curred with the plants that make up these sediments, few studies have been undertaken with these organisms because of the lack of definitive character suites upon which to make comparisons with living forms.

We describe chlamydospores of Pennsylvanian age (*4*) that are morphologically and structurally identical with those produced by living endogonaceous (*5*) fungi assigned to the genus *Glomus*. The fossil chlamydospores occur singly (Fig. 1, A and C) and in loose clusters throughout the plant matrix, but they are most frequently encountered in the cortical tissues of the roots and underground organs of arborescent lycopods, cordaites, and the marattialean tree fern *Psaronius*. The majority of the spores are spherical and range from 100 to 400 μm in diameter. The wall is about 10 μm thick and constructed of two to three distinct wall layers (Fig. 1B). The outer surface is smooth.

Several fossilized spores contain a portion of the nongametangial hypha upon which they were formed (Fig. 1A). Hyphae range from 10 to 20 μm wide, increasing in diameter to 30 μm near the spore to form a funnel-shaped stalk. The outer wall of the hyphal stalk is continuous with the wall of the spore, and the contents of the chlamydospore are separated from the hypha by a curved inclusion in the stalk (Fig. 1B). A number of spores were also found to possess a simple, unoccluded stalk with a constricted opening at the spore base (Fig. 1E).

On the basis of the morphology and structure of the spores (*6*) and the funnel-shaped hyphal stalk with curved inclusion (Fig. 1, D and F), we believe that these fossil remains have affinities with the fungus *Glomus*. *Glomus* chlamydospores are borne terminally on single (Fig. 1D) undifferentiated, nongametangial hypha either in sporocarps, loose in open clusters, or singly in the soil (*7*). At maturity the chlamydospores may be separated from the subtending hypha by a septum which may consist of a thin membrane at the base of the spore, or a curved extension of the inner wall of the stalk (Fig. 1F). Studies of the living *Glomus* chlamydospores from different geographic regions (*8*) indicate that a number of features (spore size, shape, and stalk structure) are variable within a species, and this same variability appears to exist among the fossil specimens collected at different localities.

Interest in the genus has centered on its role in the production of vesicular-arbuscular endomycorrhizae. These fungi may be found in most habitats in nature associated with an extremely diverse group of plants, including those that inhabit swamps and marshes and even some aquatics that have been regarded as being nonmycorrhizal.

The material described here is the most convincing evidence assembled to date that establishes the presence of modern endomycorrhizal fungi as early as the Pennsylvanian. The existence of well-preserved fungal chlamydospores in the underground organs of a number of Carboniferous vascular plants provides an opportunity to investigate both the biology and evolutionary history of a mycorrhizal fungus that is exceptionally cosmopolitan today. The identification of endomycorrhizal fungi in Carboniferous plants also affords an opportunity to consider questions of a more biological nature, such as some of the intermediate stages in the evolution of the mycorrhizal system.

CYNTHIA A. WAGNER*
THOMAS N. TAYLOR
Department of Botany,
Ohio State University,
Columbus 43210

References and Notes

1. S. A. Tyler and E. S. Barghoorn, *Science* **119**, 606 (1954); J. W. Schopf, *J. Paleontol.* **42**, 651 (1968); *ibid.* **44**, 1 (1970); ———, T. D. Ford, W. J. Breed, *Science* **179**, 1319 (1973).
2. B. H. Tiffney and E. S. Barghoorn, *Occas. Pap. Farlow Herb. Cryptogam. Bot. Harv. Univ.* **7**, 1 (1974).
3. R. W. Baxter, *Univ. Kans. Paleontol. Contrib. Pap.* **77**, 1 (1975); R. L. Dennis, *Mycologia* **62**, 578 (1970).
4. Stratigraphically the specimens come from sediments that range from the Lower [C. W. Good and T. N. Taylor, *Palaeontology* **13**, 29 (1970)] through the Upper Pennsylvanian [M. A. Millay and D. A. Eggert, *Am. J. Bot.* **61**, 1067 (1974)].
5. Modern members of the Endogonaceae currently include seven genera characterized by the organization of the reproductive structures. Living species of *Glomus* possess vesicular-arbuscular mycorrhizae surrounded by a hyphal network that extends into the soil and penetrates the host plant. Both short-lived arbuscules and vesicles may be produced and, under adverse conditions, such as the death of the host, endotropic chlamydospores are the only structures able to survive.
6. B. Moose and G. D. Bowen, *Trans. Br. Mycol. Soc.* **51**, 469 (1968).
7. J. W. Gerdemann and J. Trappe, *Mycol. Mem.* **5**, 1 (1974); J. W. Gerdemann, *Annu. Rev. Phytopathol.* **6**, 397 (1968); T. H. Nicolson, *Trans. Br. Mycol. Soc.* **43**, 132 (1960); D. J. Bagyaraj, A. Manjunath, R. B. Patil, *ibid.* **72**, 164 (1979); M. Sondergaaed and S. Laegaard, *Nature (London)* **268**, 232 (1977).
8. L. K. Abbott and A. D. Robson, *Aust. J. Bot.* **27**, 363 (1979); I. R. Hall, *Trans. Br. Mycol. Soc.* **68**, 341 (1977).
9. Supported by NSF grants DEB77-02239 and DEB 8001803 to T.N.T.

* Present address: Department of Botany, Ohio State University, Athens 45701.

17 October 1980

Alternative Male Strategies: Genetic Differences in Crickets

Abstract. *Male field crickets,* Gryllus integer, *call and attract mates, or they silently intercept females attracted to calling males. Selection experiments demonstrate that the duration of nightly calling has an important genetic component. Mean calling times in high and low lines were significantly different and had realized heritabilities of 0.50 and 0.53, respectively. Selection can operate in such a way that each of the alternative forms of male reproductive behavior is associated with a specific genetic substrate. This has not yet been shown for other species in which males adopt contrasting modes of mating behavior.*

Conspecific males in the same population may have different types of mating behavior. Some male field crickets, *Gryllus integer*, call very regularly and attract females, whereas other males (satellites) call infrequently, or not at all, and intercept females attracted by the calling of neighboring males (*1*). The male *G. integer* show definite tendencies for calling or for satellite behavior (*2, 3*), but population density, male aggression, and time since sunset influence the duration of calling (*2–4*). Similar patterns occur in vertebrates and other invertebrates (*2, 3, 5, 6*), and a genetic model has been proposed to explain the coexistence of alternative male reproductive strategies (*7*). There is, however, no direct evidence that this type of variation in male behavior has a genetic component. I now report the results of selection experiments demonstrating that male field crickets differ genetically with respect to the amount of time they call each night.

Gryllus integer were raised in the laboratory from eggs laid by females that were collected in San Antonio, Texas, during July 1979. After the final molt, males were placed in separate 4.2-liter glass jars fitted with sound-operated relays to monitor the total calling time each night (*8*). In the initial generation, males were monitored for 21 to 45 days. Most males began calling at 3 to 6 days of adult age, a time corresponding to the initial production of spermatophores (*9, 10*). There were nightly variations in individual calling times, but average calling did not correlate with age or weight of the males (*9*). Calling time was therefore computed as the average calling per night from 7 to 16 days of adult age for each male (*11*) (Fig. 1).

Two to four males from each end of

0036-8075/81/0501-0563$00.50/0 Copyright © 1981 AAAS

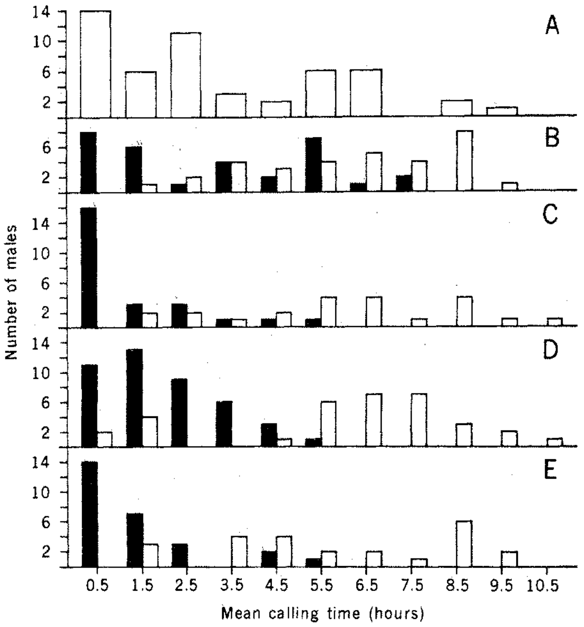

Fig. 1. Frequency distribution of mean calling time per night for *G. integer* on days 7 to 16 of adult age. (A) Parental generation. (B to E) First through fourth generation of selection (low line is shown by closed bars; males who never called are included in the 0.5 interval).

the distribution were mated with nonsister virgins from stock cultures. The same procedure was followed with succeeding generations. High and low lines differed significantly in calling time per night each generation (Mann-Whitney U test, $z = 3.16, 5.22, 5.38$, and 5.24 for generations 1 to 4, respectively; $P < .0003$ in all cases) (Fig. 2). Realized heritabilities, calculated as the ratio of selection response to the selection differential (*12*), were 0.50 and 0.53 for the high and low calling lines, respectively.

These data demonstrate that the amount of calling in *G. integer* has an important genetic component. Calling and satellite behavior in *G. integer* are probably separate genetic strategies whose expression is conditional on extrinsic variables. For example, males progammed as satellites should be selected to call if singing males are not present. Isolation from conspecifics results in increased calling behavior in male field crickets (*2–4*). Observations in a large outdoor arena on another group of males, both before and after placement in sound-monitored jars, showed that males called more when they were isolated in jars. Calling times in the jars and in the arena were, however, positively and significantly correlated (*9*). The percentage of males who never called varied from 7 percent in the parental generation, to 3, 44, 11.6, and 33.3 percent in generations 1 to 4, respectively, of the low line. Only one male in the high selected line never called. Most males should call, at least infrequently, when isolated in laboratory jars (*13*).

The hypothesis that little genetic variation should underlie traits under sexual selection (*14*) assumes that there is a high level of sexual selection and an otherwise stable or predictable environment. Such conditions may be met in the bullfrog, *Rana catesbeiana*; male bullfrogs live for several years and switch from satellite to calling behavior as they grow older and larger (*6*). Alternative forms of male behavior in *R. catesbeiana* apparently reflect low genetic variation. Genetic homogeneity of male sexual traits is, however, a largely untested hypothesis. A counterproposal is that fluctuating selection may be responsible for maintaining genetic variation underlying male sexual traits (*15*). One form of shifting selection in *G. integer* is represented by parasitoid flies, *Euphasiopteryx ochracea*, which orient to the cricket calling song. Female flies deposit larvae that consume their hosts in about 7 days. Calling *G. integer* are parasitized much more often than satellites, but the frequency of fly parasitism varies yearly (*9, 16*). In addition, the relative number of matings by calling and satellite male *G. integer* fluctuates greatly (*2, 3, 9*). Fluctuating selection may be common in many species, and my data indicate that high genetic variation underlying male sexual behavior may persist under these conditions.

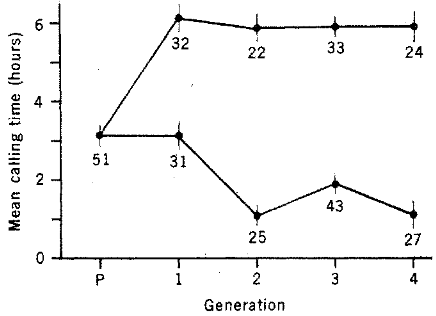

Fig. 2. Mean (± 1 standard error) calling time per night for parental and selected generations of *G. integer* (sample sizes are indicated).

WILLIAM H. CADE
Department of Biological Sciences,
Brock University, St. Catharines,
Ontario, Canada L2S 3A1

References and Notes

1. This species commonly occurs in central Texas where it inhabits old fields, lawns, or any grassy area.
2. W. Cade, in *Sexual Selection and Reproductive Competition in Insects*, M. S. Blum and N. A. Blum, Eds. (Academic Press, New York, 1979), pp. 342–379; *Fla. Entomol.* **63**, 30 (1980).
3. ——— and D. Wyatt, in preparation.
4. R. D. Alexander, *Behaviour* **17**, 130 (1961); in *Insects, Science and Society*, D. Pimentel, Ed. (Academic Press, New York, 1975), pp. 35–77.
5. J. Alcock, in *Sexual Selection and Reproductive Competition in Insects*, M. S. Blum and N. A. Blum, Eds. (Academic Press, New York, 1979), pp. 381–402; W. D. Hamilton, in *ibid.*, pp. 167–220; R. Thornhill, in *ibid.*, pp. 81–121; K. D. Wells, *Anim. Behav.* **25**, 666 (1977).
6. R. D. Howard, *Evolution* **32**, 850 (1978).
7. M. Gadgil, *Am. Nat.* **106**, 574 (1972); ——— and C. E. Taylor, *ibid.* **109**, 470 (1975).
8. Relays were maximally sensitive to sounds at 4 to 6 kHz and at 50 dB+, a frequency and minimum intensity characteristic of the *G. integer* calling song. Males were observed calling in jars, and the relays were checked routinely. Jars were placed 0.5 to 1.2 m apart, a distance corresponding to the minimum distance between males in the field (*2, 3*). Newly eclosed males were placed randomly in jars in different areas of the room. Tests in foam-lined jars showed that the echoic properties of glass did not affect individual calling times (*9*). Trials were conducted in a 12:12 photoperiod and at 19° to 24°C.
9. W. Cade, unpublished observations.
10. Calling in field crickets requires the presence of a spermatophore in the spermatophoric pouch of the male [F. Huber, *Evolution* **16**, 429 (1962)].
11. Six of 51 males in the initial generation first called after 11 to 23 days of age. These males had spermatophores by 7 days as shown by gentle squeezing of the abdomen. They were therefore capable of calling during the 7- to 16-day period. Calling times for these males was low, but some males may switch to calling at an advanced age when they are isolated in jars. Observations in a large outdoor arena, however, showed no tendency for males to start calling later in life when they were not isolated (*3*).
12. D. S. Falconer, *Introduction to Quantitative Genetics* (Ronald, New York, 1960).
13. R. D. Alexander [*Evolution* **16**, 443 (1962)] described cricket songs. Sound analyses of tape-recorded songs of low and high selected males in the fourth generation and of calling males in the field were carried out with Uher 4000 Report L and Sony TC-105 tape recorders and a Hewlett-Packard 1741 A storage oscilloscope. The species-specific characteristic of wing stroke rate was 72 to 79 per second at 25°C for laboratory and field males.
14. H. C. Harpending, *Am. Nat.* **113**, 622 (1979); J. Maynard Smith, *The Evolution of Sex* (Cambridge Univ. Press, Cambridge, 1978); R. Thornhill, *Fla. Entomol.* **63**, 5 (1980); M. J. West-Eberhard, *Proc. Am. Philos. Soc.* **123**, 222 (1979); G. C. Williams, *Sex and Evolution* (Princeton Univ. Press, Princeton, N.J., 1975).
15. G. Borgia, in *Sexual Selection and Reproductive Competition in Insects*, M. S. Blum and N. A. Blum, Eds. (Academic Press, New York, 1979), pp. 19–80.
16. W. Cade, *Science* **190**, 1312 (1975).
17. Supported by Natural Sciences and Engineering Research Council grant A6174. Sound relays were designed and built by J. Ross, J. Rustenberg, and A. Struyk, Technical Services, Brock University. I thank E. Cade, A. Joern, P. Mason, R. Morris, G. Pollack, T. J. Walker, and D. Hickey for comments on the manuscript.

29 September 1980; revised 13 January 1981