Cambrian (*10*). The group possess orthoconic shells that taper to a point at the apical end. Well-preserved specimens of *Salterella* (*11*) are septate and have a central siphuncle-like tube connecting the apex and body chamber. Well-preserved specimens of *Salterella* (*S. mexicana* Lochman from Caborca, Mexico; and *Salterella* sp. from York County, Pennsylvania) were examined (*12*) and compared with *Wyattia reedensis*. The specimens have an outer shell formed by superposed sinuous laminae of calcite separated from a series of conical septa, an internal phragmocone-like structure being formed. In other species of *Salterella*, such as *S. rugosa* (*11*), the outer wall is formed by the invaginating septa so that two distinct structural elements seem to be absent.

In *Salterella* sp. from York County, Pennsylvania, the phragmocone-like structure must have been very fragile since it is not always preserved even in a rock showing only slight evidence of diagenetic alteration. When *Salterella* is preserved in this manner the shell takes on the appearance of a simple cone, so that some apparent similarities with *Wyattia* result. For this reason the possibility exists that *Wyattia* may be a poorly preserved salterellid-type fossil shell. The remaining difference between *Salterella* and *Wyattia* that cannot be explained by this hypothesis is the presence of a globous apex in *Wyattia*, in contrast with a tapering apex in *Salterella*. This difference may not be of great systematic significance since some groups of molluscs (for example, gastropods) have developed highly diverse apical structures.

The molluscan class Calyptoptomatida was established in 1962 by D. W. Fisher (*13*) for " . . . the long-known group of hyolithids and their allies." The calyptoptomatids consist of " . . . bilaterally symmetrical, conoid, calcium carbonate shells that taper to a closed point or rounded apex and are open at their widest portion, the aperture." The class was subdivided on the basis of morphology of the initial chamber or embryonic portion of the shell. On the basis of this criterion Fisher recognized three orders: Hyolithida (conical embryonic stage) (*14*), Globorilida (globular embryonic stage), and Camerothecida (cylindrical embryonic stage) (*13*).

The order Globorilida is a monotypic taxon consisting of one genus, *Globorilus*, based on the species *Globorilus globiger* (Saito) from the Lower Middle Cambrian of northwestern Korea (*13*). *Globorilus* has a bilaterally symmetrical, small, smooth, conical shell slightly curved ventrally near the apex, and has a slightly inflated initial chamber at the apex (*15*). The slight curvature of the distal end of the shell results in the initial chamber being asymmetrical to the main axis of growth as in *Wyattia reedensis*. Whether internal structures were present in *G. globiger* is unknown, but the shell was probably operculate (*15*).

Examination of the earlier portion of the shell of *G. globiger* (*15*) shows that the early curvature of the shell and asymmetrical position of the initial chamber are results of curvature immediately after the development of the earliest part of the shell. In *Wyattia reedensis* the asymmetry results within the initial chamber, with the later formed shell being essentially orthoconic.

Based on the similarity in embryonic portions of the shells and general shell shape, *Wyattia* is tentatively classified in the calyptoptomatid order Globorilida. However, since the type of preservation reflected by the *Wyattia* fossil material does result in apparent similarities with some occurrences of *Salterella* it seems desirable to query the higher classification of *Wyattia* until more data are available.

MICHAEL E. TAYLOR
Department of Paleontology, University of California, Berkeley

References and Notes

1. C. A. Nelson, *Bull. Geol. Soc. Amer.* **73**, 139 (1962).
2. C. A. Nelson and P. Hupé, *Compt. Rend.* **258**, 621 (1964).
3. R. A. Gangloff, thesis, Univ. of California, Berkeley (1961).
4. P. Hupé and G. Choubert, *Notes Mém. Géol. Serv. Maroc No. 103* (1952). P. Hupé, *Intern. Geol. Congr. 21st Rept.* **8**, 75 (1960).
5. A. Katz and G. M. Friedman, *J. Sediment. Petrol.* **35**, 248 (1965).
6. J. W. Koenig, *J. Paleontol.* **28**, 76 (1954).
7. R. K. Folk, in *Dolomitization and Limestone Diagenesis*, L. C. Pray and R. C. Murray, Eds. (Society of Economic Paleontologists and Mineralogists, Tulsa, Okla., 1965).
8. Bedrich Bouček, *The Tentaculites of Bohemia* (Czech. Acad. Sci., Prague, 1964), 215 pp.
9. H. K. Erben, in *Treatise on Invertebrate Paleontology*, R. C. Moore, Ed. (Univ. of Kansas Press, Lawrence, 1964), vol. K, pp. 491–505.
10. C. Teichert, *ibid.*, pp. 484–490.
11. C. Poulsen, *Meddel. Grønland* **87**, 6 (1932).
12. Specimens of *Salterella* from Caborca, Sonora, Mexico, and York County, Pennsylvania, were provided on exchange with the Museum of Paleontology, University of California, by the United States National Museum through the courtesy of Dr. G. A. Cooper.
13. D. W. Fisher, in *Treatise on Invertebrate Paleontology*, R. C. Moore, Ed. (Univ. of Kansas Press, Lawrence, 1962), vol. W, pp. 98–143.
14. L. Marek and E. L. Yochelson, *Science* **146**, 1674 (1964), considered the Calyptoptomatida a heterogeneous group. They removed the hyolithids from the Calyptoptomatida and raised them to a separate molluscan class—Hyolithida. The remaining calyptoptomatid orders—Globorilida and Camerothecida—are also of questionable monophyletic origin. However, because of the enigmatic character of these poorly known and relatively scarce fossils, the use of embryonic development (as deduced from apical morphology) by Fisher (*13*) represents a reasonable tentative approach to their classification until more data become available.
15. K. Saito, *J. Fac. Sci. Imp. Univ. Tokyo* **4**, 345 (1936).
16. I thank E. C. Allison, W. B. N. Berry, D. B. Blake, P. E. Cloud, Jr., J. W. Durham, R. L. Hay, C. A. Nelson, C. M. Nelson, and C. J. Stubblefield for reading the manuscript and offering criticism. I also thank M. Blos for drawing the reconstruction of *Wyattia reedensis*, and J. H. Peck, Jr., for providing technical assistance.

18 April 1966

Mexican Freetail Bats: Photography

Abstract. *A method is described for photographing bats or other rapidly moving objects as they intercept in space a particular area which is covered by a camera system. Photographs taken at Carlsbad Caverns show that the tail membrane of the Mexican freetail bat is extended when the animal is in flight.*

Bats in free flight were photographed, with electronic flash, at the mouth of the Carlsbad Caverns. The timing of the flash was determined with a photomultiplier trigger system. About one-quarter of a million bats leave the cavern each night for the Pecos River feeding area, some 64 km away. Since bats must circle many times to clear the cave entrance, there are numerous opportunities for pictures. The cave entrance is about 30 by 45 meters at a steep angle (some 30°).

The operation of the equipment (Fig. 1) was as follows. First, a white object was placed on a collapsible tripod at the desired distance (about 3 meters) from the camera lens (15-cm focal length at $f/11$). Then a battery-operated spotlight was directed onto the white object. Next a photomultiplier tube at the focus of a 15-cm lens was pointed at the white object, and the gain was adjusted so that a signal was received from the light reflected from the white object. The signal triggered a spotlight-type of lectronic flash unit which had three FX-33 flash lamps at the focal point of a (17.5-cm) reflector. Each lamp was excited from two 250-μfarad capacitors in series at 900 volts. The output was 3200 beam candle power seconds (BCPS) with a flash duration of 70 μsec. Finally the camera

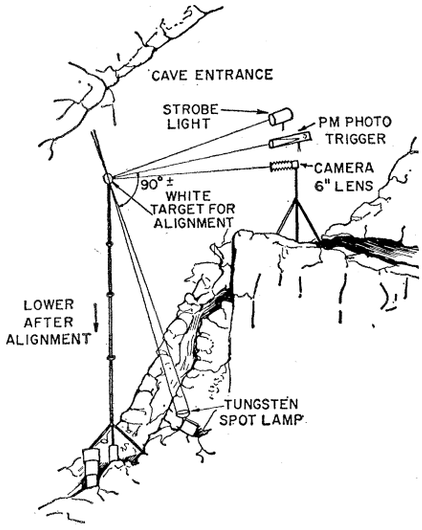

Fig. 1. Automatic method of triggering an electronic flash lamp when a "target" reflects light into a photomultiplier tube.

was critically focused on the white subject. The darkness required in the cave was obtained by directing the PM tube against the dark wall of the cave after sunset or shortly before.

After all was adjusted and rechecked the artificial white target and tripod were removed. The camera shutter was opened on "time" in anticipation of a bat's flying through the field of action. After each flash the shutter was closed, and a new film was introduced into the camera.

A Mexican freetail bat (*Tadarida brasiliensis mexicana*) in flight was photographed when it passed into the beam of light which intersected the senstive area of the photomultiplier (Fig. 2). The tail membrane is extended characteristically in flight whereas in other kinds of bats (such as the little brown bat *Myotis lucifugus*) the tail membrane is so extended when the bat is *not* in flight. Figure 3 shows the tail of the Mexican freetail bat in a normal resting position.

High-speed photographs (*1*) of bats in flight show that the interfemoral membrane extends along the length of the tail and the characteristic "free tail" virtually disappears. The hind limbs are thrust outward and the calcar is pointed backward so that the membrane is spread to its fullest extent—almost to the tip of the tail. Thus the tail vertebrae act as a slide, and the loose tail skin slips along them when the interfemoral membrane is extended. When at rest the membrane is retracted by pulling the hind limbs back in alongside the body.

The advantages seem obvious and threefold. First, the interfemoral membrane of bats, when present, no doubt plays an important role in flight for climbing, diving, turning, and braking. The expansion of the tail membrane of the freetail bat would obviously create a greater surface area for more efficient maneuverability.

Second, the wide expanse of the naked wing and tail membranes can at times be disadvantageous, for bats have difficulty in maintaining body heat and water which is lost easily through the thin skin. It would be advantageous for the freetails to have adapted the ability to retract the tail membrane when at rest and thereby reduce the exposed surface area to conserve body heat and water.

Third, others (*2*) have shown through similar high-speed photographs that in *Myotis lucifugus*, at least, the interfemoral membrane is used as a "tail scoop" to catch insects in midair. In half a second the bat can scoop a food item into its tail membrane and transfer it to its mouth. If this procedure holds true for other insectivorous bats, as the Mexican freetail, then the expansion of the interfemoral membrane would be a considerable aid in the foraging activities of this bat. Until the photographs revealed that the tail membrane was expanded it was difficult to understand how the tail of the freetail could act as a scoop,

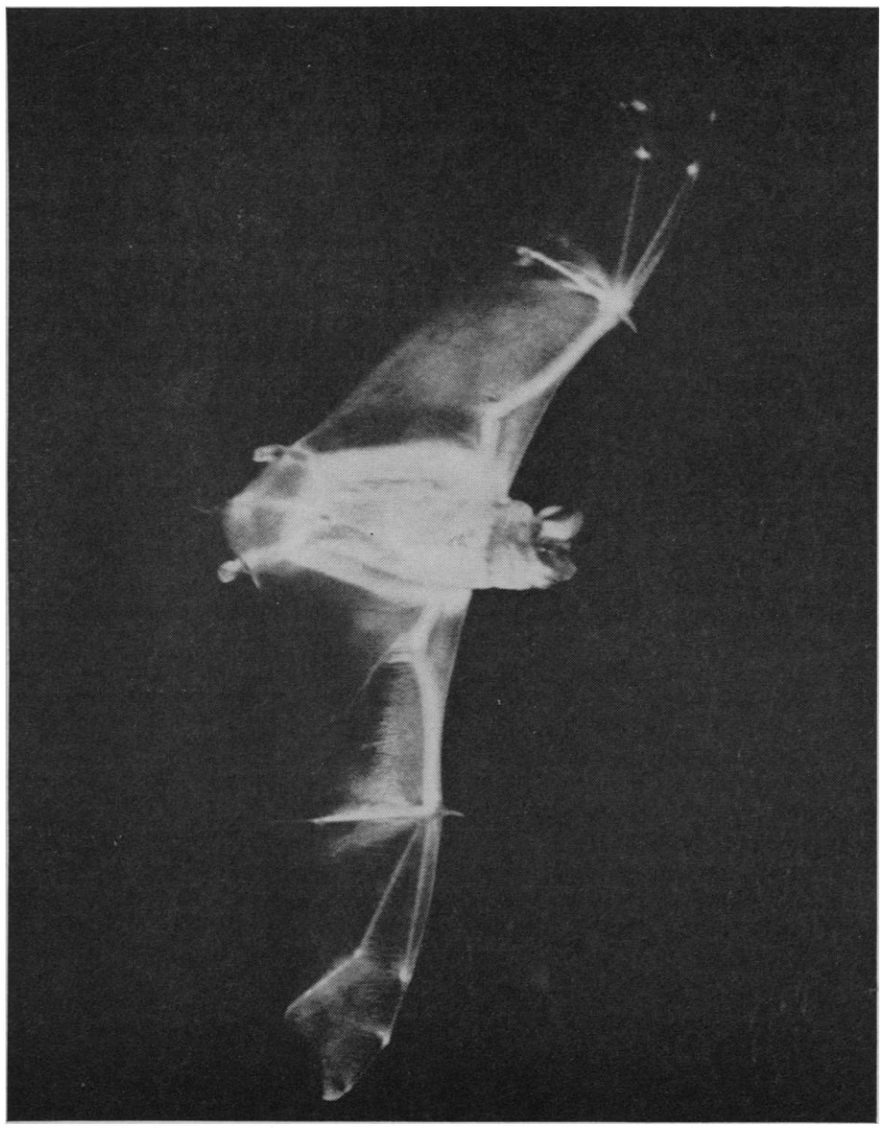

Fig. 2. A high-speed photograph of a Mexican freetail bat in flight, as timed by the equipment shown in Fig. 1. The tail membrane is extended.

since, when the bat was at rest, the membrane was so drawn up into itself that there appeared only very little tail membrane; at least, there was nothing to compare with the tail membranes of other insectivorous bats. (In noninsectivorous bats, such as the fruit eaters and the nectar and blood feeders, there is only a very short tail and almost no tail membrane.)

The early morning dive of the bats into the cave was observed and photographed by a different method. The camera was located on the surface near the edge and flashed at random with a focal distance setting of about 4 meters at $f/4.5$ and 1/60 of a second exposure, an electronic flash (Heiland with 1500 BCPS) being used.

One Kodachrome slide showed seven bats silhouetted against the early morning sky. The cover picture is an enlargement showing the position of the wings in the power dive into the cave. The wings made a characteristic fluttering sound, which we believe is caused by the air action as the bat exceeds his normal flying speed. A blur against the light of the sky shows the motion in the 1/60 second shutter time. If the bat is 10 cm in length, head to tail, the blur caused by motion during 1/60 of a second from this photo is 25 cm. The velocity of the diving bat is 1500 cm/sec, as estimated very roughly from the above-mentioned blur.

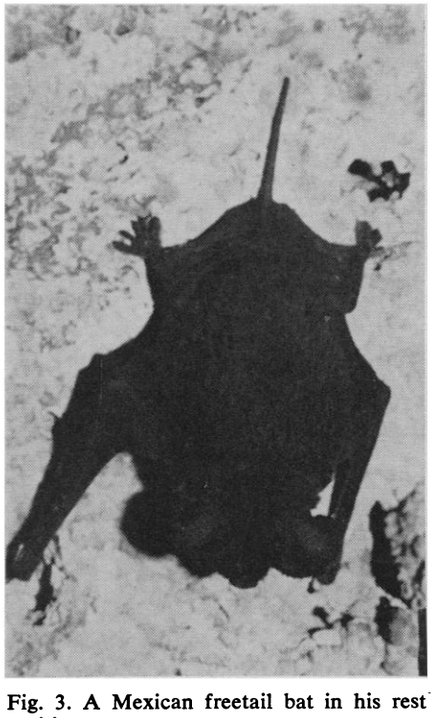

Fig. 3. A Mexican freetail bat in his rest position.

The photographic blur of the wings against the sky indicates that the bat does not flutter his wings in a normal manner, but uses them in a half-folded position as air brakes to limit his velocity during the dive.

HAROLD E. EDGERTON
Massachusetts Institute of Technology, Cambridge

PAUL F. SPANGLE
Western Museum Laboratory, San Francisco, California

JAMES K. BAKER
Joshua Tree National Monument, California

References

1. J. K. Baker and P. F. Spangle, *Southwest. Nat.* **7**, 76 (1962).
2. F. A. Webster and D. R. Griffin, *Animal Behavior* **10**, 332 (1962); F. Webster, *Proc. Int. Congr. Technol. Blindness* **I**, New York, 1963; J. J. G. McCue, *Nat. Geogr. Mag.* **119**, 571 (1961).

18 April 1966

Mating Speed in Male *Drosophila melanogaster*: A Psychogenetic Analysis

Abstract. *A diallel analysis of mating speed as measured by the copulation frequency of male* Drosophila melanogaster *revealed strong directional dominance for high frequency involving a minimum of five genes. The trait as measured is highly correlated with sexual drive and fitness. Consequences for artificial selection and the nature of the heterosis displayed by the crosses are discussed. High copulation frequency of the male is probably the result of unidirectional natural selection.*

Mating speed in *Drosophila melanogaster*, measured in both sexes simultaneously, has been subject to artificial selection by Manning (*1*), thus demonstrating that genetic variation exists for this trait. Parsons, following recent trends in behavioral biometrical genetics (*2*), has partitioned this variation and calculated heritabilities (*3*).

However, mating speed measured in both sexes at once relates to the behavioral interaction of a particular pair of genotypes only, and generalization to other possible genotypic combinations, such as would certainly arise in natural populations, is consequently dubious. This report is concerned, therefore, with mating speed in males only, measured against a broad range of female genotypes. Mating speed was taken as the number of successive copulations accomplished by a male during a 12-hour period, and not the time to first mating, as previously used. These variations allowed a more extensive observation of behavior and a simple and valid method of scoring to be devised.

In the first experiment each 36-hour-old male fly was placed in a tube containing six virgin females. The females were chosen one from each of six available inbred lines to provide a heterogeneous, but standard, test situation for the males. The tubes were set in a rack and observed every half minute during the first 30 minutes, and thereafter every 2 minutes, to detect further copulations. Observation was carried out at 25°C for 12 hours, after which time each female was placed, singly, in a fresh tube, and scored for the yield of progeny produced during 8 days. In this experiment four measures were therefore obtained for each male—time to first copulation, number of copulations, number of copulations resulting in fertilization, and the total number of progeny he produced. The sixty males tested were obtained from the same six inbred lines as the females and also from a sample of six F_1 crosses made from these lines, five males being taken from each of these twelve genotypes. The 12 male genotypes and their average scores on the four measures are given in Table 1.

Table 1 shows that there were few repeat matings between males and particular females, since the number of copulations that occurred resulted in almost as many individual fertilized females (mean discrepancy = 0.7).

The product-moment intercorrelations of measures, presented at the foot of Table 1, indicate that males which mate fast on the first occasion also copulate more often, more successfully, and leave more progeny. The four measures thus appear as aspects of a general characteristic of male mating behavior. The intercorrelations further suggest the number of copulations resulting in fertilization as a convenient method of measuring mating speed, since, with $r = 0.96$, the two measures are practically interchangeable. This proposal has the advantage that it avoids constant observation during the 12-hour period of mating. This method was used in the second experiment involving the genetic analysis of a diallel set of crosses.