A morphogenetic study of sporangia-partitioning complex

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Abstract

The bilobed sporangia in the species of *Anthoceros*, *Isoetes* and *Ophioglossum* are described.

The morphogenetic importance of the process of "fission" in evolutionary development of sporangia in pteridophytes is discussed.

INTRODUCTION

A little known part of a classical discovery by Kidston and Lang has been their find of a bilobed (divided) sporangium in *Hornea* (now, *Horneophyton*) *ligneri* (Kidston and Lang, 1921). Bower 1926, 1935) however, conceived of a common relationship among *Psilophytales*, *Psilotales* and Ferns through this unique process of "fission" of the sporangium. With a view to explaining all variables he assumed fission and two adjuvant processes, fusion and condensation, to be effectively operative on a sporangium culminating into synangium and sori of ferns. Under abnormal situations in *Psilotum* and *Tmesipteris* he indicated that a single distal sporangium had replaced the synangium or the fission remained incomplete. In *Danaea* (Bower, 1926; Bierhorst, 1971) the imperfect synangium was found in a depression comparable to the fovea of *Isoetes* but occasionally, fission had resulted in situations normally present in *Christensenia*, *Dipteris* and *Metaxya*. Bower thus opined that the individuality of a sorus was lost by the processes of fission and fusion. For instance, in *Saccoloma*, *Nephrolepis* and *Lindsaya* various stages of linkage of the sori have been seen and the fusion sorus became typical of *Pteris*. Suggesting evolution in *Ophioglossaceae* Bower has

indicated that separate sporangia of *Botrychium* and *Helminthostachys* have led to the synangial state of *Ophioglossum*. Similarly he mentioned that the synangial states in *Marattia*, *Protomorattia* and *Danaea*, a series parallel in soral form to that of *Angiopteris*, *Archangiopteris* and *Danaeopsis*, have also resulted from a secondary fusion of their sporangia to form synangia. This is of particular interest because the Palaeozoic ferns *Stauropteris*, *Botryopteris* and *Zygopteris* exhibit (Scott, 1920) separate sporangia; although of course, early synangial sori are known in *Ptychocarpus*.

Most pertinently Eggert (1974) has recently described numerous sporangia of *Horneophyton ligneri* from the original locality where it was first discovered by Kidston and Lang. He emphatically mentioned "The branched sporangia of this genus are unique among bryophytes and vascular plants and provide some evidence that certain synangia may have arisen from a single sporangium rather than from multiple sporangia borne singly at the tips of ultimate branches" (p. 405).

The theme of this paper therefore is to emphasize the morphogenetic importance of the process of "fission" by discovering bilobed sporangia in *Anthoceros*, *Isoetes* and *Ophioglossum*.

MATERIALS AND METHODS

An *Isoetes* plant showing irregularly partitioned sporangia was first collected in September 1968 in a village pond near Guna (M.P.). A plant of *Anthoceros himalayensis* showing two long cylindrical capsules enclosed by a single involucre was presented by Mr. Arya in August 1970. Subsequent field collections also brought forth fissioned sporangia in the genus *Ophioglossum* (=synangia; used rather reluctantly to keep uniformity in description). Thus, a survey was planned and all three genera, incidentally, simultaneously available during rainy season in India (July-September), were collected from different parts of the country. Numerous other genera have been examined for this trait. All plants were first counted at the spot and examined to reveal any sort of abnormality. Afterwards, these were randomly taken out with a caution that some of the abnormal plants must be left with normal plants in each population. *Isoetes* plants, however, were taken out of the ponds and at certain places from rice fields, but all counts were made in the laboratory.

Abnormal specimens were photographed and fixed in Newcomer's fixative. Each sporangium, after 24 hours' fixation was dissected and spores released in 1.5% aceto-orcein with a view to stain their nuclei. Normal, joined and abortive or disfigured spores were counted from mature sporangia. *Lycopodium* plants were obtained from the depart-

mental collections. Their, and young and mature sporangia of *Anthoceros*, *Isoetes*, *Selaginella* and *Ophioglossum* were also processed for microtomy; sections were cut at 10-12 μ m and double stained with Erythrosine-Crystal Violet.

OBSERVATIONS

Bipartite sporangia are most common in the genus *Isoetes* (Table 1); these are either incompletely or irregularly fissioned or partitioned by a thick wall. Serial microtomed sections revealed that partitioning is initiated at a very young stage of the development and at maturity, the sporangium is split into two halves. In *Anthoceros erectus* (Figure 1) two capsules enclosed by an involucre have been observed to be 'one' at their bases. The foot was comparatively broad and flat. It did not reveal any overlapping of the tissue which otherwise, would have suggested the fusion of two adjacent venters of fertilized archegonia. *A. himalayensis* exhibits a clearly bipartite capsule (Figure 2) and the dissection of this specimen also depicted fission at the base of sporangium.

Table 1
Plants exhibiting "fissioned" sporangia

Plant	Collection No.	Total No. of plants	No.* of sporangia observed	No. of partitioned sporangia
1. <i>Anthoceros himalayensis</i> Kas	G/An, 1—2	488	127	4
2. <i>A. erectus</i> Kashyap	G/An, 2—3	470	186	9
3. <i>A. species</i>	-do-	240	154	—
4. <i>Lycopodium cernum</i> L.	BI/GW	14	40	1
5. <i>L. clavatum</i> L.	-do-	7	28	—
6. <i>Selaginella krausiana</i>	-do-	20	42	—
7. <i>Selaginella species</i>	G/Simla	18	87	—
8. <i>S. species</i>	G/Ngh	29	58	1
9. <i>Isoetes pantii</i> (A) Goswami&Arya	G/I, 2—4	855	1000	16
10. <i>I. pantii</i> (B)	G/I, 2B	240	800	92
	G/I, MK.			
11. <i>I. dixitei</i> Shende	G/I-12	220	300	—
12. <i>I. coromandelina</i> L.	G/I, 1—3	50	486	—
13. <i>I. sampathkumarini</i> Rao	G/I—8	190	408	—
14. <i>Ophioglossum costatum</i> R.Br.	G/0—3	472	95	12
15. <i>O. nudicaule</i> L.	G/0, 1—2	180	84	7
16. <i>O. gramineum</i> Willd	G/0, — 1	40	28	4
17. <i>O. petiolatum</i> Hook	G/Shv.	32	7	—
Total		3565	3910	146

* Actual no. of sporangia searched for "Fission".

Table 2
Spore statistics from normal sporangia obtained from normal plants

Lp.	Plant	No. of sporangia	No. of spores	Abnormal spores			
				Joined		Anunculate	
				number	frequency	number	frequency
1.	<i>A. himalayensis</i>	3	780	—	—	19	0.024
2.	<i>A. erectus</i>	2	408	14	0.034	—	—
3.	<i>L. cernuum</i>	9	2580	—	—	72	0.028
4.	<i>L. clavatum</i> (?)	4	545	—	—	8	0.014
5.	<i>S. krausiana</i>	13	433	—	—	7	0.016
6.	<i>S. species</i>	7	344	—	—	8	0.023
7.	<i>I. pantii</i> (A)	12	4964	810	0.163	48	0.009
8.	<i>I. pantii</i> (B)	10	3120	36	0.011	28	0.008
9.	<i>I. coronandolina</i>	5	1720	4	0.002	59	0.034
10.	<i>I. sampathkumaranii</i>	5	540	3	0.005	—	—
11.	<i>I. panchananii</i>	5	860	24	0.028	7	0.008
12.	<i>O. costatum</i>	4	2445	87	0.035	24	0.009
13.	<i>O. nudicaule</i>	4	1200	34	0.028	—	—
14.	<i>O. petiolatum</i>	5	550	—	—	—	—
	Total	88	20489	1012	0.047	280	0.013
						212	0.010

Table 3
Spore statistic from bipartite sporangia

	Plant	No. of sporangia		No. of spores	Normal spores		Abortive spores	
		Observed	Spores analysed		number	frequency	number	frequency
1.	<i>A. himalayensis</i>	4	3	1140	948	0.825	202	0.175
2.	<i>A. erectus</i>	9	4	1200	1120	0.334	80	0.066
3.	<i>I. pantii</i> (A)	16	6	2580	2544	0.987	36	0.013
4.	<i>I. pantii</i> (B)	42	10	2956	2802	0.948	154	0.052
5.	<i>O. costatum</i>	12	2	284	247	0.834	37	0.166
	Total	83	25	8170	7661	0.937	509	0.062

Lycopodium plants exhibited no such observation except two sporangia which were deeply furrowed at their apex. None of the plants of *Selaginella* and other species of *Isoetes* (Tables 1 & 2) except *I. pantii* (Figs 3 & 4) and a single observation of Pant and Srivastava in *I. indica* exhibited sporangial fission. Fission is also demonstrable in the genus *Ophioglossum*. Spikes of *Ophioglossum costatum* possessed two comparatively smaller sporangia in one socket (Figure 5) and in order to facilitate the dispersal of these sporangia, the conventional longitudinal dehiscence slit was obliquely split (Figures 6, 7) both in *O. costatum* as well as in *O. gramineum*.

Table 2 gives the frequencies of aborted spores in each species and Table 3 indicates the higher proportions of abortive spores from bipartite sporangia. For example, *Anthoceros himalayensis* shows 17.5% abortive spores and *Isoetes pantii* (B) indicates 5.2% abortive spores. Both these values are highly significant when compared to their natural incidence (Table 2). The enucleate spores which arise due to failure of the second meiotic division, spores joined by tubular connections and siamese twin spores are features recorded in *Isoetes* (Pant and Srivastava, 1965) and *Ophioglossum* (Goswami and Khandelwal, 1973a,b). Occurrence of such spores in high ratios in the abnormal plants of certain species of a genus and their such regular association with other genera (Table 3) strengthens an assumption that the trait in question is in some way related to the sterility of spores.

DISCUSSION

Professor F. O. Bower was the first to emphasize to go "to the beginnings" in the area of plant morphology. Agreeing with Kidston and Lang he extended a view (Bower, 1935, p. 594) that *Anthocerotales*, *Psilophytales* and *Psilotales* were the representatives of an organographic experimentation of Early Devonian. Based on recognized similarities in the embryogeny of *Anthoceros*, *Tmesipteris* and *Rhynia* by Holloway (1921) Bower (p. 143) characteristically mentioned "The setting free of the young plant of *Tmesipteris* by shedding its connection with the hypobasal foot is the nearest approach yet attained by observation to the solution of evolutionary problem inherent in the embryogeny of archegoniatae..." Engrossed with the same theme he stated elsewhere (p. 609) "the spore parts, whether in microphyllous or in megaphyllous pteridophytes represent the persisting remains of the thalloid branch systems found in some of the oldest Land Plants..."

Cambell was very impressed by the simple gametophyte and advanced sporophyte of *Anthoceros*, and he frequently compared the genus with *Rhynia*, *Horneophyton*, *Tmesipteris*, *Isoetes*, *Danaea* and *Ophio-*

Fig. 1. *Anthoceros erectus* plant showing two cylindrical capsules enclosed by a single involucre at the base ($\times 20$)

Fig. 2. *A. himalayensis* plant showing bipartite capsule, on dissection a single large foot was seen below ($\times$ ca 20)

Fig. 3. Upper face of the megasporangium of *Isoetes pantii* showing irregular fission ($\times$ ca 10)

Fig. 4. *Isoetes pantii* sporangia exhibiting fission ($\times$ ca 1:2)

Fig. 5. A portion of the spike of *Ophioglossum costatum* showing more than one sporangium in a socket ($\times$ ca 25)

Fig. 6. Spike of *O. costatum* showing longitudinally dehiscent slit ($\times$ ca 25)

Fig. 7. A portion of the spike of *O. gramineum* showing abnormal dehiscing slit probably due to the presence of more than one sporangium in a socket ($\times$ ca 25)

Fig. 8. A portion of spike *O. gramineum* showing "fusion" of sporangia ($\times$ ca 25)

glossum (C a m b e l l, 1940). According to him (C a m b e l l, 1925) there were situations which had approached closely to early and simplest vascular plants. S e w a r d (1910, 1933) also remarked a similarity on *Horneophyton* ... "to be as little more than a slightly ramified and free growing *Anthoceros*". The genus *Anthoceros* was cited to possess identical chloroplast as is found in *Isoetes* and also exhibited similarity in forming tetrahedral spores with the later. He (C a m b e l l, 1940) also opined that the sporangiophore of *Ophioglossum* might have been derived from some *Anthoceros* like ancestor where instead of a single terminal sporangium, as in *Rhyniaceae*, a series of lateral spore masses were developed, each then discharging from an independent orifice. In order to compare the homology of gametophytes C a m b e l l (1940, p. 5) figured *Anthoceros* and *Danaea* and in the same book C a m b e l l compared the young sporophytes of *Anthoceros* and *Ophioglossum* as a caution for a remote relationship between the two. Like the sporophytes of *Rhyniaceae* a young sporophyte of *Ophioglossum moluccanum*, at first, was found to be rootless appearing comparable to the sporophyte of *Anthoceros*. Both, B o w e r and C a m b e l l, compared resemblances among *Isoetes*, *Danaea* and *Ophioglossum*. The presence of trabeculae in *Isoetes* was considered to be much like the development of a synangium in *Danaea*. Similarly, it is believed that separate masses of sporangeous tissue had transformed in to the solid synangia in *Danaea* and *Ophioglossum* and both genera thus exhibit irregular segregation of fertile and sterile areas. (B o w e r, 1926; C a m b e l l, 1940).

Lycopods have also been described to resemble *Psilophytales* on one and *Filicales*, especially *Ophioglossales* on the other hand. P a n t and W a l t o n (1961) have indicated that columella like subarchesporial sterile pads and trabeculae in the sporangia of *Lycostachys* are made up of transfusion tissue and tracheidal cells similar to xylem elements. The columella of *Horneophyton* is in direct continuation (see, E g g e r t, 1974) of the phloem in its stem and the outer wall layer of its sporangia is made up of thick walled cells with a columnar appearance, much like the outer wall layer of *Rhynia* and many sporangia of lycopods and other groups.

A simple fact emerges from the above that the process of fission leading to the partitioning of a sporangium has been demonstrable in *Anthoceros*, *Horneophyton*, *Psilotum*, *Tmesipteris*, *Lycostachys*, *Isoetes*, *Danaea* and *Ophioglossum*. These are the plant genera whose close relationships in the line of evolution have already been a dogma with classical morphologists like K i d s t o n, L a n d, B o w e r and C a m b e l l. The purpose of this paper is not to reemphasize the origin of primitive pteridophytes from *Anthoceros* and discuss intrarelationships of pteridophytic genera from phylogenetic point of view. But, this is true, that contradictory statement is also not the theme of present study. The find

of a process, its being operative on a similar structure and to result in identical situations in the morphologically related genera, which are distributed over the period from Devonian to present, cannot be considered to be a matter of chance. On the contrary, such a trait has to be believed to be inherent in the parental gene pool.

In natural populations (Stebbins, 1966) a large gene pool of genetically controlled variations has existed at all times. Most of the adaptively important mutations continue to add quantitatively to the gene pool for already existing variations. It is hypothesized, at this stage, that during early days of *Horneophyton* emergence in Early Devonian the genes for fission (Bower, 1926) or septation (Eggert, 1974) were in "dominant combinations". Because, Eggert has clearly demonstrated that the sporangia of *Horneophyton* were branched as a rule and unbranched sporangia appeared only occasionally. Gradually, with the pace of evolution, the genes resorted to the sub-gene pools which by polygenic mechanisms (and, or mutations) gave rise to sporangia in lycopods. The single, adaxially placed sporangium in lycopods must have showed adaptive significance in the arborescent lycopods which flourished during Carboniferous period (Scott, 1920). This conservatism of single sporangium on a sporophyll has been a rule among all fossil and living lycopods (Bower, 1935) and the only exceptions now known are in *Lycostachys protostelicus* (Pant and Walton, 1961) *Isoetes indica* (Pant and Srivastava, 1962) and the present series of variously partitioned sporangia in a strain of *Isoetes pantii*.

A record of large number of fissioned sporangia in *Isoetes pantii* and their complete absence in other simultaneously growing plants of the same and different species supports the view that the trait fission has appeared due to rare genetic combinations. We may sometime even discover an *Isoetes* synangium? Thus, the fission may be defined "as the partitioning of a sporangium due to internal reasons in such a way that the sporogenous mass is functionally divided into two or more parts". Concomitant with the views of Scott and Bower it can be visualised that the free sporangia represent the original form of fillicinean fructification and the task has been mainly performed by the unique process of fission. This thesis gets massive support by the transitional states of sporangia and sori in closely as well as distantly related ferns and ferns' allies. Quite pertinently *Ophioglossum* synangia demonstrate fission as well as fusion (Fig. 8).

To me therefore fissioned sporangia in *Anthoceros*, *Isoetes* and *Ophioglossum* appear to be "evolutionary shunts" made possible by extremely rare genetic combinations which, would have been arisen due to reverse mutations. Conversely, the sub-gene pools constituting *Anthoceros*, *Hor-*

neophyton, *Isoetes*, *Danaea* and *Ophioglossum* must have received some common genes from the parental gene pool in their earliest phase of evolution.

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Studium morfogenetyczne nad procesem formowania się sporangiów

Streszczenie

Na podstawie badań nad wykretem i dwudzielnymi sporangiami w rodzajach *Anthoceros*, *Isoetes* i *Ophioglossum* omówiono rolę morfogenetyczną procesu podziału sporangiów w rozwoju ewolucyjnym paprotników.