

THE BEARING OF CYTOLOGICAL STUDIES ON THE PHYLOGENY OF THE MARCHANTIALES

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Introduction

ONE of the chief aims of the "Natural System" of classification of plants, first propounded by Antoine Laurent de Jussieu in 1789 and adopted subsequently by all the botanists, is to arrange various groups of plants in an order indicative of their relationship or affinities. In building up our phylogenetic schemes in such a system we have to use all the possible data collected from various sources and view them in a proper perspective. Up to the end of the last century such data were forthcoming mainly from the morphological studies; but since the beginning of the present century the science of cytology has opened up a new line of enquiry the findings of which have helped much to clear up some tangles in the mass of morphological evidence at our disposal. The greater part of this evidence pertains to the Angiosperms and that is but natural. The lower plants, however, have not been neglected and the pertinent data gathered in this field though not so vast as in the case of Angiosperms are likely to prove useful in our phylogenetic speculations. It is proposed to review here briefly the evidence obtained from the cytological studies on the liverworts and to indicate its bearing on the phylogeny of the Marchantiales.

The researches on the cytology of the Marchantiales go as far back as Koch (1890-91) and Schottländer (1892) but the most important advances in our knowledge of the cytology of this group are of recent origin. They are mainly due to the work of Allen (1917, 1924, 1925, 1926, 1937), Showalter (1921, 1923, 1928), Haupt (1932, 1933), Heitz (1927, 1928), Lorbeer (1927, 1930, 1934), Höfer (1932), Siler (1934), Wolcott (1939) and others. It is to these authors that we owe much of our knowledge of the chromosomes in the principal genera of the liverworts, though of course, many genera still remain unworked. About 235 genera comprise this group and our cytological knowledge extends to about 50 of them. Apparently we have gained but little insight in the cytology of this group. Similar investigations on the cytology of the Indian forms have been made by workers like

Kashyap and Pande (1922), Pande (1924, 1932, 1933, 1934, 1936), Mehra (1938), Mehra and Mehra (1939), Chavan (1937 *b*), Srinivasan (1939, 1940), Mahabalé and Gorji (1941), but looking to the richness of the liverwort flora in this country a large portion of this field remains to be covered. About 525 species of Indian liverworts have been described by Stephani (1898–1925) to which Kashyap (1929, 1932) and Chopra (1932) added about 50 more; some more forms have been added by Gola (1914), Khanna (1929, 1932, 1936, 1937), Verdoorn (1931, 1932 *a*), Chavan (1937 *a*) and others, while our knowledge of their cytology does not extend beyond a dozen forms. Fragmentary as our knowledge is regarding the cytology of the liverworts an attempt is made here to apply it, more in the way of offering some comments on the existing phylogenetic speculations, than for making any original observations.

The Data and Their Analysis

For the sake of convenience the data available have been grouped under the following four headings:—

1. Data pertaining to sex chromosomes,
2. Data pertaining to hybridization,
3. Data pertaining to polyploidy and gene-mutations,
4. Data pertaining to the morphology and number of chromosomes in different genera and species.

1. *The sex chromosomes in the Hepaticæ.*—The first discovery of the sex chromosomes in plants was made by Allen (1917) in 1917 in *Sphaerocarpus Donnellii* and led the way to similar investigation in other dioecious species of liverworts. They have been reported to be present in genera like *Pellia*, *Riccia*, *Pallavicinia*, *Riccardia*, *Lunularia*, *Tesselina*, *Makinoa*, etc. in all about 22 species. But there is some confusion yet regarding their occurrence in species like *Riccardia pinguis* and *Riccia Courtsii* due to faulty nomenclature as has been pointed out by Allen (1935, p. 275). The mechanism so far discovered is of the XY-type differing in detail only in genera like *Lunularia* and *Frullania*. Heteropycnosis was observed in some of them, e.g., in *Pellia Neesiana* by Showalter or in *Hookeria lucens* by Heitz but not in all. We have not yet been able to observe the occurrence of sex chromosomes in many other genera of the liverworts. There is not much difficulty about the dioecious species. The real difficulty is about the hermaphrodite ones. The issue before us is to know how these hermaphrodite forms have come into existence. Have they descended from the diploid races of the originally haploid dioecious parents as Heitz and Allen (1932,

p. 107) suggest, or is the sex metabolic in them as Correns (1928) believes? We are not yet in the possession of any definite answer to this question.

2. *Hybridization*.—Another line of cytological enquiry takes us back to the work of Marchal (1906–1911), Weittstein (1924–1930), Schratz (1924) and others on the hybrid races of mosses. These investigations have been successfully followed by Allen (1924, 1925, 1926, 1937), Burgeff (1930), Haupt (1932, 1933) and others who have worked on the Hepaticæ. It is well known that the crosses in liverworts under natural conditions are very rare. But since many of the species live in clones, interspecific hybridity may have occurred in them as is known to exist in some species of *Commelina* leading mostly a clonal life. For example, it has been found by Deodikar* that in India there exists a hybrid *Commelina* in nature formed by a cross between *Commelina nudiflora* and *Commelina benghalensis*. There is a common belief among the plant cytologists that many of the species of higher plants to-day have arisen as a result of hybridization among related species of plants. It is well known that many species of garden plants like *Iris*, *Viola*, *Tulipa* and others owe their origin to hybridity. This point of view has been stressed with regard to this and other groups of plants by such eminent investigators as Allen (1935), Tischler (1928, 1935) and Anderson (1937).

3. *Polyploidy and gene-mutations*.—One of the most interesting phenomena from the evolutionary point of view is the phenomenon of polyploidy. Sometimes the whole set of chromosomes forming a basic complex undergoes doubling or trebling and gives rise to polyploids of higher valence. These may be auto- or allo-polyploids and are found in many plants like *Rosa*, *Crepis*, *Chrysanthemum*, *Solanum*, *Primula*, *Carex*, *Agave*, etc. They occur more frequently in plants than in animals. *Apropos* the flowering plants Anderson (1937, p. 343) says: "It is already safe to say that at least half the species and varieties of flowering plants belong to polyploid series (Müntzing, 1936)." But in the lower plants like the Hepaticæ, as has been remarked by Mehra (1938, p. 6), they are rather rare. They have, however, been recorded in *Pellia epiphylla*, *Pellia borealis*, *Androcryphia confluence*, *Marchantia polymorpha*, *Dumortiera nepalensis*, *Sphærocarpus Donnellii* var. *bivalens*, *Aneura multifida*, *Aneura sinuata*, *Calobryum Neesiana*, *Calobryum trichomanis*, *Riccia Gougetiana*, *Riccia Donnellii*, etc. Whether these are auto- or allo-polyploids, it is difficult to say from the mere numbers of

* I owe this observation to an unpublished work of Mr. G. B. Deodikar working on the genus *Commelina* in India under the guidance of Prof. L. S. S. Kumar of the College of Agriculture, Poona.

chromosomes. Observations on the gene-mutations, chromosomal translocations and on aneuploidy in the Bryophyta are very few and they are mainly due to the work of Heitz (1927, 1928) and Wolcott* (1939) on *Pellia*.

4. *The chromosomes: Their morphology and numbers.*—What holds good for our knowledge of the chromosomal translocations in the Hepaticæ, also holds good partly at least for our knowledge of the karyotypes of the different genera and species in the liverworts. Some 27 species have been described karyologically by Heitz (1927, 1928), some by Lorbeer (1930, 1934), a few like *Fegatella*, *Riccardia*, *Pellia* and *Pallavicinia* by Showalter (1921, 1923, 1928) and Wolcott (1939) and some of the Indian representatives of the Codoniaceæ by Mehra (1938). We have, however, to describe them in many more genera and find out the homologous pairs of chromosomes. Much work in this direction on the chromosomal complexes of the Orthopteran insects has been done by McClung (1914) and on the homologies of the karyotypes of Reptiles by Matthey (1931, 1933). Obviously there is a great scope for similar work on the karyotypes of liverworts in India. In these circumstances the only recourse left to us for considering our phylogenetic speculations in the light of the cytological data is to make use of whatever scientific information is available regarding the number of chromosomes found in the various forms of liverworts which have been investigated for this purpose. Such information is available in the lists of chromosomes prepared by Ishikawa (1916), Heitz (1927), and Tischler (1931, 1935–1936). Table I gives an abstract of our knowledge of the chromosome numbers in the various groups of the liverworts.

The following points emerge from the table:—

1. In the Ricciaceæ the basic number of chromosomes seems to be 8 as it occurs in all the genera worked out and in the great majority of the species.
2. In the Marchantiaceæ the basic number seems to be 9 as it occurs in the most of the genera worked out.
3. In the Jungermanniaceæ the basic number seems to be 9 as it occurs in most of the genera studied.
4. The chromosome numbers in the Anthocerotaceæ are quite different from those in the majority of the Marchantiales and their separation, therefore, into a distinct family is justifiable even on cytological grounds.

* See also Wolcott, *Science*, 1940, 91, 593.

TABLE I

Family	The total no. of genera known	Number of genera worked out	Number of species worked out	Analysis of the chromosome numbers	Probable basic numbers	Aberrant chromosome numbers	Poly-ploid species
Jungermanniaceæ	192	29	40	13 genera with $n = 9$ 6 genera with $n = 8$ 2 genera with $n = 18$ 1 genus with $n = 16$ 1 genus with $n = 10$ 1 genus with $n = 20$ 1 genus with $n = 30$	8, 9, 10	..	5
Ricciaceæ	3	3	23	11 species with $n = 8$ 4 species with $n = 9$ 1 specie with $n = 10$ 1 specie with $n = 16$ 1 specie with $n = 18$ 2 species with $n = 4$	8, 9, 10	..	2
Corsiniaceæ	3	1	1	1 specie with $n = 16$	8
Targioniaceæ	3	2	2	1 specie with $n = 24$ 1 specie with $n = 9$	8, 9	6	1
Sauteriaceæ	4	2	4	4 species with $n = 9$	9
Rebouliaceæ	6	2	6	1 specie with $n = 9$ 5 species with $n = 16$	8, 9	..	5
Marchantiaceæ	26	13	38	11 species with $n = 9$ 3 species with $n = 8$ 2 species with $n = 10$ 2 species with $n = 18$ 2 species with $n = 27$	8, 9	11, 17, 25	4
Anthocerotaceæ	5	3	6	2 genera with $n = 6$ 1 genus with $n = 4$	4, 6	5	..

5. Examples showing aberrations from the usual basic numbers are very few.
6. Polyploidy and aneuploidy are of rare occurrence.
7. Numbers 8 and 9 occur very frequently in many genera and families known to be quite unrelated on other grounds. They may have, therefore, arisen polyphyletically.
8. As most of the genera in the Hepaticæ have 8, 9 or 10 or the multiples and submultiples of these numbers in their haploid, *i.e.*, gametophytic state, the basic numbers in the Hepaticæ seem to have reached a great stability as in the Gymnosperms where the great majority of the genera are referable to four basic numbers 10, 11, 12 and 13.

Phylogeny of the Marchantiales

It is necessary at the outset to remark that this is a much vexed question and there will be many who will not agree with the view that will be propounded here, and perhaps with good reasons. The crux of the whole situation lies in the consideration of the simple forms. Have they given rise to more complex forms in evolution or have they passed through an ordeal in course of time and got themselves reduced to simple forms from some complex ancestors? Many eminent investigators like Bower, Campbell, Schiffner, Müller, Cavers and others favour the former alternative while there are other authors equally eminent like Goebel, Kashyap, Weittstein, Church, Howe, Buch, Meyer, Verdoorn, Evans, Pande who favour the latter alternative. The first view considers that the complex forms of the Marchantiales like *Marchantia*, *Pressia* and *Asterella* are the culminating forms of a progressively advancing series beginning with simple forms like *Riccia*. By far the most elaborate statement of this view is given by Cavers (1911) who has summarised his view-point in the following scheme in *New Phytologist*, Vol. IX, p. 180:—

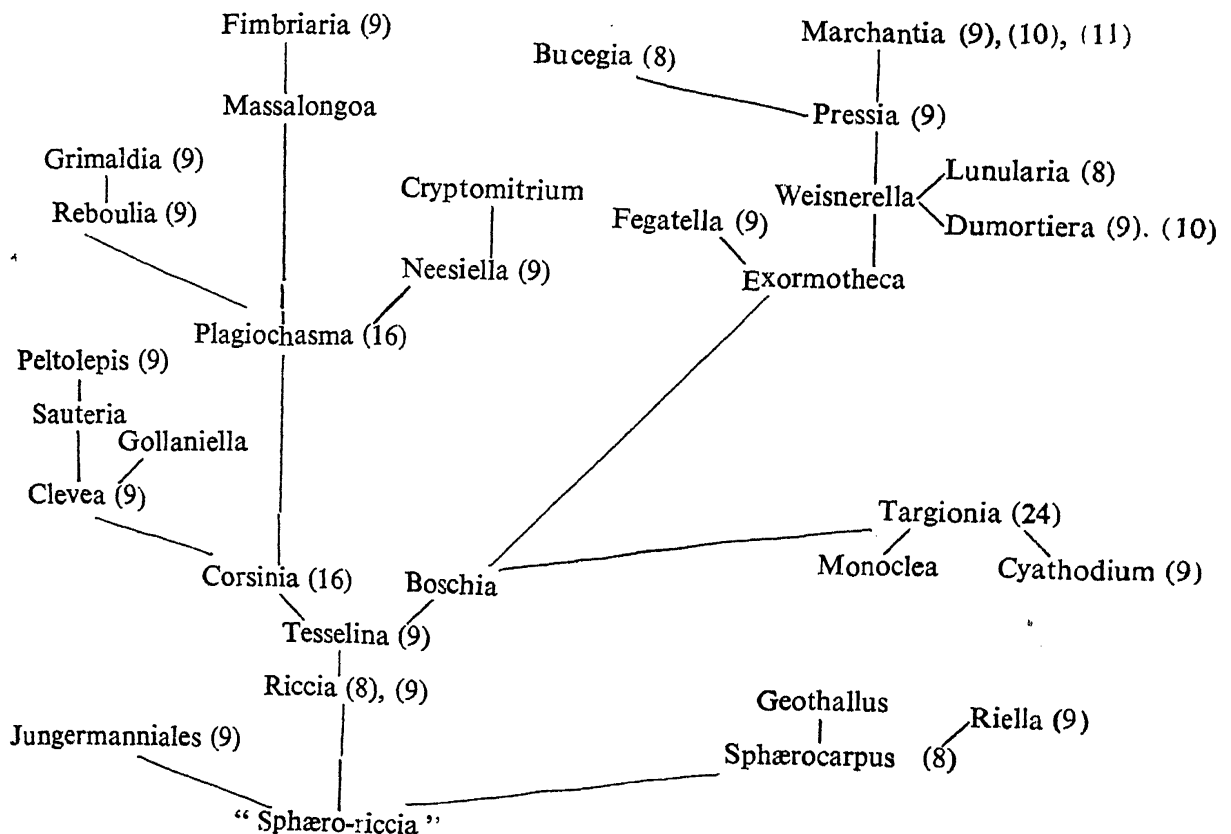


FIG. 1. Phylogeny of the Marchantiales as suggested by Cavers.

The other view, which was brought to the fore by Goebel (1910), was based on his researches on the genus *Monoselenium*, then imported in Germany

by an accident along with some tea plants from Canton, later derived support from Kashyap's masterly discoveries on the peculiar Himalayan genera *Stephensiella*, *Aitchisoniella*, *Sewardiella* and others. The reasons which led Kashyap to accept this view are given in his early papers on the Himalayan liverworts in the *New Phytologist*, Vols. XIV and XV, and have been restated in detail in his presidential address to the Botany Section of the Indian Science Congress, 1919 (see Kashyap, 1919). They are schematically summarised by him in the following diagram (Kashyap, 1914, p. 209) in which as he says (Kashyap, 1932 a, p. 2): "*Riccia* is the last term in another series of reduction."

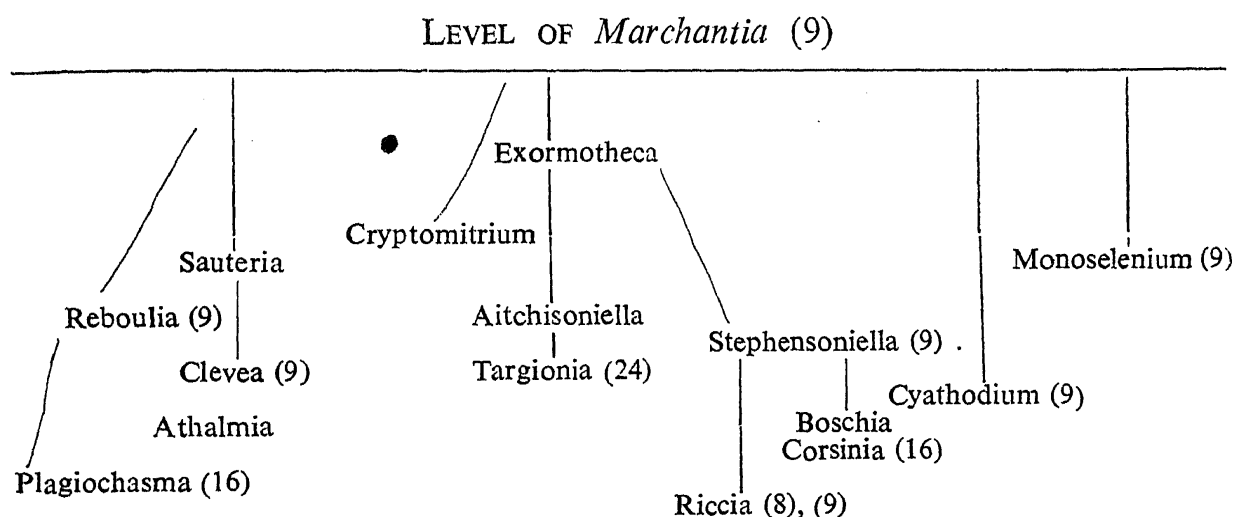


FIG. 2. Phylogeny of the Marchantiales as suggested by Kashyap

Buch, Verdoorn (1932 b) and Evans (1939) lend their support to this view and they have elaborated it still further. This modified scheme was first published in the *Annales Bryologici*, Vol. X and later transferred to *Manual of Bryology* by Verdoorn (1932 b). It has been published again by Evans (1939) in *Botanical Review*, Vol. V, p. 94. It is as follows:—

- Order 1. Jungermanniales.
- Order 2. Marchantiales.
- Order 3. Sphærocarpales.
- Order 4. Anthocerotales.

Order 2. MARCHANTIALES

Family 1. Marchantiaceæ

- | | |
|--|--|
| 1. <i>Marchantia</i> L. (9), rarely (10) | 7. <i>Lunularia</i> Adans. (8) |
| 2. <i>Marchantiopsis</i> Ch. and Douin | 8. <i>Exormotheca</i> Mitt. |
| 3. <i>Pressia</i> Corda (9) | 9. <i>Corbierella</i> Douin and Trabut |
| 4. <i>Boucegia</i> Radian (8) | 10. <i>Stephensiella</i> Kashyap (9) |
| 5. <i>Conocephalum</i> Web. (9) | 11. <i>Dumortiera</i> Nees (9), (10) |
| 6. <i>Wiesnerella</i> Schiffn | 12. <i>Monoselenium</i> Griff. (9) |

Family 2. Rebouliaceæ

- | | |
|---------------------------------|---|
| 14. <i>Reboulia</i> Raddi (9) | 17. <i>Cryptomitrium</i> Aust. |
| 15. <i>Mannia</i> Opiz | 18. <i>Massalongoa</i> Steph. |
| 16. <i>Asterella</i> Beauv. (9) | 19. <i>Plagiochasma</i> Lehm. and Lind.
(16) |

Family 3. Sauteriaceæ

- | | |
|----------------------------------|------------------------------|
| 20. <i>Peltolepis</i> Lindb. (9) | 22. <i>Sauchia</i> Kashyap |
| 21. <i>Sauteria</i> Nees | 23. <i>Clevea</i> Lindb. (9) |

Family 4. Targioniaceæ

- | | |
|-----------------------------------|---------------------------------|
| 24. <i>Targionia</i> L. (24) | 26. <i>Cyathodium</i> Kunze (9) |
| 25. <i>Aitchisoniella</i> Kashyap | |

Family 5. Corsiniaceæ

- | | |
|--------------------------------|--------------------------------|
| 27. <i>Corsinia</i> Raddi (16) | 29. <i>Funicularia</i> Trevis. |
| 28. <i>Cronisia</i> Burkeley | |

Family 6. Ricciaceæ

- | | |
|-----------------------------------|--------------------------------------|
| 30. <i>Oxymitra</i> Bisch. (9) | 32. <i>Riccia</i> L. (8), rarely (9) |
| 31. <i>Ricciocarpus</i> Corda (4) | |

FIG. 3. Phylogeny of the Marchantiales as suggested by Evans.

We shall now consider whether either of these schemes gains any support from recent cytological investigations in this field. In this connection, I have to invite the attention of the reader to the number of chromosomes placed in brackets against the name of each genus, wherever they were available, in all the three schemes of classification. It will be seen that the numbers 8 and 9 occur repeatedly along many lines in genera known to be quite unrelated. This being so we cannot speak of wholesale reduction or wholesale progression along any particular line suggested by the scheme of Cavers or Kashyap. Reduction as well as progression seem to be responsible for what the species are to-day. The question arises which one of the three probable basic numbers 8, 9 and 10 represents the number of chromosomes in the basic complex of the progenitors of the Marchantiales—let us say Pro-Marchantiales. It is perhaps easy to understand the sporadic occurrence of the number 10 in the basic complex of some genera like *Marchantia* or *Dumortiera*. If one of the chromosomes in a basic set of 9 chromosomes of a genus had undergone fragmentation, it might have added one more element to the basic complex, as has been found to be the case in the genom of *Crepis sibirica* by Swezy* (1935, p. 383). Our choice of the basic number of chromosomes in the Pro-Marchantialean complex,

* See also Swezy, *Cytologia, Fujii Jub. Vol.*, 1937, 1, 149-55.

therefore, should be between 8 and 9. If it be supposed that the basic complex of the Pro-Marchantiales consisted of 8 chromosomes, then we can say that there has been an advance from a series consisting of 8 chromosomes to one having 9 chromosomes. Let us see how far the suggestion is borne out by the scheme of Cavers based on the progression hypothesis. If the number of chromosomes alone were the criterion to judge the advance of a genus, then we would be obliged to suppose that *Bucegia* is not more advanced than *Marchantia* or that *Grimaldia* and *Fimbriaria* are more reduced than *Plagiochasma* which is not consistent with the morphological evidence on which Cavers's scheme is based. The deduction of a complex group like that of *Plagiochasma* from that of a comparatively simple genus like *Corsinia* is logical but the deduction of the chromosomal complex of *Corsinia* from that of *Tesselina* does not follow logically as the latter genus has the basic number 9 and the former has 8. In the same way it is difficult to derive a complex of 9 chromosomes in *Clevea* from that of *Corsinia* with 16 chromosomes, unless of course we suppose that the chromosomal complex of *Corsinia* underwent reduction and then progression. The suggested relationship between *Neesiella* and *Plagiochasma*, the latter with 16 and the former with 9 chromosomes, or that between *Cyathodium* with 9 chromosomes and *Targionia* with 24 chromosomes is likewise inexplicable on the basis of progression hypothesis. These are, therefore, some of the difficulties to be solved by the supporters of the hypothesis that a genus like *Riccia* or what Cavers calls "*Sphæro-riccia*" has given rise to several advanced genera of the Marchantiales. Anyway the verdict of the cytological evidence as it stands to-day is not unequivocal on the progression hypothesis.

We may next consider the other two schemes of classification stressing the reduction hypothesis as a factor in the evolution of the Marchantiales. Kashyap's scheme suggests that a form like *Riccia* has been derived from the level of *Marchantia* by a process of reduction. It will be seen from the scheme given on page 147 (Fig. 2) that there are no discrepancies in this scheme along any particular line undergoing reduction. If we consider that the chromosomal complex at the level of *Marchantia* consisted of 9 chromosomes and in course of time got reduced to 8, and occasionally underwent diploidy as for example in *Corsinia* or *Plagiochasma*, then there is little difficulty in interpreting this scheme on the hypothesis of reduction.

The other scheme proposed by Verdoorn, Buch and Evans may now be considered. As regards the arrangement of the genera in this scheme Evans (1939, p. 89) says: "The families in this scheme so far as possible have been

arranged in phylogenetic sequence. This sequence represents a compromise between Verdoorn's and Buch's earlier classification, except that the Anthocerotales are not separated as a sub-class from the rest of the Hepaticæ." He further states that "in families containing more than one genus the attempt has been made to place genera with primitive characters at the beginning and genera with advanced characters at the close." A careful consideration of the chromosome numbers, so far known, written against several genera in the brackets in this scheme (Fig. 3) will show that there has been a general tendency towards reduction in the whole plexus of the Marchantiales. This tendency seems to have manifested itself in different families independently, so that in each one of them there are certain genera with 8 chromosomes. Thus in the Marchantiaceæ *Bucegia*, in the Rebouliaceæ *Plagiochasma*, in the Targioniaceæ *Targionia* and in the Corsiniaceæ *Corsinia* have 8 chromosomes in their basic complex. When the level of the Ricciaceæ has been reached the tendency becomes more uniform as is evident from the fact that in *Oxymitra* as well as in the great majority of the species of *Riccia* the number of chromosomes in the basic complex is 8. But so long as many genera of the liverworts remain uninvestigated it is difficult to say how far this analysis on cytological grounds alone contains any grain of truth. Provisionally it may be said, however, that cytologically there seems to be some justification for a view which considers that reduction has played an important part in the phylogenetic story of the Marchantiales. At the same time there is no denial of the fact that some progress has been made in some genera like *Fimbriaria* or *Plagiochasma* due to polyploidy and similar phenomena.

But in our attempt to correlate morphological with the cytological data so far known, with a view to seeking support for the validity of any of the phylogenetic schemes mentioned above, we must not lose sight of the fact that the main cytological observation brought in evidence, either for support or criticism of a scheme in the aforesaid discussion is the difference of only one chromosome between the two chromosomal garnitures, one of 8 and the other consisting of 9 elements. It may well seem doubtful whether this cytological observation could be adequate scientific evidence to prove or disprove the validity of any of these hypotheses.

Can we put any other interpretation on the same existing cytological data and press them into the service of reconciling these conflicting phylogenetic theories based on morphological investigations? Instead of regarding either the 8 or the 9 chromosomal complex as the primitive one, would it not be more plausible to postulate a chromosomal complex of 17 complements as the parental or ancestral garniture from which both the existing

complexes with the reduced numbers 8 and 9 have been descended? Why not say that the chromosomal complex of the Pro-Marchantiales contained both 8 and 9 chromosomes in their basic complex, as we find for example in the Rosaceæ? The great majority of the Rosaceæ has got 9 chromosomes in its basic complex but the sub-family Pomoideæ has only 8. We explain the occurrence of two basic numbers in this family by supposing that both of them were present in the chromosomal complex of the ancestors of the Rosaceæ from which the modern Rosaceæ with the small deterrent group of the Pomoideæ took their origin. The argument *pari passu* can be applied to the two basic numbers found in the living Marchantiales. Instead of saying that the Marchantiaceæ with 9 series got reduced to Ricciaceæ with a series of 8 chromosomes or progressed *vice versa*, we should rather say that both these groups, the 8 and the 9 series, came into existence independently of each other from the basic complex of the Pro-Marchantiales consisting of 17 chromosomes.

As a matter of fact a view somewhat similar to the one propounded here, suggesting a polyphyletic origin of the Marchantiaceæ and the Ricciaceæ, has been maintained by Meyer (1914, 1931), though of course on absolutely different grounds. Meyer's view is based on ontogeny. In genera like *Marchantia* or *Fegatella* the embryo is of the *filamentous type* whereas in the genera *Riccia* and *Corsinia* it is of the *quadrant type*. On this basis he divides the whole group of the Marchantiales into two classes: those in which the embryo is of the *filamentous type* and those in which it is of the *quadrant type*. From these observations it is argued, that as the embryos of the Ricciaceæ are simpler than the filamentous embryos of the Marchantiaceæ, the progenitors of the Ricciaceæ were perhaps more simpler forms than the modern complicated Marchantiaceæ. Meyer's conclusion stands true to-day though in a different perspective. The cytological analysis clearly suggests a polyphyletic origin for the Ricciaceæ and the Marchantiaceæ. They rather represent end products of two distinct series which have moved along parallel lines but which tend to converge in their evolutionary history in the past.

Considered as a whole the Bryophyta seem to be a very conservative group of plants in the process of evolution, as is evident from the great stability of their basic numbers. It resembles in this respect an equally ancient and conservative group of plants, the Gymnosperms, in which also the known chromosomal complexes are reducible to three or four basic numbers. For example, in the whole of Coniferæ the great majority of the genera of the Taxaceæ and Abietinæ has 12 chromosomes and the Taxodinæ and Cupresseæ have 11. The delicate structure and the flabby parts of

the liverworts are not very well suited for fossilisation, and therefore, their fossil record is bound to be imperfect. The only authentic record of the fossil Marchantiales, so far as I am aware, is the Jurassic genus *Marchantites* of Dr. Scott. Some more forms like *Hepaticites* have also been described by Walton (1925, 1928) from the Carboniferous strata of England. But what happened to them in subsequent epochs we do not know from the fossil record. Our only clues, therefore, regarding the course of their evolution are those from the living forms. And to unravel these we have to follow several lines of investigation before their phylogenetic story can be reconstructed. This brings us back to the point from where we started. After all in building up our phylogenetic schemes of a particular group or groups of plants or animals cytology furnishes us with the data obtained by following only one line of enquiry which in themselves are not so important as in their relation to the data obtained by following the other lines of enquiries like morphology, ecology, geographic distribution, etc.; and our phylogenetic notions, therefore, should be based on the sum-total of all the data available from different sources rather than on this or that factor affecting the course of evolution.

Summary

The paper gives a brief account of the cytological studies on the Hepaticæ and indicates the bearing of these on the problem of the phylogeny of the Marchantiales. The data available have been analysed and grouped under the following four headings: the sex chromosomes, hybridization, polyploidy and gene mutations, and the morphology and numbers of chromosomes. The information regarding the chromosomal numbers has been tabulated and the probable basic numbers in different families have been indicated. From the table given on page 145 it will be seen that the basic number of chromosomes (gametophytic number, *i.e.*, *n*-number) for the majority of the genera of the Marchantiaceæ and the Jungermanniaceæ seems to be 9, and for the genera of the Ricciaceæ it seems to be 8. In the light of this cytological observation the existing schemes of classification of the Marchantiales have been examined with a view to knowing how far the morphological data and the cytological data are correlated. If it be supposed that the basic complex of the ancestors of the Marchantiales called Pro-Marchantiales in this paper, had 8 chromosomes in their genome and changed to a 9 chromosomal condition later by fragmentation, then there is some justification for the progression hypothesis. On the contrary, if it be imagined that the Pro-Marchantiale complex consisted of 9 chromosomes originally and got reduced to 8, the reduction hypothesis may seem plausible. But when either of these ideas are pressed further and

the number of chromosomes in different genera in the various schemes of classification given by Cavers, Kashyap, Verdoorn and Evans are considered, the verdict of cytology on either of these schemes is not unequivocal, as the main argument brought in the discussion for or against a theory is based on the difference of a single chromosome only; and it may well seem doubtful whether that alone can constitute sufficient proof for or against a scheme.

In these circumstances a third reading of the same cytological data is proposed by the author. It is postulated that the Pro-Marchantialean complex consisted of 17 chromosomes from which the Marchantiaceæ and the Ricciaceæ took their origin independently of each other polyphyletically, by the segregation of the ancestral complex into two series one having 9 and the other having 8 chromosomes. The Rosaceæ have been cited as a parallel example which has a bearing on this point. The great majority of the Rosaceæ has 9 chromosomes in their basic complex (*n*-number), but the small subfamily Pomoideæ have only 8. The presence of two basic numbers in this family is accounted for by supposing that the ancestors of the modern Rosaceæ had 17 chromosomes in their basic complex. The argument *pari passu* may hold good for the Marchantiaceæ and Ricciaceæ also. On this assumption the cytological analysis clearly suggests a polyphyletic origin for the Marchantiaceæ and the Ricciaceæ in the evolutionary history of the Marchantiales.

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LITERATURE CITED

- Allen, C. E. .. *Science*, 1917, 46, 466; *Genetics*, 1924, 9, 530; 1925, 10, 1; 1926, 11, 83; *Amer. Naturalist*, 1932, 66, 107; *Proceed Nat. Acad. Sci.*, 1934, 20, 147; *Bot. Rev.*, 1935, 1, 269; *Cytologia*, 1937, *Fujii Jub. Vol.*, 1, 494.
- Anderson, E. .. *Bot. Rev.*, 1937, 3, 335-50.
- Burgeff, H. .. *Zeitschrift f. induk. Abst. und Vererb.*, 1930, 54, 239.
- Cavers, F. .. "The Inter-Relationships of the Bryophyta," *New Phytologist*, Reprint, 1911.
- Chavan, A. .. *The Bryologist*, 1937 a, 40, 58; *Amer. Journ. Bot.*, 1937 b, 24, 484.
- Chopra, R. S. .. See Kashyap, 1932 b.
- Correns, C. .. *Handb. Verebungswiss.*, 1928, II C.
- Evans, A. W. .. *Bot. Rev.*, 1939, 5, 49-96.
- Goebel, K. .. *Flora*, 1910, N.F. Band 1, 43.
- Gola, G. .. *Atti Della R. Acad. Delle Sci. Di Torino*, 1914, 49.
- Haupt, G. .. *Zeit. induk. Abst. und Vererb. L.*, 1932, 62, 367; 1933, 63, 390.

- Heitz, E. .. *Ztschr. f. Bot.*, 1927 a, 18, 625-81; *Abh. d. naturwiss. Ver.*, Hamburg, 1927 b, 21, 3/4 Heft, 48-58; *Jahrb. f. wiss. Botan.*, 1928, 69, 762.
- Höfer, K. .. "Karyologie" in Verdoorn's *Manual of Bryology*, 1932 b, 159-206.
- Ishikawa, M. .. *Bot. Mag.*, 1916, 30, 404.
- Kashyap, S. R. .. *New Phytologist*, 1914, 13, 206-26 and 308-22; 1915, 14, 1; *Proc. Asiatic Soc. of Bengal (New Series)*, 1919, 15, 152; "Liverworts of the Western Himalayas and the Punjab Plains," Part I, 1929; "Supplement" to the above, 1932 a.
- and Chopra, R. S. .. *Ibid.*, Part II, 1932 b.
- and Pande, S. K. .. *Journ. Ind. Bot. Soc.*, 1922, 3, 79.
- Khanna, L. P. .. *Ibid.*, 1929, 8, 103; *Bot. Gaz.*, 1932, 93, 103; *Journ. Ind. Bot. Soc.*, 1936, 15, 235; *Journ. Bombay Nat. Hist. Soc.*, 1937, 39, 358.
- Koch .. *Malpighia*, 1890-91, 4.
- Lorbeer, G. .. *Zeitschr. f. induk. Abst. u. Vererb. L.*, 1927, 44, 1; *Zeitschr. f. Bot.*, 1930, 23, 932; *Jahrb. wiss. Bot.*, 1934, 80, 567.
- Mahabalé, T. S., and Gorji, G. H. .. *Curr. Sci.*, 1941, 10, 28.
- Marchal, El. and Em. .. A series of papers in *Mem. Cour. and Bull. Acad. Roy. Belg. Cl. Sci.*, 1906-11.
- Matthey, R. .. *Rev. Suisse de Zool.*, 1931, 38, 118; 1933, 40, 281.
- McClung, C. .. *Journ. Morph.*, 1914, 25, 651.
- Mehra, P. N. .. *Proc. Ind. Acad. Sci.*, 1938, 8, 1.
- and Mehra, H. L. .. *Ibid.*, 1939, 9, 287.
- Meyer, K. .. *Ber. Deut. Bot. Ges.*, 1914, 32, 262; *Planta*, 1931, 13, 210.
- Müntzing, A. .. *Hereditas*, 1936, 21, 263.
- Pande, S. K. .. *Journ. Ind. Bot. Soc.*, 1924, 4, 117; 1932, 11, 169; 1933, 12, 110; *Proc. Ind. Acad. Sci.*, 1934, 1, 205; *Journ. Ind. Bot. Soc.*, 1936, 15, 221.
- Schottländer .. *Cohn's Beitr. Biol.*, 1892, 6.
- Schratz, E. .. *Arch. mikr. Anat.*, 1924, 63, 197.
- Showalter, A. .. *Bot. Gaz.*, 1921, 72, 245; *Amer. Journ. Bot.*, 1923, 10, 170; *Proc. Nat. Acad. Sci.*, 1928, 14, 63.
- Siler, M. B. .. *Proceed. Nat. Acad. Sci.*, 1934, 20, 603.
- Srinivasan, K. S. .. *Proc. Ind. Acad. Sci.*, 1939, 10, 88; *Journ. Madras Univ.*, 1940, 12, 59.
- Stephani, F. .. "Species Hepaticarum," Genève, 1898-1925, 1-6.
- Swezy, O. .. *Amer. Nat.*, 1935, 69, 383; *Cytologia, Fujii Jub. Vol.*, 1937, I, 149-55.
- Tischler, G. .. *Biolog. Zentralbl.*, 1928, 48, 321; "Pflanzliche Chromosomen-Zahlen," in *Tabulae Biologicae Periodicae*, published by W. Junk, 1931, 1935-36; *Bot. Jahrb.*, 1935, 67, 1.
- Verdoorn, Fr. .. *Ann. Bryol.*, 1931, 4, 123; 1932a, 5, 125; *Manual of Bryology*, 1932 b.
- Walton, J. .. *Ann. Bot.*, 1925, 39, 563; 1928, 42, 707.
- Weittstein, F. .. *Bibliogr. Gen.*, 1925, 1, 38; early papers in *Zeitschr. induk. Abst. Vererb.*, 1924, 33, etc.
- Wolcott, G. B. .. *Amer. Journ. Bot.*, 1939, 26, 41.