytokinesis occurs forming jointed diads. It is difficult to say anything about the germinating capacity of the diad spores. The $2n=108$ chromosome of this form as against $n=36$ with normal meiosis of the form α, and the complete morphologic similarity between the two would lead us to believe that this is an autotriploid asynaptic form. But the question arises as to what is the explanation of complete asynapsis at metaphase.

Praaken (1943) has summarized and Johnsson (1944) has supplemented all the previously examined cases of asynapsis, which are mostly based on investigations in flowering plants. The former distinguished the following groups of asynapsis:

(1) Asynapsis due to the action of a distinct gene or genes (or some slight structural change).

(2) Asynapsis caused by loss of a chromosome pair.

(3) Asynapsis induced by external conditions.

(4) Asynapsis as a normal process in apomictic organisms.

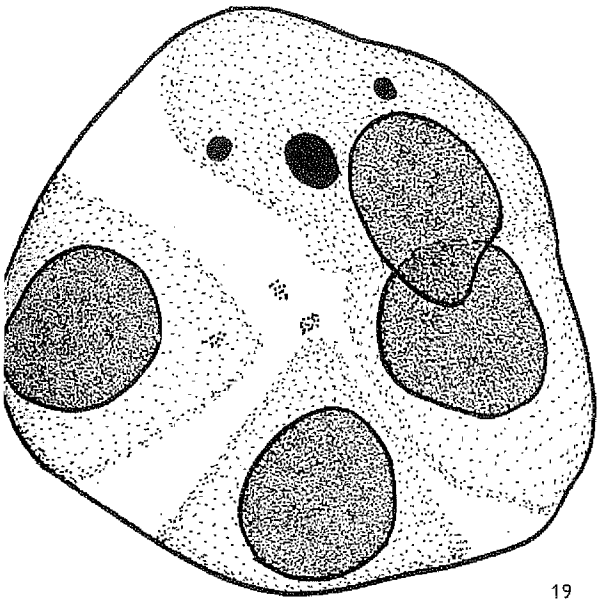
(5) Asynapsis depending upon mechanical chromosome condition (structure number).

(6) Asynapsis in species hybrids.

Out of these items (2)–(5) are ruled out as being inconsistent with the data available. In view of the complete morphological identity of this form with the previous, to the point of being externally indistinguishable, it is impossible to conceive it as a hybrid. The most plausible explanation seems to be the one due to action of gene or a group of genes. This is known to cause asynapsis in *Zea* (Beadle, 1933), *Rumex* (Yamamoto, 1934), *Datura* (Bergner, Cartledge & Blakeslee, 1934), *Crepis* (Richardson, 1935), rye (Praaken, 1943) and *Picea* (Andersson, 1947). In most of these cases, however, asynapsis is not complete, and a certain, often good, number of bivalents is organized. The most parallel case with which the present species agrees is that of *Allium amplectens* in which Levan (1940) described a triploid asynaptic form. This form exhibited complete asynapsis forming 21 univalents. But the further behaviour of these univalents was perfectly regular. These divided mitotically, and diads were organized, each containing an exact 21 chromosome number. In the present triploid asynaptic form of *T. insigne* the formation of perfect diads has not been completely stabilized, as they frequently contain micronuclei.

Forma γ. As previously stated this variety was collected from Mussoorie Hills and is somewhat different morphologically from the previous two in the cutting of the fronds, although the differences are not well marked. Mehra (1939) reported it to be common in the Mussoorie Himalayas under the name of *Trichomanes bipunctatum* Poir, growing in the form of tufted mats on rocks or tree trunks in ravines.

At diakinesis we find 33 normally paired bivalents and 6 univalents, so that the $2n$ number comes to 72 (Pl. 17, fig. 20; Text-fig. 18). One univalent chromosome marked *A*



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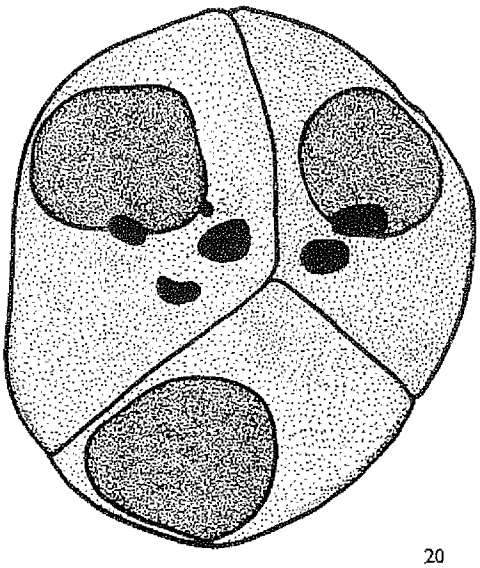

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Text-figs. 18–20. *T. insigne*, forma γ. 18. Metaphase showing 33 bivalents and 6 univalents (2=72), × 2156. (E.D. to Fig. 20). 19, 20. Tetrads with micronuclei, × 2240.

is particularly conspicuous by its minute size and has been observed in all the preparations. The number of chiasmata in the bivalents does not exceed two. At anaphase I the pairs separate normally, but the univalents are left suspended on the spindle. These may divide longitudinally, and the daughter chromatids reach either of the two poles or may be left undivided and form micronuclei inside the binucleate mother cell. At the second division chromosome behaviour is conditioned by the number of univalents that entered into the first division. Thus all those which divided in the first division, being unable to divide a second time, are left behind as laggards and later form micronuclei inside the tetrads and spores (Text-figs. 19, 20). As a result of this irregularity the spores mostly get shrivelled and abort, but occasionally a few normal-looking ones may be produced. A total of 32–48 spores are formed per sporangium of which on the average 5 are apparently normal-looking, but it is doubtful if these would be viable.

This variety, which is obviously a diploid, may be considered either as a hybrid between two closely related genotypes, one of which differs from the other in possessing a micro-chromosome, or a cytotype which has undergone structural changes and deletion resulting in meiotic irregularities and consequent sterility. The profuse multiplication in nature must be purely apomictic.

Conclusions

So far eighteen species and varieties belonging to the family Hymenophyllaceae have been investigated. This, indeed, is a poor number for deducing sound phylogenetic conclusions considering that over 600 species are represented in the family. Table 1 gives a summary of the results hitherto reached, together with the status of polyploidy of the species (and varieties) within the family based on the monoploid numbers.

Manton on the basis of her investigations concluded on three base numbers 7, 18 and 13 for the family. In view of *Hymenophyllum polyanthos* from Darjeeling having $n=27$, the base number 18 will now have to be reduced to 9. A perusal of Table 1 shows that the number 9 is more deep seated, as it is represented in eleven members out of eighteen investigated. The number 7 is represented in three members and 13 in only one. It seems not unlikely that the numbers 33 and 34 exhibited by *Trichomanes obscurum* and *T. motleyi* respectively may be synthetic from a combination of prime monoploid base numbers.

Polyploidy has played its part in the evolution of species and forms in the family, as it has done in other families of ferns. It is, however, not clear how three base numbers have been evolved. In view of the generally stereotyped nature of characters in the family, these seem interrelated and possibly may have been evolved one from the other rather than having come from different ancestral stocks. While it is premature to test the classification of Copeland, the present cytological data seems to lend a partial support in that all the six members of *Crepidomanes* have a uniform multiple of 9 and so have the three members of *Vandenboschia*, while 33 and 34 are restricted to *Solenodesmium* and *Microgonium*. Seven is the number met with in the single member of *Meringium* investigated. The exceptions, however, are *Mecodium*, in which two base numbers 7 and 9 are manifested, and *Hymenophyllum* with base numbers of 13 and 9.

We confirm Manton's observations that the overall size of the chromosomes in Hymenophyllaceae is the largest in the Fern kingdom. This observation is based on over 150 species of ferns belonging to different families so far investigated in this Laboratory.

Table 1

Serial no.	Species name	Natural habitat	Author	Chromosome number	Meiosis	Status in the family	Genus according to Copeland's classification	Base number
1	*Hymenophyllum exsertum* Wall.	Ceylon	M. & S. (1954)	$n=21$	Normal	6-ploid		
		Darjeeling	Authors	$n=21$	Normal	6-ploid		
2	*H. javanicum* Spr.	Ceylon	M. & S. (1954)	$2n=72$	Unpaired	8-ploid		
		Darjeeling	Authors	$2n=108$	Irregular	12-ploid	*Mecodium*	7 (2), 9 (3)
3	*H. polyanthos* Swartz	Darjeeling	Authors	$n=27$	Normal	6-ploid		
		Malaya	M. & S. (1954)	$n=28$	Normal	8-ploid		
4	*H. flabellatum* Lab.	Australia	M. & S. (1954)	$n=36$	Normal	8-ploid		
5	*H. serrulatum* Presl.	Malaya	M. & S. (1954)	$n=21$	Normal	6-ploid	*Meringium*	7 (1)
6	*H. tunbridgense* (L.) Sm.	Scotland	Manton (1950)	$n=13$	Normal	diploid	*Hymenophyllum*	13 (1), 9 (1)
7	*H. unilaterale* Bory = *H. peltatum* Poir	England	Manton (1950)	$n=18$	Normal	tetraploid		
8	*Trichomanes radicans* Swartz	Ireland	Manton (1950)	$n=72$	Normal	16-ploid	*Vandenboschia*	9 (3)
		Darjeeling	Authors	$n=72$	Normal	16-ploid		
9	*T. auriculatum* Bl.	Darjeeling	Authors	$n=36$	Normal	8-ploid		
				$2n=108$	Irregular	12-ploid		
10	*T. pyxidiferum* L.	Darjeeling	Authors	$n=36$	Normal	8-ploid		
11	*T. bipunctatum* Poir	Malaya	M. & S. (1954)	$n=c.\ 36$	Normal	8-ploid		
12	*T. plicatum* (v.d.B.) Bedd.	Darjeeling	Authors	$n=36$	Normal	8-ploid	*Crepidomanes*	9 (6)
13	*T. insigne* (v.d.B.) Bed. var. α	Darjeeling	Authors	$n=36$	Normal	8-ploid		
14	*T. insigne* var. β	Darjeeling	Authors	$2n=108$	Irregular	12-ploid		
15	*T. insigne* var. γ	Mussoorie	Authors	$2n=72$	Irregular	8-ploid		
16	*T. bilabiatum* Nees & Bl.	Hakgola	M. & S. (1954)	$n=36$	Normal	8-ploid		
17	*T. obscurum* Bl.	Ceylon	M. & S. (1954)	$n=33$	Normal	?	*Selenodesmium*	33? (1)
		Malaya	M. & S. (1954)	$n=c.\ 33$	Normal	?		
18	*T. motleyi* v.d.B.	Malaya	M. & S. (1954)	$n=34$	Normal	?	*Microgonium*	34? (1)

The *Trichomanes insigne* complex requires further investigations to resolve certain taxonomic issues revealed in the irregular cytological behaviour exhibited in some forms.

The family Hymenophyllaceae, though archaic, seems to be in active state of speciation.

Summary

Ten members of the family Hymenophyllaceae distributed mostly in the Darjeeling Himalayas have been cytologically investigated.

Hymenophyllum javanicum Spreng is a 3*n* form with irregular meiosis. In *Trichomanes auriculatum* both the diploid and triploid forms, which are morphologically indistinguishable, occur in nature. The triploid has an abnormal meiosis.

The so-called *T. insigne* v.d.B. is a species complex with at least three forms with different cytological behaviour.

The base numbers in the family should be revised from 7, 18, 13 to 7, 9, 13.

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EXPLANATION OF PLATES

PLATE 14

Fig. 1. *Hymenophyllum exsertum*, $n=21$.
Fig. 2. *H. polyanthos*, $n=27$.
Fig. 3. *H. javanicum*, $2n=108$.
Fig. 4. Univalents splitting at equator during first division.

PLATE 15

Fig. 5. *H. javanicum*. Four unequal nuclei within a mother cell.
Fig. 6. A microspore of the same containing micronuclei.
Fig. 7. *Trichomanes radicans*, $n=72$.
Fig. 8. *T. auriculatum*, diploid, $n=36$.
Fig. 9. Same, but a tetraploid mother cell, $4n=72$.
Fig. 10. *T. auriculatum*, triploid form, $2n=108$.

PLATE 16

Figs. 11, 12. Irregular I division in triploid *T. auriculatum*. Note splitting univalents in Fig. 12.
Fig. 13. *T. auriculatum*, tetrad formation with micronuclei.
Fig. 14. *T. pyxidiferum*, $n=36$.
Fig. 15. *T. plicatum*, $n=36$.
Fig. 16. *T. insigne*, forma α, $n=36$.

PLATE 17

Fig. 17. *T. insigne*, forma β at pachytene. Note the bivalent and trivalent pairing.
Fig. 18. Same with univalents, $2n=108$.
Fig. 19. Same forming a diad.
Fig. 20. *T. insigne*, forma γ, with 33 bivalents and 3 univalents.