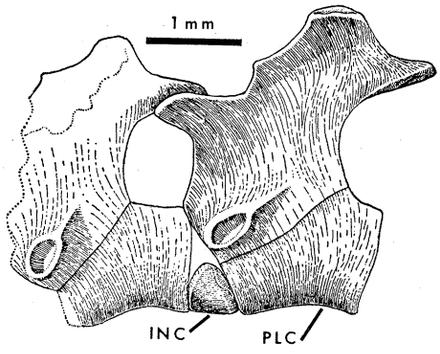

Fig. 4. *Doleserpeton annectens* UR 1332, two dorsal vertebrae in left lateral view; *INC*, intercentrum; *PLC*, pleurocentrum.

teeth, and (iii) bicuspid teeth. The first character is not particularly convincing by itself, as it is shared with other fossil amphibian groups [although among rhachitomes in the broad sense, only with *Peltobatrachus* (*12*), which otherwise does not seem to resemble *Doleserpeton* very closely (*9*)]. Parsons and Williams (*13*, p. 48) have listed seven characters which they feel "most clearly and uniquely link the three modern orders"; I would add an eighth, corresponding to (iii) above. Three of these eight characters might be determinable in a fossil. Two correspond to (ii) and (iii) above; the third, an operculum-plectrum complex, may or may not be present in *Doleserpeton*. Characters (ii) and (iii) have not been observed previously in any nonlissamphibian fossil tetrapod. Parsons and Williams argue for the recognition of Lissamphibia as a phyletic unit. They list 19 characters [I would expand this to 20, by including (iii) above] which might be present in an ancestral lissamphibian and might be recognizable in a fossil. [I question the advisability of postulating that pleurocentra would be "the dominant, if not the only, central elements." Despite Williams' (*14*) review, the homology of central elements in living amphibians is not secure (*15*). Rather, the vertebral centra should be monospondylous, or nearly so, thus leaving in abeyance the question of homologies.] On the basis of either the amended or original list, *Doleserpeton* has a higher "score" than any other nonlissamphibian tetrapod (*15*). *Doleserpeton* does not appear to possess any characters which clearly point to exclusive affinity with any one modern order. It is thus structurally a "protolissamphibian." Whether it is also such phyletically is an open question. Although a morphologically plausible protolissamphibian, *Doleserpeton* might well be ancestral to only part of the Lissamphibia. Its discovery does not solve the problem of the phyletic unity of the Lissamphibia.

The tetrapod faunas of upland, terrestrial environments are poorly represented in Upper Paleozoic deposits in North America. Most of our knowledge of such faunas comes from occasional finds of animals which were transported into lower-lying, more aquatic areas and buried there. The Fort Sill deposits, however, contain large numbers of upland terrestrial tetrapods, especially the reptile *Captorhinus*, and lack significant numbers of stream and pond dwellers. With the exception of the extremely rare aïstopod *Phlegethontia*, the only amphibians identified in the fissure fills were two genera of gymnarthrid microsaurs whose habits are problematic (*1*, *16*). Labyrinthodonts other than *Doleserpeton* occur at Fort Sill but are comparatively quite rare. *Doleserpeton* is probably second in abundance only to *Captorhinus*. Bones of *Doleserpeton* in the D-concentrate generally show no signs of transportation. This and their abundance indicate that *Doleserpeton* is a member of the terrestrial fauna.

Throughout their long history, labyrinthodonts have occurred in association with aquatic or periaquatic vertebrate faunas. Several groups experimented with a more terrestrial mode of life, however, the best-studied case being that of the dissorophids and trematopsids (*8*). In certain respects, *Doleserpeton* was possibly adapted more completely to terrestrial existence than any other known labyrinthodont. *Doleserpeton* shows striking differences from other labyrinthodonts in both dentition and vertebrae. These changes in locomotor and feeding systems, together with its occurrence in a presumably very terrestrial situation, suggest that *Doleserpeton* was exploiting the terrestrial environment in a basically different fashion, and perhaps more fully than most contemporary labyrinthodonts. This could be a fundamental reason for the persistence of the Lissamphibia to the present. In this view the doleserpetontid protolissamphibians were a terrestrial group in the sense that early members were dependent for food on animals that lived on land (possibly insects, by analogy with living amphibians). If insects did constitute their major food source, then by implication most labyrinthodonts either fed upon insects in a basically different way, or did not feed upon them to the same extent, or both.

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17. I thank Drs. H. Barghusen, R. DeMar, E. Olson, and D. Wake for criticism and discussion, A. Gorman for photography, and Miss M. Moran and R. Parshall for drawings. A. Graffham supplied several fine skulls. J. Yingling, superintendent of the Dolese Brothers Richards Spur plant, allowed me to collect in the quarry on several occasions and aided in other ways. Supported by a NSF graduate fellowship at the University of Chicago and by a grant from the University of Illinois at the Medical Center, College of Medicine.

12 June 1969; revised 29 July 1969

Acoustic Synchrony: Two Mechanisms in the Snowy Tree Cricket

Abstract. *Snowy tree crickets synchronize their chirps by responding to the preceding chirp of their neighbors. If a neighbor's chirp precedes his own, a cricket shortens his chirp and the following interval. If it follows his own, he lengthens his chirp interval and sometimes the following chirp. A single response of the first type may advance his phase of chirping 160° and one of the second type may retard it 200°.*

The snowy tree cricket *Oecanthus fultoni* Walker (*1*) is a common dooryard species throughout most of the United States. Since 1889, its synchronous chirping has been a subject for comment in scientific literature (*2*, *3*). However, only two previous investigators have reported experimental approaches to the phenomenon, and both established only that the synchrony is real and depends on auditory stimuli—Fulton found that males without tympanic organs chirped asynchronously, and Allard noted that individuals quickened their chirps in response to rapidly delivered imitations (*4*). I now report the first quantitative description of synchrony in the snowy tree cricket and the first detailed account of stimulus-response mechanisms in this or any other insect with comparable synchrony (*5*).

The song of the snowy tree cricket

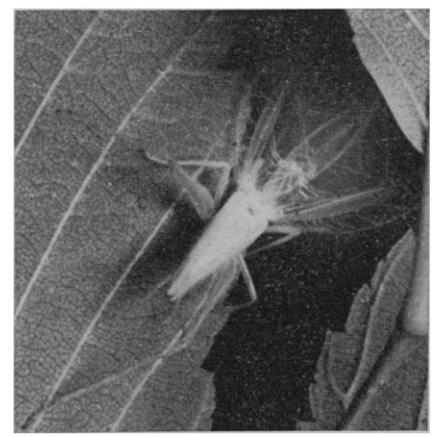

Fig. 1. Posterior view of male snowy tree cricket stridulating with elevated forewings. Neighboring males synchronize their chirps and the chirp rate varies directly with temperature. The chirp rhythm attracts sexually responsive females. After the female accepts a spermatophore from the male, she feeds 10 to 30 minutes at the glandular cavity visible at the base of the male's forewings. She then removes the just-emptied spermatophore and eats it.

(Fig. 1) is a long-continued sequence (Fig. 2A) of chirps produced when the male elevates his specialized forewings and rubs them together. Each chirp consists of 2 to 11 pulses (most often 8 or 5) that correspond to wing closures (*6*). The chirp rhythm is highly regular in choruses and is usually so for solitary singers. Irregularities in chirp rhythms of solitary singers most often result from occasional hesitations between chirps and from mixing five-pulse chirps with the more usual eight-pulse ones. The effect of a five-pulse chirp on the regularity of the rhythm is exaggerated by the interval following being shorter than that following an eight-pulse chirp (*7*). For 50 consecutive periods (chirp and following interval) of a solitary individual producing all eight-pulse chirps, the coefficient of variation was 2.3; of one producing one-third five-pulse chirps the coefficient was 9.6.

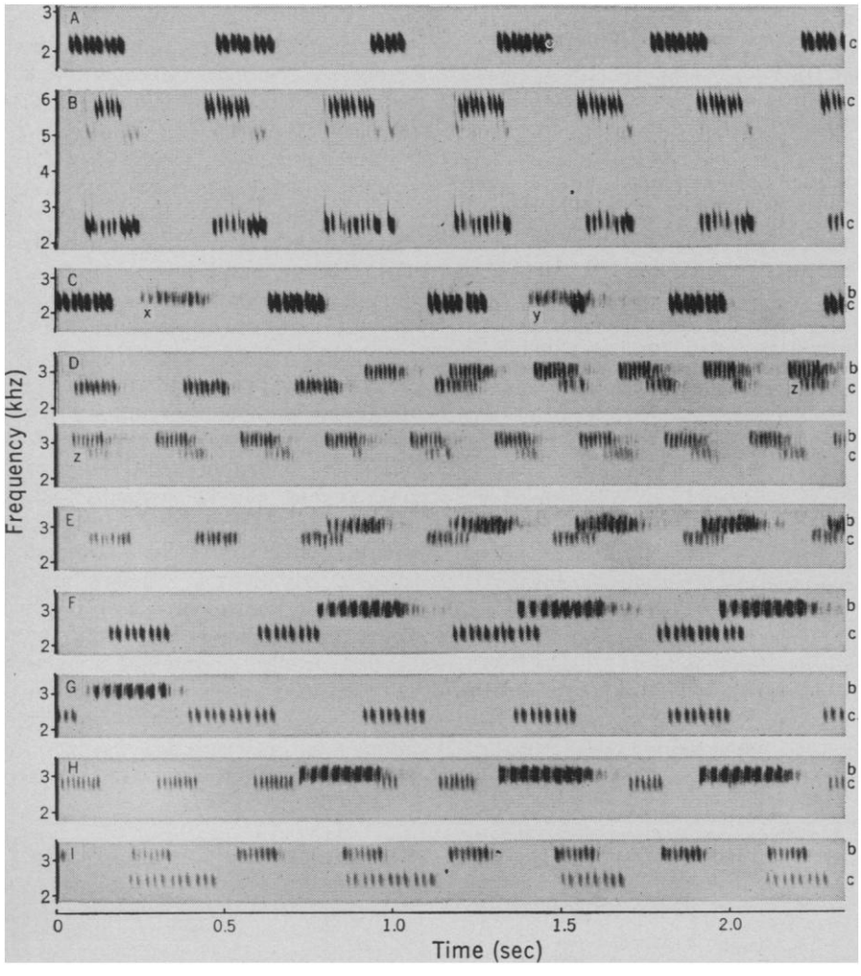

Fig. 2. Audiospectrograms of songs of the snowy tree cricket. *b*, Broadcast sounds; *c*, sounds of test cricket. (A) One individual; Franklin Co., Ohio, 24.5°C. (B) Two individuals synchronizing; 25.0°C. Upper individual (frequency electronically doubled): Santa Cruz Co., Ariz., unusually fast pulse rate. Lower individual: Pima Co., Ariz. (C) Two types of responses to broadcast, isolated eight-pulse chirps (*x*, *y*); same cricket as in (A); 24.5°C. Chirp interval is lengthened in response to *x* (type L response) [see intervals in (A)]; chirp and following interval are shortened in response to *y* (type S response). (D) Response of same individual at 29°C to onset of artificial chirps at 242 chirps per minute (equivalent to cricket at 34°C). Chirp rate prior to broadcast signal was 185. Lower audiospectrogram is a continuation of the upper. Chirp labeled *z* is common to both. First two responses are L, remainder are S. (E) Response of same individual at 29°C to onset of artificial chirps at 166 chirps per minute (equivalent to cricket at 25°C). Chirp rate prior to broadcast signal was 192. All L responses. (F) Response of another individual (Franklin Co., Ohio), at 21°C, to onset of artificial chirps at 103 chirps per minute (equivalent to cricket at 17°C). Chirp rate prior to broadcast signal was 133. All L responses; chirps as well as chirp intervals lengthened. (G) End (after 21 seconds) of broadcast signal of (F). Original chirp rhythm resumes immediately after the last L response. (H) Response of individual in (A) at 31.5°C to onset of artificial chirps at 103 chirps per minute. Chirp rate prior to broadcast signal was 211. The response to the first broadcast chirp is first L (a lengthening of the chirp interval) and then S (a shortening of the next chirp and its interval). Cricket maintained the rate of the broadcast signal for 11 seconds and then stopped singing. (I) Response of individual in (F) at 20.5°C to artificial chirps at 195 chirps per minute (equivalent to cricket at 28.5°C). Chirp rate prior to broadcast signal was 128; rate during broadcast was 97.5. All L responses.

The dramatic and linear effect of temperature on chirp rate makes the snowy tree cricket a passable thermometer (*8*). Chirp rates as divergent as 50 and 200 chirps per minute are produced in the field. The average pulse rate within a chirp is also temperature dependent, and chirp durations as well as chirp intervals shorten or lengthen with increasing or decreasing temperatures (*8*).

Neighboring crickets synchronize chirps but not pulses, and one cannot identify individual songs in conventional tape recordings of choruses. However, by electronically doubling the carrier frequency (hz) of one of two synchronizing individuals, I was able to make a tape recording that showed, upon audiospectrographic analysis, the performance of each individual (Fig. 2B (*9*). During 100 consecutive chirp pairs, the lead changed 74 times, with one individual leading 51 times and the other 49. The difference in the chirp starting times of the two individuals for the 100 pairs was never more than 72 msec with the average being 27 ± 17 ($\bar{x} \pm$ S.D.), much less than the approximately 60 msec minimum delay between an acoustic stimulation and a forewing response (*10*). Evidently the crickets used cues from the preceding chirp or chirps to maintain synchrony.

To investigate the means of synchrony in the snowy tree cricket, I played tape-recorded sounds to males singing on perches in individual, organdy-closed glass cylinders (15 by 20 cm). The tapes of test sounds were spliced into loops that could be played continuously. The sounds were broadcast at approximately natural intensity, and the acoustic response of the test cricket was tape recorded and later analyzed.

In one series of tests, I played isolated naturally produced eight-pulse chirps, anticipating that the cricket might alter its chirp rhythm and reveal how synchrony is achieved and maintained. The tests were made at 24.5°C, and the test chirps had been tape-recorded previously at the same temperature (*11*). In a second series of tests, I played long sequences (10 to 30 seconds) of artificially produced chirps at

five different rates to individuals singing at various temperatures between 18° and 32°C. At each rate the chirps were uniform in quality and timing, and the pulse rate within the chirps was adjusted to agree with that appropriate to the chirp rate. The frequency was maintained at 3.0 khz, slightly higher than the natural frequency. Consequently the broadcast chirps and the cricket's chirps could be distinguished easily in audiospectrograms (Fig. 2, D–I) (*12*).

The tests with isolated chirps demonstrated two contrasting types of response, each consisting of a change in a single period (chirp and interval). One type (L, period lengthened) occurred when the broadcast chirp began during the latter part of a cricket's chirp or during the first part of a cricket's chirp interval and consisted of the cricket delaying its next chirp and sometimes lengthening it (Fig. 2C, *x*; Fig. 3, right). The other type of response (S, period shortened), occurred when the broadcast chirp began during the latter part of a chirp interval and consisted of the cricket abbreviating its next chirp from a presumed eight pulses to five or two and shortening the following chirp interval (Fig. 2C, *y*; Fig. 3, left). The response to be made by the cricket was predictable from the timing of the broadcast chirp except when the broadcast chirp was approximately +220° (= −140°) out of phase with the rhythm of the test cricket. Then either an L or an S response might occur (Fig. 3).

Either type of response brought the test cricket closer to agreeing in phase with the broadcast chirp (Fig. 3). The L response lengthened a single period by as much as 55 percent; however, if the broadcast chirp was more than 70° out of phase, the response failed, by about 60°, to fully adjust the phase of the cricket to the broadcast sound. A second L response would have been expected had broadcast chirps continued at a natural rate, and synchrony would have occurred with the third broadcast chirp. The S response shortened a single period by as much as 45 percent and changed the phase of the cricket either enough or a little too much to result in synchrony in a single response. In the case of too great a phase shift for synchrony, an L response would have next been expected had the broadcast sound continued at a natural rate, and synchrony would have occurred with the third (rather than the second) broadcast chirp.

The results with isolated chirps thus suggested that (i) maintenance of synchrony in the snowy tree cricket may involve nothing more than two types (L and S) of graded responses to the immediately preceding chirp of the chorus and (ii) no more than two consecutive responses (L, L or S, L) may be required for a cricket to achieve synchrony with any song like its own. Both of these hypotheses were supported by the results of tests with sequences of artificial chirps.

In response to broadcast sequences of artificial chirps, crickets showed the same two types of responses as they had with broadcast isolated natural chirps. When the broadcast chirp rate matched or nearly matched the solitary rate of the test cricket, the cricket achieved and maintained near-perfect synchrony. When the broadcast rate deviated from the cricket's solitary rate by more than about 10 percent, the cricket either failed to match the broadcast rate (Fig. 2I) or matched it while remaining perpetually out of phase (Fig. 2, D–H).

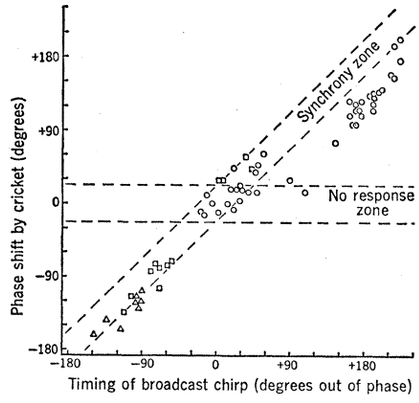

Fig. 3. Response of singing snowy tree cricket to isolated eight-pulse chirps (Franklin Co., Ohio, 24.5°C). Degrees out of phase calculated from difference between start of broadcast chirp and start of cricket's chirp compared to 465 msec, the mean period of an eight-pulse chirp and its following interval (*7*). For broadcast chirps that produced a detectable response the measurement was from the beginning of the broadcast chirp either forward or backward to the beginning of the chirp starting the period (potentially 465 msec) that was affected. Otherwise the nearest chirp was used. Symbols indicate the number of pulses in the first chirp that could have been influenced by the broadcast chirp (△) two-pulse; (□) five-pulse; (○) eight-pulse. Before the test began the cricket was mixing eight- and five-pulse chirps at a ratio of 2 : 1. Broadcast chirps that fell near presumed natural five-pulse chirps are omitted but discussed in (*17*). The zones include an estimated 95 percent of the expected variation about the lines of perfect response for synchrony and of no response and were drawn ± 22.2° based on a standard deviation of 14.4 msec or 11.1° for an eight-pulse chirp and following interval.

Failure to match the broadcast rate occurred at rates as near the solitary rate as +31 or −18 percent. At faster broadcast rates, the cricket sometimes chirped only once for two broadcast chirps. Indeed certain faster rates caused only L responses, and the cricket chirped at a slower rate (Fig. 2I). At lower broadcast rates, the cricket sometimes inserted extra chirps (through S responses) and hence exceeded the broadcast rate.

The limits for rate matching were +31 percent (Fig. 2D) and −51 percent (Fig. 2H) of the cricket's solitary rate. The degree to which the cricket remained out of phase with the broadcast signal depended upon how much the broadcast rate differed from the cricket's solitary rate. At very slow broadcast rates alternation resulted (Fig. 2, F–H).

The Bucks (*3*) emphasized the importance of distinguishing synchrony that depends on responses to the antecedent signal or signals from synchrony that depends on responses to the concurrent signal. They termed the first *anticipatory* or "sense of rhythm" synchrony and the second *paced* synchrony. The snowy tree cricket synchrony belongs to the first category, yet neither name seems appropriate because (i) the mechanisms demonstrated are apparently merely reflexes influencing a single period, (ii) the cricket fails to improve its phase relations with a faster or slower broadcast signal that it is equaling in chirp rate (Fig. 2, D–H), and (iii) it returns immediately to its original chirp rate when the broadcast signal is discontinued (Fig. 2, F–G). In the 16 instances that a test cricket equaled the rate of the broadcast signal and continued singing after the signal was discontinued, not even the first chirp after the signal stopped appeared significantly different from the chirps made just prior to the test signal (*13*).

A more explicit terminology for the types of synchrony distinguished by the Bucks must focus on the stimulus causing an occurrence (episode) of synchronized signal production. Either the stimulus precedes the episode (proepisodic) or it is concurrent with the episode (homepisodic). Thus the snowy tree cricket has two proepisodic mechanisms of synchrony, and Alexander and Moore (*14*) have demonstrated hom-

episodic mechanisms for the periodic cicada *Magicicada cassini*.

Synchrony in the snowy tree cricket is understandable in terms of the function of the song. Sexually responsive females come to the song, and the chirp rhythm is essential to their response (*15*). When males sing in proximity, synchrony allows the rhythm to remain evident to females outside the chorus. The chirp rhythm is so rapid that only proepisodic mechanisms can effectively preserve it. Individuals in choruses may have an advantage over solitary singers as to safety from acoustically orienting predators (*16*), and it is possible that females respond sooner or more readily to the louder more regular chirp of a chorus than to the song of a solitary male.

Except for two other tree crickets (*Oecanthus allardi* and *O. rileyi*), other insects known to have proepisodic mechanisms of synthrony have evolved them independently of the snowy tree cricket (*O. fultoni*). The mechanisms I have studied in other species are similar though not the same as for *O. fultoni* (*5*).

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References and Notes

1. Prior to 1960 [T. Walker and A. Gurney, *Fla. Entomol.* **43**, 10 (1960)] the snowy tree cricket was known as *Oecanthus niveus*.
2. See, for example, A. E. Dolbear, *Amer. Natur.* **31**, 970 (1897); J. McNeill, *Entomol. Amer.* **5**, 101 (1889); H. A. Allard, *Amer. Natur.* **51**, 438 (1917).
3. J. Buck and E. Buck, *Science* **159**, 1319 (1968).
4. B. B. Fulton, *Ann. Entomol. Soc. Amer.* **21**, 445 (1928); H. A. Allard, *Annu. Rep. Smithson. Inst.* **1928**, 563 (1929).
5. Fireflies of the genera *Pteroptyx* (*3*) and *Photuris* [J. E. Lloyd, *Fla. Entomol.* **52**, 33 (1969)] and sound-producing insects of at least seven genera in the families Cicadidae (Homoptera), Gryllidae (Orthoptera), and Tettigoniidae (Orthoptera) [T. Walker, in preparation] synchronize rapid rhythmic signals with such perfection that they must use cues from one or more previous signals rather than from the contemporary one. Among other animals only human beings are known to have this ability (*3*).
6. The pulses within a chirp are delivered at two rates: The interval after the second pulse and every third pulse thereafter is slightly longer than the other intervals. The pulses are therefore grouped 2–3–3. The cricket produces long or short chirps by adding or dropping groups of three pulses.
7. In an individual from Franklin Co., Ohio, at 24.5°C, the average ($n = 43$) five-pulse chirp lasted 102 ± 3 msec ($\bar{x} \pm$ S.D.) with a following interval of 279 ± 14 msec for a period of 381 ± 14 msec, while the average ($n = 53$) eight-pulse chirp lasted 167 ± 4 msec with a following interval of 298 ± 15 msec for a period of 465 ± 14 msec.
8. First noted by M. W. Brooks [*Pop. Sci. Mon.* **20**, 268 (1882)] and recently discussed by B. C. Block [*Ann. Entomol. Soc. Amer.* **59**, 56 (1966)]. In eastern United States, the relation between chirp rate and temperature is chirps per minute $= 8.21T - 38.6$, where $T =$ temperature in degrees Celsius. Westward, the relation varies. The average pulses per second during a chirp approximates $2.24T - 4.16$; T. Walker, *Ann. Entomol. Soc. Amer.* **55**, 315 (1962).
9. Audio frequency doubler made by Alton Electronics Co., Gainesville, Fla., used between the tape recorder and microphone for one individual.
10. Female of *Montezumia modesta* in reply to male lisp at 25°C; J. D. Spooner, *Anim. Behav.* **16**, 200 (1968). The shortest delay that the snowy tree cricket demonstrated in the present experiments was approximately 90 msec.
11. Four chirps were spliced with blank tape to form a 6.7 second loop having chirps at 0, 2.2, 2.9, and 4.1 seconds. The loop ran continuously during a test.
12. The equipment used to produce artificial cricket songs is described in T. Walker, *Ann. Entomol. Soc. Amer.* **50**, 629 (1957).
13. When the period of the first chirp that the last broadcast chirp might not have influenced (by S or L responses) was compared with the mean period of the last 2 to 5 chirps prior to the beginning of the broadcast signal, ten of the first chirps were within 3.2 percent [$< \simeq 1$ S.D. (*7*)], five were within 6.4 percent ($< \simeq 2$ S.D.), and one was a two-pulse chirp evidently caused by an S response to the voiced announcement that the signal was off. Analyses of second and third chirps gave similar results.
14. R. D. Alexander and T. E. Moore, *Ohio J. Sci.* **58**, 107 (1958).
15. T. J. Walker, *Ann. Entomol. Soc. Amer.* **50**, 634 (1957).
16. – → –, *Fla. Entomol.* **47**, 163 (1964).
17. In the tests illustrated, 21 broadcast chirps fell near presumed natural five-pulse chirps. When the test chirp fell −50° to +83° out of phase with such a chirp ($n = 19$), the chirp remained five-pulse but the interval (normally 279 msec) usualy equalled or slightly exceeded the interval normal for eight-pulse chirps (298 msec) (*7*). Since the broadcast chirp was eight-pulse, the response was appropriate for achieving synchrony. In two cases the test chirp followed a five-pulse chirp by nearly 180°, and the response of the test cricket was to lengthen the period by nearly 180°.
18. Supported by NSF grant GB4949 and the Graduate School, Ohio State University. I thank D. J. Borror, J. E. Lloyd, and J. Buck for help and advice. Florida Agricultural Experiment Stations Journal Series No. 3329.

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Cellulosic Wall Component Produced by the Golgi Apparatus of Pleurochrysis scherffelii

Abstract. *The Golgi apparatus of a marine chrysophycean alga* Pleurochrysis scherffelii *Pringsheim produces wall fragments (circular-to-ellipsoidal "scales") which are released to the periphery by an exocytotic process involving the fusion of cisternae and the plasma membrane. The cellulosic component of the scales is a complex network of fibrils (10 to 25 angstroms in diameter) that resist treatment with strong alkali. Untreated washed scales yield galactose, ribose, arabinose, and traces of glucose; alkali-purified scales yield much more glucose. The fibrillar scale constituent shows a positive iodine dichroism of the intact wall, a positive zinc chloride–iodine reaction, breakage sites characteristic of highly crystalline cellulose, and solubility in Schweizer's reagent.*

Pectic cell-wall polysaccharides are formed within the Golgi apparatus and extruded in typical vesicles by an exocytotic membrane-flow mechanism (*1–4*). The same process is very likely for formation of hemicellulosic components (*5, 6*); however, it is generally agreed that cellulose is not made within the Golgi cisternae. Instead, the cellulose fibrils are thought to be formed outside of the plasma membrane from intracellular precursors (*1, 4, 6, 7*).

The difficulty of assigning to the Golgi apparatus the role of cell-wall formation comes principally from the lack of morphological evidence for equivalent structures within the Golgi cisternae in comparison with constituents of the cell wall *in situ*. Such morphological proof for the role of the Golgi apparatus in the production of the cell wall of a marine chrysophycean alga *Pleurochrysis scherffelii* (*8*) was recently demonstrated by Brown (*9*), who suggested that the cell wall was composed of cellulosic substances as indicated by a positive iodine dichroism and a negative spherite birefringence of the intact wall. Pectic substances were also demonstrated in the wall by a positive reaction with Ruthenium Red and uptake of Alcian Blue at *p*H 0.5. This report provides biochemical and additional morphological evidence that at least one component of the cell wall produced by the Golgi apparatus is composed of a cellulosic glucan.

Axenic cultures of *P. scherffelii* were grown in agar slants of von Stosch's medium (*10*) modified to include 4 grams of vitamin-free Casamino acids (Difco) in each liter of medium. Pure fractions of cell-wall fragments or "scales" were obtained from dissolution of mother-cell walls during zoospore production (*11*). The scale fraction was separated from the zoospores by centrifugation (1600*g*, 20 minutes), and the supernatant containing the scales was again centrifuged at 70,000*g* for 20 minutes. The resulting pellet consisted of circular-to-ellipsoidal scales (Fig. 1A). Whereas some of the scales produced an image of a distinct network of concentric microfibrils with an underlying layer of radial