STUDIES ON THE CYTOLOGY AND PHYLOGENY OF THE PTERIDOPHYTES

II. OBSERVATIONS ON THE GENUS *LYCOPODIUM*

by C. A. NINAN, *Department of Botany, University College, Trivandrum*

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ABSTRACT

1. The cytology of nine species and a few varieties of the genus *Lycopodium* indigenous to South India is described.

2. The different species of the genus investigated in this study are found to possess chromosome numbers like $n = 48$, $n = 104$, $n = 136$ and $2n = c.405$. These data taken together with previous observations show that basic numbers like 11, 12, 13 and 17 are characteristic of this genus. In the possession of more than one base number in the different species of a single genus, *Lycopodium* is remarkably different from the other genera of primitive Pteridophytes.

3. It is observed that species with a predominant vegetative mode of reproduction like *L. selago*, *L. lucidulum* (and *Phylloglossum drummondii*) show irregular meiotic behaviour.

4. *L. lucidulum* is shown to be probably of hybrid origin.

5. Cyto-taxonomic evaluation of the various subgenera of the genus *Lycopodium* has shown that the scheme of Walton and Alston is more acceptable. It is suggested that the genus *Lycopodium* may be retained with due recognition of the subgenera, the arrangement of which should be revised, taking into account data of chromosome numbers to supplement other relevant criteria.

INTRODUCTION

The Lycopods are a great group of primitive microphyllous Pteridophytes, consisting of four living genera, *Lycopodium*, *Phylloglossum*, *Selaginella* and *Isoetes*. Traceable back in geological history to the Carboniferous period in which they reached the climax of their development, the Lycopods were represented by many genera and a great number of species, most of which were characterised by an arboreal habit. Though the living genera differ markedly from their fossil relatives in habit, in the lack of secondary growth and in many other features, the fossils *Lycopodites* and *Selaginellites* from the Upper Carboniferous strata have shown the probability that forms similar in habit to *Lycopodium* and *Selaginella* and perhaps referable to these genera existed even in such a remote period (Eames 1936). The finding of the Devonian *Drepanophycus* and the Silurian *Baragwanathia* (Lang and Cookson 1935) and the discovery of Lycopodiaceous shoots in the Middle Cambrian of East-Siberia (Kryschtofowitch 1953) indicate that the Lycopodiaceous stock can be traced still further back in time.

The living genera can be sharply separated into two groups: (1) eligulate forms with homosporous fructifications and (2) those which are ligulate and heterosporous. *Lycopodium* and *Phylloglossum* are assigned to the former group while *Selaginella* and *Isoetes* come under the latter. The monotypic *Phylloglossum* is confined to Australia and New Zealand, and as no material was available it is excluded from the present study. The cytology of *Isoetes* and *Selaginella* is reported elsewhere (Abraham and Ninan 1958, Ninan 1958*a*). The present paper deals with the cytology of nine species and a few varieties of *Lycopodium* indigenous to South India.

The genus *Lycopodium*, with nearly 100 species (Eames 1936), possesses very distinctive features and has a cosmopolitan distribution though it occurs in greater abundance in the tropical and subtropical forests. In spite of the world-wide distribution and the great phylogenetic importance of this group, the cytology of only a few species has appeared in previous reports. Difficulty in procuring fresh material at the right stage and the peculiar technical problems associated with their study account for this. Manton (1950) has very rightly pointed out that "*Lycopodium* is the most awkward genus of the Pteridophytes for cytological study".

Material and Methods

The materials used in this study were collected from different localities in South India and grown in the Botanical Garden of the Kerala University. Some of the epiphytic species of *Lycopodium* like *L. squarrosum*, *L. macrostachys*, *L. phlegmaria* etc. thrive very well under green house conditions. The terrestrial species like *L. vernicosum*, *L. lucidulum*, *L. wightianum* etc. characteristic of higher elevations do not grow satisfactorily when brought to the plains, though they may survive for a few seasons in the green house.

Fixations for cytological study were made from wild materials wherever possible. In certain cases the transplants also provided material for study. The fixative used was a modified proportion of Carnoy's fluid (Ninan 1955). Actively growing tips of strobili (or shoot apex with young sporangia) were fixed for study of meiosis in spore mother cells. In nearly all cases successful fixations for meiosis were made between 1 p.m. and 3 p.m.

Lycopodium is a difficult cytological material ; the spore mother cells are thick-walled and it is not easy to break them and get well spaced out chromosome preparations. Secondly, the spore mother cells in most cases are found to contain globule-like bodies making exact cytological interpretation difficult. Added to these, the peculiar chromosome structure in certain species and the tendency for clumping make the *Lycopodiums* the most difficult cytological material among the Pteridophytes. The fixative containing chloroform proved to be very helpful in dissolving out the globule-like bodies and facilitating spreading of the chromosomes when pressure was applied to the cover glass. Sporangia were fixed for nearly a week and a change to fresh fixative was made before smearing. Certain species like *L. lucidulum* combine all these difficulties with irregular pairing and extreme diffuseness of chromosomes, making exact cytological interpretation almost impossible.

Cytological Observations

Lycopodium hamiltonii Spring.

The first material to yield a satisfactory preparation was *L. hamiltonii* Spring. This was collected from Ponmudi (3,500 ft.) and Kodaikanal (7,000 ft.). The Kodaikanal material was epiphytic and pendulous on tree trunks while the Ponmudi material was found to grow on the surface of moist rocks along with mosses and grasses in exposed areas. *L. hamiltonii* Spring. var. *petiolatum* C.B. Clarke (*L. taxifolium* Spring.) was also obtained from Kodaikanal. *L. hamiltonii* is characterised by the lack of specialised cones ; the sporangia were distributed in the axils of unaltered leaves in the upper part of the stem. Cytological examination of the Ponmudi materials showed 136 bivalents at first metaphase of meiosis (Pl. V, fig. 1 and Text-fig. 1). The same number of bivalents has also been observed in the Kodaikanal material. The meiotic chromosomes of this species are fairly large compared to those of the other species and have quite normal shapes unlike the "antenna-like" bivalents reported for *L. inundatum* (Manton 1950).

TEXT-FIGS. 1–6

Explanatory diagrams of figures 1–6 on Plate V, reproduced at the same magnification as the photographs, (all × 1000).

Fig. 1. *Lycopodium hamiltonii* spring. $n = 136$ Fig. 2. *L. macrostachys* Spring $n = 136$
Fig. 3. *L. squarrosum* Forst. $n = 136$ Fig. 4. *L. squarrosum* Forst. $n = 138$
Fig. 5. *L. wightianum* Wall ex. Hook & Grev. $n = 48$ Fig. 6. *L. vernicosum* Hook & Grev. $n = 136$

L. vernicosum Hook. & Grev.

Baker (1887) considers this as a form of *L. hamiltonii* with "much reflexed leaves". They resemble the latter species in external appearance ; but are usually of shorter stature with a number of lower leaves almost always drooping down and persistent even after drying up. The stem is densely tufted. This species has been collected from Ponmudi (3,500 ft.). They are seen to occur in plenty at the top of an exposed hillock on moist rocks along with mosses and grasses. Cytologically, this species is similar to *L. hamiltonii* ; one hundred and thirty-six bivalents are present in spore mother cells (Pl. V, fig. 6 and Text-fig. 6). The metaphase chromosomes of this species, unlike those of *L. hamiltonii*, are more fuzzy and exhibit a tendency for clumping. There is no appreciable difference in chromosome size.

L. squarrosum Forst. [= *L. ulicifolium* (Vent.) Hook.]

The largest epiphytic species of *Lycopodium* indigenous to this area is *L. squarrosum*. This species occurs in several places in the Western Ghats and was collected from Ponmudi and Munnar areas (2,500–3,000 ft.). This is characterised by the possession of pendulous shoots, one to two feet long and two to three times dichotomously forked. Preparations of meiosis from wild materials of this species collected from Ponmudi (epiphytic on a large rock) showed the presence of 136 bivalents in spore mother cells (Pl. V, fig. 3 and Text-fig. 3). The Munnar material also showed the haploid number of $n = 136$. However, materials from one of the earlier collections from Ponmudi (epiphytic on tree trunks) showed 138 bivalents in a spore mother cell (Pl. V, fig. 4 and Text-fig. 4). The meiotic chromosomes of this species are almost comparable to those of *L. hamiltonii* in size and appearance.

L. macrostachys Spring. (*L. phyllanthum* Hook. & Arn.)

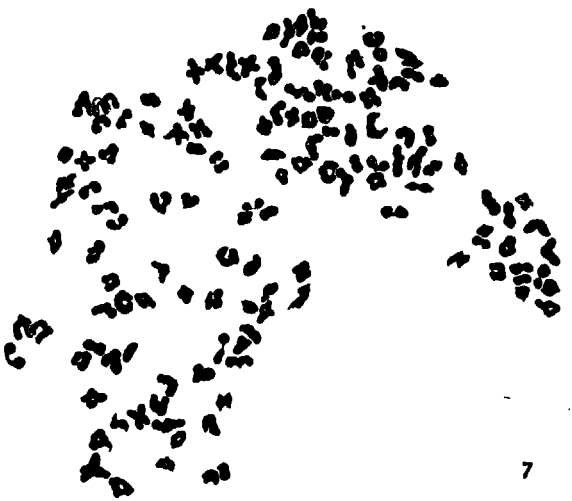
This is another epiphytic species usually found growing on the trunks of huge trees at higher elevations. They form very big clumps and are characterised by luxuriant vegetative growth. One such clump was recently collected from Ponmudi. The enormous size of this can be well appreciated from the fact that it had over 500 shoots. In this species, the shoots are more fleshy and stout and the leaves are moderately dense, spreading, with revolute edges and distinct midrib, and larger than those of any other species collected so far. The strobili are highly differentiated from the vegetative axis and are dichotomously branched a few times. In certain materials of this species, the growth of the strobili is seen to continue and give rise to vegetative shoots. This species occurs in several places in the Western Ghats namely, Ponmudi (3,500 ft.), Poringalkuthu (2,500 ft.), Thekkady (2,000 ft.) etc. Cytological examination of the Ponmudi material showed 136 bivalents in spore mother cells (Pl. VII, fig. 11 and Text-fig. 11). The bivalents are of quite normal shapes and closely resemble those of *L. squarrosum*. The same number of bivalents has also been observed in spore mother cells of all the other materials of this species collected from different localities.

Another variety of *L. macrostachys* obtained from Kodaikanal hills (7,000 ft., showed much thicker strobili, reaching almost a foot in length. Cytological examination of this also showed the chromosome number to be exactly $n = 136$ (Pl. V, fig. 2 and Text-fig. 2). The bivalents here again are of normal shapes and almost comparable to those of the Ponmudi material.

L. phlegmaria L.

This is another epiphytic species occurring in similar habitats as *L. macrostachys* and almost resembling it in external appearance. Unlike the former, the vegeta-

tive axis in *L. phlegmaria* is less stout and pendulous. The strobili which are highly differentiated from the vegetative shoots are profusely branched in a dichotomous manner and are very slender. In external appearance, this closely resembles *L. nummularifolium*. *L. phlegmaria* grows in several places in the Western Ghats, like Ponmudi, Munnar, Thekkady and Poringalkuthu. This is the only species of *Lycopodium* so far found in coastal areas. It was collected from Sherthalai



TEXT-FIGS. 7–8

Explanatory diagrams to figures 7–8 on Plate VI, reproduced at the same magnification as the photographs. (both figures × 1000).

Fig. 7. *L. phlegmaria* L. $n = 136$
Fig. 8. *L. lucidulum* Michx. $2n = c.405$.

(sea-coast), from a *Calophyllum inophyllum* tree on which it was growing epiphytically. Epiphytic races of this are also seen to occur in the plains. Chromosome counts of $n = 136$ were made from materials collected from all the above localities. The meiotic chromosomes in the Sherthalai material of this species are illustrated in Pl. VI, fig. 7 (see also Text-fig. 7).

L. setaceum Hamilt.

This epiphytic species was collected from Ponmudi, Poringalkuthu and Muthukuzhivayal in the Western Ghats. The Muthukuzhivayal material was considerably different from the other two in external appearance. However, cytological examination of all the three gave identical results. One hundred and thirty-six bivalents were counted from spore mother cells. The illustration (Pl. VII, fig. 13) shows the meiotic chromosomes of this species collected from Poringalkuthu. Meiosis in the Muthukuzhivayal material is illustrated in Text-figure 14. The meiotic chromosomes of this species are slightly smaller than those of all the other species with $n = 136$.

L. cernuum L.

This terrestrial species is very common on way sides at higher elevations. It is also seen to occur in certain areas in the plains. The vegetative shoots are highly branched, each branch at maturity ending in a compact cone. The branching in this species is apparently monopodial. Chromosome counts from materials of this species collected from Trivandrum showed 104 bivalents at metaphase of meiosis (Pl. VII, fig. 12 and Text-fig. 12). The bivalents in this species are seen to be much smaller than those of all the other species investigated in this study.

L. wightianum Wall. ex Hook. & Grev.

This is typically a terrestrial species occurring in abundance around the Fairy Falls, Kodaikanal hills. This is characterised by the possession of wide-trailing stems with many ascending branches and branchlets. Cytological examination of materials of this species fixed at Kodaikanal and brought to Trivandrum showed the presence of 48 bivalents in spore mother cells (Pl. V, fig. 5 and Text-fig. 5). The bivalents at diakinesis exhibit very peculiar shapes and are of different sizes, presenting difficulties in interpretation. Hence it is very difficult to get clear chromosome counts even though the number of bivalents is relatively low. This species exhibits the lowest number of chromosomes in any species of *Lycopodium* investigated in the present study.

L. lucidulum Michx. (= *L. reflexum* Sw.)

This terrestrial species was obtained from Bear Shola, Kodaikanal hills. Il grows abundantly on the sides of a stream in a shady place. The plant is smalt and the stem suberect and one to three times dichotomously forked. The stem is covered by a large number of closely arranged leaves which diverge away in a drooping manner. This species is further characterised by the presence in the axils of the upper leaves, of "bulbils" which drop to the ground and develop into new plants. From careful examination made in several seasons it appears that vegetative propagation is well established in this species.

The cytological difficulties inherent in the *Lycopodiums* reach the climax in *L. lucidulum*. The meiotic chromosomes in this species are very fuzzy structures with diffuse outlines and the pairing is very irregular. Some of the bivalents (or multivalents, if they are present) can hardly be distinguished from some of the univalents. This makes quantitative enumeration of chromosome number very

difficult. Chromosome counts even from very clear and well spaced out preparations can therefore be only approximate. As Manton (1950) has suggested, the actual number is not as significant as the presence of univalents. One hundred and eighty bivalents and 45 univalents were counted from a clear preparation of a spore mother cell (Pl. VI, fig. 8 and Text-fig. 8). The sporangia used in the study

TEXT-FIGURES 11–14

Fig. 11. Explanatory diagram to fig. 11 on Plate VII, showing 136 bivalents in *L. macrostachys* Spring. (variety with short strobili). ×1000.

Fig. 12. Explanatory diagram to Plate VII; fig. 12 $n = 104$. ×1000.

Fig. 13. Explanatory diagram to Plate VII, fig. 13 showing $n = 136$ in *L. setaceum* Hamilt. ×1000.

Fig. 14. Diagram of meiosis in *L. setaceum* Hamilt. (variety from Muthukuzhivayal). $n = 136$. ×1000.

of meiosis were fixed in the field and preparations of meiosis were made in two consecutive years. Irregular pairing was seen to be a constant feature in all the preparations of meiosis and it is believed from this, that the failure of pairing is not due to metabolic causes (as is seen in certain garden materials in the first season of transplanting), but to lack of homology among the chromosomes. This was further confirmed from spore mother cells showing bivalents and lagging univalents at first metaphase of meiosis (Pl. VII, fig. 9). Laggards were also seen at first anaphase of meiosis (Pl. VII, fig. 10). The irregular pairing therefore is in all probability an indication of hybridity. If it is really so, it would suggest comparison to the situation encountered in *L. selago*, described by Manton (1950) as "the most ancient impure species cytology has so far detected". Failure of chromosome pairing at meiosis has also been demonstrated in the related species *Phylloglossum drummondii* Kunze (Blackwood 1953). On comparison of these three species it is seen that vegetative propagation through "bulbils" is characteristic of *L. selago* and *L. lucidulum* while *Phylloglossum* propagates through "tubers". The prevalence of accessory methods of propagation in these species may be related in some way with the abnormalities in the meiotic process—the disadvantages arising from a defective meiosis might be counter-balanced by the parallel attainment of a vegetative mode of reproduction.

Though other species like *L. serratum*, *L. clavatum*, *L. nummularifolium*, *L. subulifolium*, *L. casuarinoides* etc. were obtained, they could not be studied due to lack of sporangial material at the proper stage of development. It may be possible to report on them on a later occasion.

Discussion

Phylogenetic considerations :

On comparison of the observed chromosome numbers with previous reports on the cytology of this genus, the first and the most striking thing that one gathers is the remarkable variation of chromosome numbers exhibited by the different species of this genus. The list of chromosome numbers of the species so far investigated is given in the table below.

Table I

Chromosome numbers in Lycopodium

(Present study)

species	source	chromosome number
L. lucidulum Michx.	S. India	irregular meiosis ($2n$ = c.405)
L. hamiltonii Spring	,,	n = 136
L. vernicosum Hook & Grev.	,,	n = 136
L. squarrosum Forst.	,,	n = 136
L. macrostachys Spring	,,	n = 136
L. phlegmaria L.	,,	n = 136
L. setaceum Hamilt.	,,	n = 136
L. cernuum L.	,,	n = 104
L. wightianum Wall. ex Hook. & Grev.	,,	n = 48

TABLE I (*contd.*)

(Previous reports)

species	source	chromosome number		author
		n	2*n*	
L. inundatum L.	Scotland	78	—	Manton 1950
L. annotinum L.	Sweden	34	—	,,
L. annotinum L.	Lake District	—	c. 68	,,
L. clavatum L.	,,	34	68	,,
L. selago L.	,,	irregular	c. 260	,,
L. alpinum L.	Wales	24-25	c. 48	,,
L. clavatum L.	N. America	—	c. 60	Dunlop 1949
L. complanatum	,,	—	40	,,
L. annotinum L.	,,	—	c. 50	,,
L. obscurum	,,	—	c. 50	,,
L. complanatum	——	22	—	Harmsen (cf. Delay 1953).
L. clavatum L.	——	14	—	Baranov 1925
L. clavatum L.	N. India	34	—	Mehra and Verma 1957
L. nikoense	Japan	34	—	,,
L. lucidulum Mich.	N. India	132	—	,,
L. setaceum Hamilt.	,,	165-170	—	,,

(In scrutinising the above list it is at once obvious that some of the earlier observations are incorrect and based on erroneous interpretations. Manton (1950) alone of all the authors has given credible photographic evidence of chromosome preparations. Others have provided only diagrams of chromosomes, which by itself is no convincing evidence, especially in view of the fact that they are conflicting observations. In the present study the author has adopted the principle : "what cannot be photographed cannot be used as evidence" (Manton 1950). For purposes of discussion therefore only those data which are well authenticated alone will be referred to.)

The haploid numbers $n = 78$ and $n = 104$ in *L. inundatum* (Manton 1950) and *L. cernuum* (present study) respectively are traceable back to a basic number of 13. It is already shown from evidences of chromosome numbers in ancient genera like *Psilotum*, *Marattia*, *Matonia*, *Hymenophyllum*, *Dicranopteris* etc. that chromosome number 13 might have been widely prevalent in the past in primitive groups of Pteridophytes (Manton 1950, 1954 ; Manton and Sledge 1954 ; Ninan 1956*b*,*c*). It is very interesting to note that the primitive genus *Lycopodium* also exhibits in some of its species numbers which are referable to 13 chromosomed ancestral types. Haploid numbers like $n = 34$ in *L. clavatum* (Manton 1950, Mehra and Verma 1957), *L. annotinum* (Manton 1950) and *L. nikoense* (Mehra and Verma 1957) and $n = 136$ in South Indian species like *L. hamiltonii*, *L. macrostachys*, *L. vernicosum*, *L. setaceum*, *L. phlegmaria* and *L. squarrosum* observed in the present study clearly show that they might have had a common cytological origin, presumably from 17 chromosomed ancestral types. *L. alpinum* (Manton 1950) and *L. wightianum* (present study) with haploid numbers like $n = 24-25$ ($2n$ = c.48) and $n = 48$ respectively represent another distinct evolutionary line, probably from ancestral types with 12 as the basic chromosome number. Harmsen's report (Delay 1953) of $2n = 22$ in *L. complanatum* and the purported presence of chromosome numbers in multiples of 11 in a few species of *Lycopodium* (Mehra and Verma 1957) show that the basic number 11 is characteristic of some species of this genus. Other primitive genera like *Isoetes* (Abraham and Ninan 1958) and *Osmunda* (Manton 1950, 1954 ; Ninan 1956*d*) also show the base number 11. It is thus seen that all the investigated species of the genus *Lycopodium* (with authentic chromosome counts) are referable to basic numbers like 11, 12, 13 and 17. In

this respect the genus *Lycopodium* provides a striking contrast to the situation in other genera of Pteridophytes, most of which show in the different species of a genus, numbers which are exact multiples of a base number characteristic of that genus. Haploid chromosome numbers like $n = 120$, 240, 480 etc. in species of *Ophioglossum* (Ninan 1956*a*, 1958*b*) and those like $n = 11$, 22, 33, c.55 etc. in *Isoetes* (Manton 1950, Abraham and Ninan 1958) are examples to this. In the leptosporangiate ferns also, the same relationship between the various species of a genus is found to hold good. However *Lycopodium* shows a different cytological situation in possessing different basic numbers in different species. But fossil history tells us that the Lycopodiaceous stock is referable back to the Siluro-Devonian strata, and the surviving species need be regarded only as representing end members of distinct phyletic lines, though in view of the stereotyped morphological features and close similarity in technical characters, some of them have come to be considered as constituting different species of a single genus. As Manton (1950) has remarked "the cytological evidence as a whole can only underline their complete dissimilarity from one another, and one must recognize in them representatives of phyletic lines which have been so long separated that their cytological connexion, if it ever existed, has become completely obscured. They seem now to be far more different from each other than are the genera or even groups of genera of the Polypodiaceous ferns. This is perhaps a sign of antiquity".

Cyto-taxonomy of the genus Lycopodium :

All the species of the Lycopodiaceae, with the exception of the monotypic *Phylloglossum*, are united into the single genus *Lycopodium*. Goebel (1930) divides this comprehensive genus into five groups, taking into account the characters of the gametophyte. The five groups according to Goebel are *Selago*, *Phlegmaria*, *Cernuum*, *Clavatum* and *Complanatum*. Pfitzer recognizes two subgenera based on the character and arrangement of the sporophyll, namely, *Urostachya* (including two sections, *Selago* and *Phlegmaria*) and *Rhopalostachya* (with three sections, *Inundata*, *Cernuua* and *Clavata*). Baker's (1887) scheme of classification, again based on character and arrangement of sporophylls, recognizes four subgenera, *Selago*, *Subselago*, *Lepidotis* and *Diphasium*, each of which is again subdivided into different sections. Walton and Alston (1938) proposed another scheme following that of Herter in the main. This recognizes six subgenera, *Urostachys*, *Clavatostachys*, *Complanatostachys*, *Cernuostachys*, *Inundatostachys* and *Lateralistachys*.

The above systems of classifications, with the exception of that of Goebel, are based on the character and arrangement of sporophylls. It is clearly evident that any classification which does not take into account data for comparison from as many criteria as possible cannot be natural. Taking Baker's scheme, for instance, it is seen that there are certain obvious discords in it in the light of evidence from cytology. The table provided below would serve to illustrate this.

It is clear from the table that Baker's subgenus *Lepidotis* is a heterogeneous assemblage of species with haploid numbers like $n = 136$, 104, 78, 34 and 24–25 which in turn are traceable to base numbers like 17, 13 and 12. In the *Clavatum* section of *Lepidotis* itself are included species like *L. clavatum* and *L. annotinum* with $n = 34$ and *L. alpinum* with $n = 24$–25. In a natural arrangement of these species, it is essential that if morphological evidences would provide sufficient warranty, species which are evidently related in a cytological sense should be grouped together. In that case, it is necessary to remove the *Phlegmaria* section of Baker's subgenus *Lepidotis* to the subgenus *Selago* to which may be merged the next subgenus *Subselago*. The single large group which would thus result would be traceable to a basic number of 17. Turning now to the scheme of Walton and Alston (1938), it is seen that exactly these three sections (*Selago*, *Subselago*

TABLE II

Chromosome numbers in Lycopodium species

(arranged according to Baker's system)

section	species	chromosome number	basic number
	Subgenus : *Selago*		
	**L. selago*	$2n$ = c.260	17?
Selago	*L. lucidulum*	$2n$ = c.405	17?
	L. hamiltonii	n = 136	17
Taxifolium	*L. setaceum*	n = 136	17
	Subgenus : *Subselago*		
	L. squarrosum	n = 136	17
	Subgenus : *Lepidotis*		
Inundatum	**L. inundatum*	n = 78	13
Phlegmaria	*L. phlegmaria*	n = 136	17
	L. macrostachys	n = 136	17
Cernuum	*L. cernuum*	n = 104	13
	**L. clavatum*	n = 34	17
Clavatum	**L. annotinum*	n = 34	17
	**L. alpinum*	n = 24–25	12
	Subgenus : *Diphasium*		
	L. wightianum	n = 48	12

*Reports of Manton (1950). Other determinations are made in the present study.

and *Phlegmaria*) are united by them to form the subgenus *Urostachys*. Species with a basic number of 17 in the *Clavatum* section (*L. clavatum* and *L. annotinum*) are evidently related to the *Phlegmaria* section in a cytological sense. However, Walton and Alston regard the *Clavatum* group of species as a distinct subgenus, the *Clavatostachys*. Both the *Urostachys* and the *Clavatostachys* of Walton and Alston are thus seen to have the same basic chromosome number. However, in view of the morphological differences exhibited by the two groups, Walton and Alston's treatment of them as two distinct subgenera seems quite justified. The morphological distinctness of the *Inundatum* and *Cernuum* sections has been stressed by all the authors. Walton and Alston raise them to the status of subgenera. The present study of representative species of these two subgenera has shown that despite morphological differences they are cytologically related in the possession of a common basic number 13. To make further discussions on the scheme of Walton and Alston, knowledge of chromosome numbers from representative species of the other subgenera is necessary. However, as far as is known, the scheme of Walton and Alston seems to be the most satisfactory. Further knowledge of chromosome numbers of different species is likely to be helpful in arriving at more correct taxonomic grouping of this complicated genus.

The question now remains whether or not the various subgenera should be raised to generic rank. Campbell (1939) remarks : "the differences shown by the

gametophyte and sporophyte are so great that it does not seem logical to refer all the species to a single genus." Herter raises the subgenus *Urostachys* to generic rank (Walton and Alston 1938). As far as this genus is concerned, the erection of new genera out of one or more of the subgenera is not warranted in the light of cytological evidence, since the same basic number is seen to be repeated in more than one section. The genus *Lycopodium* may be retained as such with due recognition of the various subgenera, the arrangement of which should be revised on the lines indicated above.

It is generally conceded that forms without definite cones are the more primitive and that specialisation into definite strobili is an advanced character. Bower (1935) holds that vegetative leaves are sterilised sporophylls and that the most primitive types are those in which almost every leaf bears a sporangium. *L. compactum*, *L. trencilla*, *L. lucidulum*, *L. selago* etc. would accordingly represent the most primitive types, while *L. wightianum*, *L. cernuum* etc. have to be taken as relatively advanced. Cytological study shows that species like *L. selago*, *L. lucidulum* etc. have comparatively high chromosome numbers ($2n = 260$ in *L. selago* and $2n = c.405$ in *L. lucidulum*) and while this may be taken as an indication of relative antiquity of the species concerned, it is by no means a primitive chromosome situation.

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Explanation of Plates

Plate V

Fig. 1. First meiotic metaphase in a spore mother cell of *Lycopodium hamiltonii* Spring. from Ponmudi showing 136 bivalents. ×1000.
Fig. 2. A spore mother cell from the Kodaikanal material of *L. macrostachys* Spring. (with long strobili). The number of bivalents is 136. ×1000.
Fig. 3. Meiotic metaphase in *L. squarrosum* Forst. from Ponmudi showing 136 bivalents in a spore mother cell. ×1000.
Fig. 4. Meiosis in *L. squarrosum* Forst. from Ponmudi area showing 138 bivalents in a spore mother cell. ×1000.
Fig. 5. Meiotic metaphase in a spore mother cell of *L. wightianum* Wall. ex Hook. & Grev. from Kodaikanal. $n = 48$ ×1000.
Fig. 6. A spore mother cell from the Ponmudi material of *L. vernicosum* Hook. & Grev., showing 136 bivalents at metaphase of meiosis. ×1000.

Plate VI

Fig. 7. Meiosis in *L. phlegmaria* L. from Sherthalai (sea-coast). $n = 136$. ×1000.
Fig. 8. Diakinesis in *L. lucidulum* Michx. 180 bivalents and 45 univalents are present (for explanatory diagram see Text-fig. 8). ×1000.

Plate VII

Fig. 9. A side view of the metaphase plate in a spore mother cell of *L. lucidulum* Michx. showing bivalents and univalents. ×1000.
Fig. 10. Anaphase in a spore mother cell of *L. lucidulum* Michx. showing irregular separation and lagging of chromosomes. ×1000.
Fig. 11. First meiotic metaphse in *L. macrostachys* Spring. (with short strobili). $n = 136$. ×1000.
Fig. 12. Meiotic metaphse in a spore mother cell of *L. cernuum* L. 104 bivalents are present. ×1000.
Fig. 13. Metaphse I in a spore mother cell of *L. setaceum* Hamilt. showing 136 bivalents. ×1000.

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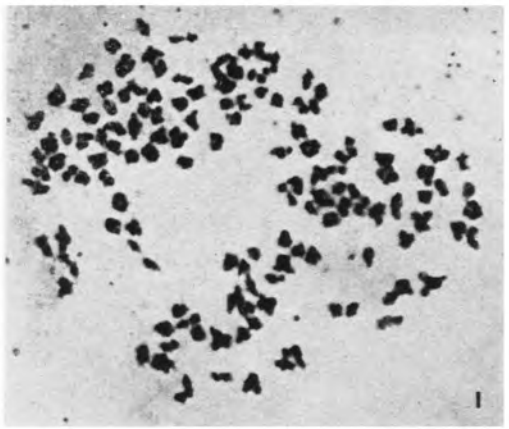
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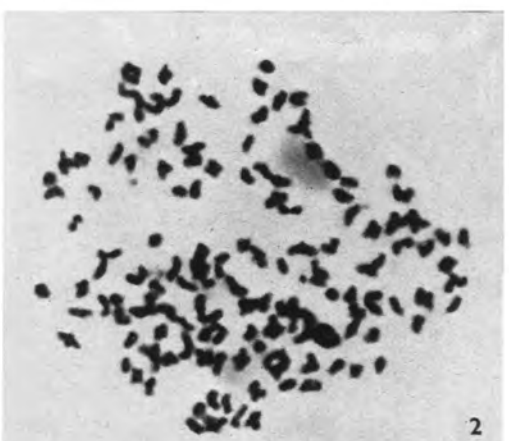
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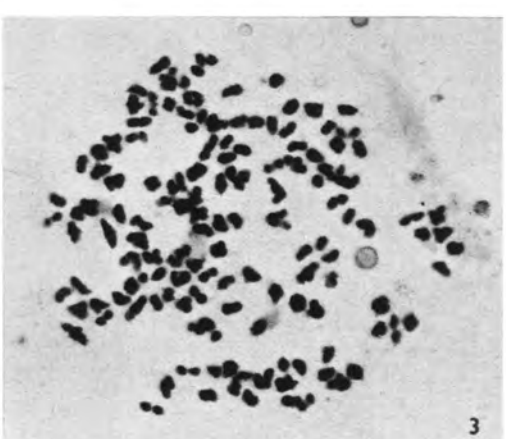
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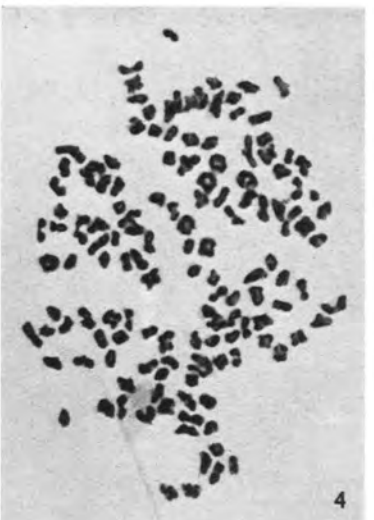
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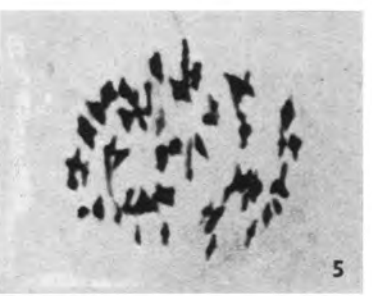
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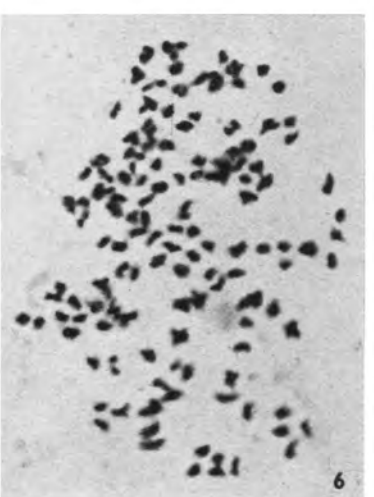
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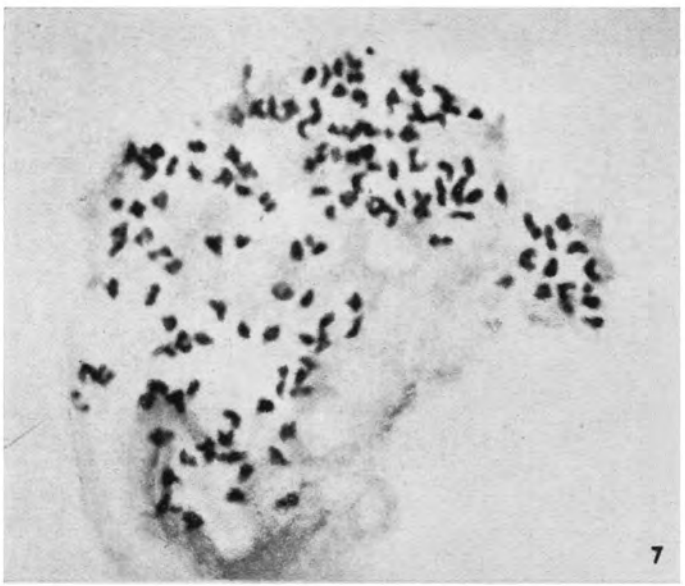
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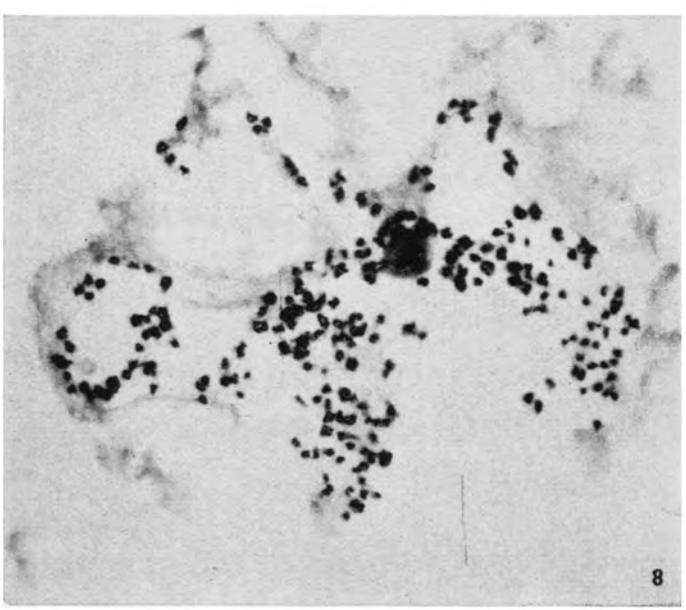
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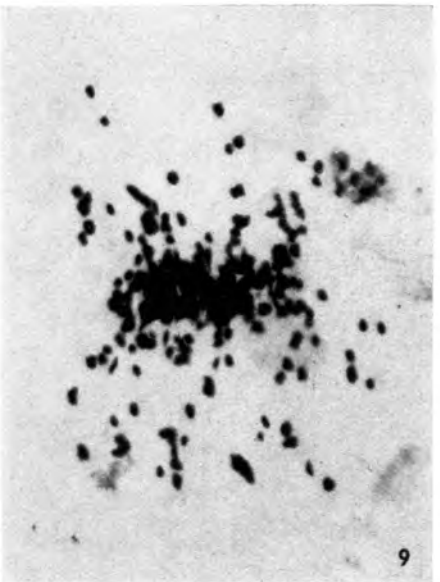
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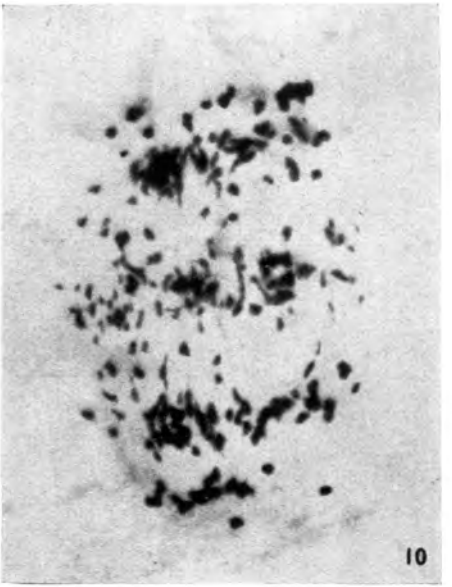
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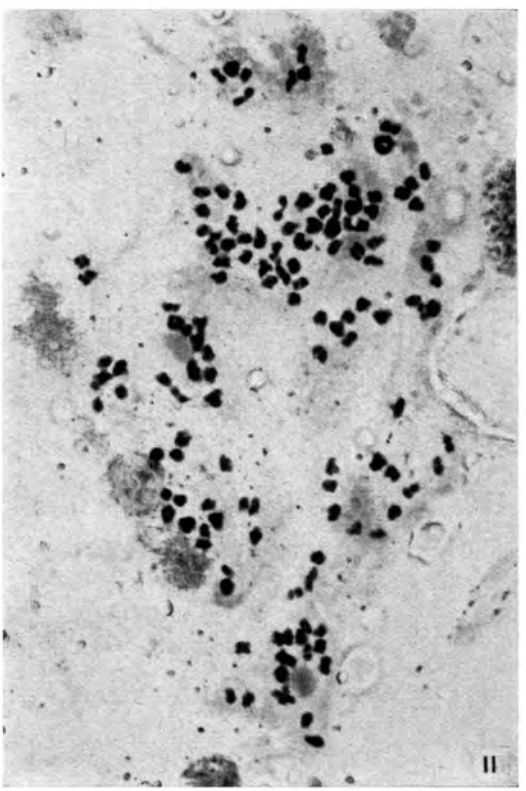
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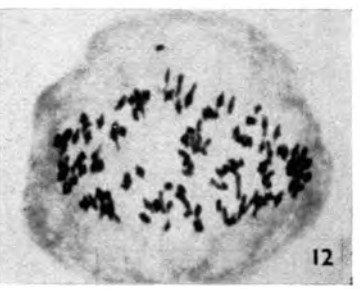
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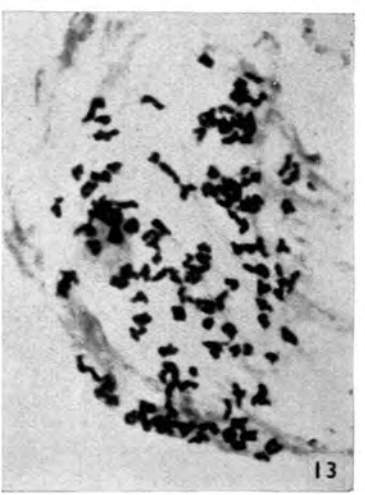
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