

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 121

**The Evolutionary Relationships
of 17-Year and 13-Year Cicadas, and
Three New Species
(Homoptera, Cicadidae, *Magicicada*)**

BY
RICHARD D. ALEXANDER
AND
THOMAS E. MOORE

ANN ARBOR
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN
JULY 24, 1962

But in flowery meads I dwell,
Lingering oft in leafy dell,
Where the inspired cicada's gladness,
Swelling into sunny madness,
Filleth all the fervid noon
With its shrill and ceaseless tune.

Aristophanes, *The Birds*, 414 B.C.

(Modified from translation by B. H. Kennedy, 1874, p. 103.)

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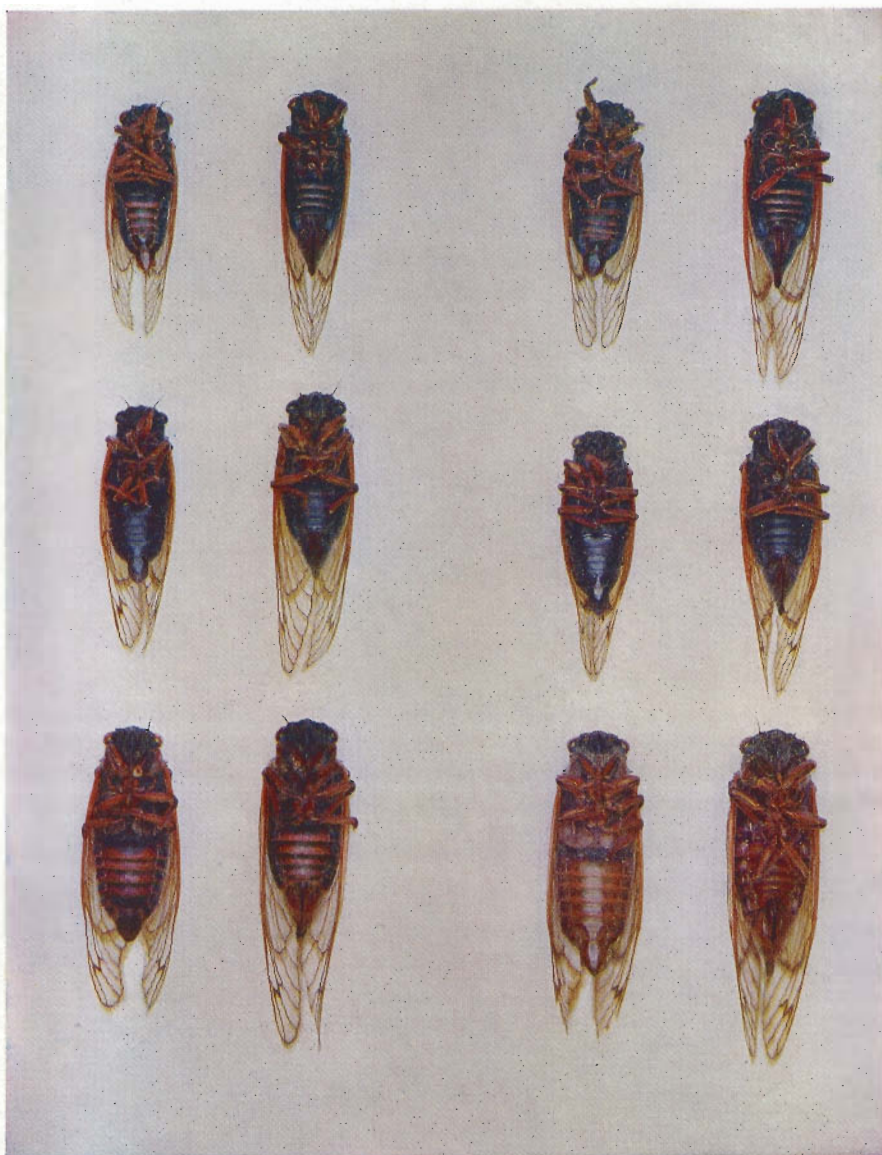
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FRONTISPIECE

Ventral Views of the Six Species of *Magicicada*.

17-Year Species

Male	Female
<i>septendecula</i> , n. sp.	
<i>cassini</i> (Fisher)	
<i>septendecim</i> (Linnaeus)	

13-Year Species

Male	Female
<i>tredecula</i> , n. sp.	
<i>tredecassini</i> , n. sp.	
<i>tredecim</i> (Walsh & Riley)	

THE EVOLUTIONARY RELATIONSHIPS
OF 17-YEAR AND 13-YEAR CICADAS, AND THREE NEW SPECIES
(Homoptera, Cicadidae, *Magicicada*)*

INTRODUCTION

THE periodical cicadas make up a truly amazing group of animals; since their discovery over 300 years ago, the origin and significance of their extended life cycles have been a continual source of puzzlement to biologists. Their incredible ability to merge by the millions as noisy, flying, gregarious, photo-positive adults within a matter of hours after having spent 13 or 17 years underground as silent, burrowing, solitary, sedentary juveniles is without parallel in the animal kingdom.

The number of species of periodical cicadas has been in doubt since Fisher (1851) described *cassini* as a result of John Cassin's observations on the distinctiveness of two 17-year forms. Prior to that time only Linnaeus' (1758) species, *septendecim*, had been recognized (*costalis* Fabricius, 1798, has never been regarded as other than a synonym of *septendecim*; cf. Distant, 1906). In 1868 Walsh and Riley distinguished a 13-year species, *tredecim*, from the 17-year forms, bringing to four the total number of formally designated species. No additional species have since been described. Marlatt (1923) in his extensive treatment of this group recognized but a single species, *septendecim*, with three "races" or "varieties," and until recently this suggestion had been almost universally accepted.

We have been studying periodical cicadas since 1956; as a result we found that Fisher's 17-year cicada, *cassini*, is indeed a distinct species (Moore and Alexander, 1958). In 1959 we observed for the first time an emergence of 13-year cicadas. Because of certain notes in the literature (e.g., Walsh and Riley, 1868, p. 63), we expected to find counterparts of the two known 17-year species. These were present, but surprisingly there was also a third, clearly distinct species. This led us to suspect immediately that a third 17-year species also existed. Re-examination of 17-year specimens showed a morphological counterpart of the third 13-year species, ironically absent or very scarce in the particular localities where we had studied 17-year cicadas in the field during 1956 and 1957. However, in Alexander's field notes there was a clear description of a song identical to that of the third 13-year species, heard repeated over and over again on a single occasion in 1957 in Ross County, Ohio, and believed then to be an aberrant *cassini*

* Funds for the publication of this monograph were derived from the income on the endowment of the Horace H. Rackham School of Graduate Studies, and made available by the Executive Board of that School as Project R No. 32—Museum of Zoology.

male. Eventually we detected the same song in the background of a tape recording made by Robert A. Champlain and Frank W. Fisk in June, 1953, in Delaware County, Ohio. Finally, in June, 1961, we found the expected species, along with the other two 17-year cicadas, in Brood I in Rockbridge County, Virginia, confirming that there are indeed three 17-year species as well as three 13-year species—six separate entities in this remarkable group. Examination of more than 10,000 specimens in 38 collections in eastern United States has indicated that three species probably occur in every one of the 20–25 recognizable broods of periodical cicadas. The history of these species, their macro- and micro-distributional relationships, and their interactions, especially with respect to acoustical behavior and other adult activities, present an unusual, perhaps unique evolutionary problem. This group seems certain to play an important role in the reconstruction of the distributional history of the fauna of eastern North America, especially with regard to Pleistocene and post-Pleistocene events. We hope that the information given here will stimulate the kind of investigation needed to fill the many important gaps remaining in our knowledge of periodical cicadas.

NOMENCLATURE AND SYNONYMY

So far as we have been able to determine (see acknowledgments), not a single specimen remains to represent any of the four names applied in this group. Consequently, along with descriptions of the three new species, we are including neotype designations and re-descriptions of the three previously named species. All type specimens, and originals or copies of all tape recordings mentioned in this paper, are deposited in the University of Michigan Museum of Zoology, Ann Arbor, Michigan.

Magicicada W. T. Davis, 1925, p. 43

Type, by original designation, *Cicada septendecim* Linnaeus; *Cicada cassini* Fisher included. The members of this genus can be separated from all other eastern North American cicadas by their reddish eyes and wing veins (yellowish or brownish in preserved specimens) and by their 13-year or 17-year life cycles. The timbals are not covered; the dorsal thorax is black without patterning; and the head including the eyes is distinctly wider than the front edge of the pronotum and distinctly narrower than the rear edge of the pronotum.

Magicicada septendecim (Linnaeus)—Linnaeus' 17-Year Cicada

Cicada septendecim Linnaeus, 1758, p. 436. "C. nigro-virescens, elytris margine flavescence, capite utrinque octo-striato. Kalm. act. Stockh. 1756. p. 101. Cicada maxilla utraque lineis octo transversis concavis, alarum margine inferiore lutescente. Habitat in America boreali."

Tettigonia costalis Fabricius, 1798, p. 511. "T. atra elytris hyalinis; costa fulva. Habitat in Philadelphia Mus. Dom. Bosc. Statura praecedentis [*Tibicen plebeja*]. Caput et thorax atra. Abdomen nigrum segmentorum marginibus subtus testaceis. Elytra aquca costa lateofulva, inprimis a basi ad medium. Pedes nigri femoribus anticus rufis."

NEOTYPE, MALE¹.—Ohio, Delaware County, Orange Township, Brown Fruit Farm, June 1953 (Brood X), D. J. Borror and C. R. Reese. Body primarily black above, primarily reddish beneath; appendages primarily reddish; lateral extensions of pronotum between eyes and wing bases reddish-yellow; prothoracic pleura reddish-yellow; wing veins yellowish-brown, radial W in forewings with yellowish-brown veins and lightly clouded with yellowish-brown; apical tarsal segments reddish-brown, darker toward their tips; abdominal tergites reddish-black with black apical borders; visible abdominal sternites almost entirely reddish; tergum and sternum reddish-yellow in the spiracular region; body length (front of head to tip of subgenital plate), 27.5 mm.; length of forewings, (L, R) 33.5 mm.; width of forewings, (L, R) 13.0 mm.; 5 timbal ribs per mm., beginning with fourth rib from base; 12 complete tinbal ribs. Preserved in 70 per cent ethyl alcohol.

REPRESENTATIVE FEMALE.—Same data as male and preserved in same bottle. Same as male except radial W in forewing heavily clouded with yellowish-brown; abdominal tergites black; reddish margin on eighth abdominal tergite; body length (front of head to tip of ovipositor sheath), 29.1 mm.; length of forewings, (L) 34.4 mm., (R) 34.5 mm.; width of forewings, (L) 13.2 mm., (R) 13.1 mm.

This is the largest and most northern 17-year species, and the most universally known periodical cicada; it is the species with the famous "Pharaoh" call. Linnaeus described it on the basis of specimens and information furnished by the Swedish botanist Pehr Kalm as a result of Kalm's observations in 1694 in Pennsylvania and New York, especially along the Schuylkill River in Pennsylvania (Kalm, 1756, in J. J. Davis, 1953). In his description, Linnaeus cites Kalm's article and copies directly the Latin descriptive phrases suggested by Kalm; but Linnaeus gives no locality.

Because some doubt must remain as to the status and relationships of the cicadas present in different broods (until these have all been studied by the means now at hand), we have designated neotypes from the broods involved in the original descriptions. The periodical cicadas emerging in 1749 in northeastern United States correspond to Marlatt's Brood X; the only other periodical cicadas emerging in large numbers during that year would have been 13-year cicadas of Brood XXX, known only from Morehouse Parish, Louisiana, and Cass County, Missouri.

We do not have individual specimens from Brood X for which songs

¹ We hereby designate this same specimen as neotype for *Tettigonia costalis* Fabricius, 1798, described without date of collection.

have been recorded. However, recordings of Brood X choruses contain recognizable songs of all three 17-year species (OSU Tape 667F). We are designating neotypes of *septendecim* and *cassini* from specimens collected by D. J. Borror and C. R. Reese in June 1953 at the same place that the recording was made.

Magicicada cassini (Fisher)—Cassin's 17-Year Cicada

Cicada cassinii Fisher, 1851, p. 272. "♂ total length of body, 9-10ths of an inch; of the wings, 1 2-10ths inches; ♀ frequently smaller.

"Colors and general appearance much like those of *Cicada septendecim*, Linn., but darker, and the segments of the abdomen below are more narrowly bordered with yellow. Note different from that of *C. septendecim*, and more like that of some of the grasshoppers. Inhabits the neighborhood of Philadelphia. . . ."

Cassin (1851), in an article immediately following Fisher's description, gives a detailed discussion of the difference between *cassini* and *septendecim*. He points out that he made these observations first in the 1834 emergence, four years following Hildreth's (1830) article in which the latter stated: "There appeared to be two varieties of the cicada, one much smaller than the other; there was also a striking difference in their notes." Cassin's conclusions were appropriate: "In short, it appears to me that the study of these insects, and the examination of their separate ranges, might result in conclusions of extraordinary importance, especially relative to modern views of the distribution of animals."

NEOTYPE, MALE.—Ohio, Delaware County, Orange Township, Brown Fruit Farm, June 1953 (Brood X), D. J. Borror and C. R. Reese. Body black above, almost entirely black beneath; appendages primarily reddish; lateral extensions of pronotum between eyes and wing bases black; prothoracic pleura black; wing veins yellowish-brown, radial W in forewings with dark brown veins and lightly clouded with yellowish-brown; apical tarsal segments reddish-brown, gradually darker toward their tips; abdominal tergites black; first four visible abdominal sternites black except for reddish-brown margins that cover one-third or less of the width of the sternites and are narrowed medially; other abdominal sternites black; tergum and sternum reddish-black in the spiracular region; body length, 24.3 mm.; length of forewings, (L) 26.5, (R) 23.8 mm.; width of forewings, (L) 11.0, (R) 10.4 mm.; 6 timbal ribs per mm., beginning with fourth rib from base; 13 complete timbal ribs; preserved in 70 per cent ethyl alcohol.

REPRESENTATIVE FEMALE.—Same data as male and preserved in same bottle. Same as male except that reddish margins on first four abdominal sternites cover one-fourth to one-third the width of the spiracular region; reddish margin on eighth abdominal tergite; body length, 26.9 mm.; length of forewings, (L) 31.1, (R) 31.0 mm.; width of forewings, (L, R) 12.3 mm.

This species is intermediate in size between *septendecim* and the next species, and differs from *septendecim* in: (1) having the pronotum and prothoracic pleura all black, (2) having the abdominal sternites either all black or marked only with narrow reddish transverse bands at the apices

of some sternites, and (3) having a distinctive call consisting of a series of ticks followed by a buzz.

Fisher named this species in honor of John Cassin who was the first to list clearly the morphological, behavioral, and song differences between this species and *septendecim*. We have shortened the original spelling by dropping the final *i*, and we suggest that it be called "Cassin's 17-year cicada." The frequently used term "dwarf cicada" is inappropriate for several reasons, not the least of which is the intermediate size of this species.

***Magiccicada septendecula*, new species—The Little 17-Year Cicada**

HOLOTYPE, MALE.—Ohio, Delaware County, Orange Township, Brown Fruit Farm, June 1953 (Brood X), D. J. Borror and C. R. Reese. Body black above, primarily black beneath; appendages primarily reddish, lateral extensions of pronotum between eyes and wing bases black; prothoracic pleura black; wing veins yellowish-brown, radial W in forewings with dark brown veins and lightly clouded; apical tarsal segments reddish-brown, gradually darker toward their tips; abdominal tergites black; first four visible abdominal sternites black except for reddish margins that cover about half the width of the sternites and are not constricted medially; other abdominal sternites black; tergum and sternum reddish-black in the spiracular region; body length, 23.9 mm.; length of forewings, (L) 26.6, (R) 27.4 mm.; width of forewings, (L) 11.1, (R) 11.0 mm.; 6 timbal ribs per mm.; beginning with fourth rib from base; 11 complete timbal ribs; preserved in 70 per cent ethyl alcohol.

REPRESENTATIVE FEMALE.—Same data as male and preserved in same bottle. Same as male except body reddish-black above (teneral?); abdominal tergites reddish-black, darker at margins, except for light margin on eighth abdominal tergite; fourth abdominal sternite only about one-third reddish; body length, 25.5 mm.; length of forewings, (L, R) 29.3 mm.; width of forewings, (L) 11.9 mm., (R) 12.0 mm.

This is the smallest and least frequently collected 17-year cicada. It is morphologically distinguishable from *septendecim* by its entirely black pronotum and prothoracic pleura, and from *cassini* by (1) its tibiae, which are either entirely reddish or else have narrow black apical markings covering no more than one-third of the segment, and (2) the prominent reddish bands on its abdominal sternites. The call of *septendecula* is most distinctive; it is a series of short buzzes (usually 20–40), each buzz prefaced by a ticking sound. Near the end of each series, the buzzes are omitted and only ticks are produced.

***Magiccicada tredecim* (Walsh and Riley)—Riley's 13-Year Cicada**

Cicada tredecim Walsh and Riley, 1868, p. 63. "There are absolutely no perceptible specific differences between the 17-year and the 13-year broods, other than in the time of maturing; but whether or not, scientifically speaking, they are to be considered as specifically distinct, we shall, for convenience sake, name the 13-year brood *Cicada tredecim*, in contradistinction to *Cicada septendecim* [sic], the 17-year brood." The sibling of *septendecim* is figured.

NEOTYPE, MALE.—Missouri, Butler County, Little Black River, 23 May 1959 (Brood XIX), R. D. Alexander and T. E. Moore. Collected in copula with representative female described below. Same as *M. septendecim* except radial W in forewings heavily clouded; visible abdominal sternites entirely reddish; body length, 28.6 mm.; length of forewings, (L) 34.1 mm, (R) 34.0 mm.; width of forewings, (L, R) 13.0 mm.; 5 timbal ribs per mm.; 12 complete timbal ribs; preserved in 70 per cent ethyl alcohol.

REPRESENTATIVE FEMALE.—Same data as male and preserved in same bottle. Same as male except abdominal tergites black, eighth tergite with slightly noticeable orange border; visible abdominal sternites dark at base; pronotum with a puncture along the outer dorsal groove behind the left eye; body length, 33.4 mm.; length of forewings, (L) 36.6, (R) 36.5 mm.; width of forewings, (L) 14.3, (R) 14.2 mm.

This is the largest of the 13-year cicadas and like its sibling, *septendecim*, it is distinguished from the other 13-year species by reddish pronotal patches between the eyes and wing bases, reddish abdominal sternites, and the "Pharaoh" call of the males.

No type locality was given by Walsh and Riley in the original description, but this species was apparently described on the basis of their observations of a simultaneous emergence of Brood XIX of 13-year cicadas and Brood X of 17-year cicadas, probably in Missouri or Illinois.

Magicicada tredecassini, new species—Cassin's 13-year Cicada

HOLOTYPE, MALE.—Missouri, Butler County, Little Black River, 15 May 1959 (Brood XIX), R. D. Alexander and T. E. Moore. Same as *cassini* except reddish margins on second and fourth visible abdominal sternites not noticeably narrowed medially; left hind leg torn off at trochanter; body length, 25 mm.; length of forewings, (L), 29.5, (R) 29.4 mm.; width of forewings, (L) 11.1, (R) 11.2 mm.; six timbal ribs per mm.; 12 complete timbal ribs; preserved in 70 per cent ethyl alcohol.

REPRESENTATIVE FEMALE.—Same data as male and preserved in same bottle. Same as male except radial W in forewings more heavily clouded; reddish margins on abdominal sternites not noticeably narrowed; reddish margin on eighth abdominal tergite; left forewing with an apical triangular notch out of wing and with a dark spot at center of a malformation in median area of wing; body length, 25.6 mm.; length of forewings, (L) 30.9, (R) 31.5 mm.; width of forewings, (L) 12.0, (R) 12.1 mm.

Like its 17-year sibling, *tredecassini* is intermediate in size between the other two 13-year species, and it is distinguished from them by the same characteristics that distinguish *cassini* from the other two 17-year species.

Magicicada tredecula, new species—The Little 13-Year Cicada

HOLOTYPE, MALE.—Missouri, Butler County, 18 May 1959, R. D. Alexander and T. E. Moore, upland woods west of the Little Black River. Same as *M. septendecim* except apical tarsal segments are reddish-brown all the way to their tips; body length, 24.4 mm.; length of forewings, (L) 27.3, (R) 27.2 mm.; width of forewings, (L, R) 10.9 mm.; 7 timbal ribs per mm.; 13 complete timbal ribs; preserved in 70 per cent ethyl alcohol.

REPRESENTATIVE FEMALE.—Same data as male and preserved in same bottle. Same as

male except margin of eighth abdominal tergite reddish; body length, 26.9 mm.; length of forewings, (L) 30.6, (R) 30.5 mm.; width of forewings, (L) 11.3, (R) 11.4 mm.

In addition to the names discussed above, Distant (1906) lists *Cicada bruneosa* Wild (1852) as a synonym of *Tibicina* (= *Magicicada*) *septendecim* (Linnaeus). However, Wild did not refer to *bruneosa* as a periodical cicada, but rather stated that it "... appears here each year ..." Further, he compared the relative ease of capturing *septendecim* with the great difficulty in capturing *bruneosa*. It would appear that *bruneosa* is a misspelling of *bruenosa* which in turn was a common misspelling of Say's (1825) species *pruinosa*, belonging in the genus *Tibicen* Latreille. In any event it is evident that Wild was not intending to describe a new species. There are at least six species of *Tibicen* in the Baltimore, Maryland, area where he worked, including *T. pruinosa* (Say).

Many of the details of morphological, behavioral, and distributional differences among the six *Magicicada* species discussed above will be found in following portions of the paper, which deal individually with these items.

SPECIES IDENTIFICATION TABLE

A. THE -DECIM SIBLINGS

SIZE AND COLOR.—Large (27–33 mm. in body length); prothoracic pleura and lateral extensions of pronotum between eyes and wing bases reddish; abdominal sternites primarily reddish brown or yellow.

SONGS OF INDIVIDUALS.—Low-pitched, buzzing phrases of fairly even intensity lasting 1–3 seconds and terminating with a noticeable drop in pitch ("Phaaaaaaraoh"); no ticks involved; the quality of this sound can be imitated very closely by simultaneously humming and whistling.

SONG CHORUSES.—An even, monotonous roaring or buzzing noise produced most intensely in the morning; there are no regular or obvious fluctuations in intensity or pitch, especially on clear, calm days.

Life Cycles:

17-year	<i>septendecim</i> .
13-year	<i>tredecim</i> .

B. THE -CASSINI SIBLINGS

SIZE AND COLOR.—Intermediate in size (20–28 mm. in body length); prothoracic pleura and lateral extensions of pronotum between eyes and wing bases black; abdominal sternites all black, or a few sternites marked with a narrow band of reddish brown or yellow on the apical third—this band is often constricted or interrupted medially; ultimate tarsal segments with apical half or more black.

SONGS OF INDIVIDUALS.—Rapidly delivered tick series that last 2–3 seconds alternated with high-pitched, sibilant buzzes that last 1–3 seconds and noticeably rise, then fall in pitch and intensity.

SONG CHORUSES.—A shrill, sibilant buzzing sound produced most intensely in the afternoon and either regularly or irregularly rising and falling in intensity; the intensity pulsation is most pronounced on clear, calm days when it occurs regularly about 12 times a minute; during these times, ticks can sometimes be heard between the peaks of intensity in the buzzing sound.

Life Cycles:

17-year	<i>cassini</i> .
13-year	<i>tredecassini</i> .

C. THE -DECUA SIBLINGS

SIZE AND COLOR.—Small (19–27 mm. in body length); prothoracic pleura and lateral extensions of pronotum between eyes and wing bases black; abdominal sternites black basally with a broad, transverse, apical band of reddish yellow or brown covering about half of each sternite and not interrupted medially; ultimate tarsal segments entirely reddish brown or yellow, or with a narrow black band covering no more than one-third of each segment.

SONGS OF INDIVIDUALS.—High-pitched, brief phrases (each like a very short buzz and tick delivered together) produced at rates of 3–5 per second in series of 20–40; the final phrases in each series are brief because they lack the short buzz; the entire call lasts 7–10 seconds.

SONG CHORUSES.—A more or less continuous repeating of short, separated buzzes or “zzzt” sounds, produced without regular fluctuations in pitch or intensity; most intense around mid-day (one should attempt to locate individuals to confirm the presence of this song because of the possibility of confusion with the courtship singing of -cassini siblings).

Life Cycles:

17-year	<i>septendecula</i> .
13-year	<i>tredecula</i> .

DISCUSSION OF BROODS

GENERAL

Nearly all of the published records (500 +) of periodical cicadas—including Marlatt's extensive studies—have failed to distinguish species, other than to separate 17-year cicadas from 13-year cicadas. Rarely has enough

information been given to enable subsequent workers to determine which species were involved. The -decula siblings have not been recognized at all, except for the unpublished observations of an amateur naturalist, the late Conrad Roth of Portsmouth, Ohio. Consequently, it is desirable to begin a thorough study of the nature and distribution of species within the broods. We have studied, in the field, Broods I, XIII, XIV, and XIX, and we have searched in vain, both in the field and among museum collections, for individuals emerging between 1956 and 1961 which would be part of the literature-designated Broods XV, XVI, XVII, XX, and XXI. The distribution maps in Figs. 1-3 are the result of examination of more than 10,000 specimens, and all locality records are based on specimens or field observations; no literature records are included. The presence of three species has been verified for 12 different broods as follows: 17-year cicadas—I, II, III, IV, V, IX, X, XIII, XIV; 13-year cicadas—XIX, XXIII, XXIV. In several cases, specimens representing three species are available from the same localities for two, three, or more successive emergences of the same brood. In addition, *septendecim* and *cassini* have been identified for emergence years that would represent Broods VI, VIII, and XII; *septendecim* and *septendecula* for years representing Brood XVII; and *tredecim* and *tredecula* for years representing Broods XVIII and XXII (cf. Table 2). Paucity of specimens, incompleteness of species representation, and questionable literature records raise doubt as to the significance of the remaining 12 broods designated by Marlatt (VII, XI, XV, XVI, XX, XXI, XXV-XXX). Most likely, specimens collected on years that would correspond to these "broods" are really stragglers that have failed to produce self-perpetuating broods. Over a period of 100 years or so, a very low rate of straggling could result in several specimens for an off year. Possibly, some of these broods may have recently become extinct, or may still remain as scattered remnants of previously more abundant ones.

We have been especially interested in the problem of stragglers, and so have tried on every possible occasion to locate cicadas on off years. We have been successful only five times, three of these relating to Brood X. Moore heard one *septendecim* male briefly in a woodlot near Danville, Illinois (Vermilion County), in 1952, the year before the heavy emergence there; in 1954, he heard two or three *septendecim* phrases in three different locations perhaps a half mile apart in the same woods on five different occasions in as many days. Alexander heard a single *septendecim* phrase during a two-day collecting trip in Hocking County, Ohio, June 4-5, 1954, one year after Brood X had emerged there. In June 1961, we found a recently cast *septendecim* nymphal skin in Jackson County, Ohio; J. N. Knull and Edward S. Thomas both supplied us with records of *septendecim* in Hocking

County, Ohio, in May 1961. It is interesting that we have heard no species other than *septendecim* in these situations.

Alexander has made the following unsuccessful searches for stragglers on years following heavy emergences: DuPage and Cook counties, Illinois, June 1957 (after Brood XIII); Pickaway and Ross counties, Ohio, June 1958 (after Brood XIV); Piatt, Macon, Johnson, and Williamson counties, Illinois, and Davidson and Cheatham counties, Tennessee, June 1960 (after Brood XIX). Moore unsuccessfully searched for stragglers of Brood XIII in early June 1957 in Lake County, Indiana, and in Champaign, Cook, Grundy, Kankakee, LaSalle, Livingston, and Woodford counties, Illinois.

A negative listening record made at the right time of day and under proper weather conditions is much more significant than failure to collect specimens. The few records that we have suggest that straggling is not significant today, in spite of the high density of the populations studied. In addition to the obvious rigidity in length of life cycles, the failure of successive broods to broadly overlap geographically suggests that competitive factors reduce the chances of successful brood establishment through straggling.

Periodical cicadas probably have been taken on more different years in southern Ohio than in any other location. This may be largely because E. S. Thomas, J. N. Knull, and other Ohio entomologists have kept this area under close surveillance for many years, and because their records are available to us. We have reliable reports of at least a few cicadas in the area of Hocking, Fairfield, Athens, and Jackson counties for the following years: 1944, 1948 (Brood V), 1949, 1952, 1953 (Brood X), 1954, 1955, 1956, 1957 (Brood XIV), and 1961; or for ten different years across a period of 18 years, during which only three large broods occurred there. It is possible that this area is not unusual, and that more careful records will show that many locations have some periodical cicadas on several different years. But, as will be pointed out later, it seems also possible that southern Ohio is unusual, and that the large number of stragglers there is related to the role this area played in brood formation during the Pleistocene.

The following summaries of field observations on Broods I, XIII, XIV, and XIX, bring our study of the broods up to date and take into account the presence of three species in each case. Information concerning the other broods will be published as it accumulates in an effort to provide detailed information through at least one complete cycle of 17 years.

BROOD XIII: 17-YEAR CICADAS

Our observations on this brood, carried out in northern Illinois in 1956, have already been published (Moore and Alexander, 1958). We distin-

guished *cassini* and *septendecim*, but did not locate *septendecula*. We have found no specimens of *septendecula* in the several quarts of cicadas we collected in 1956, and, therefore, believe that it was not present in the areas where we worked. Only a few individuals of *septendecula* have been found in the other material of this brood that we have examined, and all were from areas considerably south of the four counties where we worked. The chances of our having missed the species are very slight; in 1959 we were aware of *tredecula* in Butler County, Missouri, within a few minutes after entering the first woods containing cicadas ("lowland forest," Fig. 4), although this species was not abundant there, it was completely new to us, and we had not in any way anticipated its presence.

In northern Illinois, *septendecim* is definitely more abundant than *cassini* in Brood XIII; *cassini* was not sufficiently dense in 1956 in the areas where we studied it to achieve the striking synchrony we have since observed repeatedly, both in southern Ohio in Brood XIV (Alexander and Moore, 1958) and in Tennessee, Missouri, Arkansas, and Illinois in Brood XIX (*tredecassini*).

The three *septendecim* specimens shown from Ohio, Virginia, and Staten Island, New York, for the 1956 emergence of Brood XIII (Fig. 1) most likely represent individuals that emerged a year early for Brood XIV.

SUMMARY OF LOCALITIES

ILLINOIS.—Champaign Co.: Urbana, May 1956, *septendecim*. Cook Co.: Brookfield, 1956, *septendecim*; Orland Park to La Grange, June 1956, *septendecim*, *cassini*; Chicago Heights, May 1956, *septendecim*, *cassini*; River Grove, June 1956, *septendecim*, *cassini*; Western Springs, 17 June 1956, *septendecim*, *cassini*; Palos Park, 16 June 1956, *septendecim*, *cassini*, 30 Aug. 1922, *septendecim*; Chicago, 18 June 1939, *septendecim*, 5 July 1939, *septendecim*, 1 Aug. 1956, *septendecim*, 11 June 1888, *septendecim*; Willow Springs, 30 May 1922, *septendecim*; Park Forest, 5 June 1956, *septendecim*; Worth, 12 June 1956, *septendecim*. DeKalb Co.: Sandwich, 1956, *septendecim*. DuPage Co.: Downers Grove, June 1956, *septendecim*, *cassini*; Hinsdale, May 1956, *septendecim*, *cassini*. Edgar Co.: Paris, 1956, *septendecim*. Grundy Co.: Morris, June 1956, *septendecim*, *cassini*. Kane Co.: S of Elburn, 1956, *septendecim*. Kankakee Co.: Bourbonnais, 17 June 1956, *septendecim*, *cassini*. Lake Co.: Ravinia, 2 July 1905, *septendecim*; Lake Forest, May 1905, *septendecim*; Highland Park, 1956, *septendecim*; Libertyville, 1956, *septendecim*. La Salle Co.: Ottawa, June 1956, *septendecim*, *cassini*; NE of Ottawa, 18 June 1956, *septendecim*, *cassini*; Marseilles, 18 June 1956, *septendecim*, *cassini*. Lee Co.: Lowell Park, 18 June 1956, *septendecim*. Livingston Co.: Dwight, June 1956, *cassini*; Pontiac, 18 June 1956, *septendecim*, *cassini*, *septendecula*. Marshall Co.: near Henry, 28 May 1956, *septendecim*. Menard Co.: N of Greenview, 1956, *septendecim*. McHenry Co.: Algonquin, 12 June 1905, *septendecim*. McLean Co.: Kappa, on both sides of river, June 1956, *septendecim*, *cassini*. Ogle Co.: Oregon, June 1905, *septendecim*; Sinnissippi State Forest, near Oregon, 18 June 1956, *septendecim*. Peoria Co.: Peoria, 4 June 1905, *septendecim*, 8 June 1956, *septendecim*. Piatt Co.: White Heath, 29 May 1933, *septendecim*. Putnam Co.: Magnolia, 13 June 1956, *septendecim*. Rock Island Co.: Moline, 1956, *septendecim*. Sangamon Co.: NE of Spring-

field, 1956, *cassini*. Will Co.: Crete, 22 June 1888, *septendecim*; Joliet, 1956, *septendecim*; Mokona, 1956, *septendecim*. Woodford Co.: Kappa, on both sides of river, June 1956, *septendecim*, *cassini*. Woodward Co.: Mackinaw River along U.S. 150, June 1956, *septendecim*. County Unknown: Mt. Greenwood, 9 June 1956, *septendecim*.

INDIANA.—Lake Co.: Crown Point, 11 July 1956, *septendecim*, *cassini*; June 1939, *septendecim*. La Porte Co.: 16 July 1956, *septendecim*. Porter Co.: 11 July 1956, *septendecim*.

IOWA.—Cedar Co.: Tipton, July 1888, *septendecim*. Dubuque Co.: Dubuque, 30 June 1888, *septendecim*. Johnson Co.: Iowa City, 12 June 1956, *septendecim*, *septendecula*; 5 mi. S of Iowa City, 12 June 1956, *septendecim*, *cassini*, *septendecula*?. Linn Co.: Fairfax, July 1888, *septendecim*; Pallisade State Park, 20 June 1956, *septendecim*. Scott Co.: Davenport, 12 June 1871, *septendecim*. Tama Co.: 23 June 1956, *septendecim*, *cassini*, *septendecula*?

NEW YORK.—Richmond Co.: Staten Island, 24 June 1888, *septendecim*.

OHIO.—Hocking Co.: May 1956, *septendecim*. Pickaway Co.: Washington, 28 May 1956, *septendecim*.

VIRGINIA.—Montgomery Co.: 30 May 1956, *septendecim*.

WISCONSIN.—Dane Co.: Madison, May–June 1939, *septendecim*. Grant Co.: 1956, *septendecim*. Green Co.: Brodhead, 8 June 1922, *septendecim*. Iowa Co.: June 1939, *septendecim*. Lafayette Co.: 1956, *septendecim*. Richmond Co.: 1956, *septendecim*. Rock Co.: Beloit, 9 June 1956, *septendecim*, *cassini*, May 1956, *septendecim*, *cassini*; June 1934, *septendecim*. Walworth Co.: Lake Geneva, June 1939, *septendecim*. County Unknown: White Oak Springs, 28 June 1888, *septendecim*.

BROOD XIV: 17-YEAR CICADAS

Brood XIV is of special historical interest because it was the 1634 emergence of this brood that prompted the first published account of periodical cicadas—an anonymous letter quoted by Oldenberg (1666). Our 1957 study of Brood XIV was particularly concerned with the details of acoustical behavior (Alexander and Moore, 1958), and so was concentrated in one woods in Ross County, Ohio. In addition to several trips by Alexander to determine the northern brood limits in southern and eastern Ohio, four more extensive field trips were made during which the participants listened for and collected 17-year cicadas. During late May, D. J. Borror drove from central Ohio to Charleston, West Virginia, and back; during May 20–24, H. H. Ross and L. J. Stannard drove from eastcentral Illinois through southeastern Kentucky into southwestern Missouri and back; during June 7–9, Moore drove from southern Michigan through northwestern Ohio, northern Indiana, and northeastern Illinois, from south of Chicago to Champaign and Vermilion counties; during June 17–22, Moore drove from southern Michigan through central Maryland to the District of Columbia, down the Appalachian Mountains on the Virginia and North Carolina side to Great Smoky Mountain National Park, back north along the western slope of the Appalachians in Tennessee and Kentucky, through central Ohio

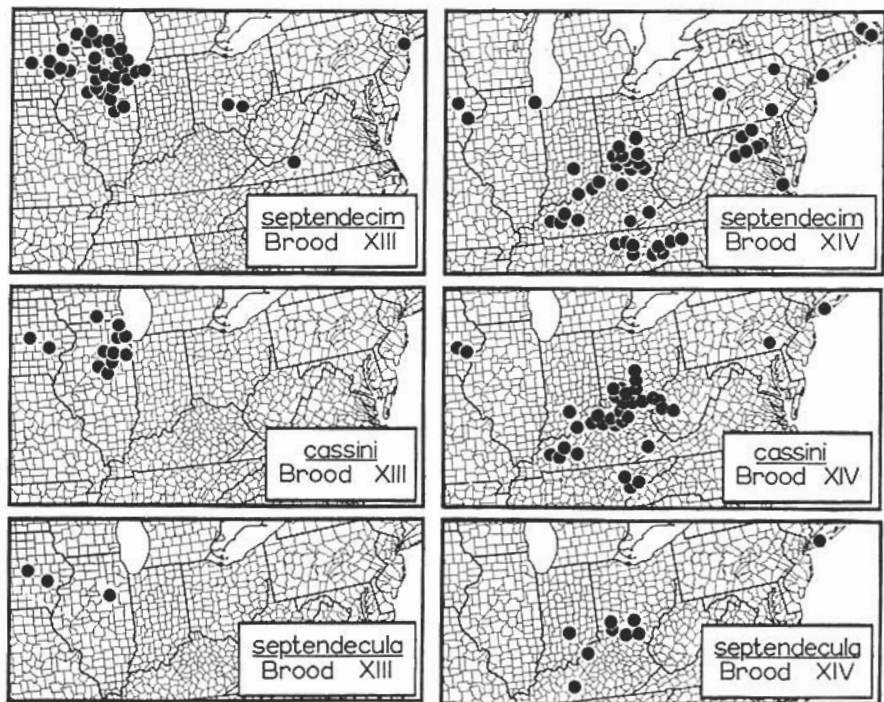


FIG. 1. Distribution of Broods XIII and XIV, 17-year cicadas.

and back to Michigan. The records from these trips and from subsequent examination of material in collections from other years are plotted by county in Fig. 1. Only in Ohio, however, are we fairly certain that an accurate picture of the brood limit is shown.

In 1957, Edward S. Thomas of The Ohio State Museum told Alexander that the late Conrad Roth of Portsmouth, Ohio, had brought to him three different kinds of cicadas which he had associated with three different songs in the 1940 emergence of Brood XIV in Adams County, Ohio. Dr. Thomas did not recall then what Roth had done with his specimens, but Moore found them in 1960 in the U.S. National Museum. In 1948, Roth sent additional specimens from Brood V to the U.S. National Museum, 40 *cassini* and 11 *septendecula*, packaged separately, and wrote that "the ones with the orange beneath [*septendecula*] are not nearly so plentiful as the ones which are black beneath [*cassini*]." Although he had sent all three species in 1940, by this time he was concentrating on the two smaller species, referring to them as "phases" of *cassini*. Thus, both of the species separations among 17-year cicadas were initially made by amateur naturalists in south-

ern Ohio: *cassini* from *septendecim* in Brood V, 1829, by Hildreth (1830) in Washington County, and *septendecula* from *cassini* in Brood XIV, 1940, by Roth in Adams County.

After listening to tape recordings of *Magicalicada* songs in 1957, Thomas believed that the courtship song of *cassini*—which superficially resembles the calling song of *septendecula*—might have been the third song described to him by Roth. Nevertheless, we were aware of Roth's observations and made a special effort to find a third species in 1957. We were unsuccessful, and we now know that this was because our study area in Ross County, Ohio, was at the very northern limit of the third species, *septendecula*. In checking over our specimens and field notes following the finding of three species in the 1959 emergence of 13-year cicadas, we discovered many specimens of *septendecula* from southern Ohio localities worked by Alexander (but only before singing had begun). As noted earlier, there was one accurate description of the *septendecula* song from Ross County in Alexander's field notes under "aberrant *cassini* songs." No specimens of *septendecula* have been found in material taken from this brood in Ross County or farther north in Ohio.

W. T. Davis (1924) indicated that both *septendecim* and *cassini* appeared in the 1923 emergence of Brood XIV on Long Island, New York; in collections we have found specimens of all three species from there. We have no evidence of the occurrence of 17-year cicadas on Long Island in 1957. The Illinois and Iowa localities for *septendecim* and *cassini* (Fig. 1) are based on single specimens and are most likely stragglers from the previous year's emergence of Brood XIII.

The earliest dates of emergence recorded in 1957 are May 6–7 in Kentucky, May 7–10 in Virginia, and May 17 in Ohio. The latest dates for which live adults are known are June 21 in Kentucky (all were dead by this time in the Norris Dam area of Tennessee and large numbers were dead on the ground in Letcher County, Kentucky), June 18 in North Carolina (all were dead by June 20 in the Asheville area), and June 22 in Ohio (large numbers still active).

Our information indicates that the approximate area of heavy emergence of both species in 1957 was bounded by Ross and Clermont counties, Ohio, Harrison County, Indiana, Hopkins and Warren counties, Kentucky, Morgan and Blount counties, Tennessee, Rutherford and Wilkes counties, North Carolina, Letcher County, Kentucky, and Kanawha to Mason counties, West Virginia. The Woods Hole area of Barnstable County, Massachusetts, experienced a heavy emergence, according to P. A. Wright and A. M. Elliott. We do not know the extent of emergence in the mountainous areas of West Virginia, Virginia, and Pennsylvania.

SUMMARY OF LOCALITIES

DISTRICT OF COLUMBIA.—13 May 1957, *septendecim*; 11 June 1906, *septendecim*.

ILLINOIS.—Cook Co.: Chicago, 17 June 1957, *septendecim*.

INDIANA.—Brown Co.: 19 May 1957, *septendecula*; Nashville, May, 1957, *septendecim*, 9 June 1957, *septendecim*. Harrison Co.: 9 mi. S of Corydon, 25 May 1957, *septendecim*. Lawrence Co.: 17 May 1957, *cassini*.

IOWA.—Johnson Co.: Iowa City, 1922, *cassini*. Linn Co.: Fairfax, 1889, *septendecim*. Muscatine Co.: Muscatine, 26 May 1940, *septendecim*, *cassini*.

KENTUCKY.—Bourbon Co.: 12 June 1957, *cassini*. Edmonson Co.: Mammoth Cave National Park, 20 May 1957, *septendecim*, *cassini*, *septendecula*. Fleming Co.: 12 June 1957, *cassini*; S of Flemingsburg, 31 May 1957, *cassini*. Franklin Co.: 12 June 1957, *cassini*. Knox Co.: Kayjay, 12 June 1940, *septendecim*. Letcher Co.: 13 mi. SE of Whitaker (near Whitesburg), Pine Mts., ca. 1000 ft. elev., 21 June 1957, *septendecim*, *cassini*. Mason Co.: 12 June 1957, *cassini*. Nicholas Co.: 12 June 1957, *septendecim*, *cassini*; Blue Lick Springs, 5 June 1957, *cassini*. Oldham Co.: Pewee Valley, 16 May 1957, *septendecim*, *cassini*, *septendecula*. Scott Co.: 12 June 1957, *cassini*.

MARYLAND.—Frederick Co.: 3.2 mi. W of Emmitsburg, 18 June 1957, *septendecim*.

MASSACHUSETTS.—Barnstable Co.: Woods Hole, 8 June–4 July 1957, *septendecim*; Osterville, June 1957, *septendecim*. Plymouth Co.: Plymouth, 3 July 1906, *septendecim*.

NEW YORK.—Suffolk Co.: Wyandanch, 25 June 1923, *septendecim*, *cassini*, *septendecula*; Yaphank, 15 June 1923, *septendecim*; Cold Spring Harbor, 14 June 1940, *septendecim*. County Unknown: Dix Hills, Long Island, 6 July 1940, *septendecim*, *septendecula*.

NORTH CAROLINA.—Buncombe Co.: Blue Ridge Parkway, 1.5 mi. N of U.S. 70, 2500 ft. elev., 20 June 1957, *septendecim* (all dead), 9 May 1957, *septendecim*; Asheville, 11 May 1957, *septendecim*. Caldwell Co.: 16 May 1957, *septendecim*; 8 May 1957, *septendecim*. Haywood Co.: 15 May 1957, *septendecim*. Madison Co.: 15 May 1957, *septendecim*. Mitchell Co.: Penland, 3000 ft. elev., 18–19 June 1957, *septendecim*.

OHIO.—Adams Co.: Duncansville, 23 June 1940, *septendecim*, *cassini*, *septendecula*; West Union, 1 June 1940, *septendecim*, *cassini*, *septendecula*; 3 mi. W of Manchester, 31 May 1957, *cassini*; Serpent Mounds, 11 July 1940, *cassini*; Jefferson Township, 11 July 1940, *cassini*. Brown Co.: Aberdeen, 31 May–12 June 1957, *cassini*. Clermont Co.: June 1957, *septendecim*, *cassini*, *septendecula*?; 22 May 1957, *septendecim*, *cassini*. Clinton Co.: 4 mi. S of Wilmington, 1 July 1957, *septendecim*. Franklin Co.: 27 May 1957, *septendecim*, *cassini*. Gallia Co.: Rio Grande to Gallipolis, June 1957, *cassini*. Highland Co.: Fort Hill, 12 May 1957, *septendecim*; 12–25 June 1957, *cassini*. Pickaway Co.: where Deer Creek crosses Route 138, 6 June 1957, *cassini*. Pike Co.: Lake White, 23 June 1940, *septendecim*; Morgantown, 23 June 1940, *septendecim*. Ross Co.: SE of Clarksburg, June 1957, *septendecim*, *cassini*, *septendecula*; 3 mi. N of Chillicothe, 16 June 1957, *septendecim*, *cassini*. Scioto Co.: Nile Township, 11 June 1940, *septendecim*, *cassini*, *septendecula*; Portsmouth, 24 May 1957, *septendecim*, *cassini*; June 1940, *septendecim*, *cassini*, *septendecula*. Warren Co.: Fort Ancient, 18–27 June 1940, *septendecim*, *cassini*, *septendecula*; 5 mi. S of Clarks-ville on Route 132, 17–22 May 1957, *septendecim*, *cassini*; June 1957, *septendecim*, *cassini*, *septendecula*? County Unknown: June 1940, *septendecim*, *cassini*, *septendecula*.

PENNSYLVANIA.—Clearfield Co.: Shawville, 23 July 1940, *septendecim*. Lackawanna Co.: Scranton, 1906, *septendecim*. Lancaster Co.: Lancaster, 27 May 1889, *septendecim*, *cassini*.

TENNESSEE.—Anderson Co.: Norris Dam, 17 May 1957, *septendecim*, *cassini*; 6 mi. SE of Norris Dam, 21 June 1957, *septendecim*, *cassini*. Blount Co.: Cades Cove, Great Smoky

Mountain National Park, 1800 ft. elev., 26 May 1940, *septendecim* (verified again for June, 1957, by A. Stupka after comparing recorded congregational songs); 23 June 1889, *septendecim*. Morgan Co.: Burrville, 19 May 1957, *septendecim*. Sevier Co.: Dry Valley, Tuckaleechee Cove, Great Smoky Mountain National Park, 1500 ft. elev., 26 May 1940, *septendecim*, *cassini* (both species verified again for June, 1957, by A. Stupka after comparing recorded congregational songs).

VIRGINIA.—Fairfax Co.: Vienna, 27 May 1940, *septendecim*. Fauquier Co.: Warrenton, 15–17 May 1923, *septendecim*. Rappahannock Co.: Amissville, June 1889, *septendecim*. York Co.: Pine Swamp, 1889, *septendecim*.

WEST VIRGINIA.—Jefferson Co.: Harpers Ferry, 26 May 1889, *septendecim*. Kanawha Co.: June 1957, *cassini*. Mason Co.: June 1957, *cassini*. Putnam Co.: June 1957, *cassini*.

BROOD XIX: 13-YEAR CICADAS

The spring of 1959 was wet and cool, and the emergence of Brood XIX may have been delayed. On May 13 and 14, we drove and listened in Illinois from Kankakee County south through Alexander County without hearing any cicadas. Still driving south on May 15, we first heard cicadas singing along the Little Black River in Butler County, Missouri. In Piatt County, in central Illinois, cicadas were heard singing first about May 28.

On May 17 and 18, we drove and listened from Butler County, Missouri, south through Clay, Randolph, Lawrence, Jackson, White, Lonoke, and Pulaski counties, Arkansas; then north through Faulkner, Cleburne, *Independence*, *Sharp*, and *Fulton* counties, Arkansas, to *Oregon*, *Ripley*, and *Butler* counties, Missouri. On May 20, we drove from *Butler* County through Dunklin and New Madrid counties, Missouri; through Lake, Obion, Gibson, Carroll, Henderson, Chester, McNairy, and Hardin counties, Tennessee; then south into Lauderdale County, Alabama, and north again through Wayne, Lawrence, *Maury*, *Williamson*, *Davidson*, *Cheatham*, Montgomery, and Stewart counties, Tennessee. Next we drove through *Trigg*, Marshall, and McCracken counties, Kentucky, and through Massac, *Johnson*, *Williamson*, Franklin, Jefferson, Marion, Clinton, Washington, and Randolph counties, Illinois. On May 23, we drove through *Perry*, *Bollinger*, Stoddard, Cape Girardeau, and Scott counties, Missouri, and arrived back in *Butler* County. Cicadas were found in all italicized counties above, as shown in Figure 2. In *Maury*, *Williamson*, *Davidson*, and *Cheatham* counties, Tennessee, we found tremendous emergences of *tredecassini* and spent two days driving several hundred miles, threading in and out of the emergence area, determining the exact limits of the brood west of Nashville, and attempting to locate *tredecula* somewhere in the area. Song choruses of *tredecassini* were recorded fluctuating (in synchrony) between 89 and 96 decibels, 20 feet from the nearest cicada; this was the most intense insect chorus we have ever heard, and *tredecassini* was more abundant here than any cicada

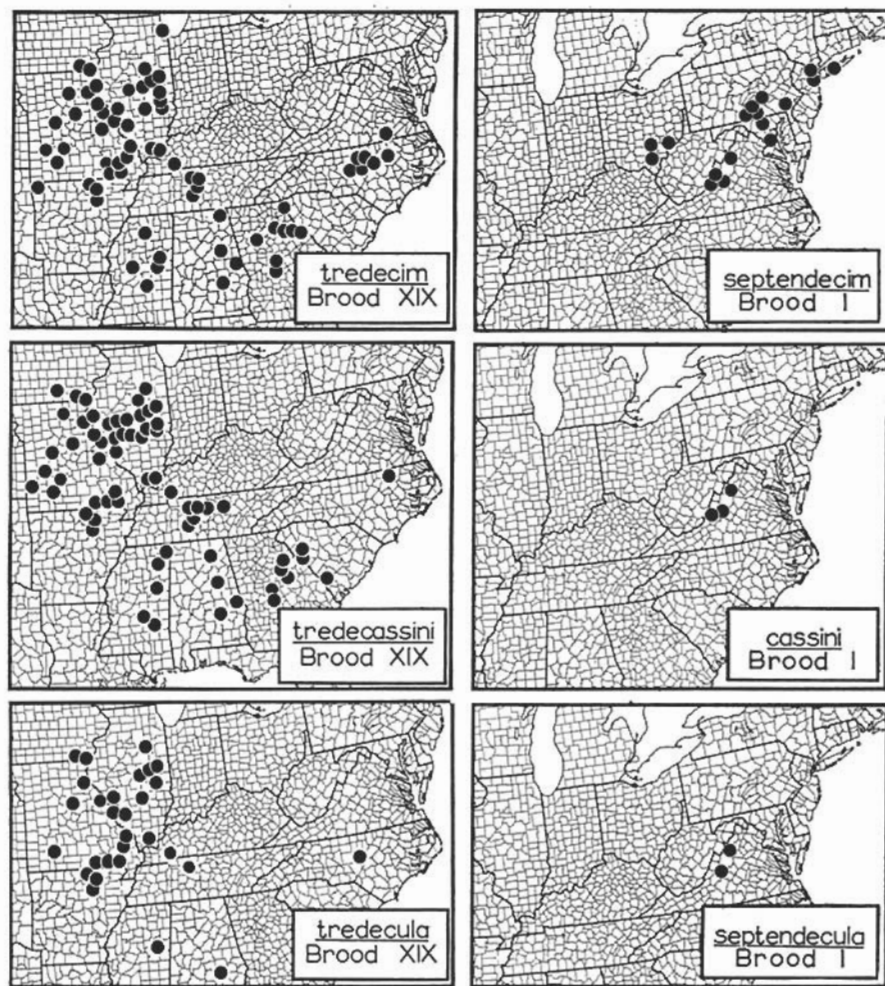


FIG. 2. Distribution of Brood XIX, 13-year cicadas, and Brood I, 17-year cicadas.

encountered elsewhere. We could not find a single strong chorus of *tredecim*, though this species was present everywhere in low numbers. We did not locate any *tredecula* individuals until we left Nashville driving northwest into Cheatham County; near Ashland City we finally heard a small chorus and tape-recorded a single individual—the first we had heard in three days of driving through periodical cicada choruses.

Our records of *tredecassini* and *tredecula* for Oregon County, Missouri, were obtained while driving through the area too fast to hear *tredecim*. One must often slow to 15 or 20 miles per hour to hear *tredecim*, even when

it is near the road, while the other two species can usually be distinguished clearly at 40–50 miles per hour.

Figure 2 includes records compiled by examination of specimens from various collections subsequent to the field work. The Cook County, Illinois, record is based on a single specimen labelled "1907." If this date is correct, the specimen may have been a straggler of Brood XIII, which emerged in 1905. However, we are skeptical of single specimen records from unusual years or places; these seem to turn up most often in student collections with university town labels! Because of the rarity and importance of positive records of stragglers, anyone hearing or collecting what appear to be periodical cicadas during an unexpected year or season should make a strong effort to confirm and publish the record.

SUMMARY OF LOCALITIES

ALABAMA.—Chambers Co.: Fairfax, 8 May 1933, 20 April 1933, *tredecim*. Jackson Co.: 9 May 1959, *tredecim*. Lee Co.: May 1959, *tredecassini*. Marshall Co.: May 1959, *tredecassini*. Montgomery Co.: Montgomery, 12–19 May 1959, *tredecim*, *tredecassini*, *tredecula*. Talladega Co.: Sylacauga, 11 May 1959, *tredecim*, *tredecassini*.

ARKANSAS.—Benton Co.: Siloam Springs, 22 May 1907, *tredecim*. Fulton Co.: 19 May 1959, *tredecim*, *tredecassini*, *tredecula*. Independence Co.: 19 May 1959, *tredecim*, *tredecassini*, *tredecula*. Sharpe Co.: 19 May 1959, *tredecim*, *tredecassini*, *tredecula*.

GEORGIA.—Bibb Co.: Macon, 11 June 1920, *tredecassini*; 10 mi. E Macon, 8 May 1933, *tredecim*. Fulton Co.: Atlanta, 7–10 May 1907, 17 May 1933, 13 May 1946, *tredecim*. Greene Co.: 5 May 1959, *tredecassini*. Hancock Co.: 12 May 1959, *tredecassini*. Houston Co.: Perry, 14 May 1959, *tredecim*, *tredecassini*. Lincoln Co.: 16 May 1959, *tredecim*. Ogle Co.: 12 May 1959, *tredecim*. Oglethorpe Co.: Lexington, 12 May 1959, *tredecim*, *tredecassini*; 5 mi. SE of Stevens, 8 May 1946, *tredecim*. Wilkes Co.: 1 May 1959, *tredecim*. County Unknown: Buffalo Creek, 12 May 1959, *tredecassini*.

ILLINOIS.—Adams Co.: near Camp Point, June 1959, *tredecassini*; Lima, 27 May 1959, *tredecassini*; 8 mi. S of Clayton, 8 June 1959, *tredecim*, *tredecassini*. Champaign Co.: St. Joseph, 31 May 1959, *tredecassini*; Mahomet, Lake of the Woods, 28 May 1959, *tredecassini*; 3½ mi. NE of Mahomet, 23 June 1959, *tredecassini*, *tredecula*; Champaign, 13 June 1959, *tredecassini*; Homer, 25 June 1907, 29 May 1959, *tredecim*, *tredecassini*; Urbana, 29–30 May 1959, first singing dates, *tredecim*, *tredecassini*, 9 June 1946, *tredecassini*, 31 June 1894, *tredecassini*; Mahomet, 1920, 22 May 1933, *tredecim*. Coles Co.: Mattoon, 4 June 1933, *tredecassini*; Charleston, 30 May 1933, *tredecassini*, 1907, *tredecim*, *tredecula*, May 1946, *tredecim*, *tredecassini*, *tredecula*, 19–26 May 1959, *tredecim*, *tredecassini*, *tredecula*; Sargent's Woods, 25 May 1959, *tredecim*, *tredecassini*, *tredecula*. Cook Co.: Riverside, June 1907, *tredecim*. Cumberland Co.: Jct. Rts. 45 and 121, 4 June 1959, *tredecim*, *tredecassini*. Fayette Co.: Lone Grove Twp., 23 May 1959, *tredecim*, *tredecassini*, *tredecula*. Jasper Co.: Newton, 2 June 1933, *tredecim*. Jersey Co.: Elsah, 13 April 1946, *tredecula*; Grafton, 5 June 1959, *tredecim*, *tredecassini*; Dow, 12 June 1959, *tredecim*, *tredecassini*. Johnson Co.: 23 May 1959, *tredecim*, *tredecassini*, *tredecula*; Parker, 12 June 1907, *tredecim*. Livingston Co.: Forrest, 20 June 1933, *tredecassini*, *tredecula*. McLean Co.: Leroy, 28 June 1907, *tredecim*, *tredecassini*. Macon Co.: Decatur, 27 May 1933, *tredecim*, *tredecassini*, *tredecula*, June 1959, *tredecim*, *tredecassini*, *tredecula*. Macoupin Co.: Beaver Dam St. Park, 8 mi.

SW of Carlinville, 16 June 1959, *tredecassini*. Montgomery Co.: 1 mi NW of Hillsboro, 16 June 1959, *tredecassini*. Morgan Co.: Jacksonville, 29 May 1959, *tredecassini*. Piatt Co.: Allerton Park, 29 May 1959, *tredecim*, *tredecassini*, *tredecula*; White Heath, 29 May 1933, *tredecim*, 3 June 1959, *tredecim*, *tredecassini*, *tredecula*; Monticello, 20 July 1946, *tredecassini*, 3 June 1959, *tredecim*, *tredecassini*, *tredecula*; Lodge Park 29-30 May 1959, *tredecim*, *tredecassini*, *tredecula*; Seymour, 30 May 1959, *tredecim*, *tredecassini*, *tredecula*; N of Monticello, 18 June 1959, *tredecassini*. Pope Co.: Herod, 14 May 1946, *tredecassini*; Eddyville, 14 May 1946, *tredecim*. St. Clair Co.: Freeburg, 24 May 1959, *tredecim*, *tredecula*. Sangamon Co.: Springfield, 31 May 1933, *tredecim*. Scott Co.: Bluffs, 26 May 1959, *tredecassini*. Shelby Co.: N of Herrick, 7 July 1959, *tredecassini*.

IOWA.—Lee Co.: 3 June 1946, *tredecassini*; 14 mi. NW of Keokuk, 2 June 1959, *tredecim*, *tredecassini*; 3 mi. W of Ft. Madison, 2 June 1959, *tredecim*, *tredecassini*, *tredecula*; Keokuk, 2 June 1959, 12 June 1959, *tredecim*, *tredecassini*, *tredecula*. Monroe Co.: 12 mi. SE of Albia, 12 June 1959, *tredecassini*. Van Buren Co.: Keosauqua, 3 June 1959, *tredecim*, *tredecassini*, *tredecula*, 14 June 1946, *tredecassini*.

KENTUCKY.—Trigg Co.: 23 May 1959, *tredecim*, *tredecassini*, *tredecula*.

MISSISSIPPI.—Holmes Co.: West, 18 May 1959, 13 April 1959, *tredecim*. Jasper Co.: Rose Hill, 4 June 1920, *tredecassini*. Lafayette Co.: 28 July 1920, *tredecim*. Lee Co.: Baldwyn, 5 June 1920, *tredecassini*. Oktibbeha Co.: State Agr. College, 2-12 May 1959, *tredecim*, 20 April 1959, *tredecim*, 1920, *tredecassini*, *tredecula*, 27 April 1920, *tredecula*, 14 May 1907, *tredecassini*. Scott Co.: Beach, 7 June 1920, *tredecim*; Hillsboro, 4 June 1920, *tredecim*; Forest, 1 June 1920, *tredecassini*. Tishomingo Co.: Cook's Landing, near Iuka, 9 June 1933, *tredecassini*. Winston Co.: Louisville, 12 June 1920, *tredecim*.

MISSOURI.—Adair Co.: Kirksville, June 1959, *tredecassini*. Barton Co.: Lamar, 5 June 1959, *tredecassini*. Bollinger Co.: 23 May 1959, *tredecim*, *tredecula*. Boone Co.: 20 May 1959, *tredecim*, *tredecassini*, 1933, *tredecula*; Columbia, July 1920, *tredecassini*, 23 May 1933, *tredecim*, *tredecula*, 30 April 1946, *tredecassini*, *tredecula*. Butler Co.: 15-25 May 1959, *tredecim*, *tredecassini*, *tredecula*. Carter Co.: Grandin, 15 June 1907, *tredecim*. Cedar Co.: 7 June 1959, *tredecim*. Dallas Co.: 7 June 1959, *tredecim*, *tredecassini*. Franklin Co.: Gray Summit, 28 May 1933, *tredecassini*; St. Albens, 27 May 1933, *tredecim*, *tredecassini*, *tredecula*? Green Co.: Willard, 6 June 1920, *tredecim*, *tredecula*, 30 May 1920, *tredecim*, *tredecassini*, *tredecula*, 13 June 1920, *tredecim*, *tredecassini*, *tredecula*. Lincoln Co.: Famous, 20 May 1933, *tredecim*, *tredecassini*, *tredecula*. Macon Co.: Macon, 11 June 1920, *tredecim*. Marion Co.: Hannibal, 1933, *tredecim*, *tredecassini*, *tredecula*. Oregon Co.: 21-23 May 1959, *tredecassini*, *tredecula*. Perry Co.: 21-23 May 1959, *tredecim*, *tredecula*. Pettis Co.: La Monte, 2 June 1920, *tredecim*, *tredecassini*. Pike Co.: New Hartford, 6 June 1933, *tredecim*, *tredecassini*. Ripley Co.: 15-25 May 1959, *tredecim*, *tredecassini*, *tredecula*. Saint Clair Co.: 3 June 1959, *tredecassini*. Saint Louis Co.: June 1959, *tredecim*, *tredecassini*, *tredecula*; St. Louis, June 1881, *tredecim*; Meramec Highlands, 30 May-7 June 1920, *tredecassini*, *tredecula*; University City, 16 June 1933, *tredecim*. Wayne Co.: Sam Baker State Park, 17 May 1946, *tredecim*, 20 June 1959, *tredecim*, *tredecassini*.

NORTH CAROLINA.—Alamance Co.: Mebane, 24 May 1933, *tredecim*. Chatham Co.: Pittsboro, 15 May 1959, *tredecim*, *tredecula*. Halifax Co.: Weldon, 20 May 1959, *tredecassini*. Nash Co.: 14 May 1959, *tredecim*. Orange Co.: 8 May 1959, *tredecim*. Randolph Co.: Asheboro, 14 May 1959, *tredecim*. Wake Co.: New Hill, 15 May 1920, *tredecim*.

SOUTH CAROLINA.—Allendale Co.: Allendale, 23 May 1959, *tredecassini*. Greenwood Co.: Greenwood, 11 May 1959, *tredecassini*. McCormick Co.: McCormick, 15 May 1946, *tredecassini*. Oconee Co.: Walhalla, May 1881, *tredecim*.

TENNESSEE.—Cheatham Co.: Ashland City, 23 May 1959, *tredecim*, *tredecassini*, *tredecula*. Davidson Co.: 22 May 1959, *tredecim*, *tredecassini*. Maury Co.: Springhill, 22 May 1959, *tredecim*, *tredecassini*. Putnam Co.: Buffalo Valley, May 1933, *tredecassini*. Williamson Co.: 22 May 1959, *tredecim*, *tredecassini*. Wilson Co.: 21 May 1920, *tredecassini*.

VIRGINIA.—Brunswick Co.: *tredecim*.

BROOD I: 17-YEAR CICADAS

On May 24 and 25, 1961, we found several cast skins, parts of adult bodies and wings, and live nymphs near the soil surface in an oak woods along State Route 259 near Mauzy in Rockingham County, Virginia. Species identification is not conclusive, but adult coloration and size of nymphs suggest that all three species were present. Near Forestville, in a grazed oak woods along State Route 42 in Shenandoah County, Virginia, we found cast nymphal skins of *septendecim* (judging by size). No cicadas were heard singing during this trip, but we could have missed the chance to hear isolated individuals because it was cool, windy, and overcast. We later realized that this was the beginning of a general emergence that was more straggling than any we had observed before.

Large, noisy, flocks of blackbirds were conspicuous in the above areas and in many other apparently suitable woods across the Shenandoah Valley. The mutilation of dead adults and the absence of any evidence of living individuals caused us to wonder if birds had cleaned out the cicadas that had emerged, and perhaps had even fed upon nymphs at the soil surface. Immature cicadas are especially vulnerable to predation during the first 24 hours after emergence, before they are capable of flight.

A month later (22–24 June 1961) we found large numbers of adults of all three species in Rockbridge County, Virginia. In addition to locating *septendecula* alive for the first time and verifying its structural and behavioral similarity to *tredecula*, we heard periodical cicadas at the following locations in Virginia: Alleghany Co.: along U.S. 60, at junction with State Route 42, and from near junction with State Route 770 to the Rockbridge Co. line, *septendecim*, *cassini*. Bath Co.: near Hotchkiss, *septendecim*, *cassini*. Rockbridge Co.: along State Route 42 and Maury River, *septendecim*, *cassini*; near two parallel creeks near Bustleburg, *septendecim*, *cassini*, *septendecula*; just north of the junction of State Routes 39 and 252, *septendecim*, *cassini*, *septendecula*; near Rockbridge Baths, just north of State Route 39 along the road to Jump, *septendecim*, *cassini*, *septendecula* (cf. Fig. 2).

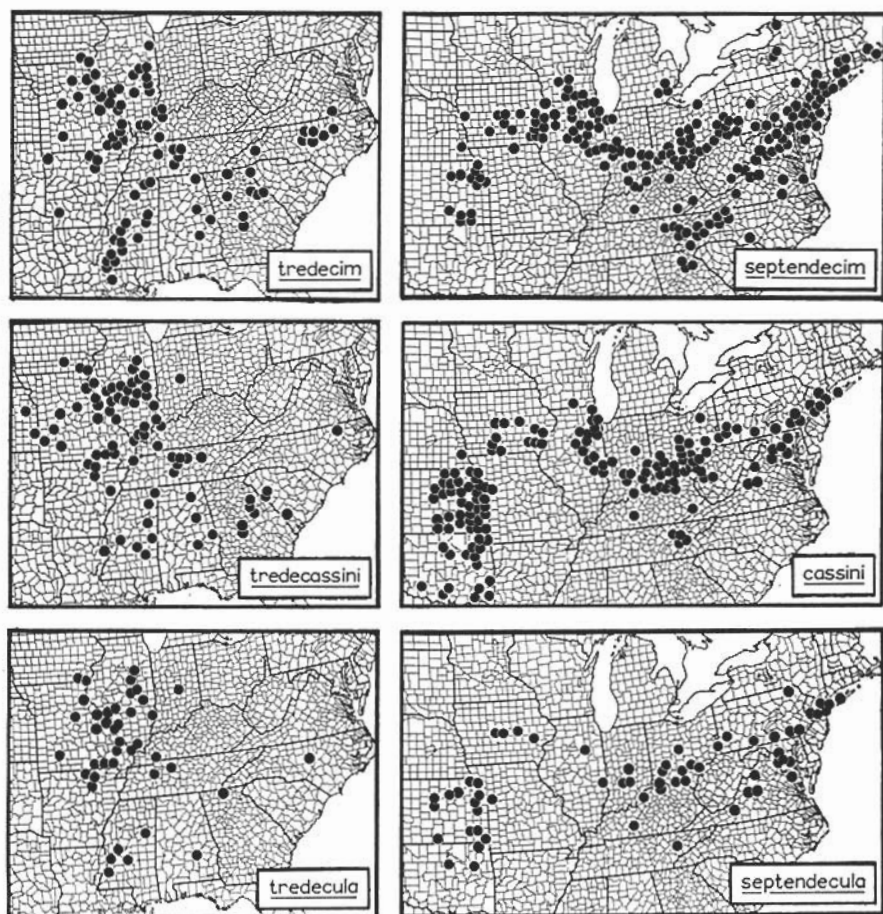


FIG. 3. Distribution of the six periodical cicadas, all broods combined.

Since preparation and mounting of the maps, the following records have been acquired, none of which can be shown on the maps as mounted: *septendecim*, Montebello, P. Quebec [Labelle Co.], Canada, 1885 (Brood X); *cassini*, Denton Co., Tex., 1947 (Brood IV), Fannin Co., Tex., 1930 (Brood IV), Dallas Co., Tex., 1879 (Brood IV).

SUMMARY OF LOCALITIES

MARYLAND.—Carroll Co.: Freedom, 29 June 1893, *septendecim*.

NEW JERSEY.—Bergen Co.: Ridgwood, 1910, *septendecim*.

NEW YORK.—Richmond Co.: Staten Island, 6 June 1893, *septendecim*, 1944, *septendecim*. Suffolk Co.: Huntington, 4 June 1910, *septendecim*. County Unknown: Long Island, 4 June 1910, *septendecim*, 1927, *septendecim*.

OHIO.—Hocking Co.: 1961, *septendecim*. Jackson Co.: 23 June 1961, *septendecim*. Washington Co.: 1961, *septendecim*.

PENNSYLVANIA.—Chester Co.: Honey Brook, 24 June 1910, *septendecim*.

VIRGINIA.—Allegheny Co.: 23 June 1961, *septendecim*, *cassini*. Bath Co.: 23 June 1961, *septendecim*. Rockbridge Co.: 23 June 1961, *septendecim*, *cassini*, *septendecula*; Lexington, 1876, *septendecim*, *cassini*, *septendecula*. Rockingham Co.: 1 July 1893, *septendecim*; near Mauzy, along State Road 259. 25 May 1961, *septendecim*, *cassini*, *septendecula*?. Shenandoah Co.: near Forestville, along State Road 42, 25 May 1961, *septendecim*.

ACOUSTICAL BEHAVIOR, MATING TESTS, AND ISOLATING MECHANISMS

As yet we have found no way to distinguish the acoustical (or other!) behavior of *tredecim* and *septendecim*, *tredecassini* and *cassini*, or *tredecula* and *septendecula*. Slight differences in frequency spectra, such as occur between the calling songs of *cassini* and *tredecassini*, may be significant (compare Fig. 5, this paper, with Figs. 1–5 in Alexander and Moore, 1958), but we have not attempted the statistical analysis of large numbers of recordings which would be necessary to see if this is so. We expect that some divergence in such respects has appeared, not only between 13-year and 17-year siblings, but also among the different broods of both 13-year and 17-year cicadas; but it seems fairly certain that none has yet appeared among the broods that we have studied which would be behaviorally significant if the individuals of the different populations could be brought together.

The following discussion of the three kinds of acoustical behavior of periodical cicadas is based largely on our study of the 1959 emergence of Brood XIX, but for the above reasons it can be regarded as applying generally to all broods of both 17-year and 13-year cicadas. We have avoided repeating information discussed in our 1958 field study, which included only *cassini* and *septendecim*, except as necessary to detail the operation of sound and the evidence of apparent identity in acoustical behavior between 13-year and 17-year siblings.

Periodical cicada males produce three basic sound signals: a *calling* or *congregating song* which is produced either individually or in chorus and is responsible for activating and assembling both males and females; a *courtship song*, produced by individual males when approaching and contacting other individuals (usually females); and a disturbance squawk, produced by males startled into flight or restrained in any way. The functions of the last two sounds have not yet been demonstrated. The three sounds of both *cassini* and *septendecim* can be heard on a published phonograph record (Alexander, 1960).

The audiospectrographs in Fig. 5–6 show that the frequency spectrum and the pulse rate (rate of tymbal vibration) are both varied in characteristic fashions within and among the sounds of the three 13-year species. We

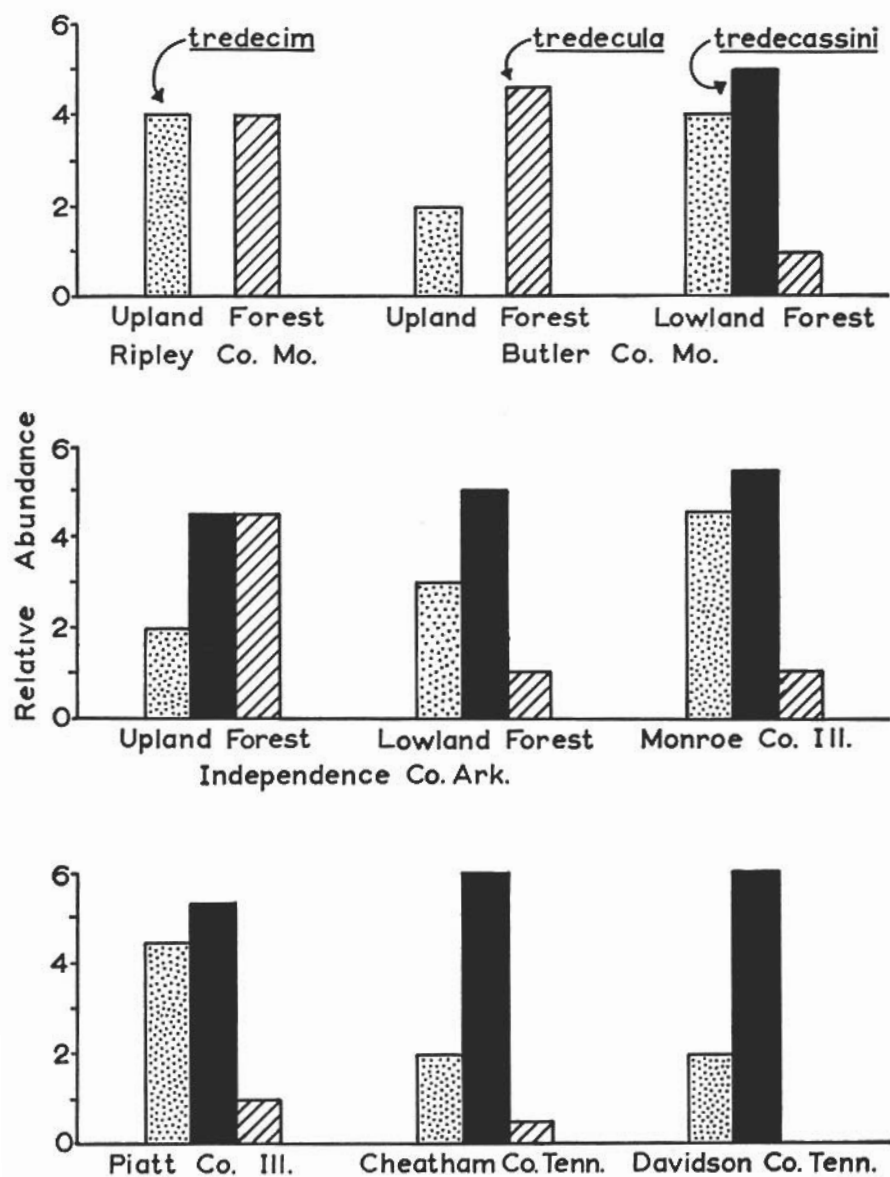


FIG. 4. Differences in distribution and abundance of the three 13-year cicadas in Brood XIX (1959 emergence).

do not yet know how all these changes are effected, but as in other cicadas, rises and drops in frequency that are associated with rises and drops in pulse rate and intensity correspond to raising and lowering the abdomen. These movements adjust tension on the timbals, on the so-called "folded" or "corrugated" membrane between the metasternum and the first abdominal sternite, and on the tympana (Pringle, 1954).

In periodical cicadas, the relationships among the three pairs of species are revealed not only by the close similarity in courtship rhythms, but also by the rhythms of the calling songs and the manners in which they are produced in chorus (Fig. 7). Each kind of calling phrase involves a terminating drop in frequency, and the song units between flights during calling are of comparable length except during the synchronized chorusing of the -cassini siblings. The acoustical signals of periodical cicadas are an apt illustration of the multiple nature of analyzable characteristics in communicative insect sounds; in spite of the obvious gross differences in acoustical characteristics among the three species pairs, one could never escape placing them together as a taxonomic unit distinct from all other cicadas. The frequency spectra and two-part nature of the sounds of the -decula and -cassini siblings, as well as morphological and other behavioral similarities, suggest that their ancestors are more recently derived from one another than either is from the ancestor of the -decim siblings—unless there has been a rather large difference in rate of change among the three pairs since their initial separation.

In addition to the differences among the three species (that emerge together) with respect to song rhythm structure, frequency spectra of individual song phrases, and the manner of chorusing, there is a difference in response to cycles of light and dark which causes the three species to chorus maximally—and to be most active in all aspects of sexual behavior—at different times of the day (Fig. 8). The difference between *septendecim* and *cassini* in this regard has been shown by successive sound intensity readings (Alexander and Moore, 1958). Among 13-year species, *tredecula* seems to fit almost exactly between the other two species in time of maximal chorusing. Thus, insofar as acoustical behavior is concerned, nearly every possibility has been exploited by these three species in reducing sexually significant interspecific contacts under the remarkable conditions of sympatry, synchrony, and population density which they maintain. The seeming incongruity in this arrangement is one of the most intriguing aspects of the study of periodical cicadas.

Species congregation during chorusing periods, and the relative inactivity of the individuals of each species during the time when that species is not engaged in chorusing and sexual activity, result in a slow but clearly

evident differential clumping of the species across its habitat. During the first few days that the adults are active, one can generally detect little in the way of differential congregation; but after a week or two of chorusing, clumping becomes so intense that a single tree may contain one species in a ratio of hundreds of individuals to one individual of the other two species combined. After the adults have been active for about two weeks, the least abundant species can usually be heard singing in only a single tree, or from one direction, while the most abundant species can be heard with about equal intensity from all directions. Nearly all matings take place in "chorus" trees. For example, in one location in Independence County, Arkansas, where *tredecim* was decidedly less abundant than either of the other two species, shaking of the single, small chorus tree late in the afternoon—after all three species had largely finished chorusing—yielded 16 mating pairs of *tredecim*, two mating pairs of *tredecassini*, and no mating pairs of *tredecula*; this in spite of the fact that the last two species should have been in copula in a higher percentage than *tredecim* at this time of day. Most of the cicadas found during the day in a strong chorus tree of another species are individuals that are more or less inactive, probably because they are not sexually responsive at that particular time.

Successful chorusing in all three species probably depends upon both auditory and visual stimuli, but visual stimuli are obviously more important in the -cassini and -decula siblings than in the -decim siblings. Sustained chorusing in the -cassini siblings is probably impossible without the males continually seeing one another. Brief synchrony can be produced by auditory stimuli alone, as was demonstrated by playing tape-recorded songs back to *cassini* males when the light intensity was too low for flight (Alexander and Moore, 1958). But *cassini* males caged under cheesecloth, while frequently achieving synchrony among themselves, rarely attain synchrony with the uncaged cicadas in the forest, largely invisible to them because of the reflectiveness of sunlit cheesecloth. In addition to being active in the brightest portion of the day, *cassini* and *tredecassini*, the synchronizing species, are the most difficult to capture by hand. Individuals frequently fly off with loud squawks when one is still several feet away in a slow, cautious approach. The -decim siblings, in contrast, are much easier to capture.

The importance of visual stimuli to all periodical cicadas is further evident in their close-range reactions to one another. When an active male sees another cicada, he often walks quickly and directly toward it; this is obvious even though the differences between situations when such an approach occurs and when it does not are unknown. An individual approached by another in this fashion seems to have several alternatives: (1)

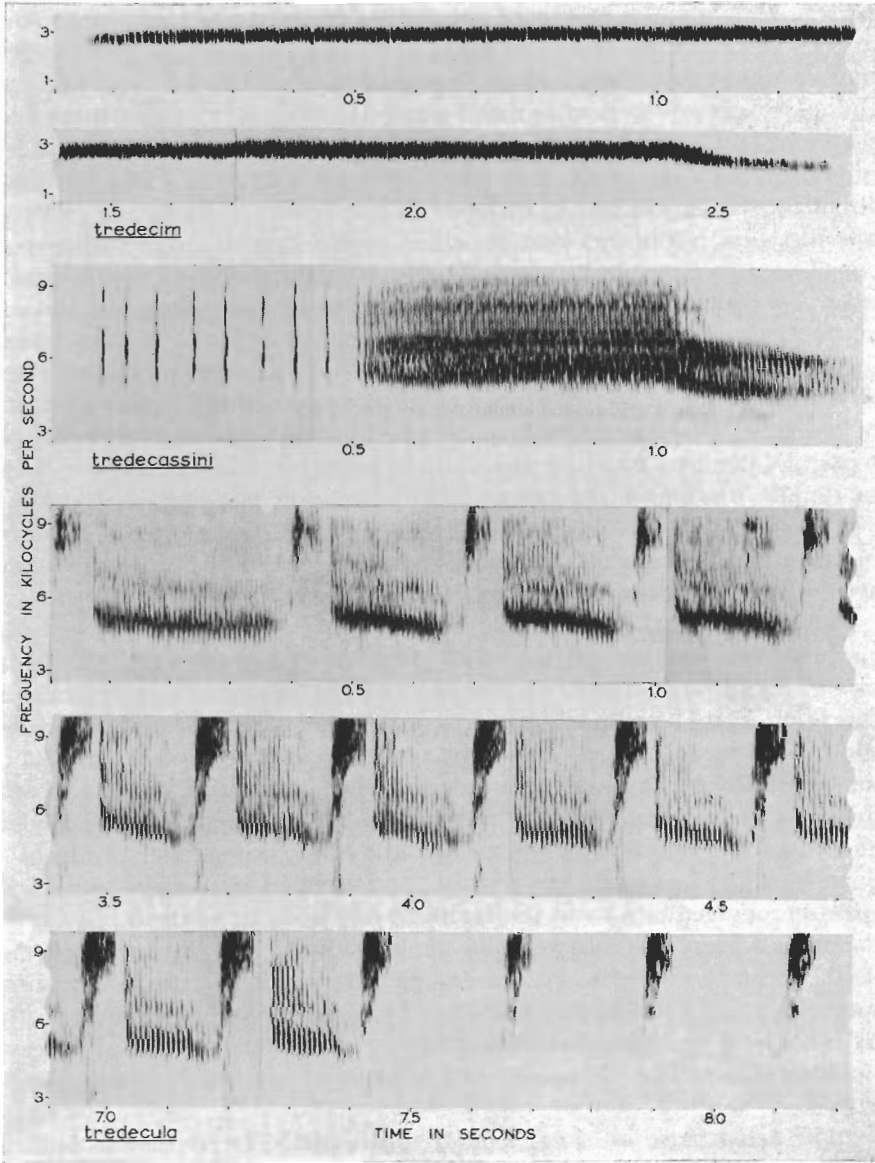


FIG. 5. Audiospectrographs of calling (or congregational) song phrases of the three 13-year cicadas (a rather short phrase was selected for *tredecassini*).

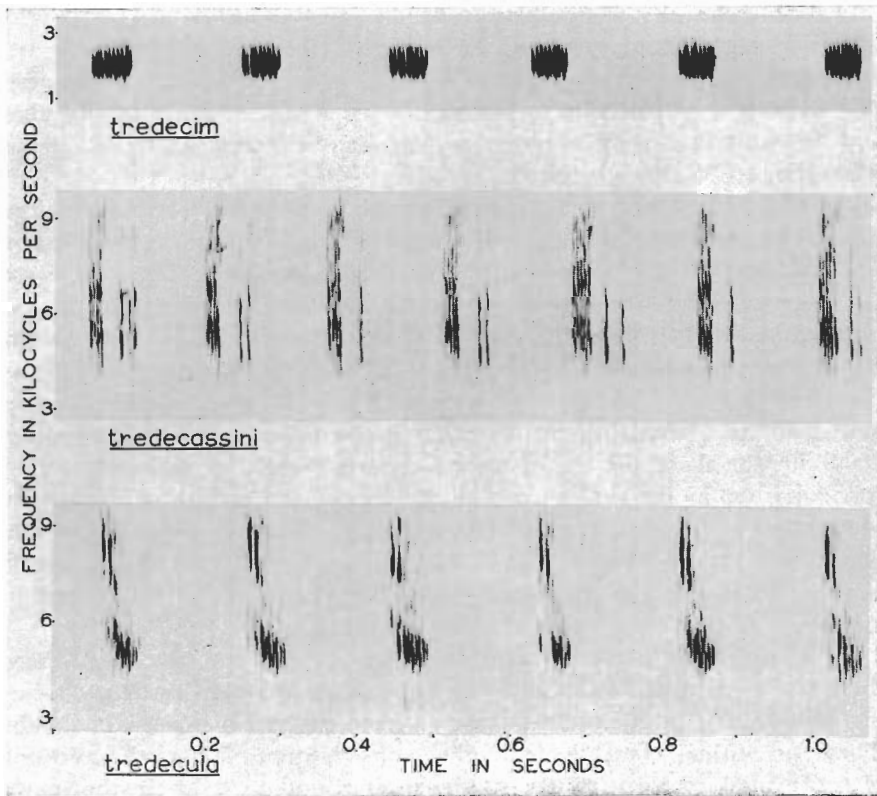


FIG. 6. Audiospectrographs of courtship song phrases of the three 13-year cicadas.

flight, (2) retreat by walking, (3) extension of the near wing, thus halting or dislodging the approacher, or (4) passivity, which seems always to lead to mounting and copulatory movements by the approaching male. We have observed all of these reactions many times in both males and females; the first three often begin before contact, obviously as a result of visualization of the approaching cicada.

Characteristically, a cicada male which has approached a female sidles alongside her, extends his near foreleg, and vibrates it rapidly near her head (and the compound eye). The distinctiveness of this behavior suggests that it plays a specific role in pre-copulatory activities. "Sidling" together and "shouldering" seem to occur among many different kinds of cicadas when they are in close proximity.

In addition to these visual interactions between cicadas, we have noticed that active chorusing in a forest is usually concentrated on the most extensive and most nearly continuous foliage surfaces available. Thus, there are far more actively chorusing cicadas along woodland borders and around bushy, isolated trees than there are inside dense foliage. In Arkansas a striking example was noted. A cut-over, upland forest in Independence County contained scattered, isolated tall trees with a solid layer of dense bushes and small trees beneath them. The very sparse foliage of the tall trees was 20 to 40 feet above the top of second growth. Nearly all active chorusing was going on in the sunlight above the continuous surface of the undergrowth, even though the cicadas concentrated along branches inside the dense undergrowth when at rest in the evening. Only scattered individuals were performing in the tall trees, which offered little in the way of landing surface.

The noticeable southern affinities of the *-cassini* and *-decula* siblings, their ecological distribution, and the importance of vision in their chorusing suggest that both sibling pairs may have evolved in open woodlands. These suggestions coincide with other considerations. Thus, the ancestor of *cassini* and *tredecassini*—the species most abundant today in the southwestern portion of the range of periodical cicadas—may have developed in the streambank, mixed woodlands of prairie areas. These are the only regions today where the lowland forest types, in which *cassini* and *tredecassini* abound (and seem to be concentrated everywhere across their ranges), are sufficiently permanent to support successive generations of 13-year and 17-year cicadas. These are not necessarily open woods, but because of their linearity they present an unusually extensive foliage surface for sunlit chorusing.

The *-decula* siblings may be southeastern or southcentral in origin. Their abundance in xeric, open woodlands and their geographic distribu-

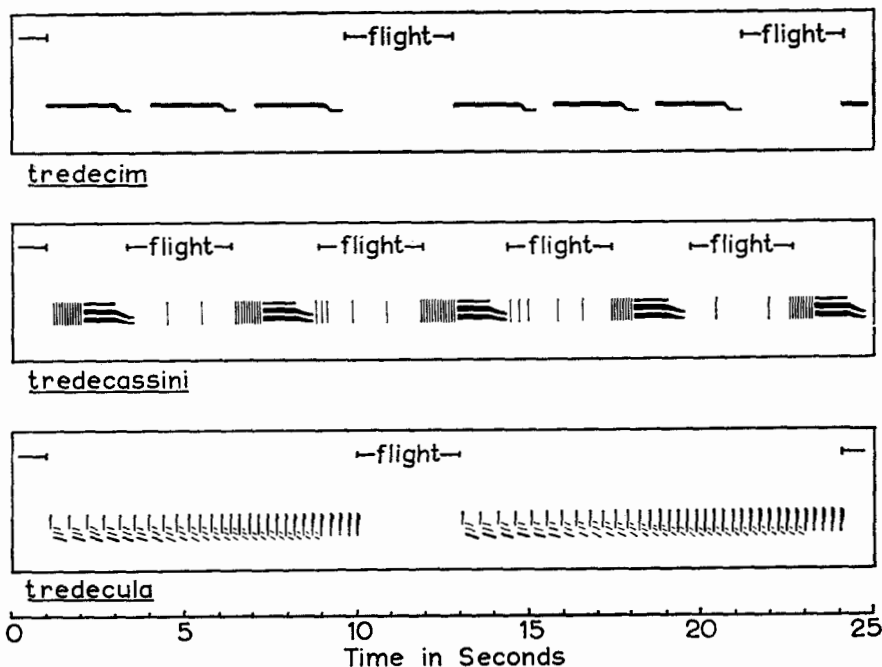


FIG. 7. Diagrams of the mode of chorusing in males of the three 13-year cicadas.

tion neither discount nor lend support to this idea. However, both species are southern, and if their ancestor was geographically separated from the -cassini ancestor, the separation surely must have been eastward. The facts that *septendecim* extends farther north than any other species today, that the -decim siblings concentrate in denser forest types all across their ranges, and that the -decim siblings are able to chorus successfully in less well-lighted situations, all support the idea that the -decim ancestor developed in the permanent oak-hickory or other deciduous woodlands of the central and southcentral portions of the present range of periodical cicadas. These different correlations are based on scanty factual details, but they correspond exceedingly well. We hope that more information to test their validity can be accumulated in the future.

As previously stated, we do not yet know the significance of the courtship songs of periodical cicadas, but it is interesting that, in general, few cicadas have specific rhythms produced during the pre-copulatory maneuvers. Perhaps this is associated with the importance of visual stimuli in close-range interactions, and the maintenance of visual acuity in connection with this and with chorusing and escape from birds and other predators. The

courtship rhythms of the six periodical cicadas are all similar, though the frequency spectra retain the species differences obvious in their other sounds. We have not been able to gather additional information on the suggestion (Alexander and Moore, 1958) that more than one courtship rhythm is occasionally produced by each species. Courtship sounds do not occur before all copulations, and the additional sounds mentioned in our earlier paper were heard on only a few occasions. There is a possibility that what was thought to be a second courtship sound for *cassini*—heard (but not observed being produced) on three occasions—was either the courtship or the calling of a *septendecula* male. More study of courtship behavior is needed to check this possibility.

Although we have purposely tabulated records of thousands of matings in the field (in Broods XIII, XIV, XIX, and I), we have never seen a single case of inter-specific mating in uncaged individuals. In an effort to check the factors responsible, we confined males and females of the three 13-year species together in cheesecloth cages covering small trees. We planned to set the cages in specific environments so that females of each species would be confined with males of each other species: (a) where surrounded by intense natural choruses of the female's species, and (b) where surrounded by intense natural choruses of the male's species. However, we were limited in the variations and extensiveness of the tests by the numbers of individuals of each species and sex that we could obtain; the variations that we were able to set up did not yield any obviously different results. The only test with *tredecim* involved large but unequal numbers of males and females of all three species caged in the midst of both *tredecassini* and *tredecim* choruses. The test cages were as shown in Table 1.

We obtained matings in every cage. In cage 7, containing males and females of all three species, every possible kind of interspecific mating took place! As soon as we discovered that interspecific matings were occurring about as frequently as conspecific matings in the first six cages, we directed our attention to the 7th cage. This cage was set up in the morning when *tredecim* was most active, and observed until afternoon when *tredecassini* was most active. During the morning, most matings (both intraspecific and interspecific) involved *tredecim* males, while afternoon matings involved the other two kinds of males exclusively. In all of the cages combined, most interspecific matings (10 of the 17 recorded) involved *tredecassini* males with females of either of the other two species; five interspecific matings involved *tredecula* males, and only two involved *tredecim* males.

We saw only one difference between interspecific and intraspecific matings; in the former there was more obvious and more active resistance by the females. This was expressed by walking rapidly away from the courting

male, by walking rapidly after the male had mounted and while he was probing with his genitalia, and by either flying or releasing hold and dropping to the bottom of the cage when approached or mounted by a male. By these actions the female frequently either removed herself from the male's presence or caused him to fly or be dislodged. The males were in every case the active members of the pairs during pre-copulatory maneuvers, and in interspecific matings they seemed to accomplish interlocking of the genitalia

TABLE 1
INTERSPECIFIC MATING TESTS

Cage	N ♂ ♂	Species	N ♀ ♀	Species	Chorus Environment Outside Cage
1	100	<i>tredecassini</i>	50	<i>tredecula</i>	<i>tredecassini</i>
2	100	<i>tredecassini</i>	50	<i>tredecula</i>	<i>tredecula</i>
3	100	<i>tredecassini</i>	100	<i>tredecassini</i>	<i>tredecassini</i>
4	100	<i>tredecula</i>	100	<i>tredecassini</i>	<i>tredecassini</i>
5	100	<i>tredecula</i>	100	<i>tredecassini</i>	<i>tredecula</i>
6	100	<i>tredecula</i>	50	<i>tredecula</i>	<i>tredecula</i>
7	85	<i>tredecim</i>	45	<i>tredecim</i>	<i>tredecim</i> and <i>tredecassini</i>
	100	<i>tredecassini</i>	100	<i>tredecassini</i>	
	50	<i>tredecula</i>	50	<i>tredecula</i>	

solely by force and only after unusual delays. Many interspecific pairs that seemed to be locked together in copulation separated immediately upon being handled, showing that the genitalia were not as firmly attached as in normal conspecific matings in which one can drop the animals, put them in alcohol, or otherwise disturb them without the genitalia becoming separated. However, we found at least one interspecific mating of every possible kind in which the genitalia seemed thoroughly locked together; all of the 17 recorded matings were of this type. Dybas and Lloyd (in press) report seven interspecific matings, all involving *cassini* males and *septendecim* females, among 771 mating pairs collected in 1956 in northern Illinois. There is no indication as to whether any of these pairs were firmly attached; all have come apart in alcohol, or have been taken apart, since their collection.

These observations suggest that there are morphological differences that delay copulation between individuals of different species but cannot prevent it in the absence of other deterrents. Also, they suggest that some difference among the males of different species causes special resistance on the part of females approached by males of other species; this must be behavioral, and it may be partly owing to the difference in courtship songs. The infrequency with which courtship songs are heard may result from their being produced only when a male and a female (or any two individuals) remain in close proximity for some time without copulating, while the male is actively

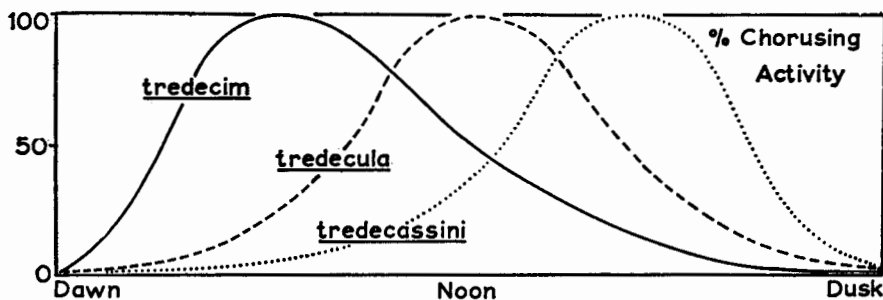


FIG. 8. Approximate times of maximal chorusing activity in the three 13-year cicadas.

promoting assumption of the copulatory position and interlocking of the genitalia. If the courtship sound does increase the receptivity of conspecific females, these are exactly the situations in which it would be most effective, both in indirectly deterring interspecific matings and in directly promoting success in conspecific matings.

As already noted, female cicadas reject the advances of males of other species—or their own species—in the following ways: (1) retreat by walking, (2) retreat by flight, (3) dislodgement or repulsion of the male by extension of the near wing, and (4) dislodgement of the courting male by walking, dropping, or flying after he has mounted. When the female can walk or fly only with difficulty, as was the case in these small cages with cheesecloth surfaces in which the tarsal claws frequently become enmeshed, then interspecific copulation becomes possible. Such matings might also occur among the imperfect individuals that are sometimes fairly abundant low on tree trunks and on low shrubs and herbs.

In view of their abundance and mixing as adults, the periodical cicadas represent an unparalleled case of efficiency in mating separation among closely related species. It is worth emphasizing that the actual barriers are combinations of behavioral characteristics. Selection for behavioral incompatibility has apparently been intense and multi-faceted, while complete

morphological incompatibility is absent in every case, and can probably develop now only through chance divergence. Because genitalic differences are not now brought into play in mating separation among the species, there is no chance for selection to operate upon them. The obvious efficiency of behavioral incompatibility as compared with morphological incompatibility makes it likely that this kind of situation is not unusual. A plausible history of the results of sympatry among these cicadas would involve early selection for divergence in many characteristics—morphological, physiological, and behavioral—both efficient and inefficient barriers to copulation by later standards. When behavioral barriers became effective, then selection for divergence in other respects more or less came to a standstill. This sort of situation explains why characters such as song and other behavioral differences are consistently excellent tools for species identification and recognition.

We have no information as to whether males of any species can actually inseminate females of other species, or whether interspecific matings of any kind can produce offspring. However, we have never heard an intermediate song, and we have seen only a few cicadas which on the basis of morphology could have been hybrids. Only rearing experiments with forced cross-copulations involving virgin females can finally answer this question.

ECOLOGY, DISTRIBUTION, AND HISTORY

VARIATIONS IN ABUNDANCE AND DISTRIBUTION

Most of our information in this regard has been gained in the field study of Brood XIX. However, additional observations on other broods and correlations with overall distribution patterns have yielded some significant generalizations.

Figure 4 shows the presence or absence and relative abundance of each of the three species in several localities within the 1959 emergence of Brood XIX. The scale of relative abundance is subjective. It is based primarily upon the volume, extensiveness, and uniformity of song choruses, and supplemented by counts of specimens collected and seen during the day, shaken from trees at night, and taken in copulation as a result of tree-shaking and other collecting methods. The heaviest population, *tredecassini* in Cheatham and Davidson counties, Tennessee, was given an arbitrary numerical value of six, and all other populations were estimated as some fraction of this value. Because of the obvious limitations in such a subjective method, we diagrammed only those areas in which there were some gross differences, and where we spent considerable time observing, collecting, and recording. Even if one considers only the more gross of the differences actually plotted,

definite trends in relative abundance are apparent, and further, these trends are in accordance with the few instances where one species or another was absent from a particular locality. Thus, *tredecula* was most abundant in upland, dry forests and least abundant in luxuriant lowland forests; it was absent only in Davidson County, Tennessee. On the other hand, *tredecassini* was most abundant in Tennessee, otherwise most abundant in lowland forests, and absent only in upland forests in Missouri where *tredecula* was most abundant. The third species, *tredecim*, showed less consistency in density variations, and it was present in every locality visited. It was scarcest in the upland Missouri and Arkansas forests, where *tredecula* was most prominent, and in Cheatham and Davidson counties, Tennessee, where *tredecassini* was so abundant.

Apparently there are only two geographic areas where but one species of periodical cicada occurs. Only *septendecim* occurs along the extreme northern border of the range of 17-year cicadas, and only *cassini* is known from the extreme southwestern portions of the range of 17-year cicadas. If the ancestors of the three sibling pairs were geographically separated prior to the sympatry which must have preceded the 17-year-13-year split—and this seems fairly certain—then we might expect traces of this early separation to persist today in the form of slightly greater extensions of one or another of the present six species in the direction from which that species originally came. If this is the case, we are brought to the suggestion that the -cassini siblings originated in the southwestern part of periodical cicada range and the -decim siblings in the central portions. In the latter case, *septendecim* may have penetrated farther north than the other 17-year species because it was originally closer to that area and has moved at a rate comparable to that of the other species, and perhaps it has retained some characteristic(s) better adapting it for survival in northern locations. We are left without evidence concerning the geographic origin of the -decula siblings. If this is a southeastern species, as is suggested by its abundance in upland, xeric forests, then our lack of evidence may be due to the scarcity of specimens of all species from the southeastern states. If it is southcentral in origin, this would be obscured by the present abundance of all three 13-year species in that region. These questions are explored further in the discussions that follow.

SYNCHRONOUS EMERGENCES AND ATTENUATED LIFE CYCLES

As with all other diapausing animals with short-lived adults—whether with a one-year life cycle or a longer one—the individuals of any species of periodical cicada must have some manner of synchronizing their maturation. They live as adults only four to six weeks, or the equivalent of about

two days in an animal with a one-year life cycle. Obviously, under such conditions there cannot be much efficiency in a straggling emergence spread out across several weeks. Furthermore, the significance of chorusing in dense groups in connection with sexual behavior surely stresses the importance of synchronous emergence of a high percentage of the population.

That synchrony exists is obvious. On some years practically all of the population in a given forest emerges on the same night, or on two or three different nights. There is almost always one night of maximum emergence. In 1957, Alexander witnessed such an emergence in Clinton County, Ohio. In a woods that during the afternoon had contained only scattered nymphal skins and no singing individuals, and in which no live adults had been found during a two-hour search, nymphs began to emerge in such tremendous numbers just past dusk that the noise of their progress through the oak leaf litter was the dominant sound across the forest. Thousands of individuals simultaneously ascended the trunk of each large tree in the area, and the next morning foliage everywhere was covered with newly molted adults. The numbers of subsequently emerging adults were negligible in comparison. In this case, it was literally true that the periodical cicadas had emerged as adults within a few hours from eggs laid across a period of several weeks seventeen years before.

Even when the emergence is not so striking, the influence of external environmental factors in synchronizing maturation is obvious. In 1959, the total emergence was spread across a period of perhaps two weeks, but nearly all emergence of consequence took place on two or three nights during that period—in each case following a warm rain.

One obvious selective advantage in synchronous emergence, both for the individuals of any one species and for those of all the species living in any particular region, is that the effects of predation would be greatly reduced during the first 12 to 24 hours when the cicadas are soft, flightless, and particularly vulnerable. In late May, 1961, we noticed large flocks of blackbirds in several oak forests where sparse and scattered emergences of Brood I had begun. Not a single living adult cicada could be found or heard, although wings and mutilated individuals could be picked up around the bases of large trees bearing nymphal skins on their trunks. It seems that a scattered emergence would be in double jeopardy, for flocks of birds would not only be able to consume a higher proportion of the emerging cicadas, but once congregated in the area of emergence they would be more likely to keep up with the newly molting cicadas appearing from day to day. The effects of predation in shaping the peculiar evolution of periodical cicadas will be taken up again later.

A second characteristic of periodical cicadas that may be associated with

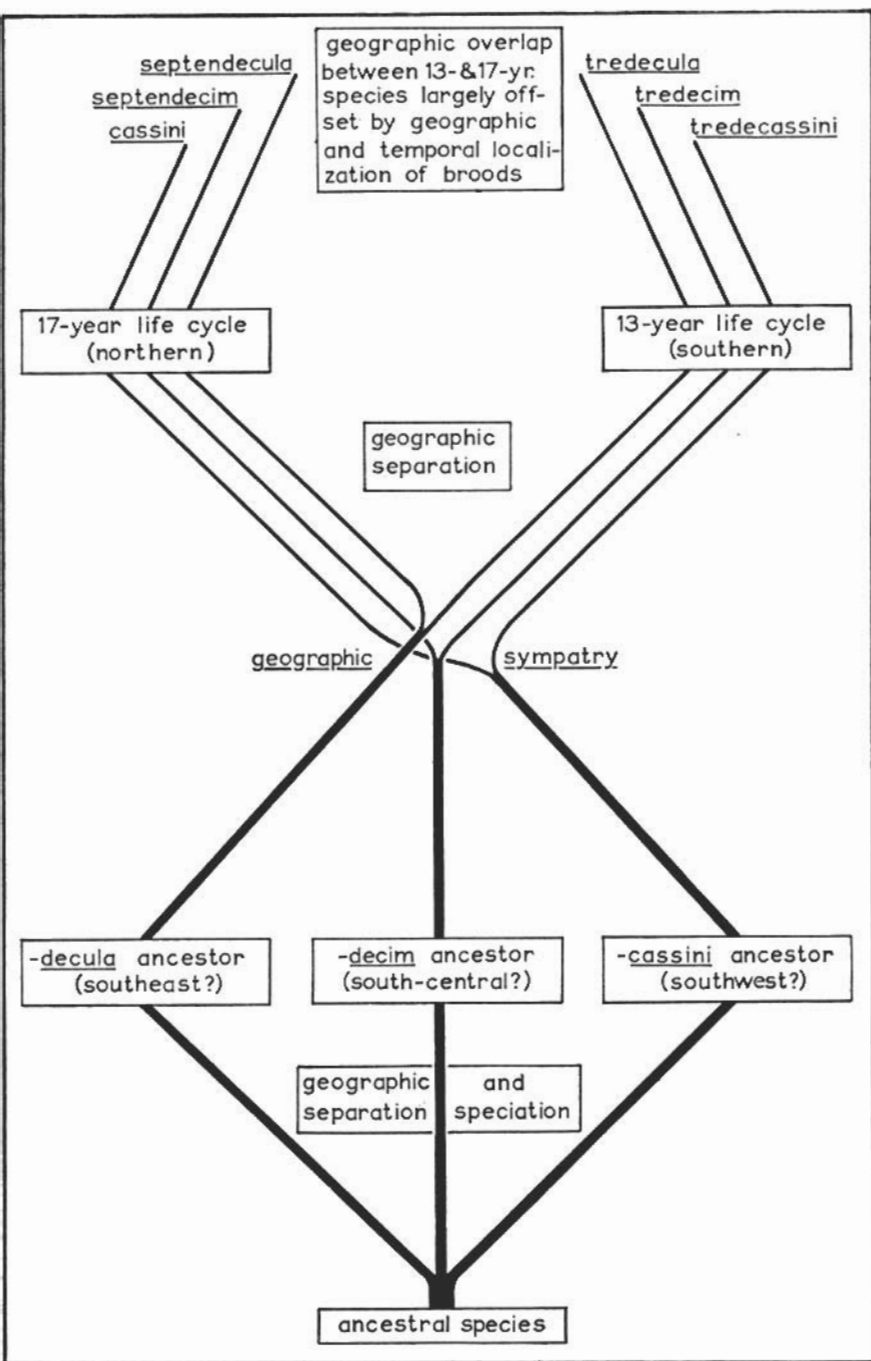


FIG. 9. The probable phylogenetic relationships of 17-year and 13-year cicadas.

synchronous emergences and with the long life cycle, is their specialized acoustical behavior. Among cicadas there is a wide range of variability in the particular behavior associated with production of the calling or congregational song. The nature of this variability and its effects are discussed in some detail by Alexander (1960). It can be summarized briefly as follows. On the one hand, individual males become residential and sing from the same perch, the same limb or part of a tree, or the same tree, for long periods of time—at least up to several days in species that we have observed, such as *Tibicen canicularis* (Harris), *T. pruinosus* (Say), *T. marginalis* (Walker), *Diceroprocta viridifascia* (Walker), *D. olympus* (Walker), and *Okanagana rimosa* (Say). In such instances, individual females must be attracted to individual males, and there seems to be little or no attraction among males. There may even be acoustical repellence among males, causing some spacing and enhancing residentiality and solitary behavior as is probably the case in various Orthoptera. At the other extreme, males perform in great clusters, as we have been describing for *Magicicada*. They aggregate and pile together, climbing over and across one another, and instead of singing continually for long, uninterrupted periods, they alternate bursts of song with bursts of flight. This activity, through an orientation that we do not yet clearly understand (does it occur during flight or at time of take-off; as a result of acoustical stimuli, visual stimuli, or both?), tends to make the group more compact and to increase its size and activity. The result in such animals is that the stationary target for females is the chorus itself, rather than the individual males. Individual males increase their chances of copulating largely through ability to join the chorus and perform as the other males are performing. As such a chorus grows, its attractiveness to both males and females must also grow, if only through an increasing range of effectiveness (but probably also through increasingly efficient group activity, such as synchronization), so that a kind of feedback results, one which should have selective effects on an evolutionary scale in addition to its direct effects.

That this range of variation in acoustical behavior exists among the Cicadidae as a group is an obvious fact. But we have observed that almost the entire range of variation also exists *within* many of the species that occur in eastern North America. That is, the individuals of a particular species (for example, all of the species of *Tibicen* and *Diceroprocta* listed above) behave sometimes one way and sometimes the other. The important influence seems to be population size and density. In sparsely populated areas, such as residential districts in towns with scattered, large old trees, individual males of any of these species can be heard day after day and continually for an hour or more at a time, singing from the same perch or

the same tree. In other areas where dense populations of the same species occur, the behavior exhibited is strikingly different and comparable to that of *Magicicada*. There is a sing-fly alternation; individuals cluster in great numbers; the daily period of activity is usually shortened; and the percentage of individuals active at the same time is greatly increased.

The selective advantage of the maintenance of such variability in acoustical behavior among species that are subject to wide fluctuations in population size and density from generation to generation is obvious. Maximum effectiveness in breeding populations is promoted in times of high and low population density by kinds of activity that are almost diametrically opposed to one another. Some species are more characteristically associated with one of these extremes than with the other, not only because of their usual population structure but also because of their particular kind of song. Thus, species of *Diceroprocta* and *Okanagana* have continuous songs and are more frequently found behaving individually than species of *Tibicen* which have intermittent songs (though low-intensity buzzes connect the different songs produced by an individual performing alone) and for the most part can be found behaving in choruses of greater or lesser density and singing only during restricted portions of the day.

The factors which directly bring about this intraspecific variation in acoustical behavior are somewhat obscure. However, some clues are available. At least three events increase a male cicada's propensity to fly: (1) producing a song burst, (2) hearing a song burst, and (3) seeing another cicada fly (or seeing motion of any kind). In *Magicicada*, at least two events increase a male's propensity to sing: (1) hearing a song burst (either a partial phrase or a complete phrase under certain conditions) and (2) taking a short flight. Now under these conditions, placing a group of males together on a warm, bright day would stimulate the sing-fly rhythm and group performance. But keeping a male away from intense acoustical stimulation and the sight of other flying males would decrease the likelihood of his flying between song bursts and increase the likelihood that he would sing from the same location for a longer period of time whenever light intensity and other external factors were suitable for singing.

The manner in which the above variability in acoustical behavior arose is not clear. Specialized chorusing behavior, along with the intense, synchronized, sing-fly behavior of males in clusters, is probably an innovation that appeared among cicadas which were already coming together as adults through acoustical behavior that was more similar to that of orthopterans. Simple, individual performances—and attraction between individuals—is a less complicated kind of behavior than elaborate, synchronized chorusing, and seems the more likely precursor. An alternative to this explanation is

the possibility that cicadas aggregated in a highly specialized fashion prior to the development of acoustical behavior, and that acoustical behavior originated in some way not presently clear to us, perhaps in a context in which the action of the group as a result of disturbance, rather than during reproductive behavior, was the first effective communication.

A specialization that may be important to the understanding of directions and rates of evolution among periodical cicadas is a possible loss of flexibility in acoustical behavior. We have never seen individual males of *Magicicada* perform alone in the field as residential, non-flying singers. In the few instances where we have observed straggling individuals, they did not sing continuously for long periods of time. In the laboratory and on the edges of dense populations in the field, individual males still seem to perform in a sing-fly rhythm. Even the misshapen individuals that one often finds singing low in trees and bushes sometimes drop from their perches after a burst of a few phrases, and they rarely sing continuously without long breaks between short groups of phrases. It seems that a lone male *Magicicada* is unable to continue singing for a very long time without stimulation from other males, and thus may be more likely to stop singing than to adjust his behavior in the direction of that of males of other species with more flexible or more solitary and individual behavior.

The length of the life cycle is known in only a few cicadas, but in all cases it appears to be no shorter than four years (Beamer, 1928). The selective advantage in these long life cycles is not clear, but some possibilities are apparent. A given habitat can probably support a larger population per generation of a species that requires many years to mature than it can of a species that is comparable in body size but requires only one year to mature. We have already noted that in chorusing cicadas, dense adult populations seem to be a great deal more effective than sparse ones. How this relationship began is obscure, but at least we can be fairly certain that it exists today. Perhaps the loss in flexibility of acoustical behavior occurred in *Magicicada* as a result of a very long period of success in chorusing performance in dense populations associated with a long life cycle. Once such a loss in flexibility occurred, there would seem to be a strong probability that selection would be limited to favoring an intensification of the long life cycle—specialized chorusing trend. This might account in some part for the direction of evolution taken by periodical cicadas. In addition, predation is bound to be more severe on a short-lived, dense, active, noisy population of cicadas than on one with other characteristics. Again, if periodical cicadas had specialized far enough in this direction, then an increasingly severe predation could only accelerate and further the process—the only obvious alternative for periodical cicadas would be increasingly dense

populations, increasingly synchronous emergences, increasingly long life cycles, and increasing specialization of acoustical behavior. Such predation would tend to reinforce the failure of stragglers and off-year partial emergences, perhaps accounting in large part for the restriction to broods and the cementing of the life cycles and the synchrony among species that is evident today.

The genetic and physiological bases for the attenuated life cycles of periodical cicadas, and for the incredible synchrony that is maintained from generation to generation, are completely unknown. Possibly these cicadas undergo 13 or 17 obligate diapauses, the individuals of each species in effect "catching up" with one another developmentally every autumn as do other insects with one- and two-year life cycles and specific diapause stages. The number of instars is still uncertain, although various studies summarized by Marlatt (1923) indicate that there are five instars, as in other cicadas (Beamer, 1928). According to Marlatt, the first instar lasts about one year, the second and third about two years, the fourth three years, and the fifth five years in 13-year cicadas and nine years in 17-year cicadas.

COMPETITIVE AND MUTUALISTIC INTERACTIONS

Some competition must exist among the species of periodical cicadas within a particular brood and among the broods in a particular locality. This is suggested by the facts that: (1) there are never more than two or three major broods in one woods, (2) broadly sympatric broods are always separated by a span of at least three years (Fig. 10), and (3) there was a noticeable reduction in numbers of other species where *tredecassini* was most abundant in Brood XIX. Another kind of "competitive" or mutually excluding interaction may be involved in the failure of 13-year and 17-year cicadas to overlap broadly, especially in Illinois, Indiana, Iowa, and Missouri, where the 13-year cicadas reach northward in a peninsular distribution far into the general region of 17-year cicada range (Fig. 3). We assume that a particular woods can sustain only so many juvenile cicadas, and in certain circumstances this must reduce one species more than another. We have speculated that breeding inefficiency, due to the absence of barriers to copulation between incompatible 17-year and 13-year cicadas, might be involved in the failure of these two kinds of populations to overlap broadly where they meet.

Much more interesting than possible competitive interactions is the suggestion that there are actually some strong advantages to the different species living together and emerging at the same times. This conclusion seems inescapable in view of the several possibilities for separation that have not been exploited.

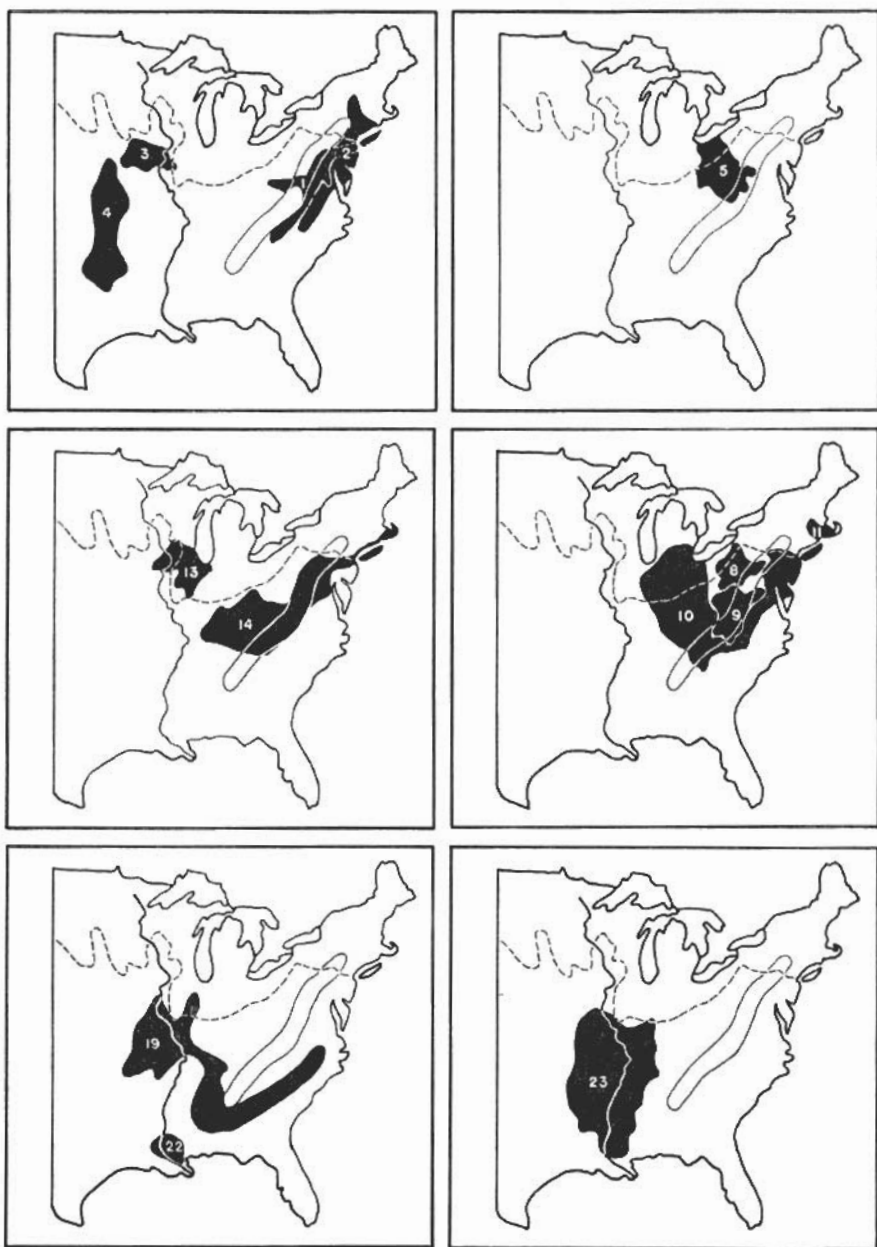


FIG. 10. Generalized distributions of the major broods of *Magicicada* in relation to the approximate limit of maximum Wisconsin glaciation (dashed line) and the Appalachian Mountains (S-shaped enclosed area).

First, microsympatry is continually offset by the rather loose habitat requirements of the three species, coupled with the tendency of the adults of each species to assemble through song. Any deciduous woodland with a fair degree of permanence seems suitable for periodical cicadas, including dry, upland, oak-hickory woods, mixed lowland forests, and several kinds of orchards. Big old lone oaks, elms, cottonwoods, hickories, apples, and other trees that we have observed supporting colonies attest to this absence of specificity. Oviposition must be clumped every generation as a result of song assembly. Differences in habitat requirements or habitat selection would tend to offset competitive interactions, and one would expect these to be swiftly elaborated whenever they appear if competition is a guiding force. This is surely not the case. Except for local instances such as reported by Dybas and Davis (in press) and Dybas and Lloyd (in press)—which, regardless of offsetting factors, should appear briefly now and then under the conditions we have described—sympatry is about as complete as it possibly could be.

Second, the three species consistently emerge precisely together, although interference in sexual behavior should cause intensive selection for divergence in this respect. Species of cicadas in various genera are active all through summer until frost in the same general habitats that periodical cicadas occupy, suggesting that the available season is much longer than that utilized.

One is inclined to speculate that there may be some advantage in overall abundance, regardless of whether one, two, or three species are involved. It has been repeatedly suggested that predation is a likely reason for such a presumed advantage. Predation on periodical cicadas would have to be non-specific and haphazard, for there are no predators with comparable life cycles, or with the ability to repeatedly build up devastating numbers at the particular times and places of emergence. The tremendous numbers of cicadas that die, apparently of old age—but certainly without predation or obvious parasitism or disease—also suggest that it might be too hasty to conclude that lowered susceptibility to predation is the principal advantage in overall abundance. Male cicadas keep up intensive chorusing long after the vast majority of females have been inseminated and are no longer sexually receptive.

That birds can effectively wipe out small populations of adult cicadas was first illustrated to us in 1957 when about a thousand cicadas were transferred from Ross County to Hocking County, Ohio, for experimental work. Shortly after release of the cicadas, birds began attacking and capturing them, and within three days there were no cicadas to be heard or seen in the entire area. Marlatt relates a similar incident involving the adults from

a population started 17 years earlier in Washington, D. C. He counted five thousand emergence holes, but blackbirds descended and attacked the cicadas in great numbers and a few days after the emergence there were no living adults in the area.

The devastating effects of predators upon small, dense populations of cicadas recall the observations made earlier upon the concentration of the sparse species in any *Magicicada* emergence into one or a few trees within the area of emergence. The breeding behavior of periodical cicadas draws them into noisy, active, concentrated masses, and as such they must be highly vulnerable to predaceous birds. But inside a major emergence of two or three species, a tiny, concentrated species population would be largely protected by its more abundant co-emergents. The result would be fluctuating abundances of the different species, each acquiring increasing immunity from predation as its total population decreased in size, *as long as there were other species present* to bear the brunt of predation by virtue of a relatively increased population size. The net effect should be that any isolated species with the particular behavior of periodical cicadas would be decimated with increased severity whenever its numbers decreased, while populations of the same species that emerged within a group of two or three species would be increasingly protected under the same conditions. Two or three species together then could operate in continual balance against the ravages of predators, and maintain the unusually specialized life cycles and behavior patterns that have been evolved in this group.

SPECIES AND BROOD ORIGINS

From the relationships that have been made evident to this point, it is clear that the general sequence of events that gave rise to the six periodical cicadas went something like this. An ancestral species was separated into three divergent populations (Fig. 9). This could have happened as a three-way split, or as one two-way split followed by another in one of the daughter populations (for example, the ancestor of the -cassini and -decula siblings, which seem more closely allied to one another than either is to the -decim siblings). Subsequently these three species must have become largely sympatric, for in a later division, each contributed a member species both to the population that was to develop a 17-year life cycle and to the one that was to develop a 13-year life cycle. It is a moot question what kind of life cycle the three ancestral species had—whether 13-year or 17-year or some other long, fixed or flexible period. Subsequently the 17-year species and the 13-year species each underwent fractionation into several allochronic broods, and at least one more fractionation took place at a still later time.

Of the above facts we can be fairly certain. But there are some vexing

questions involved. Perhaps the most perplexing is how three different species in each of two different cases could all hit upon the same odd life cycle. Yet if we order the presumed events in any other fashion, the problem becomes more difficult, for there is no possibility that the -cassini, -decula, and -decim sibling pairs did not each have a common ancestor—the siblings are too much alike to have evolved independently. Possibly gross life cycle differences in slowly maturing cicadas have a simple genetic basis; this is suggested by the evidence that the life cycle difference between 13-year and 17-year cicadas is owing to a difference in the length of the final nymphal instar (Marlatt, 1923).

A comparison of Figs. 1, 2, and 10 suggests that there has been more than one period of brood formation. Here it is clear that groups of 17-year broods are related both geographically and temporally. That is, broods which appear on successive years neighbor each other or overlap geographically—Broods I and II in the eastern Appalachians; Broods III and IV in the west central states; Broods V and VI in the central and southern Appalachian region; Broods VIII, IX, X, and XI in the Appalachian region; and Broods XIII and XIV in the central to southern Appalachian region. The indications are that each of these groups of broods arose from a single ancestral brood that occurred in the general area now occupied by the several related broods. If this is the case, then there must have been at least two major periods of brood formation.

A major climatic fluctuation must be necessary to upset the emergence times of significant portions of a brood with the life cycle as fixed as it is today. Obviously the life cycles must have been fixed prior to any brood formation to allow the appearance of the many identical broods we have today, and so we can assume that major climatic upsets were indeed necessary for the formation of the broods. The most recent major climatic fluctuations in North America occurred during Pleistocene, and glacial advances seem the only likely candidate for the events we wish to explain. It might be argued that populations isolated since Pleistocene should now have become separate species, but a species with a 17-year life cycle may have undergone as few as 600 generations since the last glacial maximum. Every laboratory *Drosophila* population that has been cultured continuously for 25 or 30 years has been isolated for more generations than this from the rest of its species.

An additional fact apparent from the brood maps in Fig. 10 affirms the suggestion that climatic fluctuations associated with the glacial advances caused the last major brood fragmentation. There are only two major broods of 13-year cicadas, and there is no grouping of temporally and geographically isolated broods. The suggestion is strong that the 13-year

cicadas did not undergo a second major period of brood formation. The southern location of 13-year cicadas may have separated them far enough from the effects of the ice advances to keep this from happening.

If 13-year cicadas were far enough from the glaciers to avoid major brood fragmentation, it follows that the 17-year broods must have been closer to the glaciers—perhaps very much closer. Present brood distributions reinforce this suggestion. No brood is either wholly inside the region of Wisconsin glaciation or restricted to the higher Appalachians, which were probably also inhospitable during maximum glaciation. Only Brood IV, which extends even farther southwest than the 13-year cicadas, is completely outside these two regions. All of the other nine major 17-year broods extend into the previously glaciated regions or across the Appalachian Mountains. But the southern limits of some of these broods are amazingly close to the glacial line. Thus, Brood XIII extends only about a hundred miles west of the glacial line in eastern Iowa, and Broods V and VIII are contained between eastern Ohio and the crest of the Appalachians in West Virginia. Other broods extend far southward from these points, demonstrating that suitable 17-year cicada habitat is not restricted to northern locations in eastern North America today. Broad geographic overlaps such as those between Broods IX and XIV, Broods X and XIV, and Broods II and X show that more than one brood can co-exist in the same general locations, at least if they do not emerge on successive years. If Broods III, V, VIII, IX, and XIII were once pushed far below the glacial boundaries, then why do they not have some persisting remnants there today? If we assume that all species and broods of periodical cicadas dispersed at similar rates into the advancing areas of suitable habitat following the retreat of the glaciers, then the fact that some 17-year broods presently extend much farther south than others is a strong indication that the dense broods that are today wholly located near the glacial boundary survived within or almost within their present locations *during the climatic fluctuations responsible for their appearance*. Further, the present distribution of 13-year cicadas in Illinois and Missouri, apparently to the exclusion of 17-year cicadas, suggests that in this particular location 13-year cicadas were not far south of the glacier, and that they were at least close enough to enter this particular region before any 17-year broods could invade it. If 17-year and 13-year cicadas cannot efficiently live together, as is suggested by our data to this point, then the 17-year species must have been greatly restricted during maximum glaciation, cut off on the north by the glaciers and on the south by the presence of 13-year cicadas. It seems reasonable to suggest that 17-year cicadas survived through the particular period during glaciation which was responsible for the last major period of brood formation in three

TABLE 2

EMERGENCE DATES FOR 17-YEAR AND 13-YEAR CICADA BROODS, AND THE SPECIES IDENTIFIED FROM EACH BROOD (A = -DECIM SIBLINGS, B = -CASSINI SIBLINGS, C = -DECUA SIBLINGS)

Broods		Species		17-year Cicadas—Emergence Years																					
I	ABC	1621	1638	1655	1672	1689	1706	1723	1740	1757	1774	1791	1808	1825	1842	1859	1876	1893	1910	1927	1944	1961	1978	1995	2012
II	ABC	1622	1639	1656	1673	1690	1707	1724	1741	1758	1775	1792	1809	1826	1843	1860	1877	1894	1911	1928	1945	1962	1979	1996	2013
III	ABC	1623	1640	1657	1674	1691	1708	1725	1742	1759	1776	1793	1810	1827	1844	1861	1878	1895	1912	1929	1946	1963	1980	1997	2014
IV	ABC	1624	1941	1658	1675	1692	1709	1726	1743	1760	1777	1794	1811	1828	1845	1862	1879	1896	1913	1930	1947	1964	1981	1998	2015
V	ABC	1625	1642	1659	1676	1693	1710	1727	1744	1761	1778	1795	1812	1829	1846	1863	1880	1897	1914	1931	1948	1965	1982	1999	2016
VI	AB	1626	1643	1660	1677	1694	1711	1728	1745	1762	1779	1796	1813	1830	1847	1864	1881	1898	1915	1932	1949	1966	1983	2000	2017
VII	A	1627	1644	1661	1678	1695	1712	1729	1746	1763	1780	1797	1814	1831	1848	1865	1882	1899	1916	1933	1950	1967	1984	2001	2018
VIII	AB	1628	1645	1662	1679	1696	1713	1730	1747	1764	1781	1798	1815	1832	1849	1866	1883	1900	1917	1934	1951	1968	1985	2002	2019
IX	ABC	1629	1646	1663	1680	1697	1714	1731	1748	1765	1782	1799	1816	1833	1850	1867	1884	1901	1918	1935	1952	1969	1986	2003	2020
X	ABC	1630	1647	1664	1681	1698	1715	1732	1749	1766	1783	1800	1817	1834	1851	1868	1885	1902	1919	1936	1953	1970	1987	2004	2021
XI	A	1631	1648	1665	1682	1699	1716	1733	1750	1767	1784	1801	1818	1835	1852	1869	1886	1903	1920	1937	1954	1971	1988	2005	2022
XII	AB	1632	1649	1666	1683	1700	1717	1734	1751	1768	1785	1802	1819	1836	1853	1870	1887	1904	1921	1938	1955	1972	1989	2006	2023
XIII	ABC	1633	1650	1667	1684	1701	1718	1735	1752	1769	1786	1803	1820	1837	1854	1871	1888	1905	1922	1939	1956	1973	1990	2007	2024
XIV	ABC	1634	1651	1668	1685	1702	1719	1736	1753	1770	1787	1804	1821	1838	1855	1872	1889	1906	1923	1940	1957	1974	1991	2008	2025
XV	A	1635	1652	1669	1686	1703	1720	1737	1754	1771	1788	1805	1822	1839	1856	1873	1890	1907	1924	1941	1958	1975	1992	2009	2026
XVI	A	1636	1653	1670	1687	1704	1721	1738	1755	1772	1789	1806	1823	1840	1857	1874	1891	1908	1925	1942	1959	1976	1993	2010	2027
XVII	AC	1637	1654	1671	1688	1705	1722	1739	1756	1773	1790	1807	1824	1841	1858	1875	1892	1909	1926	1943	1960	1977	1994	2011	2028

Broods	Species	13-year Cicadas—Emergence Years																			
		XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXV	XXVI	XXVII	XXVIII	XXIX	XXX							
XVIII	AC	1685	1698	1711	1724	1737	1750	1763	1776	1789	1802	1815	1828	1841	1854	1867	1880	1893	1906	1919	1932
XIX	ABC	1686	1699	1712	1725	1738	1751	1764	1777	1790	1803	1816	1829	1842	1855	1868	1881	1894	1907	1920	1933
XX	B	1687	1700	1713	1726	1739	1752	1765	1778	1791	1804	1817	1830	1843	1856	1869	1882	1895	1908	1921	1934
XXI	—	1688	1701	1714	1727	1740	1753	1766	1779	1792	1805	1818	1831	1844	1857	1870	1883	1896	1909	1922	1935
XXII	AC	1689	1702	1715	1728	1741	1754	1767	1780	1793	1806	1819	1832	1845	1858	1871	1884	1897	1910	1923	1936
XXIII	ABC	1690	1703	1716	1729	1742	1755	1768	1781	1794	1807	1820	1833	1846	1859	1872	1885	1898	1911	1924	1937
XXIV	ABC	1691	1704	1717	1730	1743	1756	1769	1782	1795	1808	1821	1834	1847	1860	1873	1886	1899	1912	1925	1938
XXV	B	1692	1705	1718	1731	1744	1757	1770	1783	1796	1809	1822	1835	1848	1861	1874	1887	1900	1913	1926	1939
XXVI	A	1693	1706	1719	1732	1745	1758	1771	1784	1797	1810	1823	1836	1849	1862	1875	1888	1901	1914	1927	1940
XXVII	B	1694	1707	1720	1733	1746	1759	1772	1785	1798	1811	1824	1837	1850	1863	1876	1889	1902	1915	1928	1941
XXVIII	—	1695	1708	1721	1734	1747	1760	1773	1786	1799	1812	1825	1838	1851	1864	1877	1890	1903	1916	1929	1942
XXIX	—	1696	1709	1722	1735	1748	1761	1774	1787	1800	1813	1826	1839	1852	1865	1878	1891	1904	1917	1930	1943
XXX	—	1697	1710	1723	1736	1749	1762	1775	1788	1801	1814	1827	1840	1853	1866	1879	1892	1905	1918	1931	1944

principal locations: west of the Mississippi River in Iowa and farther south; between the Appalachians and the glacier in Tennessee, Kentucky, and perhaps even Ohio and West Virginia; and along the eastern and southern borders of the Appalachian Mountains.

The particular temporal relations of the groups of broods that lie closest to the glacial boundary strengthen the suggestion that the glaciers did cause temporal splitting, and they give an indication as to how it might have come about. In nearly every pair of related broods, the brood nearer the glacier appears one year earlier than its relative. Thus, on the west, Brood III appears one year earlier than Brood IV; centrally, Brood XIII—probably ancestrally related to Brood XIV to the southeast and geographically as well as temporally separated from it during Pleistocene—appears one year earlier than Brood XIV; Brood IX in the Appalachians appears one year earlier than Brood X, slightly to the south and west. The manner of formation of the remaining broods, particularly Broods VIII and V, is more doubtful. Broods VIII and IX may have been synchronous prior to glaciation, rather than IX and X, in which case, the earlier emerging brood is still nearer to the glacial line. The strong indication is that prolonged or repeated periods of extreme cold caused summation of diapauses (which we assume regulate the developmental cycles of these cicadas), and thus caused those populations closer to the glacial boundaries to emerge earlier.

APPLICATION OF THE SPECIES CONCEPT TO PERIODICAL CICADAS

Regardless of one's viewpoint concerning species definition, there can be no doubt that the three 17-year cicadas are distinct from one another and the three 13-year cicadas are distinct from one another. The morphological and behavioral differences outlined here are more detailed and positive than those available for the majority of recognized animal species. Apparently the sole reason for earlier taxonomists being unwilling to accept *cassini* as a distinct species, in spite of numerous confirmations of Cassin's excellent original evidence, is the unusual sympatry and synchrony between *cassini* and *septendecim*. Because no other closely related species were known to co-exist in this fashion, the evidence was either doubted or ignored. As a result, the most intriguing problems regarding the history of these unusual animals have been suppressed.

We expect that there will be some divergence of opinion among taxonomists as to the most satisfactory treatment of the kinds of relationships existing between *septendecim* and *tredecim*, *cassini* and *tredecassini*, and *septendecula* and *tredecula*. Only *septendecim* and *tredecim* show morpho-

logical differences (Frontisp.), and even here a certain percentage of specimens cannot be distinguished. No behavioral differences are known between the members of the three pairs. Only the life cycle and distributional differences are consistent. There is little doubt that the differences in life cycle are hereditary, but we do not know how they are determined, and so cannot tell certainly whether or not gene exchange occurs at 221-year intervals between the few 17-year and 13-year broods that overlap geographically to a slight extent (Figs. 3, 10). Three facts suggest that such exchange of genetic materials, if it occurs at all, must be insignificant: (1) the morphological differences between *septendecim* and *tredecim* that are no less pronounced where the two species overlap, (2) the absence of evidence suggesting intermediate life cycles, especially in woods where all six species occur together, and (3) the narrow zone of geographic overlap between 13-year and 17-year cicadas. The location and unusual shape of the overlap zone (Fig. 3), together with its narrowness and the fact that different broods of either 17-year or 13-year cicadas can co-exist in the same woods without obviously affecting each other's abundance, suggest that there may be a disadvantage in the co-existence of 17-year and 13-year cicadas in the same localities. As was discussed earlier, this disadvantage could stem from a physiological or genetic incompatibility that in these slowly evolving forms has not yet become associated with behavioral or morphological barriers to copulation. This condition could render the breeding populations of both groups of species highly inefficient whenever they emerge simultaneously in the same localities.

At any rate the morphological differences between most specimens of *septendecim* and *tredecim*, and the important difference in life cycle between the two members of each species pair, indicate that 13-year cicadas have not exchanged genes with their 17-year counterparts at a significant rate as recently as the different broods of either 13-year or 17-year cicadas have with one another. Today, the individual broods are actually more completely isolated extrinsically from one another than the 13-year and 17-year species are from one another. These broods are not only separated temporally because of the exceedingly small number of stragglers and virtual absence of sympatry between successive large broods, but most are separated geographically as well (Fig. 10). We must conclude that if the different broods remain in their present status long enough without becoming extinct, then they too will diverge sufficiently to become separate species at some time in the future. Several broods are large enough to make this a strong likelihood.

We suggest that it is practical to designate extrinsically isolated populations as species as soon as one can distinguish them, if two additional

conditions are taken into account in every case: (1) the likelihood of disappearance of the extrinsic barrier before the appearance of intrinsic isolating mechanisms, and (2) the likelihood of one or the other of the populations becoming extinct prior to the appearance of intrinsic barriers to hybridization. Both of these possibilities can usually be determined with a high degree of confidence.

A simple example would be the geographically isolated populations of the house cricket, *Acheta domesticus* L., which now occur on all continents. Most of these imported populations have burgeoned from small, local introductions, and because of increasingly rigid restrictions on transport of living animals and plants they will probably never again exchange genes on a significant scale. As soon as the American house crickets develop characteristics by which they can be distinguished from the European house crickets—morphologically, physiologically, or behaviorally—then it should be most practical to regard them as different species. Rather than adding to the confusion concerning species definition, we think this practice would clarify many problems and promote use of the species concept in its proper, biological, evolutionary context. Much needless confusion regarding the use of trinomials and the evaluation of “degrees” of difference could be eliminated, so that it would actually become a more straightforward and meaningful proposition to designate species in all situations, whether dealing with preserved specimens or natural populations. Further, there is little evidence to suggest that this practice would result in a great increase in scientific names; the house cricket is a good illustration that allopatric populations do not diverge overnight. Isolated, successful populations which have developed non-overlapping differences and show no likelihood of being brought back together in the foreseeable future have already become separate evolutionary units and should be treated separately by most (if not all) kinds of biologists.

This problem comes up with periodical animals because of the temporal isolating factor, as it does with island populations that are geographically isolated. In the case of the 13-year and 17-year cicadas, there is no doubt that the six populations need to be recognized by all biologists, there is no problem in separating them, there is scarcely any possibility that they will interbreed significantly in the future, and there is certainly no good reason to designate them by trinomials. For these reasons, we consider them to be distinct species.

Both the speciation which has already occurred between 17-year and 13-year siblings and that which may be incipient among some of the different broods of 13-year and 17-year cicadas are the results of interesting combinations of geographic and temporal separation. Temporal separations due to

unusual climatic events affecting only part of a brood, or resulting from successful straggling during times when the life cycles were not so rigid as they are now, appear to have been the principal initiating factors in forming the different broods. In the first case there would have been a degree of geographic separation from the start, although it would have had little significance in the continuing failure to exchange genes; in the second case geographic separation need not have been involved in any way. On the other hand, the temporal separation present today between 13-year and 17-year cicadas has undoubtedly developed as a result of initial geographic separation. But the partial breakdown of allopatry now in evidence may have left allochrony—either at some time in the past or yet today—as the sole barrier to significant hybridization.

We should note that although temporal isolation becomes increasingly important in initiating and promoting speciation among animals with life cycles of increasing length, this added factor is counteracted with regard to its effect on overall rates of speciation by the reduction in rate of change. An extremely long time must be required for two isolated populations with 17-year life cycles to develop incompatibility or diverge sufficiently to be distinguished by biologists. Many populations with one- or two-year life cycles must have been fragmented and developed into different species since the present broods of periodical cicadas were first formed.

SUMMARY AND CONCLUSIONS

1. There are six species of *Magicicada*: three with 17-year life cycles and three with 13-year life cycles. Two new 13-year species and one new 17-year species are described, and types are designated for all species. Each 17-year species has a 13-year sibling from which it can be separated only by differences in life cycle and geographic distribution. The three species with the same life cycle can in each case be distinguished by striking differences in acoustical behavior, and also by other behavioral characteristics, as well as by size, color, and male genitalia.

2. There are at least 18 successful broods of *Magicicada*: 13 with 17-year cycles and five with 13-year cycles. These broods emerge on different years and have different geographic ranges. The presence of three species has been verified for 12 of the 18 successful broods, and two species have been found in each of the other six broods. Although more than one brood may inhabit a single forest, broods that appear on successive years do not overlap broadly. Temporal and spatial distribution of the broods indicates that there have been at least two major periods of brood formation, and that Pleistocene glaciation must have been involved in at least the last one.

3. The three species within each brood are generally sympatric, and most habitats contain all three species, individually intermingled. But there are predictable differences in species abundance in different habitats, and differential clumping of adults occurs as a result of song chorusing. In some locations along the peripheries of ranges, only one or two species occur. Although 17-year cicadas are generally northern, and 13-year cicadas generally southern, the two occur together in the same forest in some locations, and the northern extension of 13-year cicadas is far north of the southern extension of 17-year cicadas.

4. Different species of *Magicicada* which live together were not found cross-copulating, even under the most striking conditions of sympatry; and there is no evidence of hybridization. When the three 13-year species were confined together in small cages, all possible kinds of inter-specific matings were obtained, apparently because of a reduction in the females' ability to reject males of other species. It is not known whether 13-year and 17-year siblings cross-copulate or hybridize in the rare circumstances when they meet (every 221 years in narrow zones of overlap). But no intermediate life cycles are known; one pair of siblings can be distinguished about 95 per cent of the time by differences in color and in the size of the abdomen; and the peculiar shape of the narrow zone of geographic overlap between 17-year and 13-year cicadas suggests mutual exclusion, possibly because of deleterious interaction during the adult stage.

5. Periodical cicada males appear to be more specialized in their acoustical behavior than most other North American cicadas, having to all indications lost the ability to perform acoustically as residential individuals. They are thus more or less restricted to a pathway of specialization emphasizing and depending upon dense, active, chorusing clusters of adults. It is suggested that there has been selection for synchrony and sympatry among species with the same life cycle, principally because of the cushioning effect of dense, multiple-species populations with regard to predation; and that there may even have been selection for ecological identity among juveniles in connection with reducing deleterious competitive interactions among species dependent upon one another's presence for survival through the adult period.

6. Apparently the six *Magicicada* species arose from a common ancestor which first split into three species representing the ancestors of the three modern 13-year and 17-year sibling pairs. These three ancestral species must have become sympatric, for each later contributed a member species to the 17-year population and another to the 13-year population. Formation of the present broods within each life cycle must have taken place still later. The

life cycles of ancestral species are unknown, as is the basis for the life cycle differences in the modern species.

ACKNOWLEDGMENTS

This study was supported by faculty research grants from the Horace H. Rackham School of Graduate Studies of The University of Michigan.

We are indebted to the following persons for making specimens available for study.

INSTITUTIONAL COLLECTIONS.—Irene Boliek, The Florida State University; H. B. Boudreaux, Louisiana State University; D. F. Bray, University of Delaware; W. J. Brown, W. R. Mason, and J. R. Vockeroth, Canadian National Insect Collection; G. W. Byers, University of Kansas; Mont A. Cazier and Herbert Ruckes, American Museum of Natural History; Leland Chandler, Purdue University; A. C. Cole, University of Tennessee; E. F. Cook, University of Minnesota; Henry Dietrich, Cornell University; J. W. Downey, Southern Illinois University; Henry Dybas, Chicago Natural History Museum; W. R. Enns, University of Missouri; J. J. Friauf, Vanderbilt University; H. J. Grant and J. A. G. Rehn, Philadelphia Academy of Sciences; K. L. Hays, Auburn University; Ross E. Hutchins, State Plant Board of Mississippi; E. W. King, Clemson College; Josef Knoll, The Ohio State University; J. L. Laffoon, Iowa State University; Horace O. Lund, The University of Georgia; Robert Mathewson, Staten Island Museum; J. T. Medler and R. D. Shenefelt, University of Wisconsin; R. H. Painter, Kansas State University; G. H. Penn, Tulane University; C. L. Remington, Yale University; G. T. Riegel, Eastern Illinois University; H. H. Ross, L. J. Stannard, M. W. Sanderson, and L. K. Gloyd, Illinois Natural History Survey; L. M. Russell, United States National Museum; J. A. Slater, University of Connecticut; Wm. C. Stehr, Ohio University; Edward S. Thomas, The Ohio State Museum; George Wallace, Carnegie Museum; T. J. Walker, University of Florida; R. E. Woodruff, State Plant Board of Florida; D. L. Wray, North Carolina Department of Agriculture; D. A. Young, North Carolina State College; F. N. Young, Indiana University.

PERSONAL COLLECTIONS.—J. Betz, Donald J. Borrer, Jay A. Buxton, Neva Chambers, Leland Chandler, Henry S. Dybas, Alfred M. Elliott, Robert A. Evers, Frank Fisk, Dwight L. Goleman, John W. and Douglas J. B. McReynolds, Frank W. Mead, Ronald Meyer, Harlow B. Mills, Russell Mumford, Thomas H. Park, Garland T. Riegel, Elbert L. Sleeper, George Steyskal, Arthur Stupka, Thomas J. Walker, Clarence E. White, Robert E. Woodruff, and Paul A. Wright.

The following people assisted in our search for type material: Mr. R. J. Izzard, Department of Entomology, British Museum (Natural History), Cromwell Road, London S. W. 7, England; Dr. W. Tischler, Zoological Institute and Museum, University of Kiel, Kiel, Germany; Prof. Dr. E. Séguéy and Dr. Lucien Chopard, Muséum National d'Histoire Naturelle, 45 bis, Rue de Buffon, Paris V^e, France; Dr. René Malaise, Entomologiska Advelningen, Naturhistoriska Riksmuseum, Stockholm 50, Sweden; Dr. S. L. Tuxen, Universitetets Zoologiska Museum, Krystalgade- København K, Denmark; and Dr. H. K. Townes, Museum of Zoology, University of Michigan, Ann Arbor, Michigan.

Special thanks are due Dr. Donald J. Borror, Department of Zoology and Entomology, The Ohio State University, Columbus 10, Ohio, for loaning us tapes and for donating type material of all three of the 17-year species, purposely designated from Brood X. We are also very much indebted to Mr. Henry S. Dybas, Division of Insects, Chicago Natural History Museum, Roosevelt Road and Lake Shore Drive, Chicago 5, Illinois, who first noted the difference in pronotal coloration used here to separate the -decim siblings from the -cassini and -decula siblings, and who has discussed many problems concerning periodical cicada relationships with us. Finally we thank Dr. Edward S. Thomas of the Ohio State Museum for his continual interest and enthusiastic support in this study since its beginning, and Dr. Charles F. Walker of the University of Michigan Museum of Zoology for his critical examination of the manuscript.

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Accepted for publication April 3, 1962