are available at the transmitter and receiver. For example, if 1 bit is to be transmitted per accelerator pulse, bit error rates better than 10^{-3} can be achieved by using suitable demodulators. At greater depths, the signal-to-noise ratio improves, and more than 1 bit could be transmitted per pulse. For example, at a depth of 3 km, pulse position modulation could be used to transmit one 15-bit message per pulse with a message error rate better than 10^{-3}.

We have considered the possibility of neutrino communication with present and future neutrino beams, using a suitable underwater Cerenkov detector for which specific examples have been presented. These concepts could be tested by establishing neutrino communication over a modest distance, such as from Fermilab into Lake Michigan, where the neutrino beam of Fermilab is now directed. In fact, the present Fermilab neutrino experiment already provides an example of "communication" with the bubble chamber detector over a distance of about 1 km.

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9. The neutrino beam at the source (including the decay tunnel) will thus have to be aimed below the horizon.
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13. The approximately millisecond pulses of bioluminescent background should be readily distinguishable from the 20-μsec neutrino signal.
14. We thank M. Hass and M. M. Shapiro for their interest and encouragement.

* A.W.S. was on sabbatical leave at the Department of Physics, Princeton University, Princeton, N.J. 08540, during the course of this work.
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1 July 1977

Gemmae: A Role in Sexual Reproduction in the Fern Genus Vittaria

Abstract. *Gemmae are generally defined as vegetative propagules. In the shoestring ferns,* Vittaria, *gemmae grown in the presence of mature gametophyte plants or on medium containing gibberellic acid produce antheridia in lieu of vegetative growth. This suggests that antheridial differentiation in* Vittaria *is controlled by a chemical antheridogen system similar to those described in other fern genera. In natural populations of* Vittaria *gametophytes composed primarily of long-lived individuals, gemmae may provide the only source of tissue susceptible to antheridogen action and may have evolved in response to that condition.*

In lower plants such as fungi, liverworts, mosses, and ferns, gemmae are generally considered to be agents of asexual reproduction. They are units of vegetative cells which, when shed from their parental plant, can grow into new individuals. However, gemmae produced by the gametophyte generation of the shoestring ferns, *Vittaria*, in addition to their role in vegetative dispersal and reproduction (*1–3*), may play an important role in sexual reproduction.

Vittaria species are tropical and subtropical epiphytes. Their gametophytes are branching, ribbonlike plants of indeterminate growth which typically form dense, perennial mats. Gemmae, consisting of chains of 4 to 12 cells, form at the ends of aerial branches of the gametophytes (Fig. 1A). After dispersal onto a suitable substrate, the gemmae may develop vegetatively into new gametophytes or, under conditions described herein, may produce antheridia with little or no accompanying vegetative growth (Fig. 1, B to D, and Table 1).

Table 1. Induction of antheridia in *Vittaria* gemmae. Test plants were grown for 6 to 10 weeks on agar blocks opposite living, mature gametophytes (living); on agar substrates containing aqueous extracts from mature gametophyte cultures (extract); on agar substrates from which mature gametophytes were removed (medium); or on agar substrates containing gibberellic acid. The percentage of gemmae forming antheridia is the average response of a minimum of 100 gemmae in each of three or more replications. *Pteridium* extract, at dilutions of 1:2 to 1:10,000, was assayed against 10-day-old gametophytes of *Onoclea sensibilis*, which yielded a 75 to 80 percent response at all concentrations except 1:10,000, where the response dropped to 30 percent.

Source of antheridium-inducing activity	Gemmae forming antheridia (%)
None (control)	0
Vittaria lineata (living)	45
Vittaria lineata (extract)	0
Vittaria lineata (medium)	0
Gibberellic acid (5×10^{-5} g/ml)	49
Pteridium aquilinum (living)	0
Pteridium aquilinum (extract)	0

Earlier descriptions of *Vittaria* gametophytes have noted the frequent occurrence of antheridia on gemmae and very young gametophytes (*1, 4–6*). In stock cultures we have observed that antheridia are produced almost exclusively on recently shed gemmae, and that mature gametophytes usually produce only archegonia. An explanation for this developmental pattern is suggested by the antheridogen system which has been shown to operate in other fern species. In this system a chemical, termed antheridogen, is produced by certain members of a culture population and induces antheridia to form on other members (*7–12*). In *Pteridium aquilinum* (L). Kuhn gametophytes produce antheridogen only after they have reached a developmental stage at which they are insensitive to this chemical (*8*). These gametophytes proceed to form archegonia, but form no antheridia. However, gametophytes in earlier stages of development respond to antheridogen by forming antheridia without concomitant archegonial development and often cease vegetative growth.

Previously described antheridogens show varying degrees of interspecific activity. Antheridogen produced by *P. aquilinum* induces antheridia in many higher ferns, but not in species of the Schizaeaceae (*10, 12*). In contrast, the antheridogen of *Anemia phyllitidis* L. is active only within the family Schizaeaceae (*9, 12*). The chemical structure of the former has not been fully determined. The latter is gibberellin-like and various gibberellins can mimic its effects (*10, 13–15*).

In *Vittaria* we wished to test the hypothesis that gemmae respond to an antheridogen produced by the mature gametophytes. Gemmae of *V. lineata* J. E. Smith were placed in two groups of 100 each, separated by 3 cm, onto petri plates of mineral nutrient agar (*16*). Mature *V. lineata* gametophytes were placed among one group of gemmae on each plate; the other group was left as a control. After 11 weeks, no antheridia

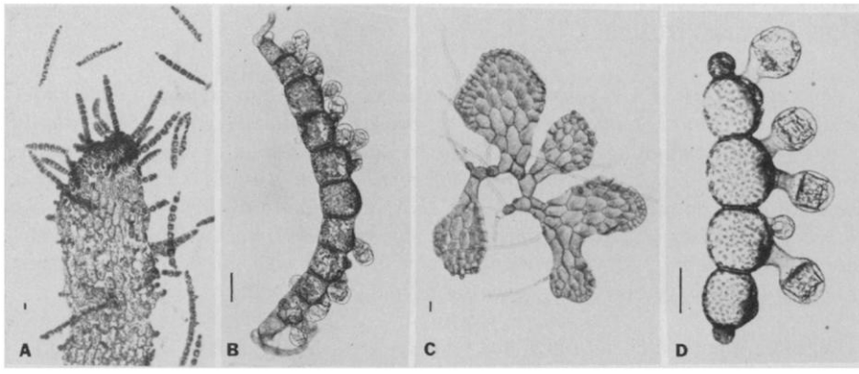

Fig. 1. Gemmae of *Vittaria* gametophytes. The scale bar in each photograph is 0.1 mm. (A) Aerial branch of gametophyte of *V. lineata* with attached gemmae in various stages of development. (B) Gemma of *V. lineata* with numerous antheridia; grown 7 weeks opposite mature gametophytes. (C) Gemma of *V. graminifolia* with vegetative growth; grown 7 weeks in the absence of any antheridogen. (D) Gemma of *V. graminifolia* with numerous antheridia; grown 6 weeks on medium containing gibberellic acid (5×10^{-5} g/ml).

were present on the control group, but approximately 20 percent of the treated gemmae had formed antheridia. The antheridium-inducing stimulus was apparently not volatile, nor did it diffuse readily over the short distance separating the two groups of gemmae. Interpretation of the results was complicated, however, by the physical contact maintained between mature gametophytes and many of the gemmae, and by the continuous shedding of additional gemmae from the mature gametophytes.

For subsequent experiments an agar block assay was devised. Gemmae and mature gametophytes were grown on opposite vertical sides of agar blocks (5 by 1 by 0.5 cm thick). Experimental blocks were cut from plates supporting mature gametophytes and placed on their cut edges. Gemmae were then placed on the vertical faces of blocks opposite the mature plants. Under these conditions, up to 50 percent of the gemmae produced antheridia (Table 1 and Fig. 1B). Gemmae placed onto control blocks did not produce antheridia (Fig. 1C). No growth penetrated the thickness of the agar blocks, showing that induction occurred through a diffusible substance.

Gemmae of *Vittaria graminifolia* Kaulf. grown opposite mature *V. lineata* gametophytes formed fewer antheridia (30 percent) than gemmae of *V. lineata*, but indicated intrageneric activity of the *Vittaria* antheridogen. *Vittaria lineata*, *V. graminifolia*, and two species tentatively identified as *Vittaria dimorpha* C. Muell. and *Vittaria stipitata* Kunze (*17*) were tested for response to *Pteridium* antheridogen. Gemmae of these species showed no response when grown opposite mature *Pteridium* gametophytes or on medium containing a 1:100 dilution of an aqueous extract (*18*) from medium on which *Pteridium* gametophytes had grown. However, gemmae of *V. lineata*, *V. graminifolia*, and *V. dimorpha*, when grown on a medium containing gibberellic acid (5×10^{-5} g/ml), produced antheridia at about the same frequency as *V. lineata* gemmae grown opposite mature *V. lineata* plants (Fig. 1D and Table 1). *Vittaria* is therefore the first known genus outside the Schizaeaceae to show an antheridogen response to gibberellin (*10*, *15*).

In our experiments, antheridial induction on *Vittaria* gemmae by natural substances occurred only when gemmae were grown simultaneously with and opposite or under mature gametophytes (Table 1). Gibberellic acid and the antheridogens of *Pteridium* and *Anemia* are relatively stable and can be stored for weeks or months without loss of activity. However, attempts to extract the antheridogen produced by *Vittaria*, using the method for extraction of *Pteridium* antheridogen, have been unsuccessful. Gemmae grown on media containing the extract did not produce antheridia. This could be attributable to the extraction procedure; however, induction also failed to occur when mature gametophytes were removed from cultures and replaced immediately by gemmae. These results plus the inability of mature gametophytes to induce gemmae 3 cm distant suggest that the antheridogen of *Vittaria* is short-lived. Possibly it is chemically unstable or is subject to enzymatic degradation.

Although as yet incompletely characterized, an antheridogen system in *Vittaria* is clearly operative and significantly different from those described previously in other fern genera. *Vittaria* is the first genus outside the Schizaeaceae to show an antheridogen response to gibberellin. The *Vittaria* antheridogen apparently is short-lived and in this respect differs from those of both *Pteridium* and *Anemia*.

Natural populations of *Vittaria* gametophytes also differ from those of *Pteridium*, *Anemia*, and most other ferns in forming dense mats of long-lived individuals. In such populations, chemical instability may be advantageous in maintaining low levels of antheridogens, which otherwise might become toxic or inhibitory. It is also apparent that populations composed principally of long-lived, mature gametophytes encounter a problem in completing sexual reproduction if antheridia can be induced only on young gametophytes. This problem is solved in *Vittaria* by the production of dispersible, young gametophytic tissue, the gemmae, which are susceptible to antheridogen activity. When germination occurs in the presence of mature, antheridogen-producing gametophytes, the gemmae produce antheridia rather than vegetative growth. These observations suggest a possible reinterpretation of the evolution of the gemmiferous habit in *Vittaria*, and perhaps other taxa, on the basis of a sexual rather than vegetative role of the gemmae.

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16. Nutrient media consisted of Bold's macronutrients supplemented with Nitsch's micronutrients plus cobalt and iron, and solidified with 0.7 percent agar. Cultures were maintained under 250 footcandles (2700 lu/m²) of fluorescent light for 16 hours per day. Temperature was 25°C during the light period and 20°C during the dark period.
17. These species were received as spores without positive identification. Their gametophyte morphology closely resembles that of *V. lineata*.
18. After the mature gametophytes were removed, the medium was frozen and thawed to obtain a liquid. The liquid was filtered, diluted as desired, and resolidified with fresh agar.

7 June 1977; revised 15 July 1977