

**DAVISPIA BEARCREEKENSIS COOPER, A
NEW CICADA FROM THE PALEOCENE,
WITH A BRIEF REVIEW OF THE
FOSSIL CICADIDAE.**

KENNETH W. COOPER.

ABSTRACT. *Davispia bearcreekensis* Cooper is described from the American Paleocene, and is the oldest cicada yet known. The wrongly placed or doubtful records of cicadas are discussed, and it is shown that *Hylaeoneura lignei* Lam. and Sev. from the Cretaceous cannot seriously be regarded as a definite record for the fossil Cicadidae. Formulae are presented which allow estimation of the relative dimensions of certain missing portions of fossil Cicadidae, and afford a means for the association of non-comparable fragments. The fore wing ascribed by Cockerell to *Cicada grandiosa* Scudd. is described and figured, and the data available for the 13 known fossil Cicadidae, representing ten species, are reviewed.

INTRODUCTION.

DESPITE the large number of fossil Cicadariae (Auchenorrhyncha) known, fossil Cicadidae are represented by nine described species only. In addition, one fossil cicada has been mentioned in the literature, but has not been described. Perhaps the oldest cicada that has been described is *Meuniera haupti* Piton, found at Menat in beds supposed by some to be of Eocene age. No other undoubted cicada has been recorded from strata lower than Oligocene, and only one Oligocene cicada is definitely certain. It is the purpose of this paper to bring to attention a new cicada from the American Paleocene, and to review briefly the fossil Cicadidae. Not only is the new Paleocene cicada of unusual interest in that it is the oldest cicada yet known, but in spite of the cicada's antiquity its wing departs in no manner from the venational pattern so typical of the Cicadidae.

In the description which follows, Tillyard's (1919) interpretation of the cubital and anal veins of the cicadid fore wing has been adopted. Nevertheless the classical interpretation of the radial veins has been adhered to in spite of Tillyard's (1926) criticism. Although his commentary on the cubital series was based largely on his study of fresh preparations of the wings of living cicadas, Tillyard's reinterpretation of the radial complex follows a study of Permian Archescytinidae and not a restudy of wing trachea. Indeed, as Myers (1928) has pointed

out, the work of Horváth (1913) and Muir (1923) brings the interpretation of the entire costal margin of the fore wing into question. A new ontogenetic study of the radial veins and costal margin is definitely desirable. According to Tillyard the veins interpreted by Comstock and Needham as R_{2+3} and R_{4+5} are actually R_1 and R_s respectively. Presumably Tillyard would designate R_2 and R_3 of the cicada as R_{1a} and R_{1b} just as in the Archescytinidae.

In describing the fore wing of *Davispia* n. gen., advantage of the geometrical qualities of the veins and cells has been taken; the description is chiefly a catalog of measurements. This course has been deemed advisable for the following reasons. Most fossil cicadas are known from wings or their fragments, and presumably in the future new fossil cicadas will be represented chiefly by wings. In many cases, therefore, generic descriptions of fossil cicadas can be based solely upon the structure of the wing.

Unfortunately the venation of the cicadid wing plays virtually no part in the current taxonomy of the Cicadidae. As the wings of living cicadas form for the most part a remarkably stereotyped lot in respect to general shape, courses of veins and shapes of cells, it is only after careful study of relative proportions of cells and vein lengths that many living species can be separated from generically different forms if wings are employed as the sole criterion. The best that can be done now, until a detailed study of the venation of the entire family has been undertaken, is to describe carefully and in detail all the structures in the fossil wings and, where possible, in a quantitative manner. The general uniformity of proportions of fore wings in living cicadas¹ suggests that such description will allow separation of many species from one another. In addition, proportions of special areas of wings may be taken from such a table of measurements, and should facilitate identification of fossil cicada wings represented by sizeable fragments.

¹ *Magicicada septendecim* (Linn.)—the seventeen-year "locust"—appears to be a flagrant exception in this respect, for abnormal veins and cells are very commonly found in the fore wing of this species. It is perhaps not irrelevant that this is the very cicada which has the longest preimaginal life. Presumably there is a longer period during which accidents might occur to the developing wings and result in an abnormal venation in the imago. Support for this suggestion lies in the fact that the abnormalities rarely show bilateral symmetry.

Lastly, such measurements largely relieve the description of such inexact terms as: "more," "less," "nearly," etc. Yet it must be emphasized that relative proportions here are held to be the significant data, and no false degree of accuracy should be read into the measurements which are given below.

DESCRIPTION.

Davisia Cooper, n. gen.

Text Fig. 1, and Plate 1, Figs. 1, 2.

Anterior wing with media forking into M_{1+2} and M_{3+4} at basal fourth of radial cell; suture of nodal line cutting through M_{3+4} slightly more than half of its length from fork M_{1+2}/M_{3+4} . M_{3+4} forks into M_3 and M_4 approximately at apical third of cell $1M_2$. The distal end of the medial cell is thus prolonged into a somewhat obliquely truncated lobe that is somewhat longer than broad apically.

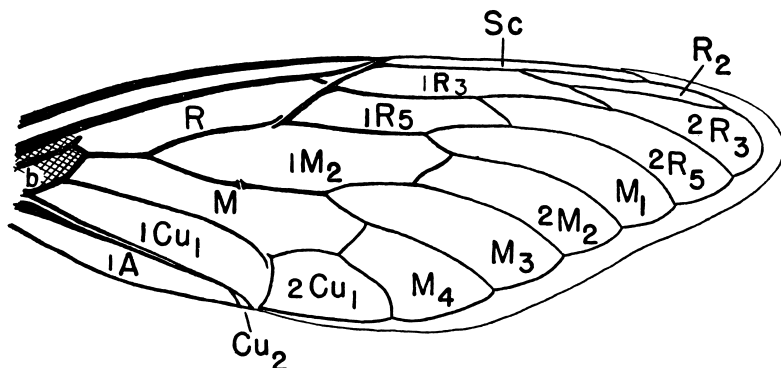


Fig. 1. Diagram of the anterior wing of *Davisia bearcreekensis* Cooper, giving the nomenclature of the cells.

Cell $2Cu_1$ broad, but slightly more than twice as long as wide, receiving the medio-cubital crossvein just proximal of the middle of vein Cu_{1a} . Apical margin (vein Cu_{1b}) of cell $1Cu_1$ evenly and shallowly curving into cell $2Cu_1$. Only Cell $2R_3$ extends into the actual apex of the wing.

Genotype: *Davisia bearcreekensis* Cooper, n. sp.

Origin of name. The name *Davisia* is derived from the name Davis and —*pia*, devoid of its usual meaning, has been appended. The genus is dedicated to Mr. William T. Davis of the Staten Island Museum, in recognition of his authority on

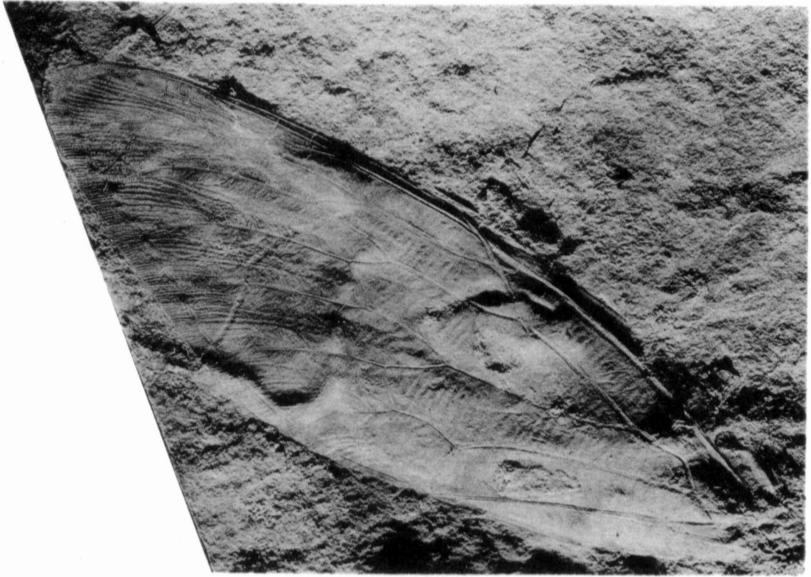


FIG. 1

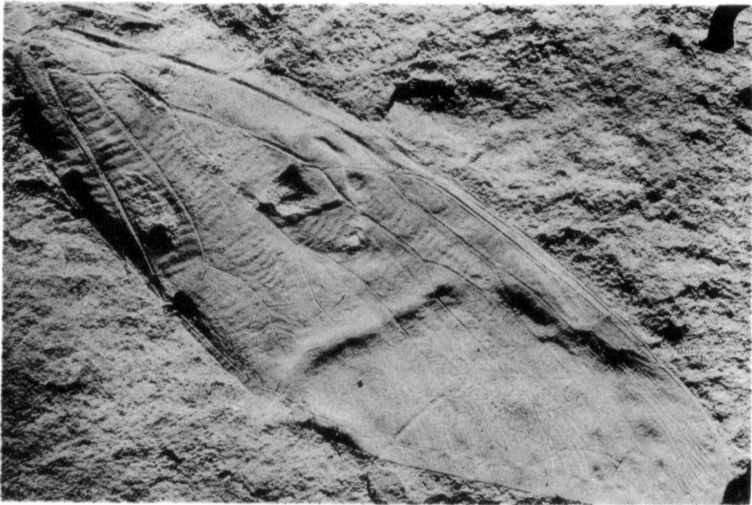


FIG. 2

FIG. 1. Dorsal impression of the left fore wing of *Davisia bearcreekensis* Cooper; Princeton no. 24001; enlargement 2x.

FIG. 2. Ventral impression of the left fore wing of *Davisia bearcreekensis* Cooper; Princeton no. 24001a; enlargement 2x.

American Cicadidae and in appreciation of his kind assistance. *Discussion.* *Davispia* probably belongs to the subfamily *Platyleurinae*, for, in size and venation the fore wing is in good agreement with those certain species of *Tibicen* (i.e.,—compare the fore wing of *Tibicen cultriformis* Davis, 1915b). Some species of *Diceroprocta* have fore wings quite similar to *Davispia*, but the robust $2Cu_1$ cell of the latter, among other characters, is strikingly distinct from the greatly elongate $2Cu_1$ so common in *Diceroprocta*. *Cacama* includes some forms with fore wings resembling that of *Davispia*, but the customarily broad coriaceous border and extremely stout cells which are closed by the ambient vein, as well as the greater length of M from the anterior arculus to M_{1+2}/M_{3+4} remove *Cacama* from further consideration.

Among American *Cicadinae*, some species of *Okanagana* (*O. mariposa* Davis, 1915a; *O. magnifica* Davis, 1919; *O. schaefferi* subsp. *tanneri* Davis, 1930; etc.) show certain venational similarities to *Davispia*, but all are very inferior to it in size. From all of these living genera, from the members of the genera of the *Tettigarctinae*, *Tettigadinae*, *Tibicininae*, and *Cicadinae*, *Davispia* may be distinguished by the unique combination of wing characters given in the diagnosis.

Of the fossil cicadas, only *Cicada grandiosa* Scudd. need be considered. From the fore wing referred by Cockerell (1911) to this species, *Davispia* strikingly differs in the relative length of the base of M, in the position of the nodal line in M_{3+4} , in the relative position of m-cu, and in the markedly different proportions of cell $2Cu_1$ (compare Figs. 1, 4 and 5 with 3). The differences of proportion between the wings of these two cicadas are strikingly brought out by comparison of Tables 1 and 2 with their equivalents in Table 3.

Davispia bearcreekensis Cooper, n. sp.

Anterior wing about 52 mm. long by 18.4 mm. wide; approximately 7.15 cm.^2 in area; costa slightly and evenly curved; coriaceous border from 1.7 mm. to 1.5 mm. wide along apices of medial cells to less than 0.7 mm. wide along cell $2Cu_1$. The dimensions and approximate areas of the cells are given in Table 1. Lengths of the veins and most of their segments are given in Table 2.

The mean area of each cell was determined by averaging not less than 12 separate polar planimeter measurements taken from photographs accurately enlarged two times. Each linear dimension recorded is the mean of at least six measurements. These measurements were made with dividers read against a Starrett steel rule graduated in half millimeters. To obtain linear measurements of strongly arched veins, photographs accurately enlarged two times were employed. With compass, straight edge and dividers the linear dimension of a bowed vein may be obtained with good accuracy.

TABLE 1.

Greatest length and width of cells of anterior wing in millimeters, area of cells in square centimeters, of *Davisia bearcreekensis* Cooper.

Cell	Length $\times$ width (mm.)	area (cm ²)
Sc	18.3 $\times$ 0.6	undetermined
R	17.4 $\times$ 2.6	0.40
R ₂	13.3 $\times$ 0.77	undetermined
1R ₃	17.5 $\times$ 1.7	0.24
2R ₃	13.3 $\times$ 3.0	0.24
1R ₅	14.3 $\times$ 2.6	0.26
2R ₅	17.7 $\times$ 3.8	0.38
M	19.9 $\times$ 4.4	0.54
M ₁	17.1 $\times$ 3.6	0.46
1M ₂	19.9 $\times$ 4.3	0.58
2M ₂	14.0 $\times$ 4.1	0.42
M ₃	16.5 $\times$ 4.5	0.49
M ₄	10.3 $\times$ 5.0	0.33
1Cu ₁	16.8 $\times$ 3.1	0.42
2Cu ₁	9.0 $\times$ 4.0	0.26
Cu ₂	1.3 $\times$ 0.41	undetermined
1A	ca. 17.6 $\times$ 2.1	ca. 0.28

The specimen described is probably a *left* anterior wing, for the normal bowing of the cicada wing ventrally and basally has been impressed on the fossil. The impressions of the wing show traces of carbonization, especially in the vicinity of the basal cell, but no traces of the color pattern of the original wing remain. *Holotype*: Dorsal and ventral impressions, Princeton numbers 24001 and 24001a.

Type locality. The impressions were discovered in 1930 by Erling Dorf, of the Department of Geology of Princeton University, while collecting fossil plants. Doctor Dorf has kindly supplied the following notes regarding the type locality.

TABLE 2.

Dimensions of veins and their segments of anterior wing in millimeters of *Davisipia bearcreekensis* Cooper. Principal veins in majusculæ, cross veins in minusculæ.

Vein or segment	length (mm.)
C from base to nodal furrow	26.1
Sc, nodal furrow to junction with R_2	18.0
R from base to nodal furrow	25.2
R_{2+3}	10.3
R_2	13.8
R_3	14.2
R_{4+5} from r-m to $r_{4+5}-m_1$	9.2
R_{4+5} from $r_{4+5}-m_1$ to r_3-r_{4+5}	9.3
R_{4+5} from r_3-r_{4+5} to ambient vein	9.5
r_3-r_{4+5}	3.4
$r_{4+5}-m_1$	3.0
r-m	3.7
M from arculus to fork M_{1+2}/M_{3+4}	4.1
M_{1+2} from M_{1+2}/M_{3+4} to nodal line at base of r-m	9.9
M_{1+2} from nodal line to M_1/M_2	8.9
M_1 to $r_{4+5}-m_1$	6.0
M_1 entire	19.0
M_2 to m_2-m_3	2.4
M_2 entire	15.4
M_{3+4} from M_{1+2}/M_{3+4} to nodal line in M_{3+4}	6.6
M_{3+4} from nodal line to M_3/M_1	5.5
M_3 to m_2-m_3	6.4
M_3 from m_2-m_3 to ambient vein	11.3
M_4 to m-cu	3.7
M_4 from m-cu to ambient vein	9.8
m_2-m_3	3.3
m-cu	3.0
Cu_1 from posterior arculus to Cu_{1a}/Cu_{1b}	15.0
Cu_{1a} to m-cu	5.0
Cu_{1a} from m-cu to ambient vein	5.9
Cu_{1b}	3.7
Cu_2	ca. 17.5
1A	ca. 18—
2A	ca. 19+

The locality is one mile south of Bear Creek, Montana, 50 feet northwest of the entrance to the Eagle coal mine in Foster Gulch, in the southwest corner of SW. $\frac{1}{4}$, Sec. 8, T. 8 S., R. 21 E. The dark, somewhat metamorphosed shales in which the fossils occur lie about 35 feet stratigraphically below coal No. 3.

Although originally referred to the Laramie group (Fisher, 1906) the beds at this locality have since been placed in the "Fort Union" group (Darton, 1907; Woodruff, 1909). The associated vertebrates and fossil plants of the Eagle Mine

locality indicate a late Paleocene age (Simpson, 1928, 1929; Jepsen, 1937; Dorf, 1938). Thirteen species of mammals including insectivores, carnivores, rodents, and primates have been described from this locality (Simpson, 1929; Jepsen, 1937). The fauna is apparently equivalent to that from the Silver Coulee of the Bighorn basin, Wyoming, and the Tiffany of S. W. Colorado, and intermediate in age between the Clark Fork of the Bighorn basin and the type Torrejon of New Mexico (Jepsen, personal communication, 1940).

A few fresh-water molluscs have also been found in the beds at this locality. These include species of *Unio*, *Sphaerium*, *Elliptio*, and *Goniobasis* (Darton, 1907; Russell, 1934). *Davisia* is the first insect recorded from these beds.

The plant remains are referable to about 25 species, including an equisetum, a fern, 2 conifers, and 21 angiosperms (Dorf, 1938). This association is apparently a lowland, humid, warm-temperate assemblage in which the dominant species are arrow-woods, katsuras, ash, redwood, hickory, staff-tree, and ginseng.

REVIEW OF THE FOSSIL CICADIDAE.

False and doubtful records. Many authors have described fossil insects as "cicadas," but in spite of a large literature no more than ten species of Cicadidae are known definitely as fossils at the present time. It may not be amiss to indicate briefly the records of fossil insects that have been wrongly or doubtfully placed in the Cicadidae.

Bloch (1776), Brodie (1845), Westwood (in Brodie, 1845), Giebel (1856), Brodie (1873), Weyenbergh (1874), Etheridge and Olliff (1890), and Buckton (1891) have mistakenly referred fossil insects to the Cicadidae. Handlirsch (1908) gives reference to their works as well as satisfactory allocation of their forms. In addition, Raffray (1875) and Bleicher (1880) mention "cicadares," and Handlirsch quite correctly indicates that by such casual mention not even the family to which the specimen belongs can be determined. Equally unsatisfactory are the "Cicadas" mentioned by Berendt (1830) and Hünefeld (1831),² for there is no reason to suppose that either author

² Attributed to Burmeister by Handlirsch. Hünefeld states that Burmeister is responsible for the identifications of the amber insects. Further confusion is created by the fact that in the index of *Isis* (p. 1158) the authorship of the article is given as "Hünefeld und Burmeister," although in the text the article is assigned to Hünefeld alone.

used the term "Cicada" to mean specifically a member of the insect family now called Cicadidae. Likewise little consideration can be given the passing mention by Flach (1890) of "einer grossen Cicaden-Larve" from the phosphorite beds of Aveyron in Caylux (lower Oligocene). It is not easy to understand why Handlirsch (1908) included these records in his list of Tertiary Cicadidae, or, as he apparently did (1925), in his numerical catalog of fossil Cicadidae. In addition, Hope (1836) listed a "Cicada?" from animé and amber. As Hope also listed *Cixius*, *Issus*, *Aphrophora*, *Iassus*, etc., his "Cicada ?" may well be correctly placed in the Cicadidae. In this connection it is of interest that Hope likewise lists the "Cicada" mentioned by Berendt.

Weyenbergh (1874, *Cicada gigantea* Weyenb.), Deichmüller (1886), Oppenheim (1888), and Haase (1890) described fossils which they took to be cicadas. Handlirsch (1908), however, grouped these forms together in the Palaeontinidae as a family of Lepidoptera resembling the Limacodidae. Tillyard (1921) disputed the correctness of Handlirsch's conclusion, and gave evidence to demonstrate that the Palaeontinidae are Homoptera related to the Mesogereonidae and, less closely, to the Cicadidae. In this view Tillyard has been supported by Myers (1928, 1929) and Martynov (1931), each of whom advanced new data to show these forms to be Homoptera. The Palaeontinidae, then, are not cicadas, but are possibly bugs fairly closely related to the Cicadidae. Nevertheless, Handlirsch (1925, 1927) has reiterated his opinion that the Palaeontinidae are Lepidoptera.

Hylaeoneura lignei, represented only by a fragmentary apical half of a wing was described by Lameere and Severin (1897) as the fore wing of a Cretaceous sialid. Handlirsch (1908, 1925), however, restored the wing of *Hylaeoneura* as that of a cicada. Until a complete wing or the corresponding basal portion is discovered, *Hylaeoneura lignei* Lam. and Sev. cannot be seriously regarded as an established record of a fossil cicada for the following reasons.

(1) Handlirsch (1908) claims an ambient vein to be evident in certain places, and this is his chief clue to the cicadid nature of *Hylaeoneura*. Lameere and Severin neither figure nor mention such a vein, and specifically speak of the thinning of the longitudinal veins at their extremities as one of the sialid characteristics of the wing. It seems clear that Handlirsch

believes the second branch of the vein designated by Lameere and Severin as "IX" to be a portion of the ambient vein. However, Handlirsch's figures of the fragment (1908, Plate 51, Figs. 46, 47) extend this vein along the margin of the wing as far as the second branch of "III." Such an illustration can follow neither from Lameere and Severin's figures nor from their descriptions; nor can Dupont's (1897) illustration be called in evidence. Unless Handlirsch has studied the original specimen, and he fails to state that he has, the presence of an ambient vein in *Hylaeoneura* remains undemonstrated.

(2) A criticism similar to the foregoing may be made for the coriaceous border which Handlirsch figures as present in the specimen. Such a *limbus enervis* is neither figured nor mentioned by Lameere and Severin (1897) or by Dupont (1897). The only apparent indication of such a border lies in the membrane below the second branch of the vein designated by Lameere and Severin as "IX."

(3) Such diagnostic features of the basal half of the wing as the nodal line are not represented, and can only be surmised.

(4) In spite of a professed attempt to restore the fragment as a cicadid fore wing (doubt may exist as to whether or not the fragment is that of a fore wing), Handlirsch's efforts awaken considerable difficulty in the interpretation of the cubital branches.

(5) The preponderance of the characteristics of the Cicadidae represented in the wing are those which are presented by Handlirsch in the reconstruction, but which apparently have not been demonstrated in the original fragment.

Catalogue of the fossil Cicadidae. In the following annotated, chronological catalogue of the fossil Cicadidae, the partial synonymies indicated have as authority Distant's (1906) catalogue; many of the generic designations, however, follow Haupt (1929) and Myers (1929). Where an author has found agreement of his specimen with a designated living species, it has been considered useful to indicate the subfamily to which the fossil species may belong. Probably the only subfamily of Cicadidae not represented by fossil forms is the Tettigadinae.

The gross dimensions of the type specimens, as well as estimates of lacking parts are given for each fossil species. These data should be of value in identifying fossil cicadas, for they allow immediate exclusion of certain forms when the specimens are being classified.

The basis for the estimation of dimensions is a series of measurements of body length and the lengths and widths of the fore and hind wings of 89 cicadas representing 67 species and 45 genera of living Cicadidae.³ These cicadas range in body size from 10.6 mm. to 66 mm., and come from North, Central and South America, West Indies, China, Siam, Sumatra, Samoa, New Zealand, Australia and Queensland. The specimens are in the collections of the Biology Department of Princeton University (largely a gift of Mr. Wm. T. Davis) and the American Museum of Natural History.⁴ A member of every identified genus available was measured. Only the data regarding the relations of wing length to body length are graphically presented in Text Fig. 2, for the full data will be published elsewhere. It is striking that only the dimensions of a greatly distended female of the very aberrant *Cystosoma saundersii* depart radically from the series.

For the purposes of this paper, each of the curves for the entire data may be treated as consisting of two intersecting straight lines although it is evident that the points fall along gentle curves. The equation of the relation of the length of the fore wing (y) to the body length (x) for all body lengths from 10 to 37 mm. and fore wing lengths up to 50 mm. may be given as: $y = 1.43 x - 3.5$ mm.; for body lengths greater than 37 mm. or wing lengths above 50 mm., calculations may be made on the basis of: $y = 1.1 x + 5.5$ mm.

The equation for the relation of the length of the hind wing (y) to the body length (x) for all body lengths from 10 to 37 mm. and hind wing lengths up to 28 mm. may be given as: $y = 0.81 x - 2.15$ mm.; for greater dimensions calculations should be based on: $y = 0.6 x + 3$ mm.

Although the data are not presented here, the relation of the

³ The genera are: *Baeturia*, *Beameria*, *Borencona*, *Cacama*, *Carineta*, *Cicada*, *Clidophleps*, *Cosmopsaltria*, *Cryptotympana*, *Cychlochila*, *Cystosoma*, *Dazu*, *Diceroprocta*, *Dundubia*, *Fidicina*, *Graptosaltria*, *Henicopsaltria*, *Herrera*, *Juanaria*, *Lyristes*, *Magiccicada*, *Melampsalta*, *Mogonnia*, *Neoplatypedia*, *Odopoea*, *Okanagana*, *Ollanta*, *Pacarina*, *Pauropsalta*, *Platypedia*, *Platypheura*, *Platytomia*, *Pomponia*, *Proarna*, *Psallodia*, *Psaltoda*, *Quesada*, *Tacua*, *Tettigades*, *Thopha*, *Tibicen*, *Tibicinoides*, *Tympanopterus*, *Uhlerioides*, and *Zammara*.

⁴ My thanks are extended to Dr. Richard Blackwelder for allowing me to study the American Museum collection, as well as for giving me access to the type of *Lithocicada perita* Cock. (AMNH accession no. 34871; mislabelled *Lithocicada perita* Cock.)

fore wing width (y) to the fore wing length (x) may be treated similarly. For wing lengths up to 50 mm. or widths to 17 mm., the equation: $y = 0.34 x - 0.1$ mm. satisfactorily expresses the relation; for wings of greater dimensions employ: $y = 0.315 x + 0.9$ mm.

For hind wings of width less than 13 mm. or of a length less than 29 mm. the relation of width (y) to length (x) is given by: $y = 0.517 x - 0.83$ mm.; wings of larger dimensions may be treated by: $y = 0.39 x + 2.6$ mm.

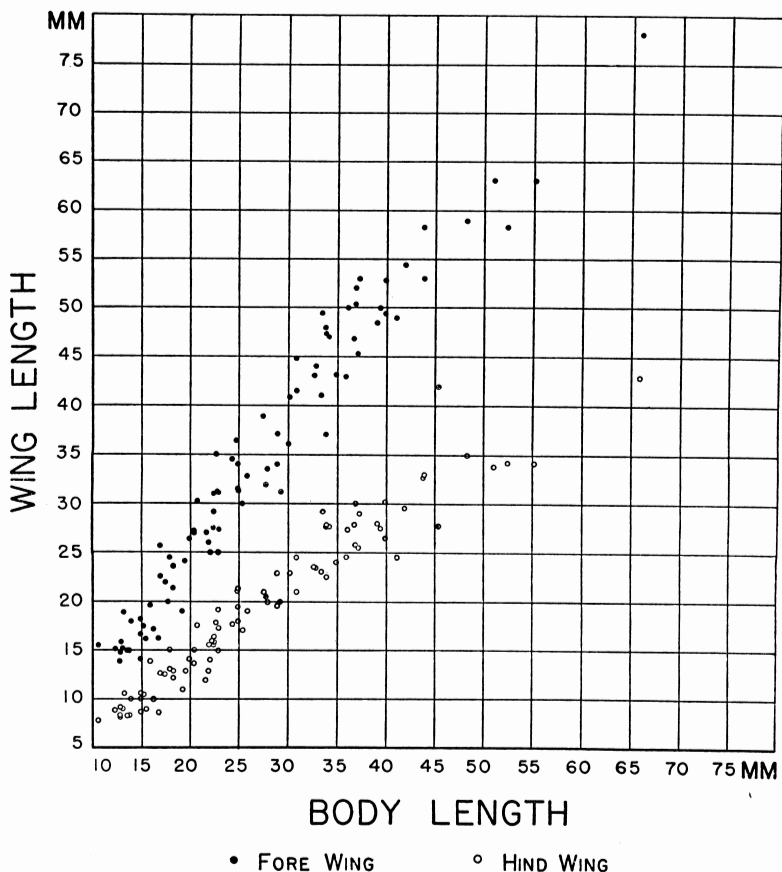


Fig. 2. Plot of wing length against body length for 89 cicadas representing 67 species and 45 genera of living Cicadidae. The circles enclosing central dots represent measurements of *Cystosoma saundersii*. Two males (of body lengths just over 27 and 29mm.) of this species are but slightly off the general trend; the fore wing of the female (of body length just over 45 mm.) is definitely away from the general trend.

The relation of the length of the hind wing (y) to the length of the fore wing (x) in cicadas is linear, and may be solved by: $y = 0.546x + 0.41$ mm.

From these equations, given any single dimension such as body length, fore wing width, hind wing length, etc., reasonable estimates of the body length and the lengths and widths of the fore and hind wings of most cicadas may be made. The degree to which the estimates may be in error can be judged from the curves in Text Fig. 2.

The least accurate of the dimensions calculated from these formulae will be the body length, for the specimens measured differed considerably in degree of distension of the abdomen and protrusion of the genitalia. Furthermore, females of *Cystosoma*-like forms and nearly all members of the Parnisini (*Platypedia*, *Neoplatypedia*) should be calculated on the basis of allied forms, for they show consistent deviations from predictions based on these formulae. Indeed, the relations shown by plots of the whole data justify estimation of dimensions of missing parts from living cicadas with proportions closely similar to those of the fossil remains. The formulae will be useful chiefly to those who do not have an extensive collection of Cicadidae at their disposal.

With these reserves, the considered use of the formulae presented here will allow judgment on the association of non-comparable fragments of cicadas from the same strata, as well as an estimate of the size of missing dimensions of fragmentary wings.

Family CICADIDAE Westwood.

(1) *Cicada emathion* Heer, 1853. Upper Miocene, Oeningen, Switzerland. Two specimens are referred by Heer to this species. One consists of a nearly complete body and two poorly preserved fore wings; of the other specimen at least the body is complete. According to Heer's measurements (in Austrian lines, = 2.20 mm.), the specimen with the incomplete body is 24.2 mm. long; its fore wing is 34.1 mm. $\times$ 11.6 mm. The body length of the complete specimen is 34.1 mm. From Heer's data and Fig. 1, Plate 11, the variation in this species may be estimated as follows: body length about 27 – 34 mm.; fore wing dimensions about 34 $\times$ 11.6 mm. to 45 $\times$ 15 mm.; hind wing dimensions about 19 $\times$ 9 mm. to 25 $\times$ 12 mm. The variation in

dimensions seems excessive and suggests that either the "complete" body has been greatly extended in fossilization, or that two species are involved. The original specimens should be restudied.

Compared by Heer with *Tettigia orni* (Linn.) and *Lyristes plebeja* (Scop.) (*Cicada plebeja* Scop. = *C. fraxini* Fabr.).

.....Cicadinae ?

(2) *Cicada aichhorni* Heer, 1853. Lower Miocene, Rado-boj, Yugoslavia. Fore wing (fragment) about 41.4×14 mm. Estimated length of body, 31 mm. Estimated dimensions of hind wing, 23×11 mm. It should be noted that Heer's Fig. 2 of the specimen and 2b (Plate 11) are not in good agreement.

(3) *Cicada ungeri* Heer, 1853. Lower Miocene, Rado-boj, Yugoslavia. Fore wing, virtually entire, about 25.6×8.5 mm. Estimated length of body, 20 mm.; estimated dimensions of hind wing, 14.4×6.6 mm.

Compared with *Tibicina haematodes* (Scop.) and *Cicadatra atra* (Oliv.) (*Cicada atra* Oliv. = *C. concinna* Germ.).

.....Tibicininae?

(4) *Cicada bifasciata* Heer, 1853. Lower Miocene, Rado-boj, Yugoslavia. An extended abdomen lacking the basal segments. The width of the abdomen of a female cicada of medium size is approximately 40 per cent of its body length. The abdomen of *C. bifasciata* is 10.5 mm. wide, and corresponds with a total body length of 26 mm. The estimated dimensions of the fore wing are 33.7×11.4 mm.; of the hind wing, 18.8×8.8 mm. The agreement with the smaller specimen of *Cicada emathion* Heer is striking, for they are apparently of similar body lengths. Association of the two forms is not warranted, for they occur in different strata.

(5) *Cicada grandiosa* Scudder, 1892. Miocene, Florissant, Colorado. Hind wing, nearly complete. Scudder records the dimensions of the venation of the hind wing as 26.5×10.5 mm., and estimates the expanse of the fore wings as about 115 mm. (thus the fore wing length would be about 50 mm.). It is fairly clear, however, that Scudder overestimated the length of the hind wing in reconstructing it, and it is probable that the hind wing including the coriaceous border did not exceed 26×12 mm. These dimensions are rendered likely by study of the relative proportions of cell and vein lengths in the hind wings of four species of *Tibicen* ranging from 10 to 14 mm. in greatest width of the hind wing. The probable dimensions of

the fore wing of the type of *Cicada grandiosa* are about 46×15.5 mm., and a corresponding estimate of the body length is approximately 35 mm.

Cockerell (1911) briefly mentioned a fragmentary fore wing of a cicada found at Florissant which he ascribed to *Cicada*

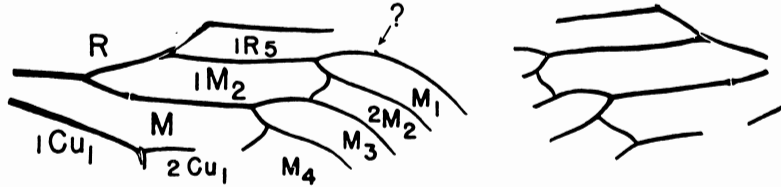


Fig. 3. Diagram of the impressions of the fragmentary fore wing of *Cicada grandiosa* Scudder, with the cells labelled for comparison with Figure 1.

grandiosa. As this fore wing has been neither figured nor adequately described, the impressions are illustrated in Text Fig. 3, and the principal dimensions are given in Table 3. The specimen is in the University of Colorado Museum, and bears the numbers "T. D. A. Cockerell 18754" and "8603." I am grateful to Professor Cockerell and Prof. Hugo Rodeck for kindly loaning me the specimen for study.

TABLE 3.
Measurements of the veins and cells of the fore wing of
Cicada grandiosa Scudder.

Vein or segment	length (mm.)
r-m	2.8
M ₁₊₂ from M ₁₊₂ /M ₃₊₄ to r-m	6.0
M ₁₊₂ from r-m to M ₁ /M ₂	10.1
M ₁ to ?r ₄₊₅ -m ₁	4.3
M ₂ to m ₂ -m ₃	1.2
M ₃₊₄ from M ₁₊₂ /M ₃₊₄ to nodal line in M ₃₊₄	3.2
M ₃₊₄ from nodal line to M ₃ /M ₄	8.4
M ₃ to m ₂ -m ₃	3.4
M ₄ to m-cu	1.8
m ₂ -m ₃	2.4
m-cu	3.0
Cu _{1a} to m-cu	5.7
Cell	dimensions
1M ₂	16.0 mm. $\times$ 2.9 mm.
1M ₂	0.37 cm ²
1R ₅ (greatest width)	2.3 mm.

The fore wing fragment represents a wing of about 43 mm. in length, and 14.6 mm. in width. These dimensions are derived from studies of the relative proportions of the central field of the fore wings of *Tibicen cultriformis* Davis, *T. duryi* Davis, and *T. chloromera* (Walk.). Although the length of cell $1M_2$ does not bear a constant proportion to the linear dimension of the wing in these species, the relation to the wing width of the distance from the base of r-m to the point of forking of Cu_1 into Cu_{1a} and Cu_{1b} gives a means of good approximation. The hind wing corresponding with the fore wing is estimated at 24×11.6 mm., and the corresponding body length is about 33 mm. As the estimates are in good agreement with the revised estimates of the proportions of the cicada corresponding with Scudder's fragmentary hind wing, it is reasonable to conclude with Cockerell that "it seems safe to assume that they belong to the same species." Such would not be the case, however, were Scudder's estimates to prove correct.

Scudder states that the venation compares well with *Fidicina* and *Cicada*. Cockerell holds that the venation of both the hind and fore wings agrees very nearly with that of the living *Tibicen marginalis* (Walk.) (= *Cicada marginata* Say). Cockerell is correct not only in likening the forking of the radius and cubitus, etc., in *Tibicen marginalis* and *Cicada grandiosa*, but the homology corresponds even in the relative position of the nodal line through M_{3+4} . Insofar as the morphology of these fragmentary wings is concerned, there is no obvious reason why *Cicada grandiosa* should not be referred to the genus *Tibicen*. Platyleurinae.

(6) *Lithocicada perita* Cockerell, 1906. Miocene, Florissant, Colorado. Nearly perfect fore wing. According to Cockerell the fore wing dimensions are ca. 23×10.5 mm.; the type in the American Museum of Natural History measures $22^+ \times 9.6$ mm. Estimated length of body, 21 mm. Estimated dimensions of hind wing, 14.9×7.7 mm. The estimates are based on the proportions of *Platypedia putnami* (Uhler). Contrary to Cockerell's statement, the radial cell extends beyond the middle of the wing. Compared with *Cicada* and *Tettigia*. Cicadinae.

(7) *Platypedia primigenia* Cockerell, 1908. Miocene, Florissant, Colorado. Nearly complete specimen. Length of body about 23 mm. Estimated dimensions of fore wing, 24×9.8 mm.; of hind wing, 15.2×7.9 mm. The estimates are based on

the proportions of *Platypedia putnami* (Uhler), a species with which *P. primigenia* is in striking agreement. From *P. putnami* and *Lithocicada perita*, *P. primigenia* is easily separated by details of venation. Cicadinae.

(8) *Cicada serresi* Meunier, 1915. Oligocene, Aix-en-provence, France. Nearly entire specimen. Length of body according to Meunier, 20 mm. Dimensions of fore wing, 24×8.2 mm. Estimated dimensions of hind wing, 13.4×6.1 mm. Compared by Serres (1829) with *Melampsalta violacea* (Linn.). Meunier merely contrasts *C. serresi* with Heer's species. It seems that Meunier's photograph could not allow the reconstruction of the wing recently published by Théobald (1937). For this reason, as well as for the obvious misinterpretation of the veins at the apex of the radial cell, Théobald's reference of *C. serresi* to the genus *Cicadatra* must be viewed with suspicion. Tibicininae ? or Cicadinae ?

(9) *Meuniera haupti* Piton, 1936. Eocene (Marty, 1937; Piton and Théobald, 1937), Menat, France. Fragmentary body and poorly preserved left anterior and posterior wings; right anterior wing beautifully preserved.⁵ Dimensions of anterior wing, 33×11.1 mm. Estimated length of body, 26 mm. Estimated dimensions of hind wing, 18.4×8.7 mm.

Piton and Haupt (in Piton, 1936) apparently misinterpreted the venation of *Meuniera*; the type should be refigured and redescribed. If their diagram of the wing is correct, the second and third branch of "subcosta" are probably R_2 and R_3 ; "radia" is R_{4+5} , and the second branch of "radia" at the ambient margin is probably M_1 . "Media" at the ambient margin includes M_2 and probably M_{3+4} . Cu_1 , Cu_{1a} and Cu_{1b} are satisfactorily indicated by "cubitus." If the wing is that of a tettigarctid, Piton and Haupt have erroneously designated Cu_2 as "nalis." Apparently the base of the wing is not complete, and the anal margin, unlabelled in their diagram, may be the true 1A. It is surprising that all mention or indication of the nodal line is lacking, in spite of the excellent preservation of this region of the wing, for this is extremely prominent and characteristic in the Tettigarctinae (Myers, 1928). Were the nodal line completely absent, *Meuniera* would necessarily be excluded from the Cicadidae (see especially Myers, 1929, p. 92). Tettigarctinae.

⁵ Piton (1933) and Piton and Théobald (1937) refer to the well preserved wing as the left, but in describing *Meuniera haupti* Piton (1936) states the wing to be the right.

(10) *Davisia bearcreekensis* Cooper, 1940. Paleocene, Bear Creek, Montana. Nearly perfect fore wing with dimensions 52×18.4 mm. Estimated length of body, 42 mm. Estimated dimensions of hind wing, 29×14 mm.

.....Platypleurinae.

In the foregoing list, the generic designation of "*Cicada*" is almost one of family rank. To these cicadas may be added one which has been mentioned but not described. Serres (1829) records, along with what is probably the very specimen that Meunier (1915) described, a *Cicada* from Aix (Oligocene), France, which he states to be about the size of *Lyristes plebeja* (Scop.).

In summary, 13 fossil cicadas representing 10 species are known. These are distributed in time as follows: Paleocene —1, Eocene —1, Oligocene —2, Miocene —9. At the present day approximately 1,900 species of Cicadidae are known.

Acknowledgment. It is a pleasure to acknowledge my indebtedness to Dr. Erling Dorf for kindly allowing me to describe the specimen, to Dr. J. Brooks Knight for aiding me with the photography, and to Dr. Glenn L. Jepsen and Dr. G. Arthur Cooper for critically reading the manuscript.

LITERATURE CITED, INCLUDING ALL OF THE RECORDS OF FOSSIL INSECTS THE
CICADID NATURE OF WHICH HAS NOT BEEN DISPROVED.

- Berendt, N.: Die Insekten im Bernstein. Ein Beitrag zur Thiergeschichte der Vorwelt, 1, pp. 1-39, 1830.
- Bleicher, M.: Note sur la découverte d'un horizon fossilifère à poissons, insectes, plantes, dans le Tongrien de la Haute-Alsace. Bull. Soc. Géol. France, 8, pp. 222-229, 1880.
- Cockerell, T. D. A.: A fossil cicada from Florissant, Colorado. Bull. Am. Mus. Nat. Hist., 22, pp. 457-458, 1906.
- : Descriptions of Tertiary insects. Amer. Jour. Sci., 25, pp. 51-52, 1908.
- : Fossil insects from Florissant, Colorado. Bull. Am. Mus. Nat. Hist., 30, pp. 71-82, 1911.
- Darton, N. H.: Coal of Carbon County, Montana. U. S. Geol. Surv., Bull. 316, pp. 174-193, 1907.
- Davis, W. T.: New species of cicadas from California and Utah. Jour. N. Y. Ent. Soc., 23, pp. 11-21, 1915a.
- : A new cicada from Arizona. Ibid., 23, pp. 239-241, 1915b.
- : Cicadas of the genera Okanagana, Tibicinoides and Okanagodes, with descriptions of several new species. Ibid., 27, pp. 179-223, 1919.
- : The distribution of cicadas in the United States with descriptions of new species. Ibid., 38, pp. 53-72, 1930.

- Distant, W. L.: A synonymic catalogue of Homoptera. Part 1. Cicadidae. Brit. Mus. Nat. Hist., 1906.
- Dorf, E.: Fort Union flora associated with the Bear Creek mammalian fauna of southern Montana. Bull. Geol. Soc. Am., 49, p. 1912, 1938.
- Dupont, E.: Guide dans les collections Bernissart et les Iguanodons. Mus. Roy. d'Hist. Nat. de Belg., 1897.
- Fisher, C. A.: Development of the Bear Creek coal fields, Montana. U. S. Geol. Surv., Bull. 285, pp. 269-270, 1906.
- Flach, K.: Ueber zwei fossile Silphiden (Coleoptera) aus den Phosphoriten von Caylux. Deutsche Ent. Zeitschr. (1), pp. 105-109, 1890.
- Handlirsch, A.: Die fossilen Insecten und die Phylogenie der rezenten Formen. Leipzig, 1908.
- : Palaeontologie, in: Schröder's Handb. d. Ent., 3, 1925.
- : Allgemeine Einleitung in die Naturgeschichte der Insecta, in: Kükenthal's Handb. d. Zool., 4 (1), 1927.
- Haupt, H.: Neueinteilung der Homoptera-Cicadina nach phylogenetisch zu wertenden Merkmalen. Zool. Jahrb., Abt. f. Syst., 58, pp. 173-286, 1929.
- Heer, O.: Die Insectenfauna der Tertiärgebilde von Oeningen und von Radoboj. 3 Abt.: Rhynchoten. Neue Denkschr. allg. Schweiz. Gesellsch. ges. Naturwiss., 13, pp. 1-138, 1853.
- Hope, F. W.: Observations on succinic insects. Trans. Ent. Soc. Lond., 1, pp. 133-147, 1836.
- Horváth, G.: Etude morphologique sur la construction de l'elytra des cicadides. Trans. 2nd Int. Congr. Ent., Oxford, 2, pp. 422-432, 1913.
- Hünefeld, L.: Bernstein-Insekten. Isis von Oken, 6, p. 1100 (2000, in error), 1831.
- Jepsen, G. L.: A Paleocene rodent, *Paramys atavus*. Proc. Am. Phil. Soc., 78, pp. 291-301, 1937.
- Lameere, A. and G. Severin: Les insectes de Bernissart. Ann. Soc. Ent. Belg., 41, pp. 35-38, 1897.
- Marty, P.: Note sommaire sur l'âge du gisement fossilifère de Menat. Rev. Sci. Nat. d'Auvergne, 3, pp. 69-75, 1937.
- Martynov, A. B.: To the morphology and the systematical position of the fam. Palaeontinidae Handl., with a description of a new form from Ust-baley, Siberia. Ann. Soc. Paléont. Russ., 9, pp. 93-122, 1931.
- Meunier, F.: Nouvelles recherches sur quelques insectes des plâtières d'Aix en Provence. Verh. d. Koninkl. Ak. v. Wetenschappen te Amsterdam, 18, pp. 1-18, 1915.
- Muir, F.: On the classification of the Fulgoroidea (Homoptera). Proc. Hawaiian Ent. Soc., 5, pp. 205-247, 1923.
- Myers, J. G.: The morphology of the Cicadidae (Homoptera). Proc. Zool. Soc. Lond., pp. 365-472, 1928.
- : Insect singers. A natural history of the cicadas. London, 1929.
- Piton, L.: Monographie de la perche tertiaire des schistes de Menat (P. -de -D.) suivi d'une note sur deux hémiptères-homoptères provenant du même gisement. Rev. Sci. du Bourbonnais et Centre de la France, pp. 60-66, 1933.
- : Les hémiptères-homoptères de l'Éocène de Menat (P. -de -D.). Misc. Ent., 37, pp. 93-94, 1936.
- and N. Théobald: Les insectes fossiles de Menat. Rev. Sci. Nat. d'Auvergne, 3, pp. 76-88, 1937.
- Raffray, A.: Morceaux de gomme copal. Bull. des Séances et Bull. Bibl., 1875; in: Ann. Soc. Ent. France, 5, pp. cxxv-cxxvi, 1875.
- Russell, L. S.: New fossil fresh water Mollusca from the Cretaceous and Paleocene of Montana. Jour. Wash. Acad. Sci., 24, p. 128, 1934.

- Scudder, S. H.: Index to the known fossil insects of the world. U. S. Geol. Surv., Bull. 71, 1891.
- : Some insects of special interest from Florissant and other points in the Tertiaries of Colorado and Utah. U. S. Geol. Surv., Bull. 93, pp. 11-25, 1892.
- Serres, M. de: Géognosie des terrains Tertiaires, ou tableau des principaux animaux invertébrés des terrains marins Tertiaires, du midi de la France. Paris, pp. i-xcii, 1-276, 1829.
- Simpson, G. G.: A new mammalian fauna from the Fort Union of southern Montana. Am. Mus. Nov., 297, pp. 1-15, 1928.
- : Third contribution to the Fort Union fauna at Bear Creek, Montana. Ibid., 345, pp. 1-12, 1929.
- Théobald, N.: Les insectes fossiles des terrains Oligocènes de France. Nancy, 1937.
- Tillyard, R. J.: The panorpoid complex. 3: The wing venation. Proc. Linn. Soc. N. S. Wales, 44, pp. 533-718, 1919.
- : Mesozoic insects of Queensland. 8 . . . The genus Mesogereon; with a discussion of its relationship with the Jurassic Palaeontinidae. Ibid., 46, pp. 270-284, 1921.
- : Kansas Permian insects. 9. The order Hemiptera. Amer. Jour. Sci., 11, pp. 381-395, 1926.
- Woodruff, E. G.: The Red Lodge coal field, Montana. U. S. Geol. Surv., Bull. 341, pp. 92-107, 1909.

PRINCETON UNIVERSITY,
PRINCETON, N. J.