

string of cells enveloped within a connective tissue membrane (Fig. 2A). Since the various members of the Cyclorrhapha have a very similar morphology, this finding in *Sarcophaga* will probably also apply to other members of the suborder. The connective tissue membrane is continuous with that over the gonad. The string of cells passes alongside a Malpighian tubule, to which it is attached by fusions of the respective connective tissue membranes and by short nucleated branches (Fig. 2B). Ultimately, the strand is traceable to the layer of ventral abdominal muscles, where it connects with a branch of the seventh lateral segmental nerve and an associated receptor-like organ. The strand has been traced repeatedly in many larvae and its position and appearance are constant. It is possible that connection is also made with the eighth segmental nerve, since it has been shown (5) that these receptor organs can connect nerve branches of two consecutive segments. The common sheath is traversed, at least in the prepupal stage, by channels similar to those contained within the dorsal nerves and receptor organ strands (Fig. 1). Whatever the exact histological nature of the strand, it is significant that it ultimately connects with the peripheral nervous system, so that the gonads of the larva, contrary to popular belief, have organic connection with the nervous system, and at the same time they are indirectly attached to a stretch receptor-like organ.

Thus, in the fly, the leg rudiments, pupal tracheal rudiments, the rudiments of the external genitalia, and apparently even the gonads themselves, have associated with them receptor-like organs which contain cells that are suspected of having a secretory function. Strands from such receptor-like organs also pass to various larval muscles, all of which in the fly histolyze at some time during metamorphosis. Differential histolysis could, in some way, be regulated by secretions of such cells [a similar suggestion was made for the apparent secretion by the dorsal nerves (8)]. Finlayson and Mowat reported recently that muscles connected with the specialized lepidopteran stretch receptors "do not degenerate when their motor innervation is severed" (10). This is in contrast to other muscles where "denervation in the larval stage could, in certain species, bring about the degeneration, during

pupation, of longitudinal muscles that would normally have persisted" (10). Hitherto, no one has suggested that the intrinsic cells of insect stretch-receptor organs may be secretory cells, in some way connected with growth regulation or muscle histolysis, and possibly intimately bound up with the neuroendocrine control of metamorphosis. Circumstantial evidence, such as that given here, strongly suggests such a possibility, but verification by histochemical and experimental study is required.

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Ameiotic Alternation of Generations: A New Life Cycle in the Ferns

Abstract. *The fern Polypodium dispersum Evans (ined.) has a completely somatic alternation of generations. During sporogenesis the sporophyte exhibits 111 unpaired chromosomes, 16 spore mother cells, and 32 viable diplospores. The sporophyte arises by proliferation from a gametophyte lacking sex organs. This is the first completely documented report of this type of life cycle in the ferns.*

The ferns have been the classic objects for teaching the biology of the alternation of haploid and diploid generations. The regular alternation of the diploid sporophyte and the haploid gametophyte is intimately associated with several interacting biological phenomena, namely meiosis—the segregation of chromosomes in connection with reduction division and the formation of spores, and syngamy—the fusion of two haploid cells or gametes which accomplish new combinations that may be selected in evolution (Fig. 1A).

Since 1874, however, when Farlow (1) discovered apogamy, it has been realized that not all alternation of generations involve both of these phenomena. The work of Döpp (2), Manton (3), Mehra (4), and others has demonstrated that a considerable number of fern species reproduce by obligate apogamy, a process termed "monotonously uniform" by Manton (3). In these ferns the new sporophytes are produced directly by proliferation from the gametophyte, thus by-passing fertilization. The chromosome number is maintained at the same level by a process in which a doubling of chromosomes (syndiploidy) occurs prior to meiosis (Fig. 1B). If the chromosome num-

ber is not doubled in the sporangium, the chromosomes will not pair and only abortive spores result. The only reproductive spores, therefore, are those which have the same number as the sporophyte, and both generations accordingly possess the same 2X chromosome number. Whereas a sexual species normally has (in higher ferns) 16 spore mother cells and 64 viable spores, the obligately apogamous species has 8 spore mother cells and 32 viable spores in some sporangia and 16 spore mother cells and up to 64 aborted spores in the rest.

Until the present study, it was generally believed that in the natural state only two types of complete life cycles, with two generations participating, existed in the ferns: the classical sexual life cycle with alternating 2X and X generations, and the obligate apogamous cycle with alternating "2X" and "2X" generations and involving syndiploidy and reduction division. It is now possible to report still a third type of life cycle, in which the two generations, as in the obligate apogamous cycle described above, have the same chromosome number. But in the new cycle, there is no change of chromosome number at all, either during sporogenesis or at the time of sporophyte produc-

tion. Thus the entire life cycle is accomplished by mitotic division.

The plant which undergoes this life cycle is *Polypodium dispersum* Evans (ined.), a close relative, as yet undescribed, of *P. plumula* s.l. of the New World tropics, a sexual species from which the present plant is distinguished on a number of morphological characters as well as the life cycle here discussed.

Materials for this study have included sporophyte plants collected by Wagner (5) and later by myself in Florida, plus a plant sent to me by Proctor (6) from Jamaica which shows the same details of life cycle. Gametophytes were obtained in the wild state in Florida and by culture of fresh spores in the laboratory. Details of sporogenesis were obtained by a modified aceto-carmin squash technique. Sporangia of appropriate age were fixed in Newcomer's solution (7) and placed on a slide in a drop of aceto-carmin with no added iron. They were squashed in the usual manner except that the sporangia were spread over the slide before the cover slip was added, and the cover slip was not tapped so that cells from each sporangium remained in close association with each other after squashing.

The basic details of the life cycle are as follows. There are 16 spore mother cells, each with 111 unpaired chromosomes, and 32 resultant diplospores which germinate to form a gametophyte, which then proliferates to form a sporophyte apogamously without formation of sex organs (Fig. 1C). This process differs conspicuously from the "usual" apogamous method, since, in the latter, only eight spore mother cells are formed which then double their chromosomes to form a temporary 4X condition; these 4X chromosomes then pair in the normal fashion, undergo meiosis, and form 2X gametophytes which proliferate to form 2X sporophytes. "Normal" apogamy is usually characterized by some spore abortion as a result of irregular meiosis. However, in the present system this problem is overcome because no chromosome doubling occurs, no pairing occurs, and the 32 spores are formed merely by mitotic division of the 16 spore mother cells. The system is not entirely perfect; occasional imperfections relate back to the familiar obligate apogamous situation, such as rare spore mother cells that have shown chromosome doubling, and in many

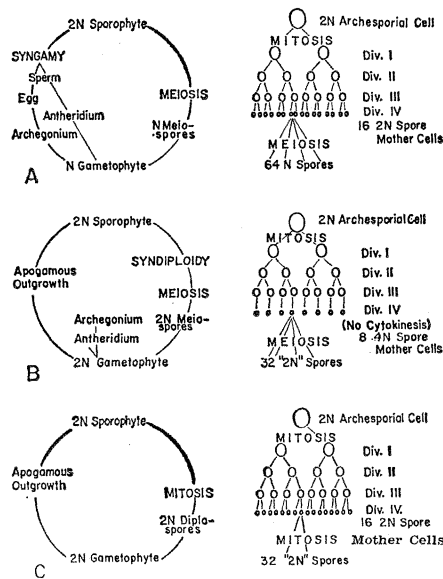


Fig. 1. Diagrammatic representations of the three types of life cycles in the ferns, the complete life cycle on the left and details of sporogenesis on the right. A. Sexual life cycle; B. meiotic obligate apogamous life cycle; and C. aneiotic apogamous life cycle.

sporangia occasional aborted spores or spore fragments can be seen among the very distinctive diplospores. The occurrence, however, of only about 10 percent aborted spores coupled with a spore germination of over 65 percent confirm that the germinating spores must indeed be those formed by mitosis and not those occasional spores formed by meiosis.

The reproductive spores of this plant are unique. Spores of related species are of a familiar and widespread type—strongly reniform, with a monolete scar. The spores of *Polypodium dispersum*, however, are considerably larger and are nearly globose. The scar is quite variable and appears to be formed in an irregular manner. Some approach a monolete condition, some are irregularly trilete, and some have an "H" shaped scar. Other spores have little or no scar at all. Aside from the variable scar patterns, the spores are remarkably uniform in size and shape, are of a high number (up to 32 spores per sporangium), and are so distinctive that they can be used for conclusive identification of the plant.

Spore germination, when compared with such near relatives as *P. pectinatum* and *P. plumula*, appears quite normal. A short green filament and a single long, brown rhizoid appear first. After a short period of filamentous growth the usual flat cordate prothallus

develops. However, no archegonia or antheridia have been observed in wild or cultured gametophytes. Sporophyte development is accomplished by the proliferation of a mass of tissue apparently anywhere on the ventral surface or margin of the gametophyte. Proliferation often does not occur until the gametophyte is well developed and typically cordate. In other cases, however, the sporophyte develops while the gametophyte is still small and elliptic in outline. It is possible to identify these gametophytes in the wild because the proliferation pad and young sporophyte leaf bear small branched hairs characteristic of the three species of the complex native to Florida. The other two species have a normal life cycle with mature gametophytes bearing sex organs, whereas all the gametophytes in question, with or without proliferating sporophytes, bear no sex organs.

The development of the sporophyte leaves is typical of the group. The first leaves are simple with a single midrib, the later leaves lobed, and the mature ones typically pectinate.

As in any obligate apogamous fern, this life cycle allows dispersal and colonization without the necessity of fertilization. It is unique, however, in that the sexual cycle has entirely the character of an asexual cycle; meiosis syngamy, and the usual associated opportunities of genetic assortment and recombination do not take place. Furthermore, the syndiploidy and meiosis characteristic of the familiar obligate apogamous life cycle is also absent. The only way to inject changes into the genome of this plant would be by random mutation, and selection for or against this mutation. But any mutations selected would then be carried by all the spores of the plant. It is significant, therefore, that this plant is a surprisingly widespread species ranging from peninsular Florida across the West Indies, Central America, and northern South America to the Galapagos Islands.

It is relatively stable morphologically throughout this broad range except for one quite distinct form with incised segments, which is confined to Cuba, where the typical form also grows. Accordingly, in spite of its seemingly limited genetic potentialities, this somatic life cycle has evidently enabled the plant to become successfully adapted to its environment.

While this appears to be the first report of a complete life cycle of this

nature, there are previous reports which suggest that other plants may actually undergo the same process as well. Bell (8) and Mehra and Singh (9), for example, reported almost identical details of sporogenesis in the filmy fern *Trichomanes proliferum* forma B. Also Verma (10) reported instances of equational divisions and formation of diaspores in sporogenesis in species of *Ophioglossum* and *Isoetes*. In none of these earlier reports, however, was the complete life cycle, including the gametophyte and formation of the sporophyte described.

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Sleep Tendencies: Effects of Barometric Pressure

Abstract. For two samples of naval aviation cadets, curvilinear relationships were obtained between barometric pressure readings and the occurrence of signs of the onset of sleep on electroencephalograms obtained during routine EEG examinations. High and low barometric pressures relative to the prevailing average pressures were associated with increased proportions of subjects showing signs of onset of sleep.

Raboutet, Lesèvre, and Rémond (1) reported a statistically significant relationship between barometric pressure and the occurrence of signs of the onset of sleep on electroencephalograms obtained during routine EEG examinations of aviation personnel. Because of

the practical and theoretical implications of this finding we undertook a further study of this relationship.

Since 1961, routine EEG recordings have been made on naval aviation trainees in the Division of Neurological Sciences of the U.S. Naval School of Aviation Medicine at Pensacola, Florida. The records of 1012 examinations made between 1 April 1961 and 30 December 1961 were obtained. Each record had been scored for the sleep signs. Two groups were identified: one group showing no signs of the onset of sleep, ($N = 641$); the other showing signs that ranged from those which were brief and occasional to those which were persistent ($N = 371$). The hour and date of examinations were available for each record.

From hourly weather records maintained by the Naval Air Station, the barometric pressure reading at the time of the examination of each subject was collated with the EEG data.

In brief, the EEG scoring criteria were as follows: The appearance of any signs of drowsiness or sleep were grouped for purposes of the study. These signs were those which have been classically associated with the onset and presence of sleep, such as a slowing of the basic resting rhythm with a desynchronizing tendency, irregular high-amplitude slow activity, or 14 cy/sec spindling. The three categories, "brief, occasional," "persistent," and "dominant," were based on the increasing appearance of these indices in a subject's record during the recording sessions of approximately ½ hour. The category "brief, occasional" included those records in which minimal sleep tendencies appeared at random for periods of less than 10 seconds, separated by much longer records showing that the subjects were unmistakably awake. The "persistent" category included records of subjects who had to be stimulated frequently by noise signals and oral prompting to stay awake so that records of wakefulness of appreciable duration could be obtained, and who lapsed into sleep again within less than 1 minute if such stimulation was delayed. The "dominant" sleep category denoted the type of subject who, despite repeated stimulation, could not be kept awake for more than a few seconds at a time. Scoring for sleep was done only on those parts of the recordings which were obtained during periods when it was intended that the subjects should be awake, as distin-

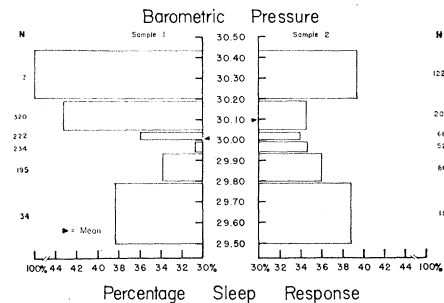


Fig. 1. Percentage of subjects showing signs of the onset of sleep, in relation to barometric pressure. N is the total number of subjects.

guished from periods when sleep was deliberately allowed or encouraged.

The results obtained from the first sample deviated considerably from those of Raboutet, Lesèvre, and Rémond, and a second sample was obtained. The EEG records from 3 January 1962 through 30 June 1962 were matched against the barometric weather records for that period ($N = 547$). Because these records were scored subsequent to the findings of the first sample, and because the scorers were more sensitive to the signs of the onset of sleep, there was a significant increase in the records scored as "brief, occasional" signs of sleep and a decrease in the records scored as "no sleep." Combining these categories in sample 2 resulted in approximately the same proportion (64.2 percent) of subjects as those classified under the "no sleep" category in sample 1 (68.2 percent). A decision was made to group the data into two categories for both samples: (i) Definite signs of sleep ("brief, occasional," "persistent," and "dominant" in sample 1; "persistent" and "dominant" in sample 2) and (ii) none or limited signs of sleep ("no sleep" signs in sample 1 and "no sleep" signs and "brief, occasional" in sample 2). In both samples, scoring was done prior to collation with the data on barometric pressure.

The results of samples 1 and 2 are shown in Fig. 1. This figure presents the percentage of subjects whose records were scored and categorized as showing definite signs of sleep in relation to the barometric pressure readings at the hour of recording. The number of subjects (N) recorded for each pressure reading is shown, as well as the mean pressure for the two samples. The relationships between barometric pressure and percentage of subjects showing definite signs of sleep are the same for both samples—that is, an in-