STUDIES ON THE CYTOLOGY AND PHYLOGENY OF THE PTERIDOPHYTES

IV. Systematic Position of *Ceratopteris thalictroides* (L.) Brongn.

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(Received for publication on June 9, 1956)

*Ceratopteris* is an aquatic annual consisting of 2–4 species widely distributed in the tropics. *Ceratopteris thalictroides* (L.) Brongn. is the only species that is indigenous to South India. It is found throughout the low lands as a weed in rice fields and by the sides of streams in shallow water.

*Ceratopteris* is a genus of very doubtful affinities and hence the assigning of a proper systematic position for this genus has for long been a difficult problem to Pteridologists. Different authors have treated it in quite different ways in their classifications. It is accepted by all that a valid phylogenetic system can be evolved only by the exercise of all available criteria for comparison (Bower, 1923 and Wagner, 1952). Due to lack of information on certain important aspects like cytology and gametophyte phase it has not been possible to come to any definite conclusion regarding the systematic position of certain problematic genera.

In *Ceratopteris*, though we have information on the gametophyte (Kny, 1875 and Mahabale, 1948) details of the cytology are not yet clearly known. The present paper attempts to fill this gap.

Materials for investigation were obtained from Veli near Trivandrum City. The cytological and photographic techniques followed were similar to those described earlier (Ninan, 1955, 1956a).

Preparations of somatic mitosis made from root tips showed 154 chromosomes at metaphase (Pl. XII, Fig. 1 and Text-Fig. 1). Meiotic counts clearly showed 77 bivalents (Pl. XII, Fig. 2 and Text-Fig. 2). Manton (1954) has reported the presence of 76–78 bivalents in Malayan materials of *Ceratopteris thalictroides*. The present study has shown very clearly that the haploid chromosome number for this genus is exactly 77.

The somatic chromosomes are fairly large in size in spite of the high chromosome number and they are all nearly of the same length. Most of them have median or sub-median constrictions and two show satellites. Some of the meiotic chromosomes show “antenna-like” shapes reminding one of the chromosomes of *Lycopodium inundatum* described by Manton (1950). Both meiotic and mitotic chromosomes take very good stain and excellent preparations could be obtained even with 12–24 hours of fixation.
Text-Figs. 1-2. Fig. 1. Explanatory diagram to Plate XII, Fig. 1 showing 154 chromosomes in root tip squash, ×1,200. Fig. 2. Explanatory diagram to Plate XII, Fig. 2, showing 77 bivalents at I metaphase of meiosis in spore mother cell, ×1,500.
The family Parkeriaceae (Ceratopteridaceae) was established by Hooker in 1825 to accommodate the genus *Ceratopteris*. Diels (1900), Ching (1940) and Copeland (1947) maintain this as a separate family. Christensen (1938) includes the genus in Polypodiaceae (sub-family Gymnogrammoideae, tribe Ceratopterideae), while Holttum (1947) relegates it to Adiantaceae. Bower (1928) associates it with the Gymnogrammoid group of genera, with many of which it shares features like the arrangement of sporangia along the veins and large short-stalked sporangia with irregular annulus. He believes that the primitive Gymnogrammoideae (including the genera *Llavea*, *Onychium*, *Jamesonia*, *Cryptogramme* and *Ceratopteris*) have originated from types with superficial sporangia like *Todea* or *Plagiogyria* and that these five genera are probably related to one another. Holttum (1947) lends support to Bower's view and regards it as more plausible than any other. He (1954) states "*Ceratopteris* is undoubtedly a specialised genus and not closely related to the other Gymnogrammoid ferns which are mainly xerophytic, but most probably it comes of the same stock". Christensen (1938) while supporting Bower's view in the main, is sceptical about the interrelationships of the various genera of Bower's primitive Gymnogrammoideae. He regards the Gymnogrammoids as a group of uncertain mutual relationship probably representing different lines of evolution. Copeland (1947) considers that the genus *Ceratopteris* is derived from indusiate ancestors. He comments: "I let the genus stand as a family because the degeneration of the sporangial structure has taken it beyond easy inclusion in any family description of Pteridaceae; but do not doubt that it is derived from that family as here construed."

Out of the 5 genera of Bower's primitive Gymnogrammoideae, the cytology of *Ceratopteris* and *Cryptogramme* are now known. The latter has a chromosome number of \( n = 30 \) a number so characteristic of most of the Gymnogrammoid, Pteroid, Adiantoid and Cheilanthoid ferns (Manton, 1950, 1954 and Ninan, unpublished observations). *Cryptogramme* therefore aligns itself very closely with the Gymnogrammoids. But *Ceratopteris* with a haploid chromosome number of \( n = 77 \) can in no way be related to *Cryptogramme*, which in the light of other evidences, is considered (Bower, 1928 and Christensen, 1938) to be a close relative of *Ceratopteris*. Though the cytological situation in *Llavea*, *Onychium* and *Jamesonia* are not yet known, the disparity in chromosome numbers evidenced by *Ceratopteris* and *Cryptogramme* is itself clear indication that the primitive Gymnogrammoids of Bower represent more than one evolutionary line. The Gymnogrammoid state as shown by these genera might be the result of parallel evolution and it cannot be construed as indicating closer relationship.

Cytological evidence also shows clearly that Holttum's inclusion of *Ceratopteris* in his Adiantaceae (1947) is the result of an inadequate
appreciation of the affinities of the genus. Recent observations have shown that all the genera of Holttum's Adiantaceae like Monogramma, Vittaria, Anthrophyum, Syngramma, Doryopteris, Hemionitis, Adiantum, Conioagramme, Pityrogramma and Cheilanthes (except Tenuitis, the cytology of which is not known) are characterised by the presence of numbers like 29 or 30 or their multiples (Manton, 1954 and Ninan, unpublished observations). The presence in Ceratopteris of a haploid chromosome number of \( n = 77 \) at once suggests discord in an otherwise cytologically homogeneous group. There is thus sufficient reason for separating Ceratopteris from Holttum's Adiantaceae.

Copeland's contention that Ceratopteris is derived from indusiate ancestors, most probably from the Pteroid ferns is also not in agreement with evidence from cytology. The close affinity of Ceratopteris with the Cheilanthes group of ferns (Copeland, 1947 and Stokey, 1951) is equally unconfirmed. However Bower's suggestion of an origin of Ceratopteris from Osmundaceous ancestors gains support in that all the living genera of the Osmundaceae and Ceratopteris are traceable back to 11 chromosomed ancestors (Ninan, 1956b).

Coming to purely cytological considerations, the nature of the somatic chromosomes in Ceratopteris also supports an ancestry from some primitive group. The chromosomes closely resemble those of some of the ancient genera of Pteridophytes like Psilotum and Angiopteris, in the large size of the chromosomes in spite of high numbers. The other genera included by Holttum in Adiantaceae and which have been investigated in this laboratory all show much smaller somatic chromosomes even where the number is appreciably smaller (Ninan and Mathew, unpublished observations). This clearly shows that on cytological grounds Ceratopteris stands in a position distinct from these genera.

Evidences already discussed provide sufficient warranty for the separation of Ceratopteris from the taxonomic groupings of Bower and Holttum. Bower's view that the genus probably represents a distinct line of evolution from some primitive stock in close relation to the Osmundaceae seems more palusible in the light of evidence from cytology. Copeland's assignment of family status to the genus appears to be the best taxonomic arrangement. In the peculiar blending of advanced and primitive characters Ceratopteris seems to be a specialised genus which occupies an isolated position.

**Summary**

The cytology of *Ceratopteris thalictroides* is described. It has a chromosome number of \( n = 77 \) and \( 2n = 154 \). The chromosomes are large in size in spite of the high number, and in this respect recall the condition in *Psilotum* and *Angiopteris*.

The systematic position of *Ceratopteris* is discussed in the light of cytological data of supposedly related genera and it is shown that Copeland's treatment of the genus as the only representative of the family, Parkeriaceae, appears to be the most satisfactory.
ACKNOWLEDGEMENT

The author wishes to express his indebtedness to Prof. A. Abraham for valuable guidance and encouragement. His thanks are also due to the Ministry of Education, Government of India, for the award of a Senior Research Scholarship.

REFERENCES


EXPLANATION OF PLATE XII

Fig. 1. Ceratopteris thalictroides (L.) Brongn. Root tip squash showing a somatic number of $2n = 154$, $\times 1,200$.
Fig. 2. Meiosis in Ceratopteris thalictroides, 77 bivalents are clearly seen, $\times 1,500$. 